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Source: *Journal of Range Management*, Nov., 1968, Vol. 21, No. 6 (Nov., 1968), pp. 355-360

Published by: Allen Press on behalf of Society for Range Management

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Conservation, Development, and Use of the World's Rangelands

ROBERT E. WILLIAMS, B. W. ALLRED, REGINALD M. DENIO, AND HAROLD A. PAULSEN, JR.

Committee on International Biological Program, American Society of Range Management.[1]

Highlight

Some 47% of the world's land area is suitable only for grazing by domestic livestock and game animals—either frequently or occasionally. These rangelands support animals which provide most of the world's meat, milk, hides, wool, and other animal products. They have major values for watershed, wildlife habitat, soil and water conservation, fuel, and important by-products. Large areas are in poor condition, primarily because of overgrazing. The American Society of Range Management has an increasingly important role in focusing attention on the world's rangelands and in stimulating effective programs of research, education, and action.

The American Society of Range Management (1964) defines range as "all land producing native forage for animal consumption, and lands that are revegetated naturally or artificially to provide a forage cover that is managed like native vegetation. Generally considered as land that is not cultivated."

Rangeland includes natural grasslands, savannas, wetlands dominated by grasses and grass-like plants suitable for grazing, and certain shrub and chaparral plant communities. Terms which often are used with similar meaning include steppe, veldt, savanna, and moor. Numerous vernacular terms are used to designate areas of native or natural plant communities used for grazing livestock and big game animals.

Rangeland most often is too dry, steep, rocky, wet, or otherwise limited for more intensive cropping use. In management of rangeland, manipulation of grazing animals in terms of numbers and season of use is the primary measure employed to improve or maintain the desired plant cover. Associated practices may include deferred grazing (resting or spelling land from grazing), rotational deferred-grazing, or other grazing systems.

Improvement in existing range cover may be too slow or even impossible under grazing management alone where deterioration is extreme. When improvement in cover requires considerable change in plant composition, seeding of desired species may be necessary. Control of undesirable plants by chemical, biological, or mechanical means may be needed to accelerate production of desirable cover and forage plants.

[1] The Committee is indebted to Dr. Roald A. Peterson, Pasture and Forage Crops Branch, FAO, Rome, Italy, for reviewing the ms and for granting permission to use previously unpublished material written by Mr. Allred.

Adequate water distributed over the range is essential to meet needs of grazing animals and to encourage dispersal and uniform utilization. Inadequate watering locations on arid grazing lands encourage concentrations around existing waterings. Lack of water and forage in times of drought lead to eventual migration to more favorable areas. In addition to water, fencing, and herding, controlled burns sometimes are employed to influence and control livestock movements and concentrations.

Range forage may be deficient in essential nutrients or minerals during some part of the year. Feeding of supplemental nutrients or minerals can be vital to livestock management and production.

The kinds of grazing animals used to convert range forage to meat, milk, wool, mohair, or hides must be compatible with each environmental situation. Under some conditions, big game animals may be more efficient rangeland users than domestic livestock.

Developing, using, and improving range resources for the benefit of man require an understanding of the physical environment, the plants that can be produced, and the animals that are the most efficient harvesters of the forage. The range resources of the world are begging for such understanding.

Kind and Location of Natural Grazing Lands

Every nation has some natural grazing land but kinds vary greatly by climate. The grasslands cover vast areas of economic importance—large areas of the arable croplands are former grasslands. Grasslands of the more humid zone include the Chernozen belt of Russia, United States prairies from Canada to the Gulf of Mexico, llanos of Venezuela, pampas of Argentina and tallgrass veldt of Africa. Plants include tall and mid-grasses, a few forbs and small shrubs. These are among the most productive rainfed farming lands of the world.

The semi-arid grasslands are composed of short and mid-grasses, forbs and a few small shrubs. Examples are the steppes of Eurasia and Africa, the Great Plains in North America and the plains of Patagonia.

Drier still are the desert and semi-desert grasslands composed of drought resistant grasses, numerous small shrubs and some forbs. Examples are found in the Middle East, much of East Africa and Southwestern United States.

Cold climate grasslands are typical of alpine and subarctic regions and are composed largely of short grasses, forbs, lichens and mosses. None are found in Antarctica.

Savannas represent another large type of grazing land and are of two major kinds.

a. Grasslands intermingled with small or me-

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dium-size trees usually in favorable moist areas.

b. Grasslands with intermingled shrub typical of semi-arid to arid climates.

Forest areas also are grazed by domestic animals and wildlife. Over half of the area classified as forest is low-producing woodland of value largely for grazing. Forbs, grasses, and low shrubs in forests are grazed by domestic animals but such areas are more widely used by wildlife.

Most deserts provide homes for many meat-producing animals, at least part of the time. Drought-tolerant shrubs, some perennial grasses, and numerous annual plants provide forage at least during years when rainfall is most abundant.

With the exception of polar caps, most of the world's land area is used by domestic and game animals at least some part of the year. About one-third of the sphere is land, or 34 billion acres. Approximately 10% is farmed, 28% is in forest which is grazed by domestic animals and wildlife part of the year; another 15% is covered with icecaps or fresh water, leaving 47% of the global land area too steep, shallow, sandy, arid, wet, cold, or saline for crops and suitable only for grazing by domestic livestock and game animals—frequently or occasionally. They vary from hot humid savannas in Brazil's Matto Grosso to Mongolia's cold arid steppes and differ widely in productivity from Saudi Arabia where 640 acres are required per camel to the Argentine pampa where 2 ha often are enough to support a cow and calf for one year.

Perhaps another 2 or 3% of the virgin land may come into crop production through drainage or irrigation.

Significance to the Human Race

Basic Source of Food and Protein.—Should some cosmic force wipe out the vegetation on the world's natural grazing land, a large percentage of our population would soon starve to death because the croplands are not great enough to feed the numbers of people already short of food. Should such a catastrophe suddenly occur, we would be deprived of most of our meat, milk, hides, wool and animal by-products.

Green plants manufacture their own food which in turn nourishes animals. Ingredients are primarily water, air, and minerals (which animals cannot use for food in their pure state) plus sunshine. In the process of making vegetable matter, plants purify the air for animals by releasing oxygen. In converting vast quantities of raw materials to food on land not suited to cultivation, plants provide much of the food for animals and eventually for man.

Grazing Lands are Watersheds.—Watershed values often are equal to forage-producing values of grazing lands. The vast areas of rangelands serve as watersheds that receive precipitation which eventually drains into rivers and small streams, or sinks into the soil to replenish springs and groundwater reservoirs.

Thrifty vegetation is the key to productive watersheds essential in supplying water for agriculture, cities, and industry. The world is suffering from exploited watersheds menaced by floods and plagued with disappearing water supplies, when need is multiplying yearly. Through cooperation between governments and landowners, many depleted watersheds are being restored to their former state of productivity. One excellent example is on Sandstone Creek, a branch of the Washita River in Oklahoma, USA. Following construction of a few reservoirs, combined with proper grazing of ranges, plus conservation farming of croplands, this wild untamed flood producer, which went dry in the summer, again has a stabilized watershed. Sandstone Creek now produces a steady stream of water all year as it formerly did before the turn of the century. Net farm income has increased.

Habitat for Wildlife and Soil Life.—Most wildlife is found on natural grazing lands and includes big game, small mammals, upland game birds, and predators. Unfortunately, numbers of many game species have been decimated and some have been eliminated because of reckless hunting or loss of habitat due to overgrazing by domestic animals. In many places where increasingly large areas are under conservation management and hunting is controlled, income from game and associated recreation facilities exceeds that from domestic animals.

Soils of well-managed natural grazing land serve as a prime habitat for countless unseen microorganisms such as bacteria, fungi, algae, and protozoa. Also the soil feeds and shelters beneficial insects, earthworms and various burrowing animals. Microscopic life prepares minerals and nitrogen for absorption in a water solution by the roots. Plants could not live if there were no microscopic soil organisms, and these organisms could not live without organic matter originating from dead stems, leaves, and roots of plants. Overgrazing has caused huge decreases in the number of soil organisms essential for full forage yields.

Value for Conservation.—A healthy cover of natural vegetation provides an effective and economic cover for soil and water conservation. As a reward for conservation management, native plants maintain a self-mulching process at little cost with generous returns. Watershed stabilization on areas of natural vegetation is accomplished largely through conservation grazing of forage plants and prudent harvesting of timber. Leftover

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protective plant cover, or litter, maintains the soil in a productive condition; water cannot get into most soils effectively without this filter of unused plant parts to let it in. On properly managed ranges and forest areas, raindrops dash harmlessly into a spongy or soft mass of litter and stubble, where water penetrates deeply into the soil and is stored safe from evaporation but available for deep-rooted plants needing it for growth.

Naturally landscaped, grassed, or wooded lands are of major interest to an increasing number of nature lovers seeking outdoor recreation and pleasant scenery provided in variety all through the growing and dormant seasons.

Fuel and Timber.—Woodlands are grazing lands. Often savannas and groves of low-value commercial timber are dependable sources of fuel and building materials for small construction. In developed countries, fuel wood has a declining use because of substitutes. However, in developing countries destruction of dwarf woodlands and browse plants continues at an alarming rate. This is doubly vexing because usually these plants are valuable for both grazing and fuel, and conservation measures are needed. Intermingled with grazing lands often are found commercial forest sites on mountains, favored exposures, or along river flood plains. A grazing program for such sites must be planned to further tree growth without damaging the timber resources. Moderate grazing often helps to control weed species and reduce the fire hazard. Animal dung is a vital by-product of grazing lands and is the prime source of fuel in some areas.

Medicines and Industrial Compounds.—Many primitive foods, medicines, and useful compounds originate from natural vegetation including sugar, nuts, seeds, turpentine, rubber, quinine, digitalis, gums, and poisons for control of insects and parasites.

Minerals and Construction Materials.—In addition to vegetation values, native grazing lands yield some of the world's great supplies of minerals and construction materials and fertilizers such as: coal, oil, precious minerals, tin, magnesium, uranium, limestone, granite, and phosphorus. Once these resources are exhausted, their raw excavation scars and heaps must again be covered with vegetation. In time nature heals them with grasses, herbs, trees, and shrubs but the process can be hurried through reclamation of destroyed surfaces by planting trees and grass for forage production or for recreation.

Dependence of World Livestock Industry On Natural Grazing Lands

We have already recognized that presently domestic animals obtain about 75% of their forage needs from natural grazing lands, while wildlife obtain most of their needs from this source. One of the great needs, howver, is to orient future animal feeding programs to provide for an increased amount of farm-grown supplements as well as more of the basic livestock ration. This is now fairly well integrated in developed nations but accomplishing it in developing countries is difficult because farming and livestock raising are generally independent operations carried out by non-related interests. Also, the traditionally small farmer has neither the size of operation nor the financing essential for successful livestock raising.

The world animal population has a colossal appetite that needs to be satisfied with nutritious forage every day but the supplies and quality are far below need. The estimated numbers of domestic animals in the world for 1963–64 are as follows:

Kind	*Number* (millions)
Horses	62.8
Mules	15.5
Asses	41.7
Cattle	992.3
Pigs	534.1
Sheep	1,008.5
Goats	356.2
Buffalo	106.0
Camels	11.6

Value of meat products alone amounts to approximately 40 billion dollars annually, second in worth only to cereals and rice. However, livestock eat one-third of all cereals produced. Over 7% of meat production goes into international trade, including live animals, carcasses, and prepared and canned meat worth around 3 billion dollars per year. In 1959–61, this trade amounted to 13% of world exports of all food and beverage sales, compared with 21% for cereals and rice, 16.5% for coffee, cocoa, and tea, and 5.5% for dairy products.

Who Owns World Grazing Lands

Probably 75% of the grazing lands are publicly owned, the amount varying widely among nations. For example, about 25% of the United States' grazing lands are owned by the public; nearly all the Arabian Peninsula is public land. The remainder is under some type of private ownership including individuals, grazing associations, cooperatives, estates, and corporations.

Outside of the United States and Canada, few nations have set up public land managing organizations for the conservation of publicly owned grazing lands. Legislation similar to that in the United States and Canada needs to be adopted and management executed in all countries.

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Destruction of Grazing Lands

The bulk of world grazing lands are in poor condition and are producing less than half their potential animal products. Unfortunately, deterioration is continuing at an alarming rate, especially in arid and semi-arid regions. In such areas, restoration is extremely slow, especially where the good perennials have been killed and only annuals and unwanted perennials are present. Many of the remaining plants are low in palatability, some like loco, *Rhayzia stricta*, and milkweed are poisonous. Many overgrazed ranges have been invaded by low-quality, but high water-using shrubs, which are plaguing an increasingly vast acreage. Replacing them is costly and generally unsuccessful because in spite of the hundreds of millions of dollars spent in brush control, the invasion is increasing faster than it is being controlled.

The shocking fact is that badly needed animal production from natural grazing lands has been cut in half as a penalty charge against mismanagement while destruction continues. A hungering world gets hungrier while a valuable natural resource erodes away for lack of rational programs and proper management. Our comfort and health are threatened for lack of foresight and use of remedial measures that will halt destruction and create new sources of protein and meat.

Half of a full animal ration goes for body maintenance. Because a vast proportion of our domestic animals are fed only a maintenance ration, they are essentially wasting forage because they are not getting enough for economic production.

If all animals were on a full diet there would be far fewer of them but animal production would be greatly raised. This point can be illustrated by an experience from one of the ancient bemas where tribal managers in Saudi Arabia had made conservation use of one range area for decades. Lamb production from this properly grazed range was about 85% and lambs weighed 65 lb at 5 to 6 months of age. On the adjoining overgrazed range, lamb crops averaged only 35% and lambs at 5 to 6 months of age weighed 30 to 35 lb.

Individual sheep production was about 60% higher on the properly grazed bema, death losses were much less and meat quality was superior.

Reasons for Grazing Land Deterioration.—Overgrazing is the single greatest cause of range degeneration according to reports of 20 FAO pasture and fodder experts made to the Pasture and Fodder Crops Branch in Rome. Two or more of the statements came from each continent and all said that staffing, budgets, economic evaluations, research, and training were far short of need in developing countries. In some areas, indiscriminate burning is a contributing factor to range deterioration.

Within the developed countries are numerous technicians with the skills required to bring immediate improvements in grazing land use. To do this, these experts would need facilities, staff, budget, legislation, and administrative support. The biggest deterrent to technical advancement of conservation use of grazing land is public inertia due to apathy and a misunderstanding of biologic laws for plant perpetuation. The specialist has not been able to inspire the public with the genius of his economics and technology. There needs to be a matching up of technologists with policy makers, financiers, planners, and legislators with the powers for mass education and motivation. The key men, the policy makers, do not know that such a serious problem exists and are not aware that they should take on the responsibility and provide the way for solving it. There is no satisfactory method for free communication between policy makers and technicians. College leaders, agency heads, and other prestige leaders need to inspire policy makers to action.

What Can Be Done to Shift from Destruction to Improvement

Properly distributed and implemented, there is a large foundation of skilled specialists in developed countries capable of heading up a rational program of world grazing land conservation. Additional budgets are needed to hire and train a supplemental staff. Also practical institutional and legislative requirements are known and could be adapted to local conditions wherever needed. Fortunately, immediate good can be achieved without great cost because much grazing land improvement comes from natural healing through correct use and management. Governments own most of these lands and their legislative bodies have the power to get action quickly by providing proper legislation and regulations, budgets, and staff.

How to Cultivate Interest and Action Among Researchers, Policy Makers, Programmers, and Budget Designers

1. Sponsor international range research through the International Biological Program.
2. Set up World Grazing Year (similar to Geophysical Year).
3. Put in motion a modern appealing educational and training program at all levels.
4. Make it a major plank in the Freedom from Hunger Campaign.
5. Set up an international grazing land improvement committee under FAO chairmanship.
6. Enlist interest and aid of both scientific and world betterment groups.
7. Develop targets and guides for action.

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Range Research Needs of an International Nature

Several areas in the International Biological Program are closely relevant to the agricultural disciplines. As succinctly stated by Byerly (1967): "Inherent in IBP is the necessity for imaginative research designed to maintain a self-sustaining chain of food production. . . . An accurate count of animal and plant species and their distribution, an examination of the interaction of communities upon each other, what sustains them and whether they have protective or adaptation mechanisms—all these and more are relevant to the agricultural disciplines. The problems are global. It is therefore axiomatic to tackle them internationally." Byerly (1968) described the four sectional committees of IBP of particular interest to rangemen in the May issue of the Journal of Range Management.

The American Society of Range Management, in fostering advancement in the science and art of grazing land management, has encountered a need for expanded research knowledge to bring all North American grazing lands under proper management. Moreover, since its organization there has been increasing appreciation and involvement by the Society with foreign grazing lands having similar and perhaps even more pressing needs for concerted effort in range management research. There has developed a general awareness of major gaps and deficiencies in the scientific and technological foundations needed for maximum production of the range ecosystem. Recognition, encouragement, and support of research on the vast complex of the world's grazing resource are sought in the following areas:

1. Range plants including forage species, weeds, and poisonous plants—life history, habits, requirements, values, genetics, and ecology.
2. Range insects, diseases, rodents, game, and other animals—life history, habits, appraisal of values, or damage.
3. Habits, requirements, and nutrition of range livestock—grazing habits, forage preferences, rations for maintenance and weight gain on different types of range, effect of range fertilization.
4. Nature of the range communities and ecosystems—composition and characteristics in relation to grazing usage and forage values, including successional and regulatory processes, community interrelations, and population fluctuations.
5. Physical environment relations of range—topographic, soil, altitudinal, and climatic conditions.
6. Range management—inventory and classification of vegetation types; determination of grazing capacity, system of grazing, timing and rate of forage use; kind, class and breed of livestock to graze; interrelations of grazing, forest production, water supplies, wildlife and recreation.
7. Range improvement—evaluation of range condition and measurement of trend in vegetation and soil stability; control of runoff and erosion; conservation of water by spreading, contour furrows, loss reduction from transpiration and evaporation; control of undesirable plants, diseases, insects and rodent pests; role of prescribed burning; planting methodology and species selection.

In view of the world's expanding population and the probable increased demands for meat and animal fiber, expansion of present range and related research is urgent. Although rangelands are often characterized by low per-acre value which precludes use of many practices of established value on arable land, their aggregate contribution is significant from the standpoint of domestic livestock and related values associated with increasingly intensified use.

Considerable effort has been made to obtain recognition of world rangelands by the Pasture and Fodder Crops Branch of the Food and Agricultural Organization of the United Nations. Several effective rangeland programs have been initiated towards improvement of rangelands to better serve the people. These programs of FAO include range-trained people.

The United States Agency for International Development (AID) has made some progress in assisting in development and improvement of the world rangelands, but the total effort in this area is far below needs. Rangemen are included in assistance teams and missions far too seldom in relation to the scope of rangelands and the opportunities for making them more useful to man.

The International Grassland Congresses include rangeland or natural pastures in their programs only after determined and persistent efforts on the part of the American Society of Range Management, individual rangemen, and some agencies. Hopefully, groups concerned with organizing future Congresses will give more attention to rangelands.

Finally, the American Society of Range Management has an increasing and continuing role in focusing attention on the world's rangelands and in stimulating effective research, education, and action programs. Symposia such as that at the 19th ASRM Annual Meeting in New Orleans in 1966, "RANGE MANAGEMENT WORLDWIDE" (Chapline et al., 1966) should be included in every annual meeting. More range scientists from foreign countries need to be encouraged to write about

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their rangelands and range work for the Journal of Range Management. The Society should also work more directly with universities and agencies to emphasize the importance of rangelands and to get more range-trained men in contract teams and missions.

Above all, positive, enthusiastic, and persistent effort is needed. The International Relations Committee of the American Society of Range Management can be the generating core within the Society to help it meet its responsibilities in relation to rangelands worldwide.

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Loco Plant Poisoning in Sheep

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Highlight

This report includes data on utilization of loco plant by sheep on winter range, a comparison of the toxicity of loco plant to sheep of different ages, influence of supplementation on the incidence of locoism, and a detailed review of the literature on locoweed poisoning in sheep. Sheep grazed locoweed readily even though other good forage and supplements were available. The amount of locoweed they consumed increased throughout the experiment. At the end (12 weeks), sheep were eating primarily locoweed and shadscale and were severely "locoed." Signs of poisoning were observed first in aged ewes and lambs. Presently the prevention of loco poisoning on winter desert ranges lies in avoiding loco-infested areas almost entirely.

Review of Literature

Loco poisoning in livestock has long been a problem to the range livestock industry of the West. "Loco" is a Spanish word, meaning "crazy." The term has been applied to livestock affected by this kind of plant and also to the plants causing the disease. The disease is caused by the ingestion by livestock of certain species of *Astragalus* and *Oxytropis*.

There may be as many as 300 species of *Astragalus* in North America, which makes this genus one of the largest in the legume family (Kingsbury, 1964). Many species of *Astragalus* are difficult to identify. Cross fertilization is common in certain loco species so their taxonomy is complicated. Fortunately, the fruits of the species differ enough to permit identification. *Astragalus* species may be annuals, biennials, or perennials. Both *Astragalus* and *Oxytropis* have a taproot (Barnaby, 1964) and are herbaceous.

Ecology.—Astragalus grows primarily on the plains and desert regions of western United States. Important species also grow in the Rocky Mountains.

The *Oxytropis* species of North America are principally perennial herbaceous plants which occur circumboreal to northern New Mexico and from Minnesota to the Pacific coast (Harrington, 1964). They are adapted to a wide variety of soil types, although many species grow only around specific range sites. Barnaby (1964) has indicated that edemism is a feature of the *Astragalus* species. The growth of many species is restricted to particular sites because of optimal moisture conditions, essential minerals, or some other confining ecological factors.

Seeds of desert *Astragalus* species retain their vitality for 30 to 40 years and perhaps longer (Barnaby, 1964), germinating readily if they become well soaked. Apparently, factors other than moisture are involved in germination since some species become epidemic only if temperature as well as moisture is optimal. Marsh (1909) indicated that locoweed, including *Astragalus mollissimus* and *Astragalus lambertii*, was abundant in high rainfall years and nearly disappeared in dry years. Under Utah conditions, heavy infestations seem to follow wet, warm, autumn seasons. Few plants are seen during the summers that follow a dry fall and winter. Locoweed species grow in a wide range of precipitation.

Coarse soil fragments are consistently associated with occurrence and abundance of loco plants. Payne (1957) found that white point loco (*Oxytropis sericea* Nutt.) grew in a wide range of soil depths. In the desert regions of western and eastern Utah, speckled loco plant or freckled milk-

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Ecological Monographs, 71(4), 2001, pp. 531–556
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LANDSCAPE-SCALE CHANGES IN PLANT SPECIES ABUNDANCE AND BIODIVERSITY OF A SAGEBRUSH STEPPE OVER 45 YEARS

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Abstract. Increasing demands on arid and semiarid ecosystems, which comprise one-third of Earth's terrestrial environment, create an urgent need to understand their biodiversity, function, and mechanisms of change. Sagebrush (*Artemisia*) steppe, the largest semiarid vegetation type in North America, is endangered because of losses to agriculture, excessive grazing, and invasive species. Establishment in 1950 of what is now designated as the Idaho National Engineering and Environmental Laboratory (southeastern Idaho, USA) created the largest existing reserve of this extensive vegetation type. We used cover, density, and frequency data for vascular plants sampled on 79 permanent plots nine times during 45 years to (1) assess long-term changes in abundance and distribution of major species and life forms, (2) assess changes in species richness and plot similarity, and (3) test the hypotheses that plant cover and stability of cover are positively associated with species richness and that invasibility is inversely related to native plant cover and richness.

From 1933 through 1957 the area was subject to severe drought, with annual precipitation exceeding the long-term mean only four times. Cover of shrubs plus perennial grasses was 18% in 1950, and the vegetation was heavily dominated by sagebrush. Perennial grass cover was only 0.5%. With elevated precipitation after 1957, shrub cover increased to 25% by 1965, and by 1975 cover of perennial grasses had increased 13-fold. Subsequent fluctuations in cover did not track precipitation closely. Cover and density of major species were often out of phase, and correlation analyses indicated lags of 2–5 yr in responses of species or functional groups to precipitation. Aggregate species richness of the area has not changed appreciably, but richness of shrubs, perennial grasses, and forbs per plot steadily increased from 1950 to 1995. Vegetative heterogeneity also increased, with mean similarity among plots declining from 72% to 40%. Plots having higher species richness tended to maintain higher levels of cover and to vary less in cover relative to their mean level, indicating links between species richness and function. Abundance of nonnative species was negatively correlated with cover, but not with richness of native species. Thus, adequate cover of native species can render these semiarid communities more resistant to invasion. Maintaining richness and cover of native species should be a high management priority for these ecosystems.

Key words: Artemisia tridentata; Bromus tectorum; *ecosystem function and species diversity; Idaho (USA) INEEL; invasibility; landscape-scale long-term data set; livestock grazing; precipitation and vegetative cover; sagebrush steppe; species richness; stability; vegetation dynamics.*

INTRODUCTION

Approximately one third of the Earth's land surface consists of arid and semiarid ecosystems (Schlesinger et al. 1990), the vast majority of which are utilized for livestock production. On all continents, heavy livestock use of these ecosystems has altered plant species composition and biodiversity and often has reduced secondary productivity and increased the proportions of non-palatable shrubs (Walker et al. 1981, West 1983*a*, 1999, Schlesinger et al. 1990, Dean and Macdonald 1994, Milton et al. 1994). In the past decade we have seen increasing concerns about habitat quality, sustainability, losses of biodiversity, and impacts of invasive species (Walker 1993, Milton et al. 1994, West 1996, 1999). These concerns, coupled with increased demands for recreation and, in many parts of the world, agricultural production, underscore the need for a better understanding of ecological processes, the nature of long-term variation in productivity and species composition, and the mechanisms driving change in semiarid lands.

In North America, sagebrush steppe occurs on some 4.48×10^5 km^2 of the Columbia and Snake River Plateaus, the northern edge of the Great Basin, and southwestern Wyoming (West 1983*a*). Similar sagebrush communities having a lower proportion of herbaceous species occupy another 1.8×10^5 km^2 of the Great Basin and Colorado Plateau (West 1983*b*). The two types constitute the largest temperate semidesert in North America (Miller et al. 1994). Despite their areal extent, however, sagebrush-dominated communities are among North America's critically endangered eco-

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systems as a consequence of losses to agriculture, conversions to exotic annual communities, or degradation due to excessive grazing by domestic livestock (Noss et al. 1995, Christensen et al. 1996, Knick 1999). Livestock were introduced to the region in the mid 1800s, and by the end of the century the grazing capacity of most sagebrush-dominated rangelands had been exceeded (West 1983*a*). The original grazing capacity of the sagebrush steppe was estimated as 0.83 animal unit months (AUM) per hectare, whereas the estimated capacity in 1970 was about 0.29 AUM/ha (West 1983*a*). Although stocking rates generally have been reduced since the 1930s, many areas have shown little recovery and may represent new steady states with reduced diversity, depleted populations of deep-rooted perennial grasses and forbs, and increased fire frequencies due to an abundance of fire-prone introduced annuals or short-lived perennials (Miller et al. 1994).

Numerous studies of semiarid ecosystems indicate that once woody species become dominant as a result of livestock grazing or alteration of natural-disturbance regimes (e.g., fire suppression) the resulting cohort of unpalatable woody plants may persist for long periods (e.g., Smeins et al. 1976, Rice and Westoby 1978, Anderson and Holte 1981, Holechek and Stephenson 1983, Sneva et al. 1984, West et al. 1984, Austin and Williams 1988, Westoby et al. 1989, Milton et al. 1994, Wiegand and Milton 1996). Dominance by woody species is often accompanied by loss of biodiversity and low productivity of palatable herbaceous plants (West 1993, 1999). The resistance to change in such communities is a consequence of the longevity of individuals of woody species, the usurping of resources by mature individuals of those species, and the relative paucity of propagules of herbaceous species. Contemporary models of vegetation dynamics in such systems postulate that the vegetation can exist in one of various relatively stable states and that transitions between states may require some biotic or abiotic force to drive the system over a threshold (Laycock 1991, Tausch et al. 1993, West 1999). Thus we might predict that, in the absence of a major disturbance, the vegetation of a shrub-steppe heavily dominated by a relatively long-lived woody species would be quite static.

To test that prediction, we analyzed data from permanent plots established in 1950 at the Idaho National Engineering and Environmental Laboratory (INEEL). We assessed changes in cover, species richness, and plot similarity through time. Our first objective was to describe and account for changes that occurred during a 45-yr period. We assumed that the major drivers of vegetative change in this ecosystem would be (1) annual or longer term variation in precipitation (Le Houerou et al. 1988, Wiegand and Milton 1996), (2) biotic and abiotic disturbances including herbivory, diseases, and fire, (3) the pool of species available for dispersal and establishment, and (4) competitive interactions (Pickett et al. 1987, Pickett and McDonnell 1989). Because livestock have been excluded from 49 permanent plots (see *Methods: Permanent vegetation plots,* below) and all of the permanent plots have been free from major abiotic disturbances such as fire since at least 1950 (except for two plots that burned in 1994), those factors could be eliminated as potential causes of change. Water is the major limiting factor in this ecosystem (Caldwell 1985, Toft et al. 1989), so we predicted that changes in abundance of plant species would be correlated with precipitation patterns, but potentially constrained by propagule availability.

Our second objective was to use the long-term data set from the permanent plots to test predictions concerning relationships between species richness and functional attributes of ecosystems. Numerous recent studies (Tilman and El Haddi 1992, Naeem et al. 1994, 1996, Tilman and Downing 1994, Tilman et al. 1996, 1997*a*, Hector et al. 1999) as well as theoretical analyses (McNaughton 1977, Tilman et al. 1997*b*, Loreau 1998) have shown or predicted positive relationships between species richness and plant cover or primary productivity and between species richness and the stability of cover or primary productivity. Exceptions to these patterns, particularly the positive relationship between productivity and species richness, have been reported (McNaughton 1968, 1985, Mellinger and McNaughton 1975, Hooper and Vitousek 1997, Wardle et al. 1997), and the design and interpretation of some studies have been challenged (Johnson et al. 1996, Grime 1997, Huston 1997). While some authors claim an emerging consensus that ''on average'' higher diversity *can* give rise to higher productivity and greater stability of ecosystem processes (McCann 2000, Purvis and Hector 2000), a lively debate continues (Hector et al. 2000, Huston et al. 2000, Naeem 2000, Wardle et al. 2000). Many studies addressing these predictions involved artificial communities grown in controlled-environment facilities (e.g., Naeem et al. 1994, 1996) or field experiments in which species composition was manipulated (e.g., Tilman and El Haddi 1992, Tilman and Downing 1994, Tilman et al. 1996, Hooper and Vitousek 1997, Hector et al. 1999). We reasoned that if such relationships were general and robust they should be apparent in the dynamics of long-term data from permanent plots. Therefore, we predicted that mean vegetative cover on the permanent plots would be positively correlated with species richness and that vegetative cover would tend to be more stable on plots having higher species richness.

The third objective of our study was to test two hypotheses concerning invasibility. Another prediction concerning the functional effects of biodiversity is that communities having more species are more resistant to invasion (Elton 1958, Fox and Fox 1986, Holdgate 1986). Conflicting results have come from studies of intact ecosystems (Lonsdale 1999, Chapin et al. 2000), but in experiments where diversity was manipulated, ''communities with more species are often more resis-

tant to invasion'' (Purvis and Hector 2000:217). We predicted that the abundance of introduced species would be inversely correlated with native-species richness on the permanent vegetation plots at the INEEL. Assuming that cover would reflect the resource space occupied on a plot, we also predicted that the abundance of introduced species would be inversely correlated with cover of native species.

Grime (1997:1261) speculated that high biodiversity might be ''vitally important'' in semiarid or other ecosystems that experience ''drastic fluctuations'' on seasonal or longer time scales. Demonstrating that any of the postulated relationships between biodiversity and ecosystem function hold for a natural sagebrush steppe could have important implications for sustainable management of semiarid ecosystems globally.

Methods

Study area

In 1950 and 1957, 2315 km^2 of sagebrush steppe on the upper Snake River Plain (southeastern Idaho, USA) were purchased or withdrawn from the public domain to form what is now designated as the Idaho National Engineering and Environmental Laboratory (INEEL, Fig. 1). About 43% of the area has been closed to grazing by domestic stock since at least 1957. Most of that area has been closed to grazing since 1950, and, before that, grazing was restricted on much of the land when it was used as a Naval gunnery range during World War II. The absence of anthropogenic disturbances over most of the area coupled with data from permanent vegetation plots provides a unique opportunity to study landscape-scale vegetation dynamics in a large area of natural sagebrush steppe.

The INEEL is on the western edge of the upper Snake River Plain in southeastern Idaho, USA (43° N, 112° W) (Fig. 1). Average elevation of the areas covered by this study is ~1500 m (range: 1460–1620 m). Mean annual temperature is 5.6°C; the frost-free period averages ~90 d but has ranged from 68 to 123 d over 45 yr of record (U.S. National Oceanic and Atmospheric Administration [NOAA], *unpublished data*). Characterized by high-magnitude diurnal and seasonal temperature fluctuations, the climate is typical of that of the region occupied by sagebrush steppe (West 1983*b*, Caldwell 1985, Smith et al. 1997). During summer, low humidities and clear skies result in high temperatures and high evaporative demand during the day and relatively low temperatures at night due to rapid radiative cooling. Winters are cold, with several months having mean temperatures below freezing. Snow cover may persist for periods of a few weeks to >2 mo.

The INEEL lies in the rain shadow of the numerous mountain ranges of central Idaho. Average annual precipitation is 220 mm. Precipitation tends to be uniformly distributed throughout the year except for a peak early in the growing season (Fig. 2). On average, 37% of the annual precipitation falls during April, May, and June; May and June are the wettest months (Fig. 2). Melting snow and spring rains account for most of the annual recharge of moisture in the soil profile (Caldwell 1985, Anderson et al. 1987). In a typical year, most of the water available to plants is depleted by early summer to midsummer (Anderson et al. 1987). The predictability of the annual cycle of moisture availability has apparently selected for similar patterns of water use among the dominant species (Caldwell 1985, Anderson et al. 1987).

Surface features at INEEL reflect a long history of volcanic activity (Nace et al. 1972). Most of the area is a relatively flat plain, but the terrain is frequently broken and undulating because of underlying Quaternary basalt flows. Most soils are of aeolian origin derived from older silicic volcanics and Paleozoic sedimentary rocks from the surrounding mountains (McBride et al. 1978). Soils are primarily orthidic Aridisols, with Calciorthids being the most common great group. Accumulations of sand on the lee sides of outcrops, in depressions, and on dunes result in abrupt gradients in soil texture that may influence plant species composition over relatively short distances (Shumar and Anderson 1986).

Vegetation at the INEEL typically is characterized by an overstory of big sagebrush (*Artemisia tridentata*); two subspecies, *A. t. wyomingensis* and *A. t. tridentata,* are common (Shumar and Anderson 1986). Other common shrubs include *Chrysothamnus viscidiflorus, Leptodactylon pungens, Grayia spinosa, Tetradymia canescens* and *Krascheninnikovia lanata* (Table 1). Perennial grasses, including *Stipa comata, Elymus elymoides, E. lanceolatus, Oryzopsis hymenoides,* and *Pseudoroegneria spicata,* are typically the most abundant herbaceous perennials, but the area also supports a diversity of forbs (Table 1). In 1995, total vascular plant cover was 38%. Shrubs contributed 52% of the cover, graminoids 15%, and perennial forbs 7.5%. Annuals and biennials accounted for 24% of the total cover, of which nearly half consisted of introduced species, primarily *Bromus tectorum* (Table 1). Anderson et al. (1996) provide a general description of the vegetation and a complete flora. Nomenclature follows USDA (1995).

Use of the area occupied by the INEEL before 1950 is not well documented. Much of the upper Snake River Plain has been grazed by livestock since the late 1800s (Harniss 1968). The area was crossed by a trail used for moving cattle to eastern markets during the late 1870s, and it was used extensively for spring and fall sheep grazing. Harniss and West (1973) concluded that the area was severely overgrazed prior to 1950. The low cover of perennial grasses in 1950 supports that conclusion (Anderson and Holte 1981), but, as shown below (see *Results: Long-term trends in precipitation*), prolonged drought during the 1930s and 1940s probably exacerbated grazing impacts.

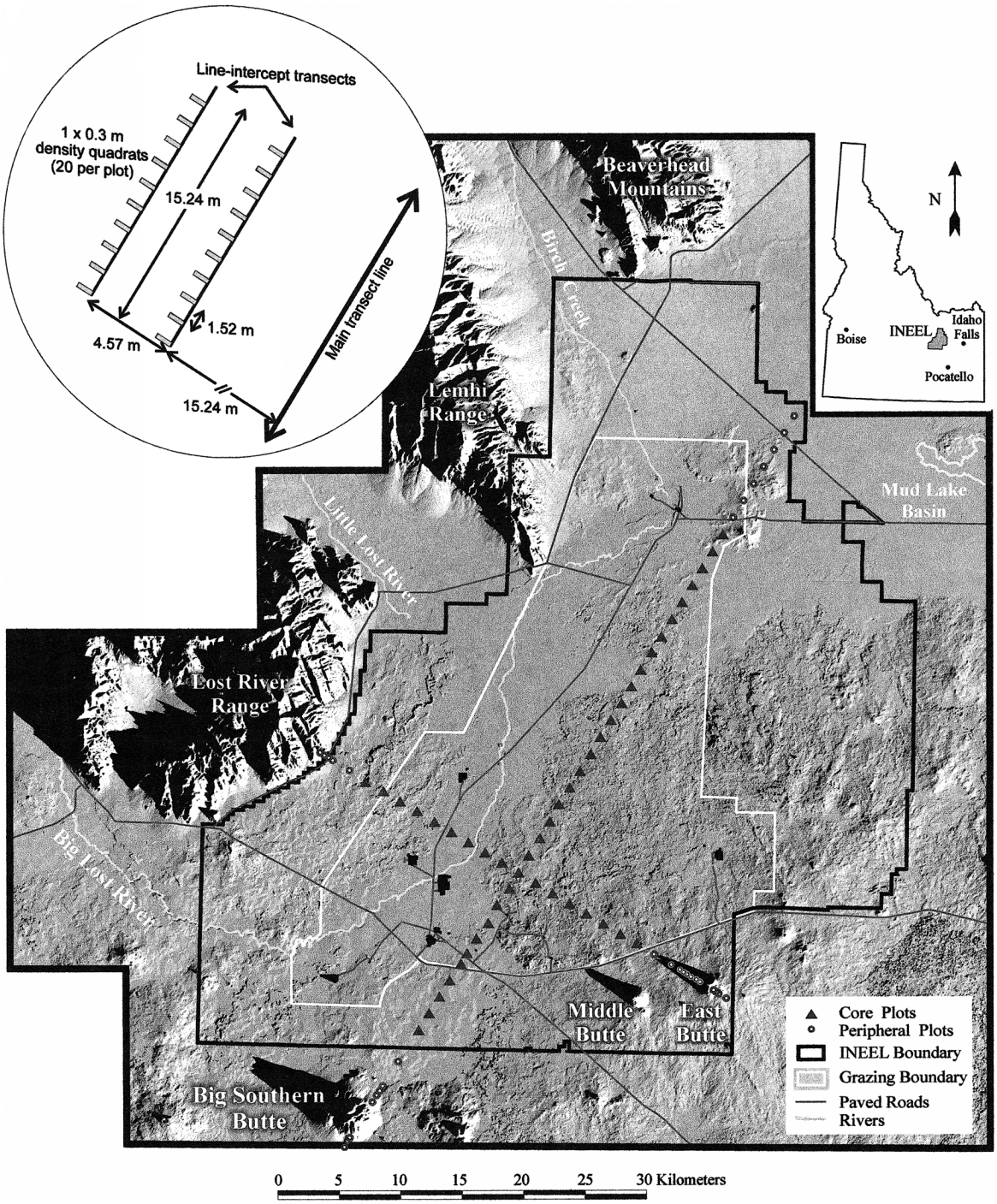


FIG. 1. Shaded relief map of the Idaho National Engineering and Environmental Laboratory (INEEL) showing the locations of the permanent vegetation plots along two perpendicular transects. The area within the white boundary is closed to livestock grazing. The left inset shows the layout of the two 15.24-m line-intercept transects and 20 density quadrats (0.3 × 1 m) at each of the plots; the right inset shows the location of INEEL in Idaho (USA). Elevations of core plots range from 1458 m to 1520 m on the southwest–northeast transect and from 1488 m to 1581 m on the southeast–northwest transect.

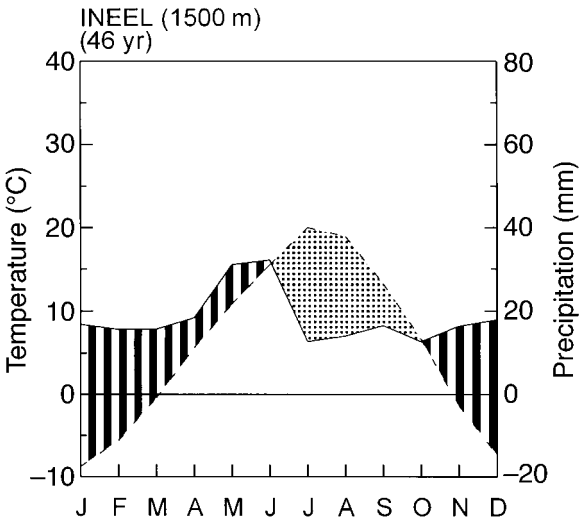


FIG. 2. Climate diagram (sensu Walter et al. 1975) for the Idaho National Engineering and Environmental Laboratory (INEEL), based on data for 46 yr from the Central Facilities Area (U.S. National Oceanic and Atmospheric Administration [NOAA], Idaho Falls, Idaho, USA, *unpublished data*). The solid curve depicts mean monthly precipitation; the dashed curve shows mean monthly temperatures. Vertical hatching indicates periods when precipitation generally exceeds potential evapotranspiration. The stippled area indicates periods when potential evapotranspiration generally exceeds precipitation.

Although domestic livestock have been excluded from a portion of the area since 1950, native herbivores are common and sometimes very abundant. The area provides winter range for large numbers of pronghorn (*Antilocapra americana*), and some pronghorn and a few mule deer (*Odocoileus hemionus*) are year-long residents. Elk (*Cervus elaphus*) colonized the INEEL during the mid-1980s (Moritz 1988), and two herds of about 80 animals each were present by 1989 (Strohmeyer 1992). Since then, numbers have varied in annual censuses from 53 in summer to >350 individuals in winter (R. Warren, *unpublished data*). Populations of black-tailed jackrabbits (*Lepus californicus*) are cyclic, reaching high densities at ~10-yr intervals (Anderson and Shumar 1986). The most recent noteworthy peak in the jackrabbit population occurred in 1981 when densities reached ~2 jackrabbits/ha. Except for a minor increase in the early 1990s (Porth 1995), jackrabbit populations have been very low since 1983 (J. Anderson and R. Warren, *unpublished data*). Scattered populations of cottontail rabbits (*Sylvilagus nuttallii*) and pygmy rabbits (*Sylvilagus idahoensis*) also exist (Wilde 1978), and small mammals can be locally abundant (Groves and Keller 1983).

Precipitation data and estimates

Precipitation data from the station at the INEEL Central Facilities Area (CFA) are available from 1950 to present. To estimate INEEL precipitation prior to 1950,

TABLE 1. Average percent cover of vascular plants (by growth form and species) for 47 core vegetation plots at the Idaho National Engineering and Environmental Laboratory (southeastern Idaho, USA), measured by point interception in 1995.

Plant species	Cover (%)	Relative cover (%)
Shrubs		
Artemisia tridentata ssp. *wyomingensis*	9.448	25.152
Chrysothamnus viscidiflorus	7.655	20.132
Artemisia tridentata ssp. *tridentata*	1.699	4.465
Leptodactylon pungens	0.539	1.417
Grayia spinosa	0.417	1.100
Atriplex confertifolia	0.352	0.926
Tetradymia canescens	0.347	0.914
Krascheninnikovia lanata	0.273	0.718
Others (n = 4)	0.148	0.423
Total shrub cover	19.74	51.88
Perennial graminoids		
Elymus elymoides	1.460	3.838
Stipa comata	1.376	3.617
Elymus lanceolatus	0.985	2.588
Agropyron desertorum	0.567	1.492
Oryzopsis hymenoides	0.405	1.066
Pascopyrum smithii	0.253	0.665
Poa nevadensis	0.181	0.475
Pseudoroegneria spicata	0.149	0.392
Poa secunda	0.139	0.367
Others (n = 6)	0.118	0.311
Total graminoid cover	5.63	14.81
Perennial forbs		
Phlox hoodii	1.136	2.986
Astragalus lentiginosus	0.306	0.805
Astragalus filipes	0.236	0.621
Erigeron pumilus	0.154	0.404
Astragalus ceramicus	0.148	0.388
Psoralea lanceolata	0.130	0.342
Phacelia hastata	0.128	0.336
Others (n = 36)	0.617	1.622
Total perennial forb cover	2.85	7.50
Succulents		
Opuntia polyacantha	0.50	1.31
Native annuals and biennials		
Descurainia pinnata	0.748	1.967
Gayophytum diffusum	0.707	1.858
Lappula redowski	0.573	1.507
Gilia sinuata	0.522	1.373
Cordylanthus ramosus	0.517	1.358
Collomia tenella	0.369	0.969
Eriastrum sparsiflorum	0.293	0.771
Machaeranthera canescens	0.273	0.718
Eriogonum cernuum	0.232	0.609
Chenopodium leptophyllum	0.204	0.537
Cryptantha scoparia	0.182	0.479
Chaenactis fremontii	0.167	0.438
Others (n = 16)	0.264	0.693
Total native annual/biennial cover	5.05	13.28
Introduced annuals and biennials		
Bromus tectorum	2.280	5.994
Sisymbrium altissimum	0.710	1.868
Descurainia sophia	0.656	1.724
Alyssum desertorum	0.563	1.479
Others (n = 5)	0.053	0.140
Total introduced annual/biennial cover	4.26	11.21
Unknowns	0.008	0.021
Total vascular plant cover	38.04	100.00

Notes: Within plant growth forms, species are listed in order of descending cover values. Cover is shown for each species having absolute cover >0.1% and for various growth forms. Relative values are based on total vascular plant cover.

data from 1950 through 1990 for three surrounding locations (Arco, Blackfoot, and Idaho Falls) were used as independent variables in a stepwise multiple regression with actual INEEL precipitation as a dependent variable. The independent variables that explained the greatest amount of variance in the actual INEEL precipitation were used to estimate precipitation from 1905 to 1949. This analysis was done separately for water-year (October through September) and for growing-season (April through July) precipitation. Data from Arco and Blackfoot together explained the greatest amount of variance in INEEL precipitation. For years in which data from one or both of these sites were missing, data from the available sites were used to estimate INEEL precipitation. None of those stations had data for 1944, so the monthly 1950–1995 data from CFA were regressed against those from Pocatello (the nearest Snake River Plain station from which 1944 data were available) to predict 1944 precipitation at INEEL. Average water-year and growing-season precipitation were calculated using estimated and actual INEEL data from 1905 through 1995. Five-year sliding averages were calculated by averaging precipitation in the current year with that in the four preceding years.

Permanent vegetation plots

Vegetation studies were initiated at the INEEL in 1950 with the establishment of 94 permanent sample plots along two perpendicular lines (Fig. 1). Most of these were at 1.6-km intervals, but intervals were shorter near the buttes on the southern and eastern sides of the INEEL. Plowing destroyed two plots before 1957. The remaining 92 plots were sampled in 1950, 1957, 1965, 1975, 1985, and 1995. A subset of 35 plots, analyzed by Anderson and Holte (1981) and Anderson (1986), was sampled in 1978, 1983, and 1990.

Forty-four plots are within the area officially closed to livestock grazing (Fig. 1). This area comprises the central portion of the INEEL, which lies at the lowest elevation. Two plots just within the northern boundary of the closed area have been grazed recently and were not included. However, we included five plots that lie outside the grazing boundary as ''closed'' because they have been inaccessible to livestock since the INEEL was established. For convenience, we refer to these 47 plots as ''core plots'' and to those in areas subject to grazing as ''peripheral plots''. For the current study, we performed numerous cluster analyses and ordinations of the data from all 47 plots within the closed area and from all years. These analyses failed to identify a consistent homogenous subset of plots (results not shown). Therefore, we used data from all 47 plots for the current analyses whenever possible. For some analyses, we used data from the 35 plots that were sampled in every census year. For analyses concerning relationships between species richness and cover or change in cover, we combined data from core and peripheral plots to make the sample as large as possible.

Vegetation sampling

Cover, density, and frequency were assessed during June, July, or August, according to the original sampling design (see Anderson et al. [1978] for details). Two parallel 15.24-m transect lines were established in 1950 at each plot (Fig. 1). Crown cover of shrubs and basal cover of perennial grasses were measured by line interception (Canfield 1941) along the two transect lines (in the original sampling design, cover estimates were limited to shrubs and perennial grasses). Ten density quadrats (each 0.3×1 m) were placed at 1.52-m intervals along each transect line. The density of each perennial species in each of the 20 quadrats was recorded. Tillers of perennial rhizomatous grasses were counted as individuals. Annuals were inventoried in a 0.1×0.1 m subsection of each quadrat.

Because the original sampling design did not estimate abundance for all growth forms on a common scale, we estimated cover of all vascular plants in 1995 by point interception (Floyd and Anderson 1982) to provide a more comprehensive description of the vegetation (Table 1) and to test the hypotheses concerning invasibility. A 0.5×1 m point sighting frame, with 36 points at 0.1-m intervals, was centered at 1-m intervals over a taut tape. The plant species or other entity (e.g., bare ground) under each point was recorded to estimate canopy cover of shrubs and forbs and basal cover of graminoids. Fifteen frames were examined on each of the original transect lines; 20 additional frames were examined on a third line 20 m in length, providing a total sample of 50 frames per plot.

Data analyses

Because of discrepancies in the identification of grass species in the genus *Poa* by different investigators over the 45-yr period, the species in this group were pooled for the current analyses. Sample sizes for analyses of density data were 46 for 1950 and 40 for 1957 because some of the original data sheets are missing.

We examined relationships between cover and precipitation using both water-year and growing-season precipitation. For total shrub or total grass cover and for four common species in each of those groups (including *Poa* spp.), we tested for significant correlations between cover and precipitation in the census year, precipitation in each of the four years preceding the census year, and precipitation of the census year averaged with 1-4 preceding years. Sample size for these analyses was nine, with each point representing average cover on the core plots and either annual or average precipitation. The resulting relationships were compared to see which precipitation value was the best predictor of average cover. Because we were interested in identifying potential relationships in these analyses, we used $\alpha = 0.05$ to indicate statistical significance despite doing repeated correlation analyses. Applying a Bonferroni-

type correction to maintain a constant alpha level would have increased the probability of a Type II error. *P* values between 0.03 and 0.05 were taken as suggestive of relationships, recognizing that additional research would be required to confirm them.

To assess changes in similarity among plots through time, we calculated percentage similarity (PS) as the sum of minimum proportional abundance of each species in a pair of plots (Whittaker 1975), using data for plots that were sampled in each census year. PS was calculated for each pair of plots and the average of all pairwise similarities was calculated for each year. These annual averages were then plotted against time.

We addressed relationships between cover and species richness in two ways, and separately for shrubs and perennial grasses. First, for each sample year we tested for correlations between total cover of shrubs or perennial grasses and species richness of the same group on individual plots. Sample sizes for these analyses ranged from 35 to 94 plots, depending on the number of plots that were sampled in a given year. Second, we tested for correlations between average cover of shrubs or perennial grasses over the nine census years and average species richness of each group over the same years. For these analyses we used the subset of 35 plots that was sampled in each of nine sample years.

We tested for relationships between species richness and the stability of cover in two ways. First, we calculated the absolute change in cover of all shrubs or all perennial grasses between each consecutive pair of censuses and averaged those eight values for each plot. We then tested for correlation between mean change in cover with mean species richness for the nine census dates. We performed this analysis for the subset of 35 plots that were sampled at every census and for a subset of 78 plots that were sampled in 1950, 1957, 1965, 1975, 1985, and 1995. Second, we calculated the standard deviation and coefficient of variation of cover separately for shrubs and for perennial grasses and tested for correlations between those values and mean species richness for the same nine sample years. This analysis was performed for the subset of 35 plots that were sampled at every census. In addition to these separate analyses for shrubs and for perennial grasses, we performed similar analyses for combined cover and species richness of shrubs and perennial grasses.

Results

Long-term trends in precipitation

In 1950 when the first vegetation samples were taken at the Idaho National Engineering and Environmental Laboratory (INEEL; Idaho, USA), the region was in the depths of an intense, sustained drought. From 1933 through 1956, water-year precipitation exceeded the long-term mean only four times (Fig. 3). Estimated precipitation was above the long-term mean in 1944 and 1945, but water years from 1949 through 1956 were very dry. Five-year sliding averages show a generally decreasing trend in water-year as well as growing-season precipitation from the early 1900s through the mid-1950s, and they clearly indicate the duration and severity of the drought in the 1930s, 1940s, and early 1950s (Fig. 3). After 1956, precipitation increased markedly, and the sliding averages generally were above the long-term averages from the late 1950s through the mid-1970s. Drought in the late 1970s was followed again by above-average precipitation in the early 1980s. The late 1980s and early 1990s water years were again very dry, but 1993 and 1995 were exceptionally wet years. June 1995 was the wettest month of record at the Central Facilities Area, and precipitation during the 1995 water year was the highest in 90 yr (Fig. 3). The five-year averages suggest precipitation cycles of about 20 yr duration (Fig. 3).

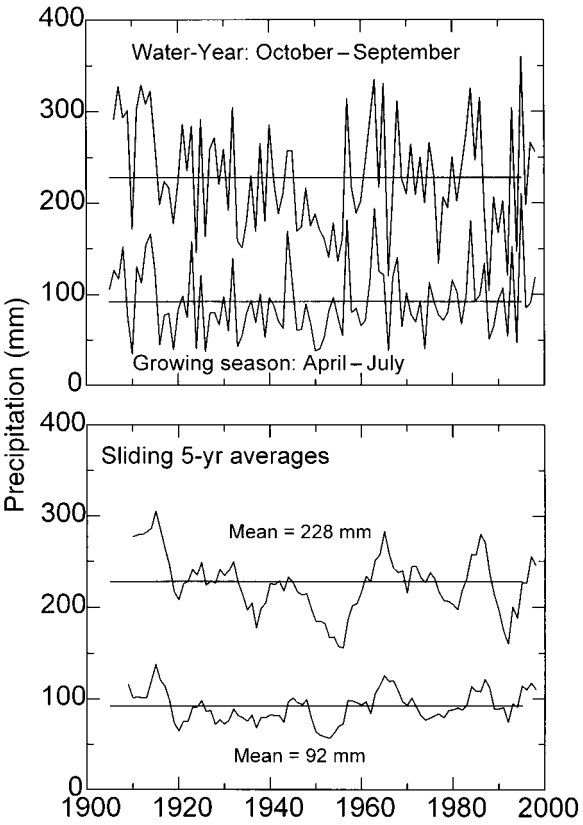


FIG. 3. Precipitation data for the Idaho National Engineering and Environmental Laboratory (INEEL). The upper curve in each panel shows water-year (October–September) precipitation; the lower curve shows growing-season (April–July) precipitation. Horizontal lines show water-year or growing-season means. Sliding averages represent the average of precipitation in the current year and four preceding years. Data for years prior to 1950 were estimated using correlations between INEEL data and precipitation at 2–3 nearby locations (see *Methods: Precipitation data and estimates*). Means shown include estimates for years prior to 1950.

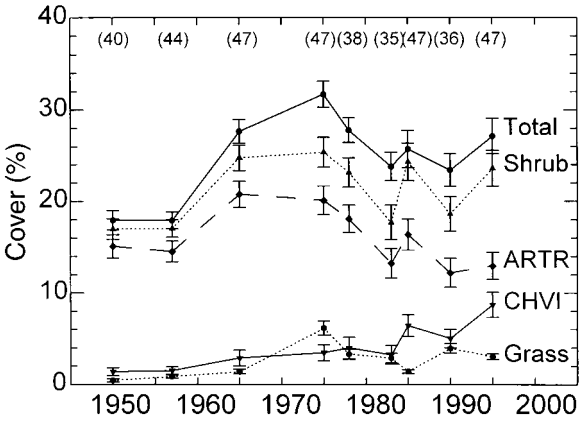


FIG. 4. Trends in total cover, shrub and perennial grass cover, and the cover of the two dominant shrubs, *Artemisia tridentata* (ARTR) and *Chrysothamnus viscidiflorus* (CHVI), from 1950 to 1995 for permanent plots at the Idaho National Engineering and Environmental Laboratory. Data are means ± 1 SE. Numbers in parentheses at the top of the frame show the number of plots for which data are available in each census year.

Long-term trends in plant cover

Shrubs dominated vegetative cover in all sample years (Fig. 4), with cover ranging from 17% in 1950 and 1957 to a high of 25% in 1975. The dominant shrub was *Artemisia tridentata,* which contributed 84% of the shrub cover in 1950. The decrease in shrub cover after 1975 (Fig. 4) was largely due to widespread mortality of *A. tridentata* (Fig. 5). The second most abundant shrub was *Chrysothamnus viscidiflorus* (Figs. 4 and 5, Table 1). Although *A. tridentata* cover decreased markedly after 1975, that of *C. viscidiflorus* generally increased over the 45 yr. Cover of *C. viscidiflorus* in 1995 was 6.3 times that in 1950 (Fig. 5).

Populations of the small shrub *Leptodactylon pungens* were apparently very small in the early census years but had increased substantially by 1983 (Fig. 5). Its cover has remained relatively high in the most recent censuses. Cover data for the only common succulent at the study area, *Opuntia polyacantha,* were not collected in all of the censuses, but the available data show an increase between 1950 and 1965 and a decline in the most recent samples (Fig. 5).

Cover of perennial grasses was much less than that of shrubs (Table 1, Fig. 4), but their cover increased quasi-exponentially from 0.5% in 1950 to 6.2% in 1975. Following this 13-fold increase, perennial grass cover decreased and has fluctuated between 1.4 and 4.0% in recent sample years. The peak in perennial grass cover apparently lagged behind that of shrubs by a decade, but this may reflect the lack of data for intervening years.

Cover of the most common grasses increased manyfold between 1950 and 1975 (Fig. 5). Cover of *Elymus elymoides, Oryzopsis hymenoides,* and *Stipa comata* declined sharply after 1975, while that of *E. lanceolatus* and *Poa* (data not shown) remained high between 1975 and 1983, but then dropped sharply by 1985. Cover of *E. lanceolatus, E. elymoides,* and *S. comata* increased between 1985 and 1990, and all but *E. lanceolatus* remained high in 1995 (Fig. 5). In contrast, cover of *O. hymenoides* has remained low over the past decade, at about the same level that it was in 1957.

Although there were cases where high cover coincided with wet periods (e.g., cover of *A. tridentata* in 1965), there was no case where the cover of a common species appeared to closely track precipitation (Fig. 5). Furthermore, neither total cover of shrubs nor of perennial grasses was correlated with either water-year or growing-season precipitation received in the years the samples were taken ($P > 0.25$ in all cases). In only one case was cover of an individual species or species group correlated with water-year precipitation of the years the samples were taken; combined cover of *Poa* spp. was positively but weakly correlated with water-year precipitation ($P = 0.050$; all others $P > 0.25$). Similarly, cover of only one species or species group was correlated with growing-season precipitation of the sample years, namely a positive correlation for *Atriplex confertifolia* ($P = 0.032$; all others $P > 0.14$).

In no case was total cover or cover of a member of either shrubs or perennial grasses correlated with precipitation received in the year preceding the sample year. However, a number of significant relationships between cover and precipitation received from three to five years earlier were found. Total cover of perennial grasses and that of *Stipa comata* were positively correlated with water-year precipitation four years earlier (Fig. 6). Total shrub cover was positively correlated with water year precipitation 2 yr earlier (Fig. 6) and with mean water-year precipitation of the sample year plus three ($P = 0.054$) or four ($P = 0.022$) previous years. Similar trends are suggested for *Artemisia tridentata* (3-yr lag) and *Chrysothamnus viscidiflorus* (4-yr lag) (Fig. 6). Surprisingly, there was a strong negative correlation between cover of *Tetradymia canescens* and growing-season precipitation received 3 yr earlier (Fig. 6). Cover of *T. canescens* was also negatively correlated with mean water-year precipitation for the sample year plus three previous years ($P = 0.018$).

Long-term trends in density of plants

There were no obvious correlations between long-term changes in plant density and precipitation patterns (Figs. 7 and 8). Mean density of shrubs has changed little over 45 yr, but the standard errors for mean shrub densities for 1950 and 1957 were much higher than those for subsequent years (Fig. 7). Density of the dominant shrub, *Artemisia tridentata,* has decreased considerably in recent decades (Fig. 8), corresponding with its decrease in cover (Fig. 5). Concomitantly, density (Fig. 8) and cover (Fig. 5) of *Chrysothamnus viscidiflorus* were higher after 1978 than at any previous cen-

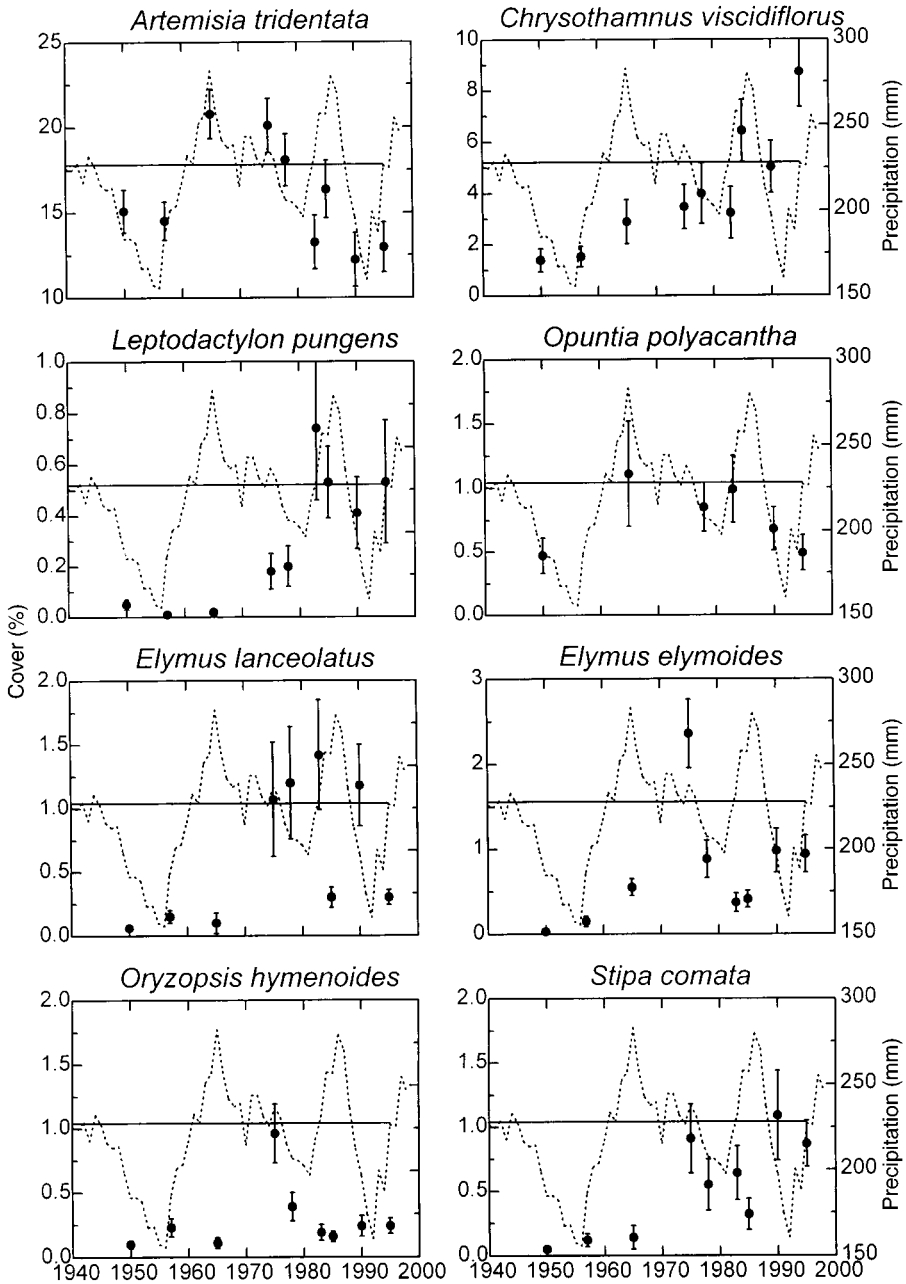


FIG. 5. Percent cover of some common perennial species at the Idaho National Engineering and Environmental Laboratory. Data are means ± 1 SE. In each panel, the dotted curve represents the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal line shows the long-term mean water-year precipitation. Cover data were not collected for *Opuntia polyacantha* in 1957, 1975, and 1985.

sus. There was no consistent trend in the density of the only common succulent on the study area, *Opuntia polyacantha* (Fig. 8).

The mean density of perennial grasses changed little between 1950 and 1978 but then increased sharply and was over two-fold higher in 1985 than in previous sample years (Fig. 7). Although the density of the most common grasses increased over the last two decades, the years of highest density did not coincide. Density of *Elymus lanceolatus* and *E. elymoides* peaked in 1985 during a wet period, while that of *Stipa comata* was highest in 1990, during a drought (Fig. 8). Density of those three groups fluctuated widely in the most recent samples, whereas that of *Oryzopsis hymenoides* has fluctuated little over the entire 45 yr (Fig. 8). Obtaining accurate density data for rhizomatous grasses is difficult, but the density data for *Elymus lanceolatus* is closely correlated with frequency data for that species

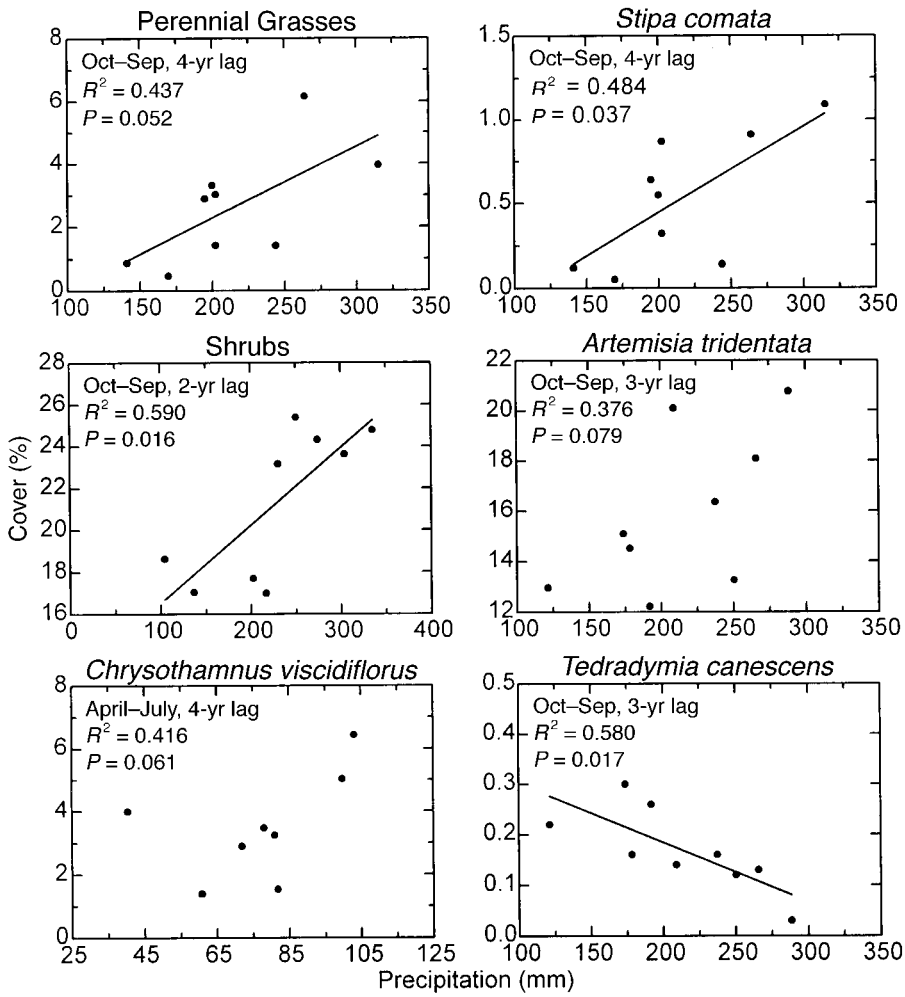


FIG. 6. Relationships between mean cover and precipitation. For each species or group of species, the figure presents the most significant relationship between mean cover and annual or growing-season (April–July) precipitation in the current year or any of the preceding five years.

across the core plots (mean R^2 for sample years = 0.60; $P < 0.001$ in each year). Thus, we are confident that the density data are indicative of the number of individual plants.

The mean density of perennial forbs remained quite low between 1950 and 1965, but increased significantly over the past two decades (Fig. 7). Forb density in 1995 was about three times that recorded in the earliest samples. Density of annuals has varied considerably, but no trend is apparent (Fig. 7). Density of annuals was much higher in 1975 than in any other sample year, apparently a consequence of abundant precipitation and a cool spring and early summer (R. Jeppson, *personal communication*). That was also the year of the highest recorded shrub and perennial grass cover (Fig. 4).

In most cases, trends for density have not paralleled those for cover. For perennial grasses, shrubs, and for all but one of the common species in those groups, mean cover was not correlated with mean density across the eight years for which both cover and density were sampled. The only species for which this relationship was significant was *Stipa comata* (core plots, $R^2 = 0.53$, $n = 8$, $P = 0.042$; all plots, $R^2 = 0.49$, $n = 8$, $P = 0.056$).

Relationships between shrub and grass cover, and changes in plot similarity through time

There were significant negative correlations between cover of perennial grasses and cover of shrubs in seven of the nine sample years (Fig. 9). This analysis also shows that the plots have become more heterogeneous in terms of vegetal cover since 1950. In 1950 shrub cover ranged from 1.2 to 30% across the plots sampled, whereas values ranged from 3 to 48% in 1975 and from 1.2 to 62% in 1995. This increase in heterogeneity is apparent in the amount of scatter on the abscissa of Fig. 9. Similarly, scatter on the ordinate of Fig. 9 indicates variation in grass cover. Cover of perennial

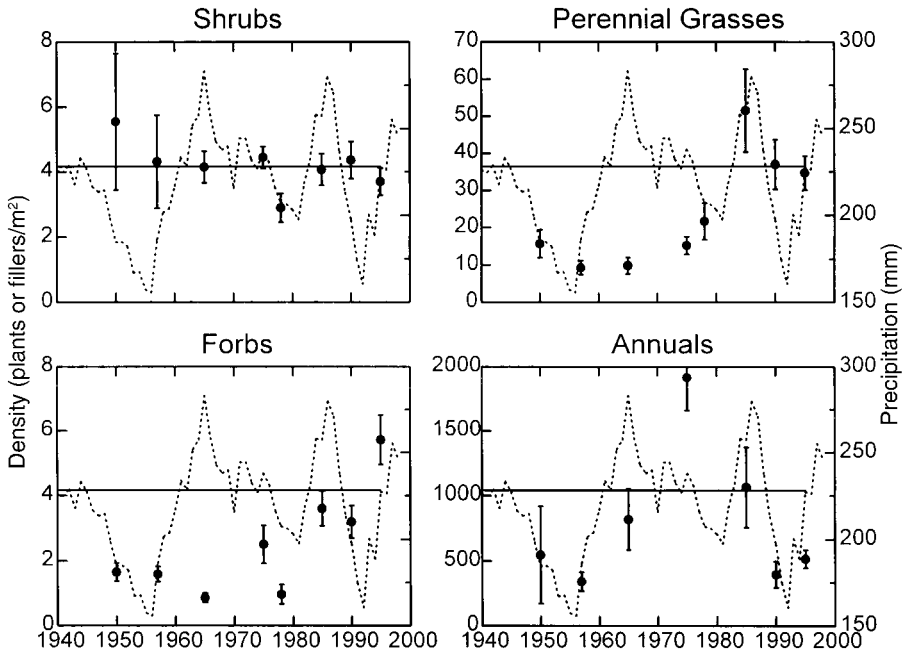


FIG. 7. Density of four plant groups at INEEL. Data are means ± 1 SE. The dotted lines represent the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal lines show the long-term mean water-year precipitation.

grasses across plots ranged from 0 to 6.5% in 1950, from 0.6 to 27% in 1975, and from 0.6 to 8% in 1995.

This increase in heterogeneity is also reflected in a large decrease in percentage similarity among the core plots over the 45 yr of record (Fig. 10). Mean percentage similarity decreased monotonically with time, from 72% in 1950 to 40% in 1995.

Trends in species richness and relationships between richness and cover

Aggregate species richness for shrubs and perennial grasses on the core plots changed little during the 45 yr (Table 2). Only three species of perennial grasses, *Sporobolus cryptandrus*, *Stipa thurberiana*, and *Elymus triticoides*, occurred in recent censuses but not in early ones. It is unlikely that any of these are new immigrants to the general area sampled by these plots. In contrast to aggregate species richness, mean species richness per plot of shrubs, perennial grasses, and perennial forbs recorded on the line-intercept transects and in the density quadrats generally increased from 1950 to 1995 (Fig. 11). The rate of increase in richness was higher for perennial grasses than for shrubs. The mean number of species of annuals was more variable, with richness highest in 1975 and 1995, census years that had high spring/early summer precipitation (Figs. 3 and 11).

Shrub cover was positively correlated with shrub species richness in the last six of nine census years (Fig. 12). Similarly, perennial grass cover was positively correlated with perennial grass species richness in five of nine sample years (Fig. 13), but the years in which those relationships were significant for shrubs and grasses did not always coincide. Cover of shrubs and perennial grasses combined was significantly correlated with combined species richness in four of nine years ($P < 0.05$), and in each case the relationship was positive.

Consistent with the results for individual years, average cover of shrubs was positively correlated with average shrub species richness, and average perennial grass cover was positively correlated with average perennial grass species richness (Fig. 14). Likewise, average cover of shrubs and perennial grasses combined, on 35 plots over nine census years, was positively correlated with average species richness of shrubs and perennial grasses ($R^2 = 0.16$, $P = 0.016$).

The average change in shrub cover and the standard deviation of shrub cover were positively correlated with average shrub species richness (Fig. 14), indicating that absolute shrub cover changed more from year to year on plots having more species of shrubs. Neither average change nor variability in perennial grass cover was related to average perennial grass species richness (Fig. 14), but for the core and peripheral plots combined, which were sampled in fewer years, the relationship between average change in cover and average species richness was significant and positive for both shrubs and perennial grasses ($P = 0.029$ and $P < 0.001$, respectively). Furthermore, for the 35-plot subset, change in cover of shrubs and perennial grasses combined was positively correlated with combined average species richness ($P = 0.037$), and the standard deviation of cover of shrubs and perennial grasses combined

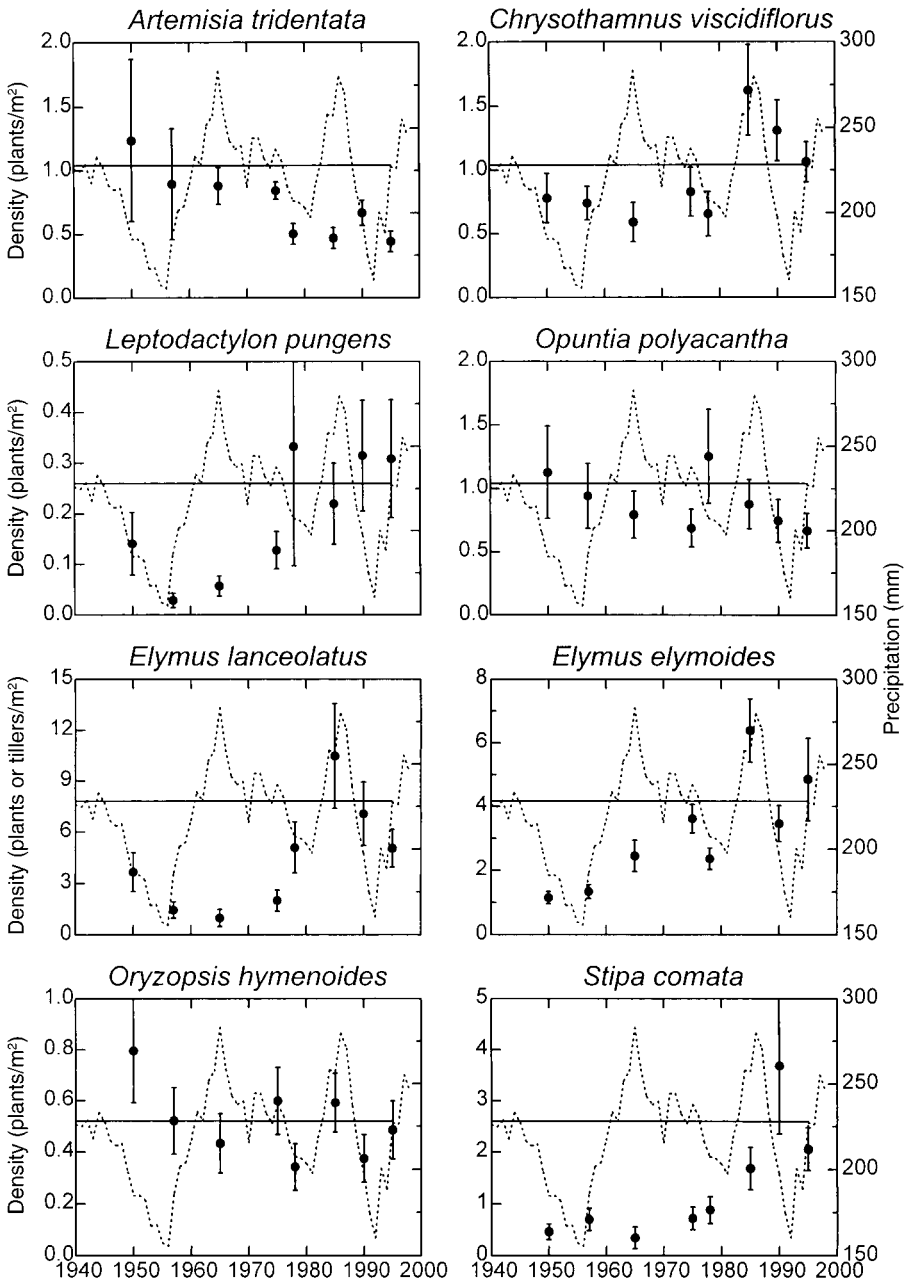


FIG. 8. Density of common perennial species. Data are means ± 1 SE. The dotted lines represent the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal lines show the long-term mean water-year precipitation.

was positively correlated with average combined species richness ($P = 0.030$).

The coefficient of variation (CV) of cover was negatively correlated with average species richness of both shrubs and perennial grasses (Fig. 14). For shrubs, CV of cover was negatively correlated with mean cover ($R^2 = 0.37$, $P < 0.001$), indicating that plots having more shrub cover tended to vary less relative to the mean cover than plots with less shrub cover. Thus, the stability of cover may be a function of some aspect of shrub cover (e.g., shrub size) rather than shrub species richness (Huston 1997). However, for perennial grasses the CV of cover was not correlated with mean perennial grass cover ($R^2 = 0.035$, $P = 0.28$). Therefore, for this functional group, stability of cover appears to be directly related to species richness. The CV of cover of shrubs and perennial grasses combined was not significantly correlated with average combined species richness ($P = 0.25$).

We found no significant correlation between species richness and the magnitude of the change in percentage similarity as measured by the minimum, the maximum,

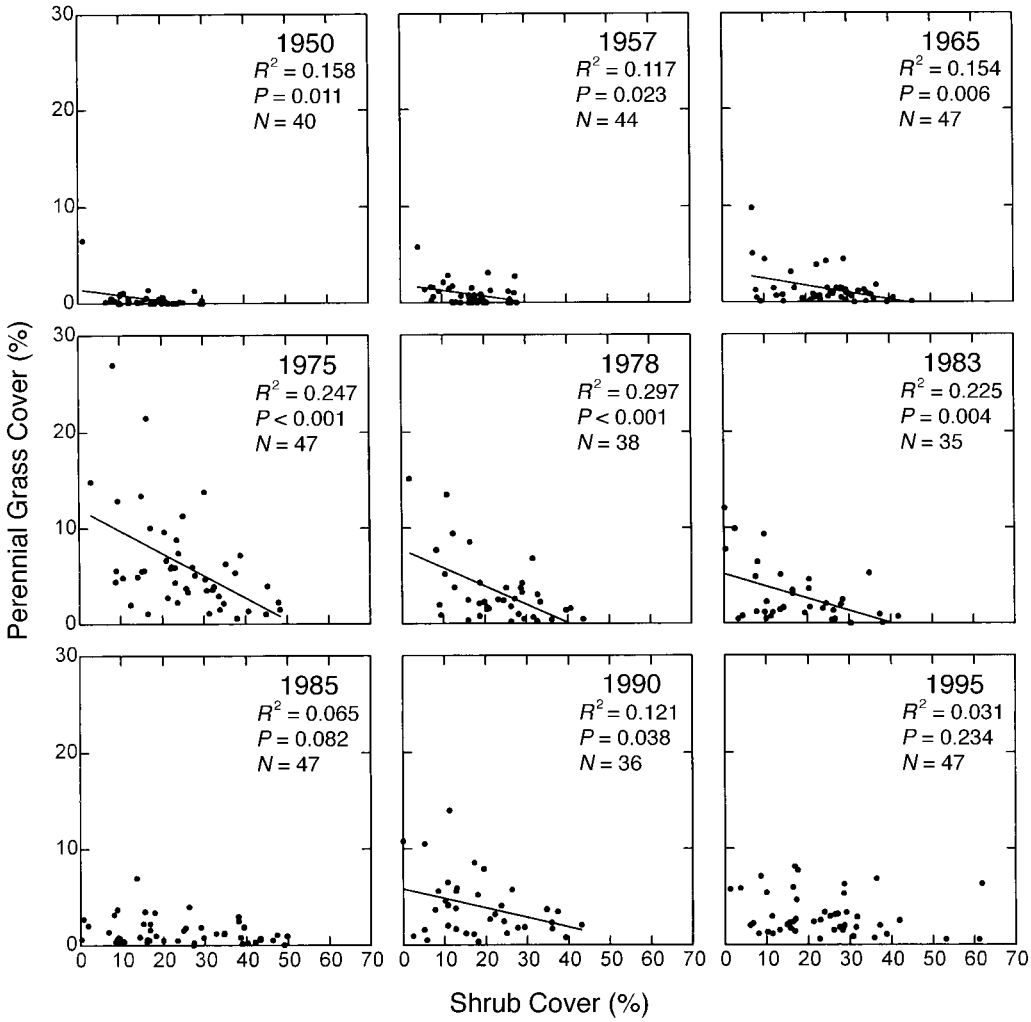


FIG. 9. Mean percent cover of perennial grasses plotted against mean percent cover of shrubs. Each graph represents one year, and each point represents one plot. Regression lines are shown for those years in which there was a significant correlation between perennial grass and shrub cover. *N* is the number of plots sampled in that year.

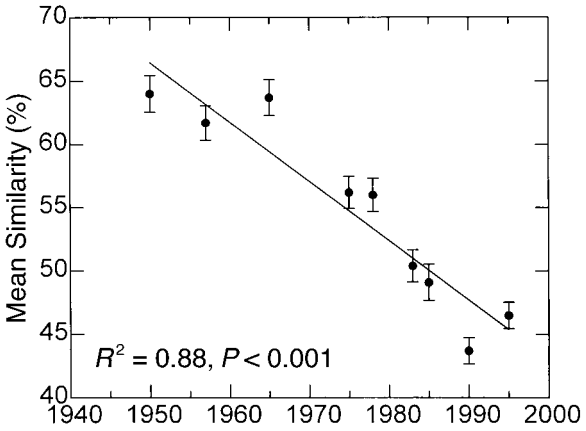


FIG. 10. Mean percentage similarity for a subset of 25 plots (see *Methods: Data analyses*), based on perennial grass and shrub cover, for each of the nine census years.

or the mean of the plotwise year-to-year comparisons ($P > 0.1$ in all cases). Thus, stability in species composition did not appear to be related to species diversity.

Relationships between cover or species richness and abundance of nonnative species

The number of plots on which nonnative species were recorded generally increased from 1950 to 1995, but the average density of nonnative species did not show any consistent trend with time (Table 3). The density of nonnative species was negatively correlated with total cover of native shrubs and perennial grasses in three of seven sample years (Table 3). Based on the 1995 point-frame data, which estimated cover for all species, cover of nonnative species was negatively correlated with cover of native species (Fig. 15A). Those

TABLE 2. Number of 35 plots on which species, or species groups, were recorded in either cover or density samples in each of eight census years, together with species richness of shrubs and perennial grasses on the aggregate 35-plot sample.

	1950	1957	1965	1975	1978	1985	1990	1995
Plant species								
Artemisia tridentata†	35	35	35	35	35	34	34	35
Chrysothamnus viscidiflorus	22	19	21	21	21	25	27	29
Leptodactylon pungens	10	6	9	11	11	11	13	11
Grayia spinosa	1	9	8	6	7	4	5	6
Tetradymia canescens	6	5	3	7	4	5	7	6
Gutierrezia sarothrae	0	1	0	7	5	6	6	5
Krascheninnikovia lanata	4	2	3	3	3	2	2	3
Eriogonum microthecum	0	0	3	4	3	4	4	1
Atriplex confertifolia	5	1	2	1	0	1	1	1
Haplopappus nanus	0	1	0	0	1	0	0	1
Artemisia arbuscula	2	0	1	0	0	0	0	0
Atriplex canescens	1	0	0	0	0	0	0	0
Artemisia tripartita	0	1	0	0	0	0	0	0
Elymus elymoides	28	27	33	34	31	30	30	30
Elymus lanceolatus	24	22	24	26	30	29	29	33
Oryzopsis hymenoides	23	22	18	29	25	25	21	28
Stipa comata	15	17	12	22	22	26	24	26
Poa sp.	10	12	16	14	17	20	22	25
Leymus cinereus	1	1	1	1	1	1	1	2
Carex douglasii	0	1	0	1	0	1	0	2
Stipa occidentalis	3	0	0	0	0	0	1	0
Sporobolus cryptandrus	0	0	0	0	0	2	1	1
Stipa thurberiana	0	0	0	0	0	1	0	1
Elymus triticoides	0	0	0	0	0	1	0	0
Species richness								
Shrubs	9	10	9	9	9	9	9	10
Perennial grasses	7	7	6	7	6	10	8	9

Notes: Thirty-five plots were used in this analysis because data are available for them for the eight census years. This table includes all species that were recorded in any of the census years in which both cover and density were sampled.

† Includes *A. tridentata* ssp. *tridentata* and *A. tridentata* ssp. *wyomingensis.*

data also showed that richness of nonnative species was negatively correlated with cover of native species ($R^2 = 0.16$, $P = 0.008$) but strongly positively correlated with cover of nonnative species ($R^2 = 0.30$, $P < 0.001$).

We found no significant relationship between native species richness based on density data and the density of nonnative species. Richness of native shrubs plus perennial grasses and of native shrubs only, based on cover data, was positively correlated with nonnative species density in only one of seven years ($P = 0.043$ and $P = 0.019$, respectively). Similarly, based on the 1995 point-frame data for nonnative species, neither cover nor richness was correlated with native-species richness.

The invasive annual grass, *Bromus tectorum,* was recorded in the first vegetation samples at the INEEL in 1950, but occurred on only nine peripheral plots on the south and east ends of the permanent transects (Table 4); it was not recorded on any core plot prior to 1975 when it occurred on 17 core plots. In 1995, it was recorded on 26 of 47 core plots (Table 4) and accounted for 6% of their vascular plant cover (Table 1). Density of *B. tectorum* on the core plots was negatively correlated with total cover of native perennials in 1990 ($P = 0.011$), and a similar negative relationship was marginally significant for 1975 ($P = 0.074$). The 1995 point-frame data showed a strong negative relationship between cover of *B. tectorum* and cover of native species (Fig. 15B).

DISCUSSION

Long-term dynamics

The 1950 data support the suggestion that the area was heavily grazed by domestic livestock before establishment of the Idaho National Engineering and Environmental Laboratory (INEEL, Southeastern Idaho, USA; Harniss and West 1973). Very low cover of perennial grasses, low density and richness of perennial forbs, dominance of plots by *Artemisia tridentata* and other shrubs, and relative homogeneity of plots are all consistent with differential responses of species to heavy grazing. Composition and structure of the vegetation in 1950 were undoubtedly also influenced by the severe and prolonged drought conditions through the 1930s and 1940s (Fig. 3), as documented for other steppe ecosystems in the region (Pechanec et al. 1937, Mehringer and Wigand 1990). Under drought conditions, stress-tolerant shrubs such as *A. tridentata* are promoted (West 1983*b*), while faster growing but less tolerant perennial grasses and forbs suffer considerable mortality. The most palatable species—perennial grass-

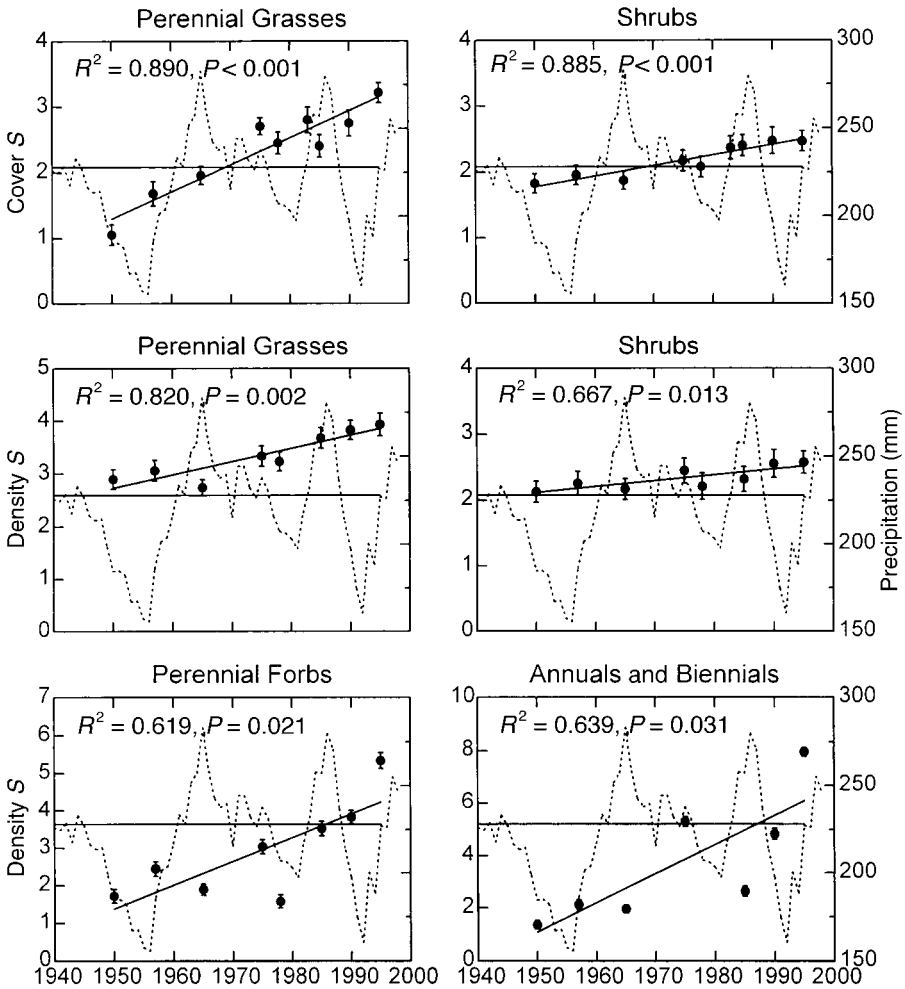


FIG. 11. Species richness (*S*) of perennial grasses and shrubs from line-interception cover samples (Cover *S*; top two graphs) and of perennial grasses, shrubs, perennial forbs, and annuals + biennials from density samples (Density *S*; bottom four graphs). Data are means ± 1 SE. The dotted lines represent the 5-yr sliding average of water-year (October–September) precipitation; the solid horizontal lines show the long-term mean water-year precipitation.

es and forbs—are likely to be the least drought tolerant. Thus, drought and grazing have similar, synergistic effects (Pechanec et al. 1937). Widespread local extinction of populations due to either cause would tend to homogenize vegetation across the landscape.

Despite the depauperate and homogeneous conditions in 1950, vegetation on the permanent plots at the INEEL has been anything but static over the past 45 yr, clearly refuting the prediction of long-term stability under shrub dominance. Mean richness per plot of all growth forms increased steadily (Fig. 11). After the first 25 yr, cover of perennial grasses was 13 times that recorded initially. Subsequently it fluctuated more than fourfold, from 6.2% in 1975 to 1.4% in 1985, but remained high relative to 1950 (Fig. 4). In this context, it is important to note that basal cover undoubtedly underestimates the importance of perennial grasses relative to that of shrubs and forbs in these communities. Furthermore, the substantial increase in cover of perennial grasses through 1975 was not at the expense of the shrub overstory. Shrub cover increased markedly in the first 15 yr and remained high through 1975.

Widespread mortality of *Artemisia tridentata* reduced cover of that species substantially after 1975. Extensive shrub die-off was observed throughout much of the Intermountain West during the late 1970s and 1980s, but there is little consensus about its causes (McArthur et al. 1990). Previous episodes of high sagebrush mortality in the region have been attributed to infestations of sagebrush webworm (*Aroga websterii*; Sneva et al. 1984) and high vole populations (Mueggler 1967). Other putative causes include anoxic soils and increased susceptibility to fungal parasites due to increased precipitation in the early 1980s. Vole populations were high at the INEEL in the mid-1980s, which may have caused some mortality, but it seems likely

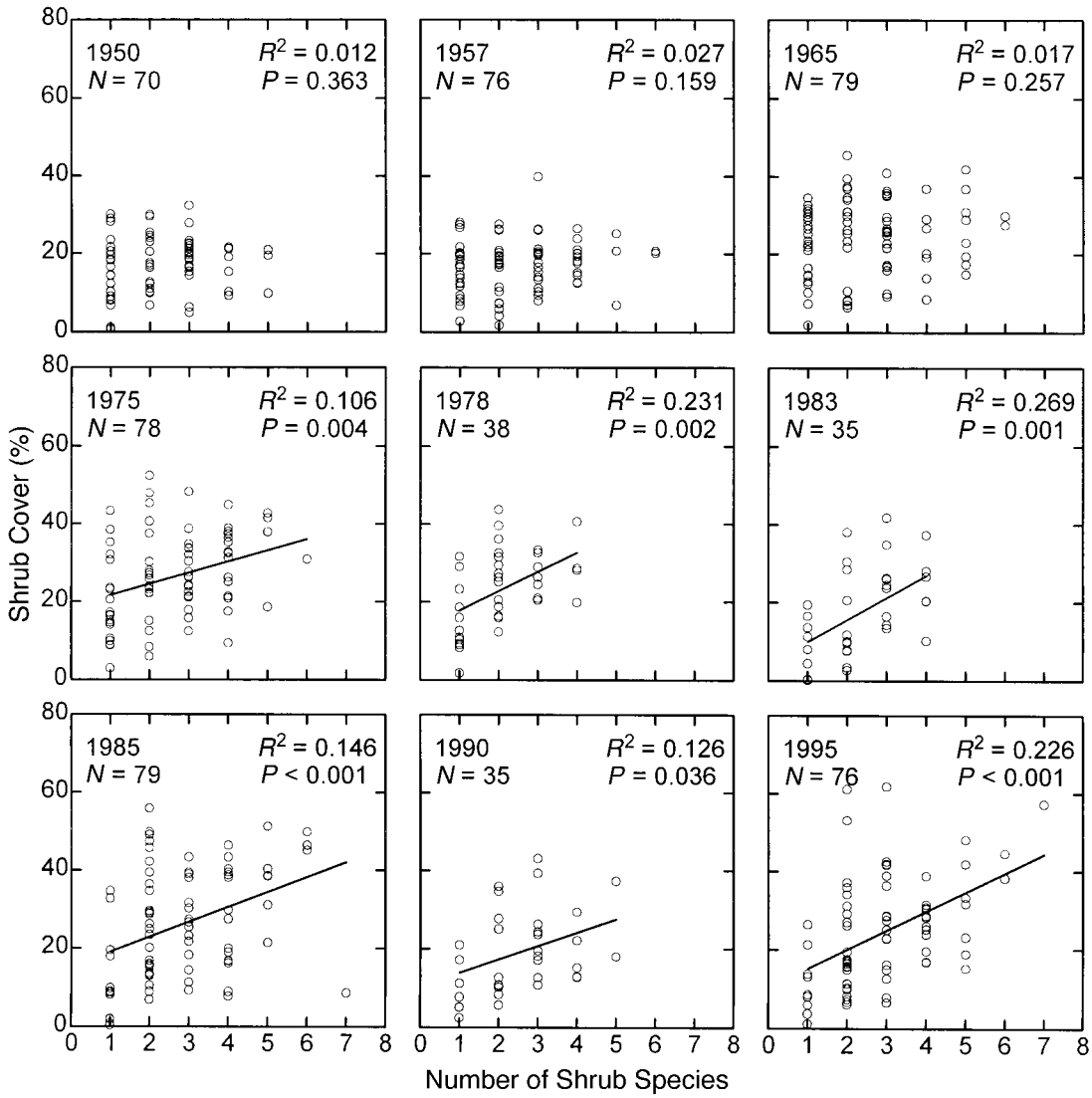


FIG. 12. Relationships between shrub cover and species richness for all plots sampled in each of nine census years. Each point represents one plot. *N* is the number of plots sampled in each census year.

that multiple stressors were involved because mortality continued well after vole populations declined (J. Anderson, *personal observation*).

Species richness for the aggregate 35-plot sample has not changed appreciably since 1950 (Table 2); however, the data show a general, consistent increase in species richness per plot (Fig. 9). These results suggest that the increase in richness of individual plots was not a consequence of immigration of new species or species that had become extinct at the INEEL. Instead, populations that were small and isolated in 1950 likely have increased in size and distribution, thereby increasing the number of species found on a given plot. Anderson (1986) documented an increase in the distribution of perennial grasses on 35 plots and attributed that trend to greater availability of propagules as previously depleted grass populations increased between 1965 and 1975. This trend is apparent in Table 2 for perennial grasses but not for shrubs.

Other than the increase in cover of perennial grasses during the first 2.5 decades and the general increase in average species richness, we found little evidence of directional changes in plant species composition. The only obvious directional change among the common shrub or perennial-grass species was a consistent increase in the cover of *Chrysothamnus viscidiflorus.* There was no evidence of seral replacement among the perennial grasses. Ordinations of the data from the core plots as well as from smaller subsets of plots having high similarity, using detrended correspondence analysis and nonmetric multidimensional scaling (McCune and Mefford 1995), failed to identify any common trajectories of plots through time (results not shown). Species abundance data, then, do not suggest directional

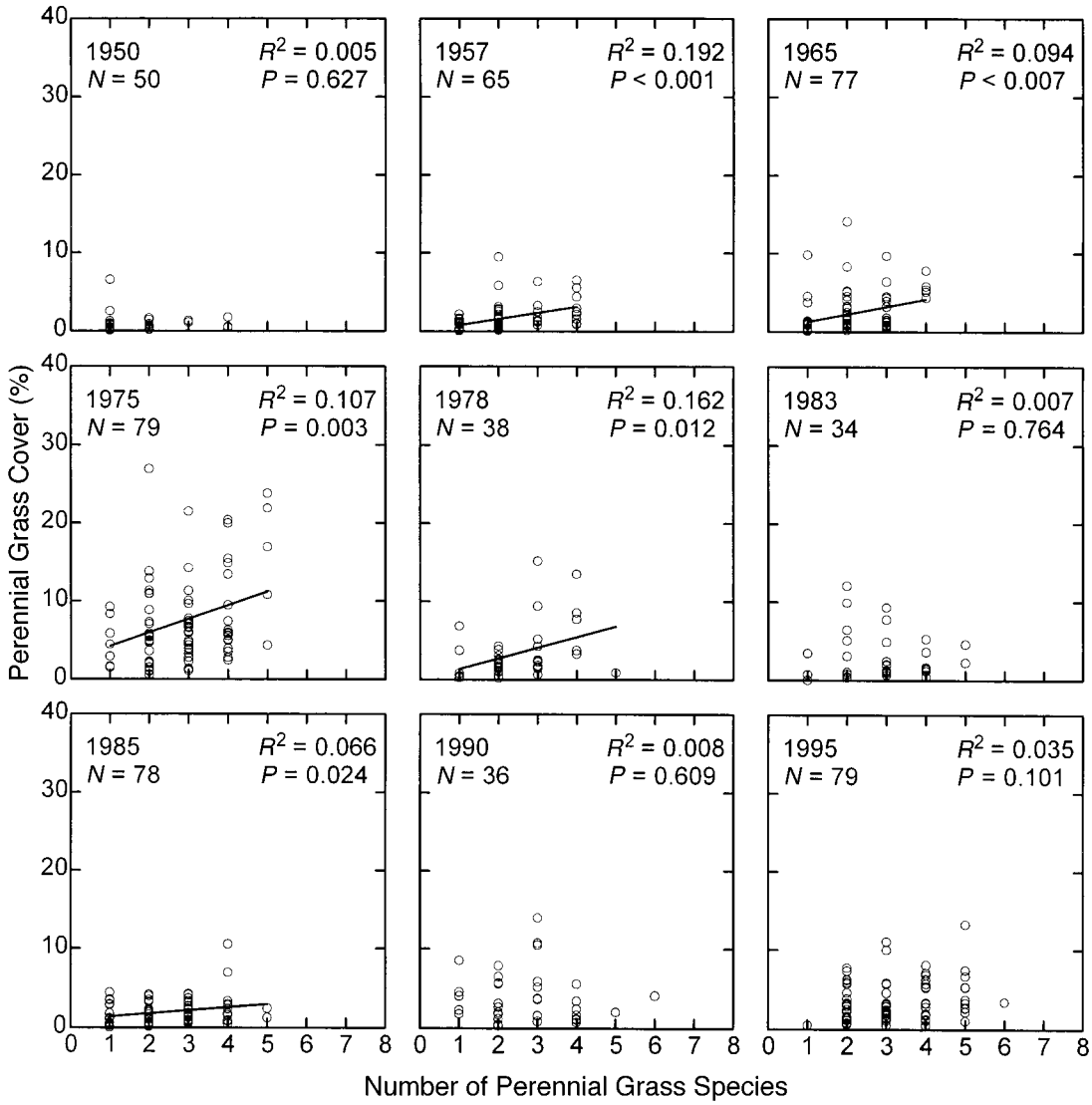


FIG. 13. Relationships between cover and species richness of perennial grasses for all core + peripheral plots sampled in each of nine census years. Each point represents one plot. *N* is the number of plots sampled in each census year.

succession as might have been predicted by classic models of rangeland succession (e.g., Dyksterhuis 1949, Huschle and Hironaka 1980). The substantial fluctuations in cover of shrubs and perennial grasses from 1975 to 1995 (Fig. 4) may represent the ''normal'' range of variation characteristic of sagebrush steppe at decadal time scales.

Contemporary state-and-transition models for sagebrush steppe (Laycock 1991, West 1999) would not have predicted the observed changes in this ecosystem either, given the state of the vegetation in 1950. State II in Laycock's (1991:431) model, ''Dense sagebrush cover; depleted perennial herbaceous understory with sagebrush seedlings present,'' is predicted to ''remain stable for long periods of time'' (Laycock 1994:269). Laycock (1991:431) argued that the threshold from that stage to an ''open stand of sagebrush with productive herbaceous perennial understory'' (Stage I in the model) is difficult to cross in the absence of fire or other force that kills adult sagebrush. Our data show that such a transition occurred in 25 yr, before sagebrush cover was reduced. Abundance of the constituent species has fluctuated since then, but composition has not differed markedly from that in nearby areas considered to be pristine (Tisdale et al. 1965, Passey et al. 1982).

Why did vegetation at the INEEL not respond as contemporary models might have predicted? We think there are two primary reasons. First, some studies that have shown long-term stability of dense shrub cover were based on data from one or relatively few exclosures (e.g., Rice and Westoby 1978, Holechek and Stephenson 1983, Sneva et al. 1984), while our data are

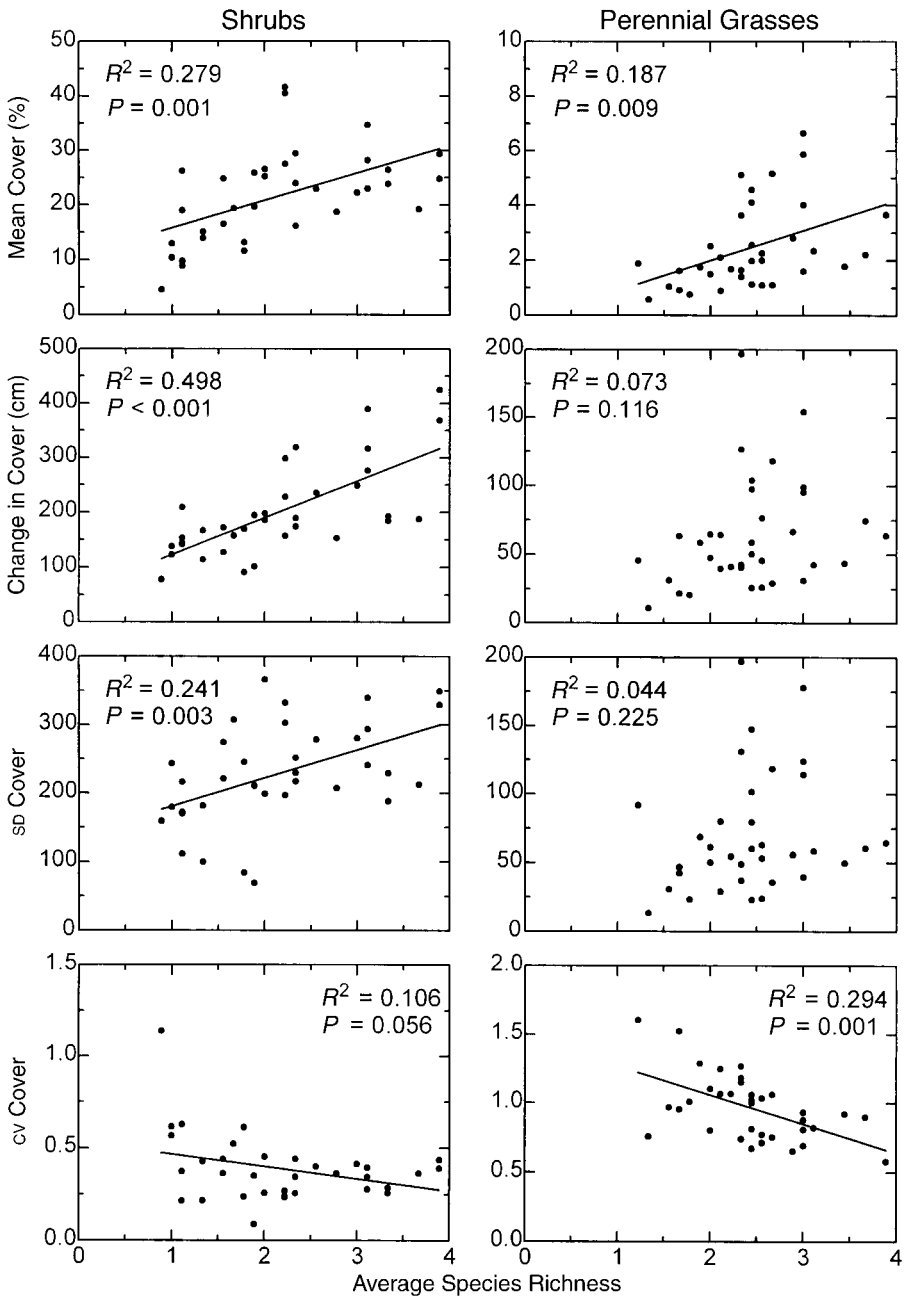


FIG. 14. Relationships between mean cover and mean species richness, for shrubs and perennial grasses, on 35 plots that were sampled in all nine census years. Mean cover is the mean from all nine census years. Change in cover is the mean of the absolute values of change in cover between subsequent censuses. Standard deviation (SD) and coefficient of variation (CV) of cover were calculated based on all nine census years.

from a large number of plots that better represent landscape-scale dynamics. Vegetation on some plots in our study has changed very little over 45 yr, while other plots have changed substantially. The second and probably more important reason for the observed changes at the INEEL is that viable remnant populations of native grasses and forbs were present in 1950 and were able to take advantage of improved growing conditions. Indeed, a few other studies have shown that arid and semiarid communities can respond to reduced stocking rates and favorable precipitation with increased production of native perennial grasses and forbs if residual populations of such natives are present (Robertson 1971, Turner 1990, Holechek et al. 1994).

Another factor that may have facilitated the transition was the rarity of *Bromus tectorum* and other in-

TABLE 3. Results of correlations between density of nonnative species and cover of native perennial species in seven census years.

Year	N†	Mean density (plants/m²)	Frequency‡	r	P
1950	39	13.33	8	−0.182	0.269
1957	44	2.7	21	0.055	0.725
1965	47	12.1	9	−0.371	0.010
1975	47	14.08	23	−0.333	0.022
1985	47	13.76	24	−0.176	0.237
1990	36	11.81	27	−0.381	0.022
1995	47	9.59	36	−0.247	0.094

† N = the number of core plots that were sampled in a given year.

‡ The number of plots upon which nonnative species were recorded.

vasive annuals on most of the core plots until 1975 (Table 4). We can only speculate about how vegetation dynamics might have differed had *B. tectorum* been abundant in 1950, but because it is so competitive with seedlings of native species (Harris and Wilson 1970, Reichenberger and Pyke 1990) it is possible that it would have slowed or precluded the growth of some native perennial populations.

Changes in plot similarity through time

The 45-yr period has witnessed a substantial increase in heterogeneity in vegetative structure among plots (Figs. 9 and 10). As the number of species per plot increased, the plots diverged in species composition and relative abundances. This is precisely the outcome that one might expect as a sagebrush rangeland recovers from the combined effects of prolonged drought and livestock grazing. Increased precipitation coupled with reduced grazing pressures allowed species to respond to the small-scale (0.1 to 100 m) differences in soil nutrients, infiltration, and runoff that create a mosaic of patches (Walker 1993) in which different species are superior competitors. Although the core plots cover an area that is fairly uniform with respect to soils, topography, and slope, these factors do vary among plots. Furthermore, samples taken at each plot cover an area large enough to include considerable variation in microtopography, soil depth, and soil resources. Substantial spatial variability in the concentrations of essential plant nutrients exists at the scale of individual plants in sagebrush steppe (Charley and West 1975, Jackson and Caldwell 1993*a*, *b*, Ryel et al. 1996). Ryel et al. (1996:299) found that ''patches of high internal uniformity'' of soil nutrients were generally smaller than 2 m in diameter in a sagebrush community of southeastern Idaho.

In addition to deterministic competitive outcomes, it is likely that stochastic factors also contributed significantly to the observed increase in heterogeneity. Plant establishment depends on availability of propagules and arrival of those propagules at ''safe sites'' for germination (Harper 1977). As depleted populations recover, arrival of propagules at suitable sites depends on a multitude of factors including proximity of source plants, dispersal characteristics of the propagules, barriers to dispersal (e.g., other plants, microtopography), and the vagaries of weather (wind speed

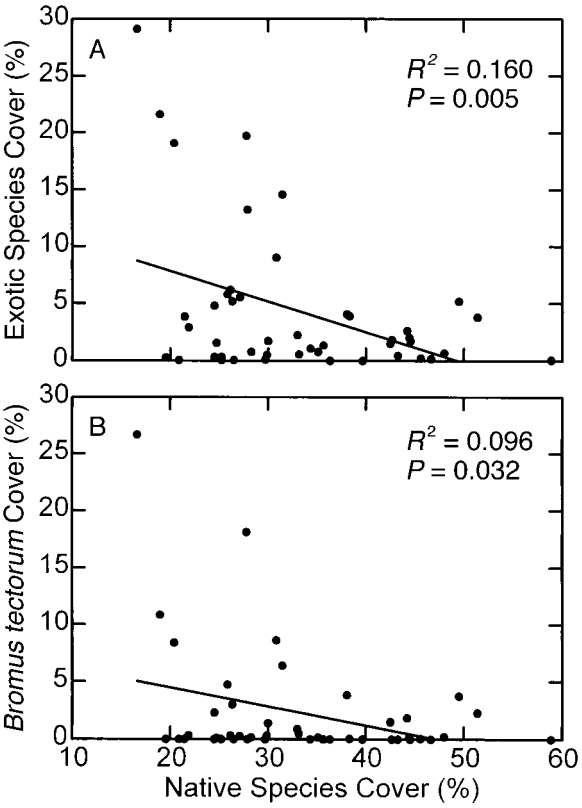


FIG. 15. Relationships between (A) exotic-species cover and native species cover and (B) between cover of *Bromus tectorum* and native-species cover based on point interception cover estimates in 1995 for the 47 core plots.

TABLE 4. Occurrence of the invasive annual grass *Bromus tectorum* based on density data.

Year	N†	Frequency‡	Mean density (plants/m²)	Density range§
1950	39	0	0	···
1957	44	0	0	···
1965	47	0	0	···
1975	47	17	11	0.5–135
1985	47	13	11	1.7–145
1990	36	21	11	0.2–67
1995	47	26	6	0.2–64

† N is the number of core plots that were sampled in a given year.

‡ The number of plots upon which *B. tectorum* was recorded.

§ The range of densities on the plots where *B. tectorum* was recorded in that year.

and direction, rainfall amount and intensity). Priority effects may also be important as propagules arriving first may gain a competitive advantage over those arriving later.

Our data do not support Laycock's (1994:272) opinion that ''if grazing were completely removed, diversity of both plants and animals on the landscape level probably would decrease on most areas of public lands'' in the United States. His prediction stems from studies in grasslands showing that grazing increases patchiness of plants and reduces ''a relatively few dominants in a system and they are replaced by more numerous secondary species'' (Laycock 1994:264). Laycock's conclusion is probably correct for grassland ecosystems having a long evolutionary history of intense grazing pressure, but it may not be applicable to semiarid ecosystems where unpalatable shrubs are dominants (e.g., sagebrush steppe) or may quickly become dominants with heavy livestock grazing or drought (e.g., desert grasslands of southwestern United States; Buffington and Herbel 1965, Gibbons and Beck 1988). As we have argued above, livestock grazing in such shrub-dominated systems intensifies shrub dominance, reduces or eliminates populations of palatable species, and tends to homogenize vegetation at the landscape scale.

Is precipitation a major driver of vegetation dynamics in this shrub steppe?

Because availability of water is the major limiting factor in semiarid ecosystems, one might expect a close correlation between cover and precipitation (Noy-Meir 1973). Several early investigations reported strong correlations between productivity and various measures of current-year precipitation in sagebrush steppe (reviewed by Sneva and Hyder [1962]). However, these studies typically only measured forage production, and some were conducted on areas seeded with exotic perennial grasses. Other investigators failed to find significant relationships between density, cover, or biomass and precipitation (West et al. 1979, Passey et al. 1982). Passey et al. (1982) measured production for 10 yr at 17 relict sites, assumed to represent ''climax vegetation;'' 10 sites were within kipukas (islands of vegetation surrounded by recent lava flows) on the upper Snake River Plain that had never been grazed by domestic livestock. They found no significant correlation between water-year (October–September) precipitation and aboveground production for any of the 17 sites. Negative correlations between production and subsets of current-year precipitation in two cases appear to be spurious (Passey et al. 1982: Table 6). They concluded that both total production and production of individual species ''are inherently erratic enough to preclude the development of precise production indices from precipitation data alone'' (Passey et al. 1982:30).

We did not find significant correlations between cover and precipitation received during the census year. However, it is likely that the 50% increase in shrub cover between 1957 and 1965 was in response to relatively high precipitation. Density of the most common shrubs did not increase during that period (Fig. 8), so the increase in cover apparently resulted largely from increases in the size of existing shrubs rather than from recruitment of new individuals. It also is likely that the exponential-like increase in cover of perennial grasses over the first 25 yr resulted from favorable moisture conditions in the 1960s and 1970s (Fig. 3). The sampling frequency is not sufficient to determine how closely changes in cover may track precipitation, but correlation analyses indicate there may be 2- to 4-yr lags in the responses of species or functional groups to precipitation patterns (Fig. 6). Similar lags were reported for arid chenopod shrublands in South Australia by Noble (1977), who attributed the long carry-over effects seen in some species to shoot longevity.

Lags might also results from pulses in recruitment or high mortality. The effect of mortality on cover would be apparent at the next census, but the relatively low sampling frequency may introduce what appear to be lags in response to precipitation. On the other hand, lags resulting from recruitment pulses are a consequence of the time required for recruits to reach sufficient size to contribute significantly to cover. Since the 1983 census, trends in cover of shrubs and of perennial grasses have been largely out of phase (Fig. 4). Similarly, density and cover of perennial grasses have been out of phase (Figs. 4 and 7). Following a generally wet period in the early 1980s, cover of both *Artemisia tridentata* and *Chrysothamnus viscidiflorus* had increased by 1985. Cover of perennial grasses in 1985, however, was anomalously low (Fig. 4), whereas their density was much higher than that recorded in any other year (Fig. 7). These data indicate substantial recruitment of perennial grasses in the early 1980s, but these recruits were apparently still very small in 1985. Density data (Fig. 7) suggest some mortality of perennial grasses during the drought of the late 1980s, but the survivors had increased sufficiently in stature to result in a 2.8-fold increase in perennial grass cover from that in 1985 by 1990 (Fig. 4). West et al. (1979) reported similar results from a demographic analysis of sagebrush-steppe plants in permanent plots at the U.S. Sheep Experimental Station in eastern Idaho. Although they did not find evidence for recruitment pulses according to their strict criteria, they did find years with exceptionally high numbers of seedlings. They reported that years having the highest plant densities coincided with or closely followed those having the lowest basal cover and argued that more space would be available for seedling establishment in years with low cover.

Our data indicate that individual species within the guild of perennial grasses responded individualistically to temporal environmental variation. Aside from a general increase in cover of grasses early on, members of this putative functional group responded differentially to environmental conditions. Cover of some species

increased between consecutive censuses, while that of others decreased, and the direction and magnitude of those differential responses varied from one census interval to the next (Fig. 8). Similar findings were reported by Passey et al. (1982:25), who observed that production of individual species ''fluctuated widely from year to year, but all species in a plant community did not fluctuate to the same degree and often not in the same direction. Growing conditions favorable for one species were often unfavorable for another.''

There is no obvious explanation for the negative relationship between the cover of *Tetradymia canescens* and precipitation received three years earlier (Fig. 6), but the strength of the relationship suggests that it is not a spurious result. It provides yet another example of the differential responses of species within a putative functional group (shrubs) to an environmental variable. Given such differential responses of species, lags between recruitment events and maturation, plasticity in the size of individuals independent of their age (West et al. 1979), and stochastic variation in timing and amounts of precipitation, we should not expect to see close correlations between precipitation and cover of individual species or functional groups, even if precipitation is a major driver of vegetation dynamics in this system.

Cover data for perennial grasses and shrubs indicate that, at least in certain years, competition may affect the abundance of some species. There were significant negative correlations between grass cover and shrub cover in years when the abundances of these groups were highest. The pattern of change in cover of these two groups suggests that grass cover is constrained on plots with greater shrub cover (Fig. 9). These data are consistent with the hypothesis that biotic interactions, such as competition or predation, can play important roles in determining the distribution and abundance of plant species at the site, but that their effect is controlled by the availability of water. Because the availability of water is highly variable in time, the responses of vegetation to changes in the type and intensity of disturbance probably take longer here than in many other systems that are limited by resources that are less variable in time. Furthermore, the large variation in precipitation on both year-to-year and longer-term time scales may be important in ensuring the coexistence of shrubs and perennial grasses in this ecosystem. This variation contributes to the dynamics that preclude convergence on a stable species composition at the scale of an individual sample plot.

Relationships between species richness and cover

Grime (1997:1261) speculated that high biodiversity might be ''vitally important'' in semiarid and other ecosystems that ''experience drastic fluctuations on a seasonal or longer time scale.'' Our results support this view by providing evidence for links between plant species diversity and function in sagebrush steppe. Our positive correlations between cover or stability of cover and species richness are consistent with those of recent studies from experimental plots in which species composition was manipulated (e.g., Tilman and El Haddi 1992, Tilman and Downing 1994, Tilman et al. 1996, 1997*a*, Hector et al. 1999). We found similar relationships in an ecosystem where water is the major limiting factor—an ecosystem having different dominant species, a different dominant growth form, and lower overall vegetative cover than the more mesic sites in Minnesota (USA) studied by Tilman and colleagues and in Europe (Hector et al. 1999).

The data clearly support the prediction that cover in sagebrush steppe is generally higher in areas having greater richness of vascular plants (Figs. 12, 13, and 14). These results imply that productivity would also be positively related to species richness. The relationship held for shrubs and perennial grasses separately, but not always in the same year (Figs. 12 and 13). These results indicate that species diversity within functional groups may be at least as important as functional-group diversity in this ecosystem type, in contrast to the results from grasslands (e.g., Hooper and Vitousek 1997, Tilman et al. 1997*a*).

We see three hypotheses to account for a positive relationship between cover and species richness. The first is that in plots having more species there is better use of limiting resources because of niche diversification in resource-acquisition patterns; consequently, those plots produce higher total vegetative cover (McNaughton 1993, Tilman et al. 1996). Tilman et al. (1996) reported positive correlations between vascular-plant cover and species diversity in experimental plots as well as in native savanna in east central Minnesota and offered evidence of more complete utilization of available soil nitrogen on plots having more plant species. It is not clear what differences in resource acquisition might have contributed to this pattern in this sagebrush steppe, but N is a limiting resource here as well (Toft et al. 1989). Bilbrough and Caldwell (1997) found differential responses to pulses of N among sagebrush-steppe species; they speculated that competition is likely intense for early spring N pulses. Thus, niche differentiation with regard to nutrient acquisition might contribute to the observed cover–richness relationship.

Unlike the grasslands of Minnesota, this shrub-steppe vegetation is clearly water limited, and plants extract virtually all of the available soil moisture each year (Anderson et al. 1987). Seasonal patterns of water use are similar among dominant perennial species because of the strongly seasonal availability of soil moisture (Anderson et al. 1987), which would limit temporal partitioning of water use within the growing season. However, there is some differentiation of rooting depths, particularly between shrubs and perennial grasses, which might increase productivity on plots where both growth forms are present. Experimental plots from which dominant *Artemisia tridentata* shrubs

have been removed show higher levels of moisture remaining deep in the soil profile at the end of the growing season (R. Inouye, *unpublished data*). Hydraulic lift of deep soil moisture allows *A. tridentata* to remain active after shallow soil moisture is depleted (Richards and Caldwell 1987) and potentially could enhance productivity of neighbors as well (Caldwell and Richards 1989). Similarly, the deep-rooted shrub *Chrysothamnus nauseosus* depends heavily on deep soil moisture reserves (Evans and Ehleringer 1994); removal of *C. nauseosus* in a natural stand indicated that it has little competitive influence on the water relations of a coexisting bunchgrass (Sirotnak 1990).

The second hypothesis to account for a positive relationship between cover and species richness is the so-called ''sampling effect,'' the idea that when more species are present it is more likely some species will be better able to take advantage of the prevailing environmental conditions in a given year (Huston 1997). While the sampling effect is viewed by some as a statistical artifact in experiments in which species composition is randomly determined (Huston 1997, Huston et al. 2000), in a natural community the sampling effect is a mechanism by which species richness could affect productivity. This sort of temporal niche partitioning with respect to year-to-year variability in climate is thought to promote co-existence among species (Chesson and Huntly 1989, 1993, 1997), and it may in turn contribute to maintenance of higher mean levels of productivity and to reduced relative variability in productivity among years.

The third hypothesis is that the observed relationships between species richness and cover reflect a productivity gradient among the plots. Along a gradient from very low to high productivity, diversity typically is highest at intermediate levels (Grime 1973). In our situation, where productivity may be severely constrained by water availability and edaphic factors including shallow soils, we would expect plots to vary in their capacity to produce biomass. A higher capacity for biomass production on some plots may allow more species to coexist (Huston 1997).

The data from the permanent plots do not provide a basis for choosing among the three hypotheses. Furthermore, these explanations are not mutually exclusive; it seems likely that the observed relationships may reflect a combination of the suggested mechanisms. For example, legumes, especially species of *Astragalus,* are quite common across the sampled landscape (Table 1). Plots having higher species richness would have a higher probability of including N-fixing species. Thus, inclusion of legumes in the species assemblage may contribute to higher productivity accompanying higher species richness, as has been observed in various experimental grassland plots (Tilman et al. 1997*a*, Hooper and Vitousek 1997, Hector et al. 1999).

Relationships between species richness and stability of cover

Species diversity has been linked to various indices of functional stability in natural communities (McNaughton 1993), including resistance to drought (Frank and McNaughton 1991, Tilman 1996) and grazing (McNaughton 1985). Data from the INEEL permanent vegetation plots provide additional evidence that cover tends to be more stable on plots having higher species richness. Whereas the magnitude of year-to-year change in absolute cover was higher on plots having more species of either shrubs or perennial grasses, the change in cover relative to the mean value per plot was lower (Fig. 14). At least for perennial grasses, greater stability appears to be directly associated with species richness (see Fig. 14). These findings have important implications for the sustainable management of semiarid rangelands. The observation that the absolute magnitude of change in cover from year to year is higher on more diverse plots implies that such plots will respond with higher increases in productivity during periods of favorable moisture. Furthermore, greater stability of relative cover on more diverse plots implies that more productive plots will tend to maintain higher levels of productivity during unfavorable times.

Relationships between species diversity or cover and invasibility

Lonsdale (1999:1533) described the idea that communities richer in native species are less invasible as ''a commonly accepted ecological truism.'' His analysis of global patterns of plant invasions failed to support that generalization; instead, he found that exotic-species richness often is positively correlated with native-species richness because ''exotic species richness responds to greater habitat diversity in the same positive way'' as does that of native species (Lonsdale 1999:1533). Similarly, we found no evidence that the number or abundance of exotic species was negatively related to native-species richness. For some census years, however, as cover of native species increased, the density, richness, or cover of exotic species decreased. Thus, good cover of perennial species in sagebrush steppe appears to increase resistance to invasion.

Bromus tectorum is among the most invasive of introduced species in the Intermountain West. By increasing fire frequency (Whisenant 1990) and out-competing native perennial grasses (Reichenberger and Pyke 1990), *B. tectorum* has effected the conversion of millions of hectares of sagebrush-steppe to annual communities. Data from the long-term vegetation plots indicate a very rapid expansion of the distribution of *B. tectorum* at the INEEL in the decade between 1965 and 1975, and the number of plots upon which it was recorded has generally increased in more recent samples (Table 4). The distribution of *B. tectorum* at the INEEL is somewhat limited by edaphic factors; it oc-

curs rarely on sites having fine-textured, clayey soils (Rasmuson 1996). Although *B. tectorum* has spread to most areas having coarser soils, it has displaced the native vegetation on those areas only infrequently. The 1995 point-frame data indicate that cover of *B. tectorum* is strongly inhibited by cover of native species (Fig. 15B). Studies of postfire vegetation on areas burned recently by wildfire show that invasion by exotic species is severely limited on areas where perennial grasses and forbs resprout in abundance (S. Buckwalter and J. Anderson, *unpublished data*). Thus, the bulk of the evidence available suggests that where native plant populations in sagebrush steppe are thriving, *B. tectorum* does not pose the threat that it does where populations of native perennials have been depleted.

Conclusions

We conclude that the increases in plant-species diversity and heterogeneity from 1950 to 1975 are largely the result of a recovery of vegetation from drought and grazing, reflecting an increase in the extent to which local variation in resource availability and stochastic variables determined the distribution and abundance of species. The increase in average species richness per plot, the increase in average frequency of perennial grasses, and the increase in among-plot heterogeneity with time all are consistent with this conclusion. Vegetation dynamics of this sagebrush steppe can be understood as the result of ongoing interactions between a spatially and temporally heterogeneous environment and a suite of species that differ in dispersal capacities and in their potential for establishing and/or persisting under varying environmental conditions (Brand and Parker 1995). These observations make it clear that a large-scale perspective is needed to understand the vegetation dynamics of even this relatively homogeneous sagebrush-steppe. It is simply not possible to infer trends accurately from one or a few plots.

We also conclude that species richness is an important factor driving the functioning of semiarid sagebrush-steppe ecosystems. The correlations among richness, cover, and variation in cover are highly significant and show that, regardless of the cause, plots having greater species richness tend to vary less in cover, and presumably in productivity, in relation to their mean level. Plots having greater species richness also tend to maintain higher levels of cover. In addition, adequate cover of native species appears to render these semiarid communities more resistant to invasion. Therefore, maintaining or recovering richness of native species should be a high priority.

Acknowledgments

We are indebted to D. L. Goodwin and colleagues who established the permanent plots in 1950, to Roy Harniss and Neil West who reexamined the plots in 1965 and contributed two papers based on their findings, and to Richard Jeppson and Karl Holte who collected the 1975 data. We thank Rae Bradish, Nancy Cole, Doug Evans, Steve Howser, Dave Humphrey, Tim Mullican, Diane Pavek, Robert Wilcosz, and numerous Associated Western University summer interns who have worked as field assistants in census years since 1975. We are especially grateful to James Glennon, who headed the field crews in 1985, 1990, and 1995 and assisted with data entry and resolving taxonomic problems, to Teresa Ratzlaff for technical support, and to Ron Rope and Randy Lee who produced the shaded relief map for Fig. 1. Steve Jackson and an anonymous reviewer provided insightful comments on an earlier manuscript. We thank Doyle Markham for ensuring the continued integrity and sampling of the permanent plots and for his continued support of the project. This report is a contribution of the Center for Ecological Research and Education at Idaho State University and the Environmental Science and Research Foundation, Idaho Falls, Idaho, through contract Number DE-AC07-94ID13268 with the U.S. Department of Energy.

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The Journal of Wildlife Management 1–17; 2021; DOI: 10.1002/jwmg.22087

Research Article

Prey Specialization by Cougars on Feral Horses in a Desert Environment

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ABSTRACT Natural controls on the distribution, abundance, or growth rates of exotic species are a desirable mode of intervention because of lower costs compared to anthropogenic controls and greater social acceptance. In the Great Basin, cougars (*Puma concolor*) are the most widely distributed carnivore capable of killing large ungulate prey. Populations of feral horses (*Equus ferus*) are widely distributed throughout the Great Basin and can grow at rates up to 20%/year. Although cougars exhibit distributional overlap with horses, it has been assumed that predation is minimal because of differences in habitat use and body-size limitations. To evaluate this hypothesis, we monitored the diets of 21 global positioning system (GPS)-collared cougars in the western Great Basin (5 males, 8 females) and eastern Sierra Nevada (2 males, 6 females) from 2009–2012. We investigated 1,310 potential kill sites and located prey remains of 820 predation events. We compared prey composition and kill rates of cougars inhabiting the Sierra Nevada and Great Basin, and among male and female cougars across seasons. We used generalized linear mixed models (GLMMs) to examine the effects of prey availability and habitat characteristics on the probability of predation on horses by cougars. Mule deer (*Odocoileus hemionus*) comprised 91% of prey items killed on the Sierra Nevada reference site but only comprised 29% of prey items in the Great Basin study area. Average annual kill rates for deer differed between the Sierra Nevada ($\bar{x} = 0.85$ deer/week, range = 0.44–1.3) and Great Basin ($\bar{x} = 0.21$ deer/week, range = 0.00–0.43). Diets of cougars in the Great Basin were composed predominantly of horses (59.6%, $n = 460$ prey items; 13 individuals). Ten cougars regularly consumed horses, and horses were the most abundant prey in the diet of 8 additional individuals in the Great Basin. Cougars on average killed 0.38 horses/week in the Great Basin (range = 0.00–0.94 horses/week). Differences in predation on horses between the sexes of cougars were striking; Great Basin females incorporated more horses across all age classes year-round, whereas male cougars tended to exploit neonatal young during spring and summer before switching to deer during winter. Within GLMM models, the probability of predation on horses compared to other prey species increased with elevation, horse density, and decreasing density of mule deer on the landscape, and was more likely to occur in sagebrush (*Artemesia* spp.) than in pinyon (*Pinus monophylla*)–juniper (*Juniperus osteosperma*) forests. Behavior of individual cougars accounted for more than a third of the variation explained by our top models predicting predation on horses in the Great Basin. At landscape scales, cougar predation is unlikely to limit the growth of feral horse populations. In the Great Basin ecosystem, however, cougars of both sexes successfully preyed on horses of all age classes. Moreover, some reproductive, female cougars were almost entirely dependent on feral horses year-round. Taken together, our data suggest that cougars may be an effective predator of feral horses, and that some of our previous assumptions about this relationship should be reevaluated and integrated into management and planning. © 2021 The Wildlife Society.

KEY WORDS cougar, *Equus ferus*, exotic prey, free-roaming horses, Great Basin, individual specialization, predator-prey dynamics, *Puma concolor*.

Management of exotic and invasive species is considered among the most pressing conservation challenges of the twenty-first century (Mooney and Cleland 2001, Clavero and Garcia-Berthou 2005, Simberloff et al. 2013). Where possible, biological control of the distribution, abundance, or growth rates of exotic species is preferable to anthropogenic interventions such as removals because of lower financial costs and greater societal acceptance. Meanwhile, activities such as livestock husbandry, urban development, fire suppression, historical overhunting, and predator

Received: 1 May 2020; Accepted: 9 May 2021

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control have altered the ecological framework of many communities, resulting in unanticipated changes in assemblages of ungulates and apex predators (Berger and Wehausen 1991, Novaro et al. 2000, Gruell and Swanson 2012). Many of those changes have resulted in predator-prey dynamics that are different from those that existed prior to those anthropogenic activities and changes to landscapes. The consequences of introductions of exotic species and unanticipated species compositions in novel landscapes are widespread but poorly understood (Hobbs et al. 2006, Moss et al. 2016). Understanding competitive and consumptive relationships between native and exotic species in altered landscapes is important for successful management of predators and their prey.

Predation and the associated cascading effects on lower trophic levels is one of the most fundamental natural processes that can limit exotic prey species (Carlsson et al. 2009, Estes et al. 2011). Some generalist predators adapt to novel prey by altering their foraging behavior (Novaro et al. 2000, Carlsson et al. 2009, Moss et al. 2016, Robins et al. 2019), especially where novel or exotic prey are vulnerable or predominant on the landscape (Novaro et al. 2000, Smith et al. 2000). Individuals that can switch to novel prey likely have a fitness advantage over those that cannot and strategies that favor successful capture of abundant and energetically profitable prey should therefore be favored (Carlsson et al. 2009).

Many factors can influence intake of a prey species by predators including relative availability of primary and alternative prey (Robinson et al. 2002, Elbroch et al. 2013, Sand et al. 2016), sex or age class of predators (Knopff et al. 2010, White et al. 2011), environmental factors (Husseman et al. 2003), size and vulnerability of prey (Knopff et al. 2010, Elbroch et al. 2013), and individual preference (Ross et al. 1997, Knopff and Boyce 2007, Elbroch and Wittmer 2013, Lowrey et al. 2016). Effects of predation by apex predators on prey populations are complex and often unintuitive (Ruth and Murphy 2009), especially considering confounding factors such as availability of multiple prey species (Knopff and Boyce 2007), level of individual specialization in a population (Festa-Bianchet et al. 2006, Pettorelli et al. 2011), and the degree of resource limitation of the prey population (Pierce et al. 2012).

Equids were extirpated in North America ≥10,000 years ago, but domesticated horses released in North America by Spaniards and later settlers increased rapidly in some areas of the Great Basin from the 1870s to the 1890s (Beever 2003, Gruell and Swanson 2012). Lack of top-down factors limiting population growth has been suggested as a potential explanation for the exceptional growth rates observed in feral horses (*Equus ferus*; National Research Council Committee to Review the Bureau of Land Management Wild Horse and Burro Management Program [NRC] 2013). Currently, 72,000 free-roaming feral horses (i.e., free-roaming horses or horses) occur in the western United States, primarily in the Great Basin ecoregion (Bureau of Land Management [BLM] 2019). As detailed in the NRC (2013) report and the BLM (2018) report to Congress, the scientific consensus has been that free-roaming horses in North America have no natural predators largely because of their large body size and lack of spatial overlap between horses and cougars (*Puma concolor*).

Cougars are the widest ranging terrestrial species in the western hemisphere (Sunquist and Sunquist 2002). Their success is at least partially attributed to behavioral plasticity facilitating varied diets associated with occupation of many diverse landscapes (Iriarte et al. 1990, Martínez et al. 2012). Cougars readily consume ungulates, including deer (*Odocoileus* spp.), elk (*Cervus canadensis*; Hornocker 1970, Clark et al. 2014), moose (*Alces alces*; Ross and Jalkotzy 1996, Knopff et al. 2010), mountain caribou (*Rangifer tarandus caribou*; Wittmer et al. 2005), bighorn sheep (*Ovis canadensis*; Ross et al. 1997), guanacos (*Lama guanicoe*; Elbroch and Wittmer 2013), domestic livestock (Cunningham et al. 1999), and feral horses (Turner et al. 1992, Greger and Romney 1999, Knopff and Boyce 2007). Although documentation of predation on horses by cougars is uncommon (Berger 1986, Murphy and Ruth 2009, NRC 2013), cougar predation has been implicated in limiting the growth of ≥2 horse populations (Greger and Romney 1999, Turner and Morrison 2001, Turner 2015). Optimizing predation by cougars on horses, for instance, through ceasing cougar hunting where horses occur, has been suggested as a panacea for managing horses with little data for support (Philipps 2018). Furthermore, cougars and horses engender strong public emotions ranging from disdain to adoration. Population control of either species remains contested, further emphasizing the need for accurate understanding of their predator-prey dynamics for efficient management.

Evidence of cougar predation on horses has primarily been anecdotal (Berger 1986), incidental (Robinette et al. 1959), or of limited sample size (Gray et al. 2008), and has been documented through monitoring horse populations (Turner et al. 1992, Greger and Romney 1999, Roelle et al. 2010), monitoring the number of overlapping cougars, or both (Turner and Morrison 2001). Although cougar predation on horses is considered rare (Berger 1986), individual variation in predator behavior could allow predation on novel or exotic prey to increase throughout a population (Bolnick et al. 2003, Carlsson et al. 2009). Few studies have documented the extent that individual cougars incorporate horses into their diet (Gray et al. 2008, Knopff et al. 2010). Cougars are one of many species in which there is increasing evidence of high variation among diets of individuals. In Alberta, Canada, only 1 of 9 cougars frequently incorporated horses into their diets, although most individuals had access to horses as prey (Knopff and Boyce 2007). Cougars can respond to changes in prey abundance by prey switching (Sweitzer et al. 1997, Novaro et al. 2000), which allows individuals to exploit novel prey (Novaro et al. 2000). Accordingly, predation on horses has previously been associated with low densities of mule deer (*Odocoileus hemionus*; Ashman et al. 1983), seasonal migration of mule deer (Turner et al. 1992, Turner and Morrison 2001), or areas where horses were relatively more abundant than deer (Berger 1986). Body size may influence

prey choice of solitary predators to mitigate risk of injury (Iriarte et al. 1990, Sunquist and Sunquist 2002). For large-bodied ungulates, this often contributes to seasonal predation on smaller, more vulnerable juveniles and neonates (Hornocker 1970, Ross and Jolkotzy 1996, Mattson 2007). Accordingly, cougar predation on horses was thought to have been limited primarily to foals during summer (Turner et al. 1992), although horses comprised 13% and 11% of male diet composition in Alberta during summer and winter, respectively (Knopff et al. 2010). Male cougars are also >50% larger than females (Sunquist and Sunquist 2002) and the stark differences observed between male and female cougars in their propensity to kill large ungulate prey such as moose and elk, and the associated risk, has largely been attributed to sexual dimorphism (Knopff et al. 2010, White et al. 2011, Clark et al. 2014).

Predators often exhibit different predation tactics with respect to landscape structure. Open landscapes, which are preferred by horses, are generally thought to be advantageous to coursing predators that may pursue prey for long distances, and a limitation for ambush predators such as cougars that require stalking and forest cover (NRC 2013). Cover, however, does not always confer an advantage for cougar predation. In the Great Basin of eastern California, USA, cougars disproportionately preyed upon mule deer in low shrub communities, even though mule deer foraged more frequently where cover was greatest (Pierce et al. 2004). Most of what we know about cougar predation comes from ecosystems where mule deer are the primary prey (Logan and Sweanor 2001).

Cougars occur at low densities in arid environments and are thought to have historically occurred at nominal levels in the Great Basin (Berger and Wehausen 1991). Vast increases in domestic livestock grazing concomitant with Euro-American expansion altered the vegetative landscape across the Great Basin from grasses to browse species, which facilitated the expansion of mule deer (Berger and Wehausen 1991, Grayson 2011, Gruell and Swanson 2012). As mule deer populations increased across the Great Basin, numbers of cougars, the primary predator of mule deer over most of their distribution across North America, also increased (Pierce and Bleich 2003).

We investigated, in an observational framework, predator-prey relationships in an altered ecosystem by taking advantage of a natural experiment presented by the occurrence of non-native horses within a desert ecosystem inhabited by cougars and mule deer. We investigated the behavioral, demographic, and habitat conditions under which cougars exploit feral horses in an altered ecosystem. If the general consensus that body size discrepancies and lack of overlap prevents cougars from effectively preying on horses is correct (NRC 2013), we would expect that cougar diets would be focused primarily on mule deer, in both study areas, regardless of the presence of horses in the Great Basin. Further, if that assumption is correct, we would predict that we would observe little spatial or habitat overlap between horses and cougars. If, however, horses are vulnerable to predation by cougars and are an important source of prey, we made 5 predictions, based on previous findings and theory outlined previously: 1) individual cougars would vary in their propensity to prey on horses (Bolnick et al. 2003, Knopff and Boyce 2007, Carlsson et al. 2009); 2) predation on horses would occur where horse densities were high and mule deer densities were low (Ashman et al. 1983, Novaro et al. 2000); 3) cougars would prey on young horses during summer when young were abundant and vulnerable to predation, with decreased predation on horses during winter months, when young horses are nearly full grown (Turner et al. 1992, Mattson 2007); 4) male cougars would prey on horses to a greater extent and kill a greater proportion of older, larger horses, compared to females (Knopff et al. 2010, White et al. 2011); and 5) cougars would spatially overlap with herd areas of horses and kill horses more frequently in sagebrush (*Artemesia* spp.), where horses are more likely to occur, compared to forests, where horses spend less time (Pierce et al. 2004).

STUDY AREA

We monitored diets of cougars in the ecotone of the western Great Basin and eastern Sierra Nevada, USA, during 2009–2012 (Andreasen et al. 2018; Fig. 1). The overall study area consisted of mountains separated by basins and covered an area of approximately 35,950 km^2. We defined the 2 study areas based on the movements of cougars studied (Figs. 1 and 2). Elevations ranged from approximately 1,190–3,440 m. The Sierra Nevada study area was centered on the Carson Range. Dominant vegetation in the Sierra Nevada included ponderosa pine (*Pinus ponderosa*), Jeffery pine (*Pinus jeffreyi*), and white fir (*Abies concolor*) at lower elevations, which gave way to red fir (*Abies magnifica*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*) above 2,285 m. Whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) occurred above 2,530 m until the treeline (~3,140 m) where alpine vegetation dominated (Grayson 2011). Shrublands and understory communities in the Sierra primarily included sagebrush, greenleaf manzanita (*Arctostaphylos patula*), curl-leaf mountain mahogany (*Cercocarpus ledifolius*), rabbitbrush (*Ericameria* spp.), and tobacco brush (*Cercocarpus velutinus*). The eastern portion of the study area was in the rain-shadow of the Sierra Nevada and was more characteristic of the arid Great Basin. Those mountain ranges were characterized by steep topography with high granite peaks and deep canyons, and were separated by desert basins 15–64 km wide that included expanses of sagebrush (Grayson 1993, Beckmann and Berger 2003), which cougars use infrequently (Beckmann and Berger 2003, Andreasen et al. 2012, Andreasen 2014). Thus, cougar habitat in the Great Basin is insular and naturally fragmented (Grayson 1993, Beckmann and Berger 2003, Andreasen 2014). Dominant vegetation in Great Basin mountain ranges included sagebrush shrublands on the lower slopes, followed by pinyon-juniper woodlands and mountain sagebrush communities as elevation increased

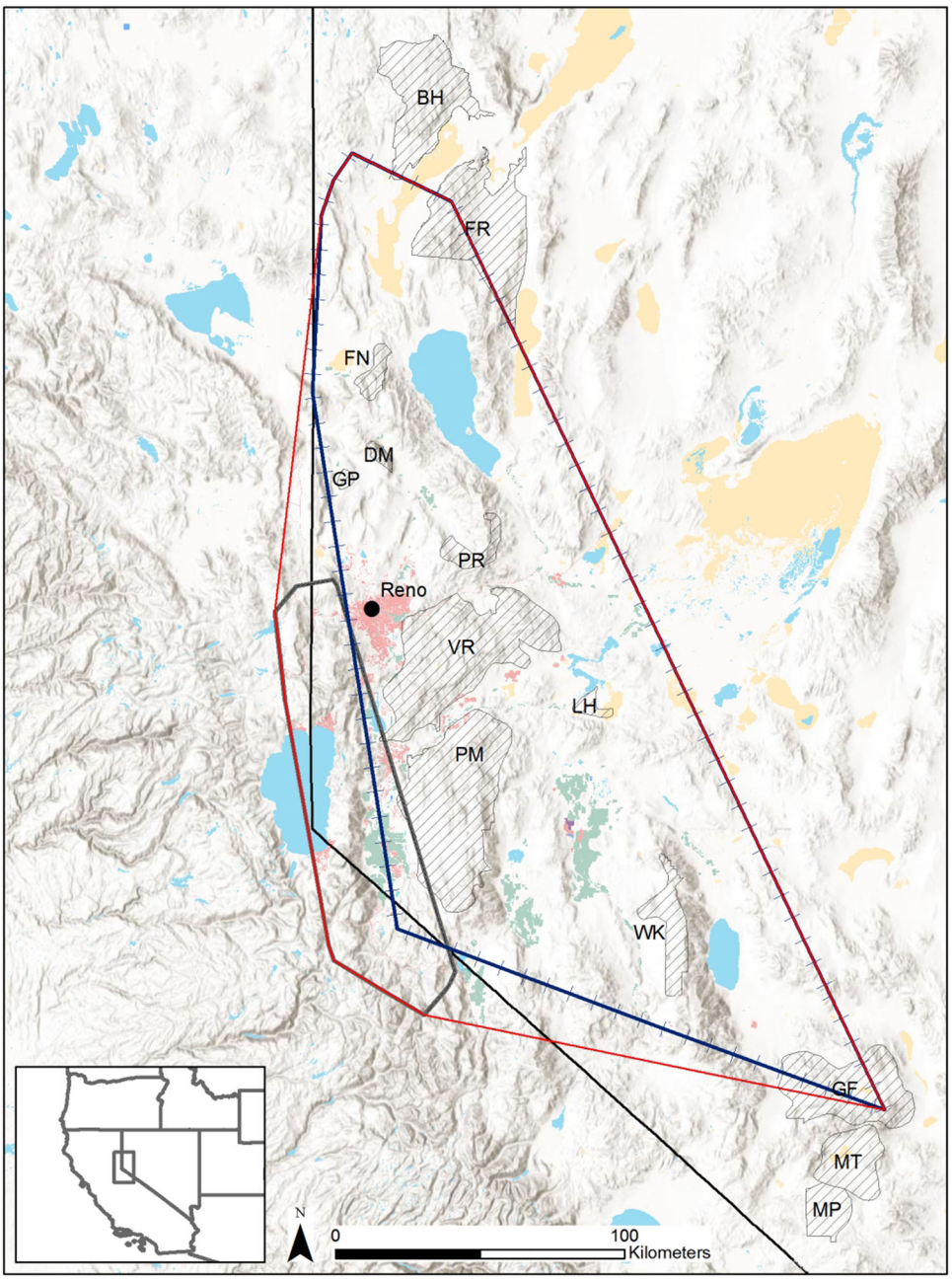
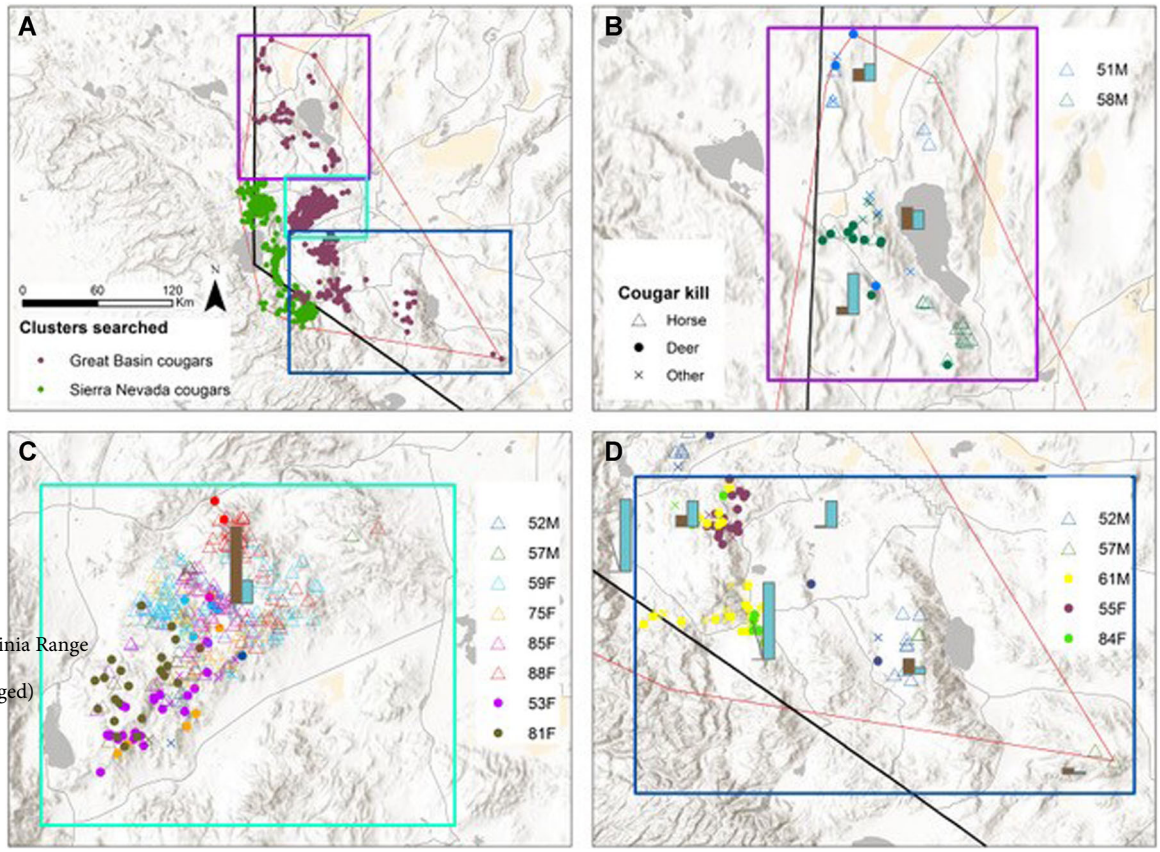


Figure 1. Overall study area (red polygon) where we monitored the diets of 21 global positioning system-collared cougars, 2009–2012, in the western Great Basin and eastern Sierra Nevada, USA. Feral horses occurred within the Great Basin study area (blue hatched polygon). We estimated horse abundance from the indicated herd management areas (BH = Buffalo Hills, FR = Fox-Lake Range, FN = Flanigan, DM = Dogskin Mountains, GP = Granite Peak, PM = Pine Nut Mountains, LH = Lahontan, WK = Wassuk, GF = Garfield Flat, MT = Marietta, MP = Montgomery Pass), herd areas (PR = Pah Rah Mountains) managed by the Bureau of Land Management, and where horses were present but managed by the Nevada Department of Agriculture (VR = Virginia Range). Collared cougars overlapped herd areas indicated except for GP, MP, and MT (with only exploratory movements near LH). Horses were not present in the Sierra Nevada study site (grey polygon). Non-cougar habitat including developed areas is shown in red with associated agricultural areas shown in green and playa represented in beige. Horse numbers in the southern portion of the study area may be underrepresented because we did not consider United States Forest Service herd territories or those in California.

(Grayson 2011). Sagebrush occurred throughout Great Basin mountain ranges in our study area, with big sagebrush species dominating lower elevations and low sagebrush at higher, colder elevations. Dominant shrubs included antelope bitterbrush (*Purshia tridentata*), rabbitbrush, and Mormon tea (*Ephedra* spp.).

Mule deer were the primary ungulate prey available in the Sierra Nevada, where other ungulates, including free-roaming horses, were largely absent. Conversely, ungulates available in the Great Basin study area included mule deer, free-roaming horses, bighorn sheep, and pronghorn (*Antilocapra americana*). We delineated seasons by birth season for horses and mule deer, such that summer included the months of March through August, and winter included the months September through February. The study area was arid with hot summers and cool



Note: this is the Virginia Range

(Nevada state managed)

Figure 2. Study area (red polygon) where we examined cougar predation, prey species killed by cougars, and location of kills for 21 global positioning system (GPS)-collared cougars in the western Great Basin and eastern Sierra Nevada, USA, 2009–2012. We searched cougar GPS clusters in the north (purple frame), central (turquoise frame), and south (blue frame) portions of the Great Basin study area. Bar charts shown within each Nevada Department of Wildlife game management unit (GMU; grey lines) represent the relative density of free-roaming feral horses (brown) and mule deer (turquoise). A) Colored dots represent GPS clusters (potential cougar kills; $n = 1{,}310$) searched in the overall study area in which 13 GPS collared cougars (5 males, 8 females) primarily resided in the western Great Basin (maroon dots) and 8 cougars (2 males, 6 females) resided in the eastern Sierra Nevada (green dots). Location of confirmed kills made by 13 Great Basin cougars in the B) northern (purple frame), C) central (turquoise frame), and D) southern (blue frame) portions of the Great Basin study area are indicated by symbols that represent the type of prey killed including horse ($n = 274$), mule deer ($n = 132$), and other species ($n = 54$). The color of each symbol represents individual cougars ($n = 13$). Sex of individual cougars, male (M) and female (F), is indicated after individual cougar identifications. Cougar identification symbol shape indicates which species was most dominant in the diet of each individual. Two male cougars are included in panels B and C because of movements from the central to the southern portion of the study area. Water bodies are colored grey. We calculated relative prey densities in GMUs as the mean of densities extracted from kill locations.

winters; average annual high and low temperatures were 20° C and 4° C on valley floors with cooler temperatures in the mountains. The majority of precipitation fell as snow in the winter with an average of 56 cm snowfall and 19 cm rainfall on the valley floor and 130 cm snowfall and 32 cm rainfall in the mountains (Andreasen et al. 2018, Virginia City; usclimatedata.com, accessed 1 Jan 2018).

A large portion of cougar habitat in the study area is public land managed by the United States Forest Service (USFS) and BLM for multiple land uses including hunting, trapping, livestock grazing, and outdoor recreation. The latter agency is also tasked with managing free-roaming horses on BLM lands; however, horses also occur in the Virginia Range, which is managed by the Nevada Department of Agriculture (Fig. 1). Urban, exurban, and residential developments along the wildland-urban interface in the study area include Reno, Carson City, Dayton, Minden, and Gardnerville, and the study area has one of the fastest growing human populations in the United States (Northern Nevada Economic Planning Indicators Committee 2015). Much of this new development is in exurban areas occurring in valley bottoms and foothills, both of which are important winter habitat components for mule deer (Andreasen et al. 2018).

METHODS

Field Methods

To evaluate predatory behavior and diet, we captured cougars between January 2009 and December 2012. We collared cougars with Globalstar satellite collars (Vectronic Aerospace GmbH, Berlin, Germany; North Star Science and Technology, King George, VA, USA). We programmed global positioning system (GPS)-collars to collect geographic coordinates at intervals ranging from 2.5–5 hours.

We captured and handled cougars using methods approved by the Institutional Care and Use committee at the University of Nevada, Reno (protocol A06/07-28) and were

in keeping with guidelines established by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011). We followed procedures outlined in the capture permit (State of Nevada scientific collection permit S33313) issued by the Nevada Department of Wildlife (NDOW). Andreasen et al. (2018) provide further details on animal capture.

We defined a potential kill using GPS clusters, defined as ≥2 GPS location points within 200 m, including ≥1 night location (Anderson and Lindzey 2003, Knopff et al. 2009). We displayed location data in ArcGIS (Esri, Redlands, CA, USA) and used an algorithm (Knopff et al. 2009) to identify clusters. Using handheld GPS to navigate, we searched the potential predation site by first visiting the centroid of the GPS cluster or the GPS location that appeared to have the most nighttime activity by the individual cougar. If we did not immediately locate remains of a prey item, we searched the site at increasing distances up to a 200-m radius. We identified the prey species at the GPS cluster based on remains (e.g., hair, skeletal remains, teeth) and attempted to distinguish scavenging from predation using criteria pertaining to the condition of remains and if they were consistent with date of cougar presence. We determined the age of prey using tooth eruption sequences or size when lower jaws were not available (Evans 1981, Schroeder and Robb 2005). We classified prey as young of year (<1 yr), yearling (1–2 yrs), or adult (>2 yrs). We further divided the age of young when possible into finer age classes (0–2 months, 3–5 months, and 6–12 months). We assigned the predation date as the first GPS location occurring at a GPS cluster, and each predation event to spring and summer or autumn and winter.

Prey Composition

We removed data for which prey species could not be positively identified. These included sites with minimal prey remains and those with remains of small animals (e.g., rabbits, skunks, squirrels) because these kills were not associated with extended feeding times. We also removed clusters associated with suspected scavenging events. We assigned prey remains shared by collared mother-offspring pairs to the mother, whereas we assigned prey items shared by 2 collared, independent animals to the individual whose GPS location indicated it was at the cluster first and assigned the second cougar as scavenging. After these removals, we included the remaining prey in the analyses of prey composition. In instances where multiple domestic sheep were killed at a cluster, we included only a single domestic sheep because typically only 1 sheep was consumed.

Individual cougars rarely crossed between the Great Basin and Sierra Nevada study areas. We thus calculated diet composition of cougars at the population level for each study area as the percent frequency of prey items made by cougars inhabiting the Sierra Nevada and Great Basin separately. To maintain sufficient sample sizes for statistical comparisons, we combined prey into 3 categories: horse, mule deer, and other. We also combined age of ungulates killed into those <1 year old and those >1 year old and further examined the frequency of predation of fine age classes within young-of-year categories. We used chi-square tests to determine differences in cougar diet composition and age class of ungulate kills across sex and season.

Modeling

We used generalized linear mixed models (GLMMs) to examine the relative contribution of potential explanatory variables at cougar kill sites to explain cougar predation on horses. We used GLMM because we were interested in identifying categorical and continuous variables important in the probability of horses being killed across the landscape compared to other prey items while accounting for and assessing the importance of random effects, including individual variation and variation among mountain ranges. We used the presence of an ungulate carcass at a cache site as the basic unit of statistical analyses with horses coded as 1 and all other species as a zero. Fixed effects variables examined included cougar sex, season, deer density, horse density, elevation, and land cover type. We included random effects (intercepts) for individual cougar identifications and groups of mountain ranges to test for variation in predation behavior among individuals, account for unequal sample sizes among individuals, and account for the correlated structure of predation events within individuals and mountain ranges (i.e., predation events within groups of mountain ranges are likely more similar than predation events occurring among ranges) using mixed effect logistic regression (Gillies et al. 2006). We approached model selection hierarchically (Hebblewhite and Merrill 2008). We selected biologically relevant variables hypothesized to be important in explaining cougar predation on horses and used Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002), Akaike weights (w_i), and parameter estimates to identify the top fixed effect model from all possible combinations of the global model (Barton and Barton 2019). We considered top models within 2 AIC_c scores to be competitive (Burnham and Anderson 2002). Further, we also used diagnostics of residuals to determine appropriateness of the models (Burnham and Anderson 2002). Finally, we evaluated the models within 2 AIC_c scores for model fit by residual analysis using the DHARMa package in R (R package version 0.2; Hartig 2019).

We added random effects to the top fixed effect model to create 3 mixed effect models. We again used AIC_c to select the top model among the 3 mixed effect models (Burnham and Anderson 2002). We considered fixed effects to be significant if 95% confidence intervals did not overlap zero (Burnham and Anderson 2002). We calculated pseudo R^2 to evaluate model efficacy and to describe the proportion of variance explained by the fixed factors (marginal R^2) and the random factors (conditional R^2 – marginal R^2; Barton and Barton 2019). We built models using the glm and glmer functions in the lme4 package (Bates et al. 2015) in the R statistical package (R Core Team 2020).

We considered 6 potential explanatory covariates for inclusion as fixed effects in predation models. We included

binary covariates to test for differences in predation on horses by sex of individual cougars (male = 1; female = 0) and season (summer, winter); and we then tested for an interaction of other fixed effect variables with sex and season. To estimate the effects of deer availability on the likelihood of cougars killing horses, we used estimates of annual density of mule deer derived by the NDOW as a relative index of mule deer abundance throughout the Sierra Nevada and Great Basin study areas. The NDOW derived annual estimates of mule deer densities by dividing the annual population estimate for mule deer by the area of the game management unit (GMU); in some instances, the GMUs were combined. This resulted in an estimate of mule deer/ha within each GMU each year for the Sierra Nevada and Great Basin study areas (C. A. Schroeder, NDOW, personal communication). We used a similar technique to estimate horse density for the Great Basin study area. We calculated a relative density index of free-roaming horses within each Nevada GMU in which we documented a kill of any species. We used annual horse population estimates published by the BLM in Nevada for horses in all herd management areas (HMAs; and herd areas where estimates were available; BLM 2012, 2013) contained within GMUs in which we discovered a kill of any species. We estimated the density of horses in the Virginia Range, where horses were managed by the Nevada Department of Agriculture, using a single estimate of horses obtained from an aerial survey in 2012 (M. Gray, University of Nevada, Reno, personal communication; Fig. 1). The result was a relative density index of horses within each NDOW GMU that varied annually, except in the Virginia Range where we used a single point estimate across all years (Figs. 1 and 2). To estimate the effect of environmental variation on horse predation, we used a geographic information system to extract elevation (m) and land cover type for each of the locations where we found a kill. We derived land cover for the study area from the United States Geological Survey Gap Analysis Project land cover dataset (U.S. Geological Survey 2001) at a 30-m × 30-m resolution and combined data into 5 land cover types: sagebrush (the reference category), desert shrub, steppe-desert scrub, forest, riparian, and other open vegetation types.

We screened variables for collinearity (>0.7) using Pearson's correlation. We also tested for collinearity of variables using variance inflation factors of the global fixed effects and top mixed effects model, further investigating variables with the generalized variance inflation factor ≥5 (Fox and Weisberg 2018). When deciding between 2 correlated variables for inclusion into models, we attempted to retain the variable that was more biologically relevant or the one that was a better predictor according to AIC_c by comparing only main effect models (models with only 1 predictor variable) AIC_c weights, and change in AIC_c (ΔAIC_c). We scaled and centered continuous variables.

Kill Rates

The number of prey removed/unit time by a cougar population can, hypothetically, be estimated as the product of the individual rate and the numbers of cougars hunting (Ruth and Murphy 2009). This metric is distorted, however, when species-specific kill rates are estimated using the inter-kill interval method (Cooley et al. 2008, Ruth et al. 2010) for individuals and populations in which individual variation in diet exists. To avoid such distortions, we used a ratio estimator to calculate the minimum kill rates of horses and deer for all cougars monitored for >4 weeks in a given season in which we confirmed ≥4 kills (Knopff et al. 2009). We calculated monitoring time for each cougar in each season as the number of days between the first day of the first cluster that we field visited and the last night of the last cluster visited. We calculated kill rates of horses and deer separately using the monitoring time as the denominator and the number of kills confirmed for those species as the numerator, resulting in frequency of kills for each species (deer/week and horses/week). We calculated first season- and species-specific kill rates for each individual. We calculated mean seasonal kill rates for individuals monitored >1 year. To provide results comparable to other studies, we calculated annual average kill rates using the mean of season-specific values and combined sexes.

We used a *t*-test to compare average annual kill rates using individuals as the sample unit to compare kill rates of mule deer among study areas. Because of limited sample sizes, and to provide results comparable to other studies, we used a *t*-test to compare species-specific and seasonal kill rates among males and females, using the mean season- and species-specific kill rates for each individual as the sample unit.

RESULTS

We monitored the diets of 21 GPS-collared cougars (7 males, 14 females) for a mean of 55 ± 35 weeks from 2009–2012. We investigated approximately 1,310 GPS clusters of telemetry locations identified as possible predation sites. We located 820 predation events, including 23 scavenging events and 35 clusters (4.4%) where we found multiple prey items. Multiple prey items were typically associated with killing of mother offspring pairs (e.g., female and juvenile), defense of a carcass (e.g., mule deer and coyote [*Canis latrans*]), or surplus killing of domestic sheep. Ten prey items were shared between 2 adult cougars with GPS-collars (mating pairs, and pairs of adult females with unknown relationships), indicated by 2 collared cougars at the same cluster simultaneously (where we assigned 1 cougar the kill and the other as scavenging). Two additional prey items were scavenged from collared cougars in which items were not shared, indicated by GPS locations from different collared individuals that did not overlap in time. After removing unknowns, scavenging, and small mammals, our dataset consisted of 771 confirmed kills ($\bar{x} = 36.7$ kills/individual, range = 9–132, $n = 21$ individuals). We visited clusters a median of 58 ± 101 days after the kill was made. Cougar GPS locations overlapped with 10 out of 13 herd areas located within study area GMUs (~52,000 GPS locations). We searched clusters in 9 herd areas with confirmed predation events in or directly adjacent to 8 of those areas (Figs. 1 and 2).

Prey Composition

Cougars killed a variety of prey across the study area including mule deer, free-roaming horses, bighorn sheep, pronghorn, domestic sheep, domestic cattle, feral goats (*Capra hircus*), coyote, American beaver (*Castor canadensis*), North American porcupine (*Erethizon dorsatum*), American badger (*Taxidea taxus*), and domestic dog. In the Sierra Nevada study area, mule deer comprised the primary prey items found for 8 individual cougars (91%, $n = 311$ prey items). Mule deer were the most common prey item in the diets of all 8 individual cougars in the Sierra Nevada, ranging from 62.8% in the diet of 1 individual to >94% of the diet of the remaining 7 individuals ($\bar{x} = 96.9\% \pm 2.3\%$, $n = 7$). One male had the lowest proportion of mule deer in the diet, but 30% of his diet was composed of beaver.

Free-roaming horses dominated the diet at the population level for 13 individual cougars in the Great Basin study area (59.6%, $n = 460$ prey items) and deer comprised 28.7% of prey items of collared cougars. Ten of 13 cougars consumed horses, comprising an average of $69.5\% \pm 25.8\%$ ($n = 10$) of those cougar diets. Horses were the most abundant prey in the diet of 8 individuals in the Great Basin, ranging from 35.7% of the diet for 1 individual to >90% for 4 individuals ($\bar{x} = 76.7\% \pm 23.6\%$, $n = 8$; Fig. 3). Among the 13 cougars in the Great Basin, mule deer accounted for 0% to 78.6% of cougar diets ($\bar{x} = 32.7\% \pm 27.9\%$, $n = 13$). Mule deer comprised the largest proportion of the diet for 5 individuals, ranging from 50% of the diet for 1 individual to 78.6% for another individual in the Great Basin ($\bar{x} = 63.4\% \pm 11.2\%$, $n = 5$).

The diets of male and female cougars varied significantly ($\chi^2_2 = 43.58$, $P < 0.001$) and the proportion of horses in the population diet of females (67.3%) was nearly 2 times that of males (35.9%; Table 1). The composition of prey did not change seasonally for females; however, males shifted seasonally to include 2 times as many mule deer and >30% fewer horses in winter (males, $\chi^2_2 = 13.34$, $P = 0.001$; females, $\chi^2_2 = 0.18$, $P = 0.915$; Table 1).

Among ungulates killed by cougars in the Great Basin, horses tended to come from younger age classes than deer ($\chi^2_1 = 75.8$, $P < 0.001$; Fig. 4). The proportion of horses in different age classes varied by season with a greater proportion of horses >1 year old killed during winter in instances where we could identify age ($\chi^2_1 = 4.17$, $P = 0.041$; Fig. 5A). Statistically, male and female cougars killed the same proportion of horses >1 year: 8.3% versus 13.8% for males and females, respectively ($\chi^2_1 = 0.81$, $P = 0.368$; Fig. 5A). Within young-of-year categories, fine age classes of horses killed differed significantly between males and females ($\chi^2_2 = 11.55$, $P = 0.003$); males predominantly killed horses ≤3 months old (74%), whereas females continued to kill older-aged horses within the young-of-year category (Fig. 5B).

Modeling

Sex of cougar was correlated with horse density, as indicated by variance inflation factors >10 in fixed effect models. The correlation between sex of cougar and horse density is likely because males have larger home ranges than females, resulting in greater variability of horse densities for males compared to females (Fig. 2). Because we examined differences in diets between male and female cougars using descriptive statistics, we opted to retain horse densities as an explanatory variable within models because it was ranked the top main effects model (model with a single variable; $w_i = 1$; $\Delta AIC_c = 11.8$). Further, when we included sex of cougar or season as an interaction term in mixed models, models failed to converge and thus we excluded this interaction. The top fixed effect model included mule deer density, horse density, and land cover type and the ΔAIC_c was 2.03 from the next best model, which also included elevation (Table 2). Based on further analysis of residuals, the model that included elevation was a better fit and we selected it as our top model. There was considerable model uncertainty within the top 2 random effect models ($\Delta AIC_c = 0.38$; Table 3). The top model included random intercepts for individual cougar and mountain range and the second-ranked model included only a random intercept for individual cougar. The top 2 models including a random intercept for individual cougar were far superior to the third-ranked model, which included a random intercept for mountain range only ($\Delta AIC_c \geq 66$). This result suggests that the models accounting for variation among individuals and individuals within mountain ranges, explain predation on horses better than differences among mountain ranges alone.

The top-ranked mixed effects model explained 78.5% (pseudo $R^2 = 0.785$) of the observed variation in horse predation. Fixed effects, including densities of mule deer and horses, elevation, and land cover type accounted for 38.7% of total variation in horse predation, whereas random effects (i.e., individual cougar identification, mountain range) accounted for 39.8% of the variation in horse predation explained by the model. The second-ranked mixed effect model, which included the same fixed effects but only a single random effect for individual cougar, explained 68.6% of the variance in horse predation; individual variation accounted for 25.1% of the total explained (Fig. 2).

For the top model including individual cougar and mountain range as random effects, confidence intervals did not overlap zero for deer density, elevation, or forest land cover (Fig. 6A). In addition to those same variables, confidence intervals did not overlap zero for horse density in the next competitive model, which included a random effect only for individual cougar (Fig. 6B). Marginal model coefficients from the top models indicated that cougar predation on horses was more likely than predation on other prey items as deer density decreased, horse density increased, at higher elevations, and was less likely to occur in forests than in sagebrush (reference category; Fig. 6).

Kill Rate

We estimated kill rates using a subset of 733 clusters where we confirmed kills during continuous monitoring of GPS-collared cougars. We calculated 58 mean season- and

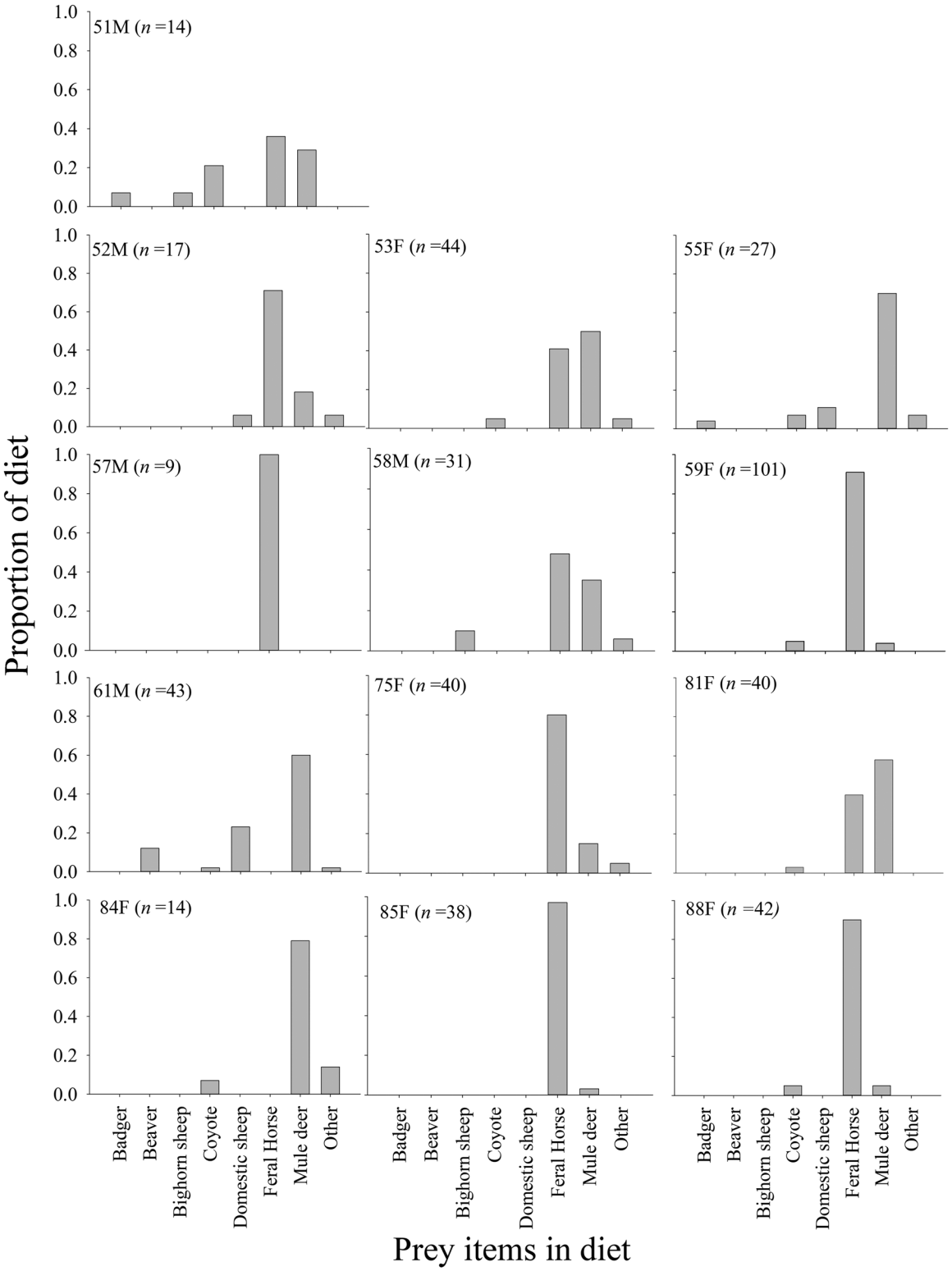


Figure 3. Proportional frequency of prey items in individual diets for 13 cougars fit with global positioning system-collars to evaluate prey composition during 2009–2012 in the western Great Basin, USA. Sex of individual cougars, male (M) and female (F), is indicated after individual cougar identifications. Sample sizes of kills by each individual cougar are indicated on each panel.

species-specific kill rates for individual cougars (Great Basin = 46; Sierra Nevada = 12). We did not calculate kill rate for 15 monitoring periods because monitoring was <28 days or <4 kills confirmed. In the Great Basin study area, monitoring times averaged 160 ± 31 days during summer and 115 ± 55 days during winter compared to 137 ± 52 days in summer and 113 ± 53 days in winter in the Sierra Nevada study area.

Annual average kill rates of deer differed between the Sierra Nevada and Great Basin study areas ($t_{9.6} = 1.69$,

Table 1. Seasonal comparisons of the proportional frequency of prey items in the diet of female and male cougars. We present results for individual prey types and condensed prey categories using data from 13 global positioning system-collared cougars (5 males, 8 females), western Great Basin mountain ranges in Nevada, USA, 2009–2012.

	Females		Males	
Prey type	Summer ($n = 214$)	Winter ($n = 132$)	Summer ($n = 74$)	Winter ($n = 40$)
Individual prey types				
Badger	0.47	0.00	1.35	0.00
Beaver	0.00	0.00	2.70	7.50
Bighorn sheep	0.00	0.00	1.35	7.50
Coyote	3.74	3.79	1.35	7.50
Domestic cattle	1.40	0.76	0.00	0.00
Domestic dog	0.47	0.00	1.35	0.00
Domestic sheep	0.93	0.76	14.86	0.00
Feral goat	0.00	1.52	0.00	0.00
Feral horse	66.82	68.18	47.30	15.00
Mule deer	26.17	24.24	28.38	57.50
Porcupine	0.00	0.00	0.00	2.50
Pronghorn	0.00	0.76	1.35	2.50
Condensed categories				
Horse	66.82	68.18	47.30	15.00
Mule deer	26.17	24.24	28.38	57.50
Other	7.01	7.59	24.31	27.50

$P < 0.001$). In the Sierra Nevada study area, the annual kill rate (not accounting for sex of cougar or season) was 0.85 ± 0.32 deer/week compared to 0.21 deer/week for cougars in the Great Basin. On average, cougars in the Great Basin killed 0.38 horses/week (Fig. 7). In both study areas, kill rates were variable among individuals (Sierra Nevada = 0.44–1.3 deer/week; Great Basin = 0.00–0.43 deer/week, and 0.00–0.94 horses/week). In the Great Basin study area, kill rates for mule deer did not vary seasonally between males and females (summer = $t_{9.9} = 1.19$, $P = 0.262$; winter: $t_{2.9} = -0.85$, $P = 0.4619$; Fig. 7). There was also no statistical difference in kill rates of horses between males ($\bar{x} = 0.32$ horses/week) and females during summer ($\bar{x} = 0.47$ horses/week; $t_{10.9} = 0.84$, $P = 0.42$; Fig. 7); however, female kill rates in winter were 16.6 times greater than winter kill rates for males (females: 0.50 ± 0.33 horses/week; males: 0.03 ± 0.05 horses/week, $t_{6.6} = 3.64$, $P = 0.009$; Fig. 7).

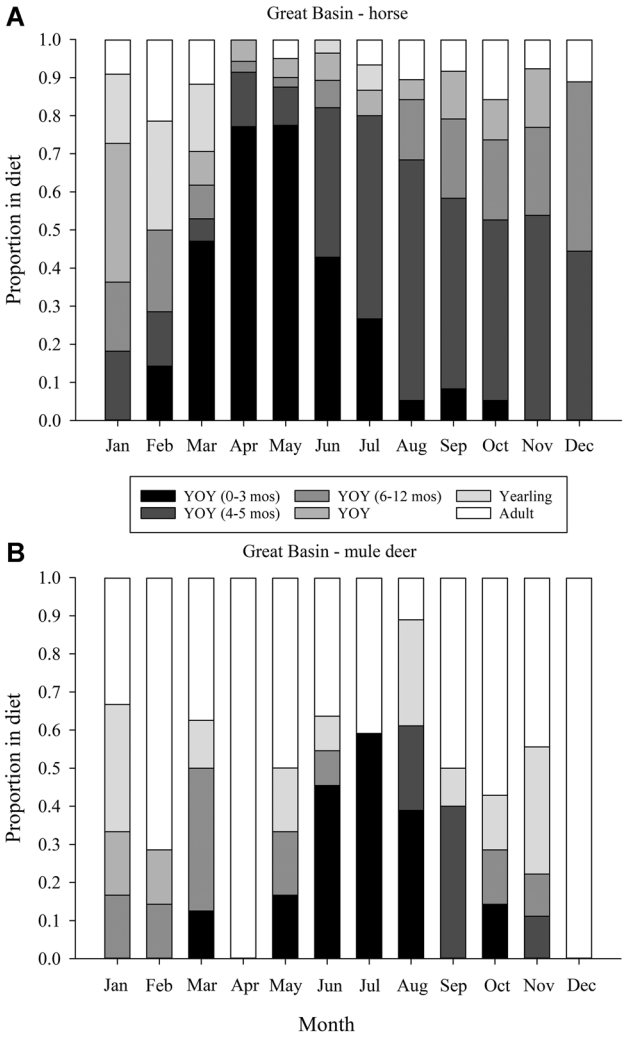


Figure 4. Proportion of age classes including adult, yearling (1 yr of age), and young of the year (YOY) of A) free-roaming feral horses and B) mule deer in the diets of 13 global positioning system-collared cougars in the Great Basin for which we studied prey composition and kill rates, western Great Basin, USA, 2009–2012.

DISCUSSION

Cougars, the most widely extant large carnivore in North America, readily integrated free-roaming horses, a locally abundant exotic species, into their diets in the Great Basin. The extent to which cougars overlapped herd areas and preyed on horses was greater than predicted given the prevailing view that, with a few exceptions, cougar predation on horses is considered to be uncommon, incidental, or opportunistic (Berger 1986, NRC 2013). Nevertheless, in the Great Basin, horses comprised the greatest proportion of cougar diets among prey species, whereas mule deer (typically considered the primary prey of Great Basin cougars) comprised less than a third of the diet. Indeed, some individuals of both sexes subsisted almost entirely on horses. Our results provide strong evidence that cougar predation on horses is partly the product of behavioral variation among individuals in addition to local environmental variability, including prey availability, prey density, elevation, and land cover.

Individual identification alone accounted for more than a third of the variation explained in the top models predicting probability of cougar predation on horses. Cougars are a generalist predator consuming a wide variety of prey (Ruth et al. 2019). There is mounting evidence, however, that within a species with a generalized dietary or habitat niche, specialization can occur, such that some individuals have diets that differ substantially from the population mean (Ross et al. 1997, Bolnick et al. 2003, Knopff and Boyce 2007, Elbroch et al. 2009, Wittmer et al. 2013, Lowrey et al. 2016). Our study provides additional support to the hypothesis that within a population, individual cougars differ in prey choice, particularly with respect to a prey species heretofore largely assumed to be invulnerable to cougar predation. Even in the Sierra Nevada, where only

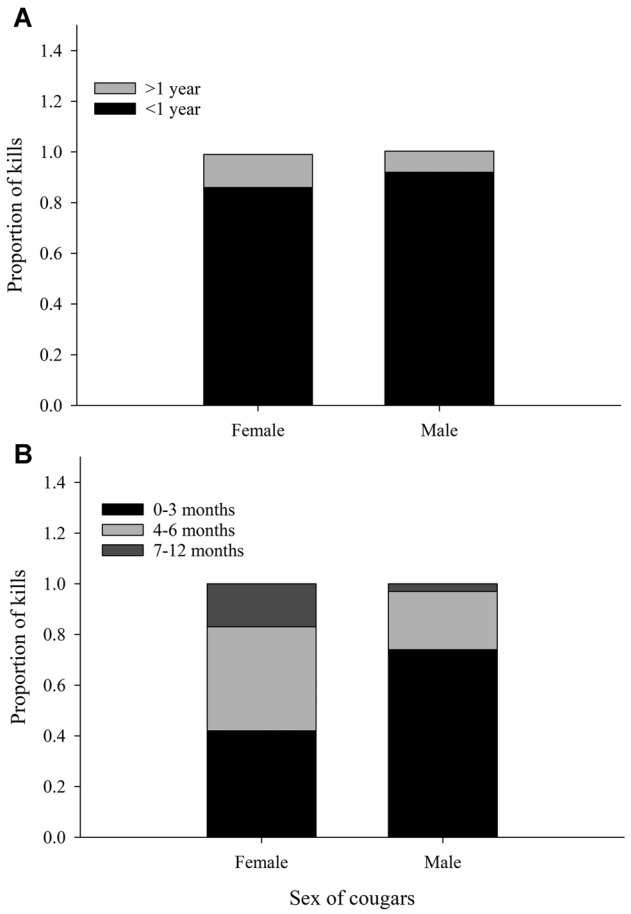


Figure 5. Proportion of free-roaming feral horses in known age classes killed by male ($n = 5$) and female ($n = 8$) cougars where horses were A) <1 year and >1 year and B) within the young of year category. We collected data from 13 global positioning system-collared cougars for which we studied diet composition, western Great Basin, USA, 2009–2012.

Table 2. Model selection results for the top 3 fixed effects models to predict predation on feral horses by cougars, western Great Basin, Nevada, USA, 2009–2012. We present log likelihood (logLik), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and AIC_c weights (w_i).

Model	logLik	AIC_c	ΔAIC_c	w_i
Mule deer density + horse density + land cover	−220.83	455.9	0.00	0.721
Mule deer density + horse density + land cover + elevation	−220.81	457.9	2.03	0.261
Mule deer density + horse density	−229.04	464.1	8.15	0.012

1 species of ungulate prey exists, individual variation in predation was evident; 1 cougar specialized on beavers. Behavioral variation among individuals has been suggested to be fundamental in allowing predation on novel prey to increase throughout a population (Bolnick et al. 2003, Carlsson et al. 2009). Such individual variation has likely facilitated the increase in cougar predation on horses throughout multiple mountain ranges varying in horse

Table 3. Model selection results from mixed effects generalized linear mixed models predicting predation on horses by cougars, western Nevada, USA, 2009–2012. Random effects included individual cougar identification (cougar) and mountain range (range). We present log likelihood (logLik), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and AIC_c weights (w_i).

Random effect	logLik	AIC_c	ΔAIC_c	w_i
Cougar + range	−180.2	380.9	0.00	0.548
Cougar	−181.5	381.3	0.38	0.452
Range	−214.4	447.2	66.3	0.000
Null	−220.8	457.9	77.0	0.000

densities within our Great Basin study area, which allowed cougars to take advantage of an abundant but novel prey source. Two male cougars dispersed long distances (~225 km, 180 km) continuing to prey on horses, even though horses were relatively less available than in the Virginia Range, where those cougars were originally captured (Fig. 2).

Probability of cougar predation on horses increased as horse density increased and mule deer decreased across the landscape. This result suggests that cougars, like other opportunistic predators, take advantage of novel prey when it is ubiquitous, especially if primary prey are less abundant (Novaro et al. 2000, Smith et al. 2000). Although native prey typically dominates the diets of cougars in North America, native ungulates comprise <50% of food items in cougar scats in South America (Murphy and Ruth 2009). In some areas of Patagonia, landscape change resulting from intense livestock grazing, introduced species, and overexploitation of native species has resulted in novel prey assemblages with <6% of overall biomass from species that were historically present. In those areas, entire assemblages of carnivores, including cougars have changed their diets to capitalize on these novel, abundant prey to such an extent that native prey have been regarded as ecologically extinct or no longer filling their role as prey (Novaro et al. 2000, Palacios et al. 2012).

We posit the question of whether free-roaming horses allow cougars to persist in portions of the Great Basin where they may not otherwise occur, or at least at densities not possible without horses (Pierce et al. 2000*a*). Cougar densities are already higher than historical levels because of habitat changes and historical expansion of mule deer across the Great Basin (Berger and Wehausen 1991). Effects of an increased number of cougars on predation rates on other prey species depend at least partly on the level of individual specialization within the cougar population; the greater the degree of generalist behavior within a cougar population, the more likely it is that apparent competition will ensue, which may affect the species of the smaller prey population (Knopff and Boyce 2007). Alternatively, horses may buffer predation on other species, such as mule deer or bighorn sheep, that would be consumed if horses were not present and abundant (Stoddart et al. 2001). For example, in 2011 bighorn sheep were reintroduced into the Virginia Range, but we recorded no predation on bighorn sheep; cougars in our study continued to focus predominantly on horses

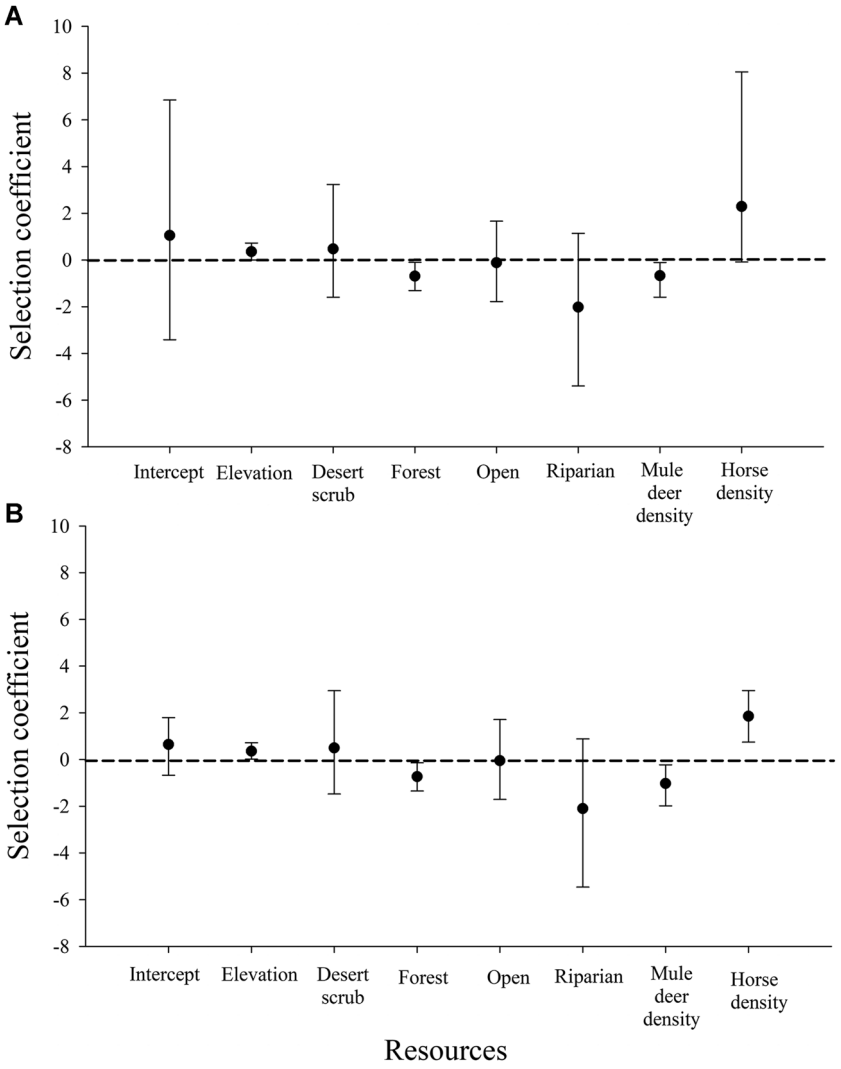


Figure 6. Parameter estimates and 95% confidence intervals for coefficients from the top 2 competitive generalized linear mixed models (A and B) predicting cougar predation on free-roaming feral horses. We collect data from 13 global positioning system-collared cougars for which we studied diet composition and predation on horses, western Great Basin, USA, 2009–2012.

despite extensive overlap with both ungulate species. The difference in predation rates on mule deer between the Sierra Nevada and Great Basin reinforces this idea in our ecosystem.

Contrary to our predictions, diets of females contained a greater proportion of horses than did males, and females preyed on horses year-round. In contrast, males capitalized on horses during spring and summer when young horses were abundant and vulnerable, and males switched from eating horses during spring and summer to primarily mule deer in autumn and winter. Female kill rates of horses were also considerably greater than that of males during autumn and winter. Those patterns contrast sharply with current literature, which generally reports that large prey species such as elk and moose are disproportionately preyed on by male cougars (Anderson and Lindzey 2003, Mattson 2007), with females capitalizing on juveniles of large prey species only during summer and typically to a lesser extent than males during this season (Knopff et al. 2010, White et al. 2011, Clark et al. 2014). Given this general rule and that predation on horses has previously been reported primarily on young <6 months old during summer (Turner et al. 1992, Greger and Romney 1999, Turner 2015), and horses are approximately equal in mass to elk and moose of the same age class (Knopff et al. 2010), it was particularly surprising that females continued to prey on horses year-round and males capitalized primarily on young. Similar to other large-bodied ungulates in the diets of cougars, including elk (Hornocker 1970, Mattson 2007) and moose (Ross and Jalkotzy 1996), horses tended to come from younger age classes than did mule deer. In the Great Basin, the proportion of horses in different age classes varied by season with a greater proportion >1-year-old horses killed during winter. This variation is because horse parturition occurs in early spring and by winter the youngest horses available are ≥7–10 months old. Young horses grow rapidly, attaining a median mass of 220 kg by 6–12 months old (Knopff et al. 2010). Risk of injury is thought to limit maximum prey size (Murphy and Ruth 2009), and female cougars often avoid large prey relative to males, presumably

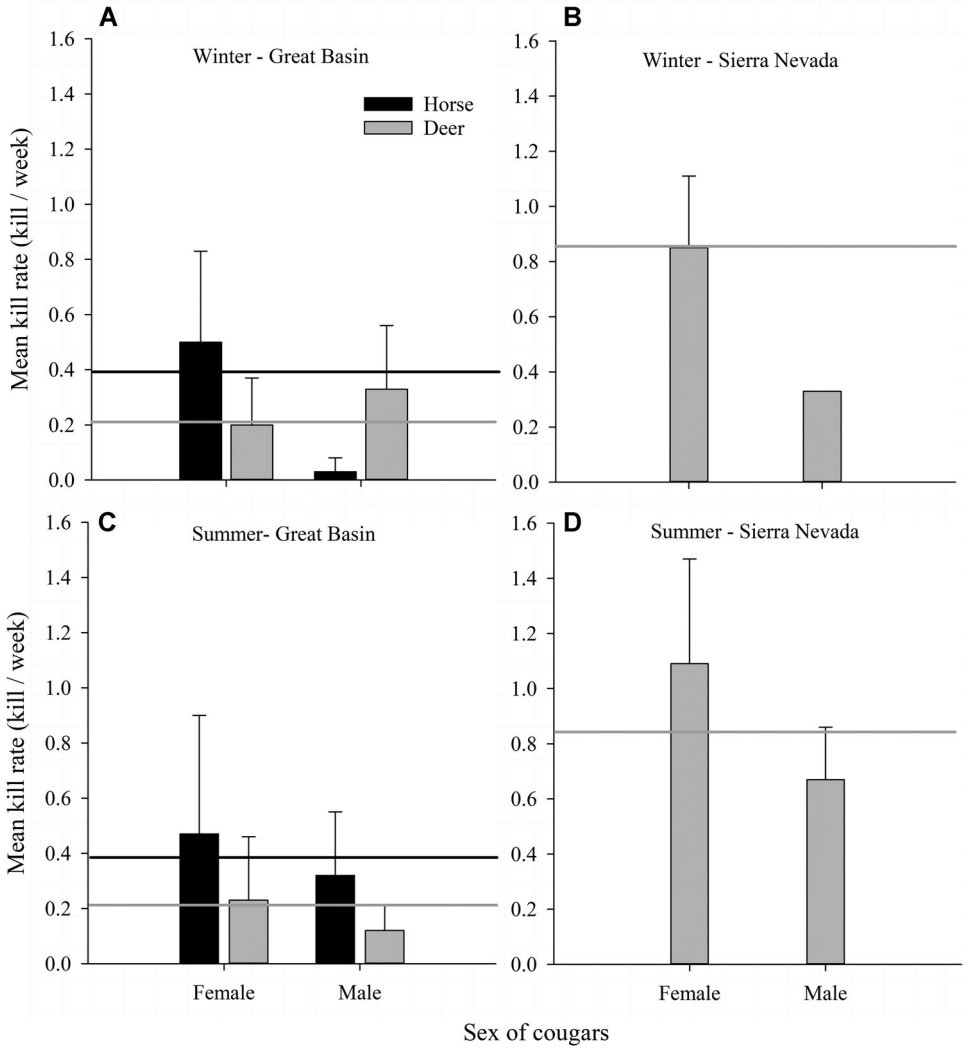


Figure 7. Mean seasonal cougar kill rates (kills/week) and 95% confidence intervals for free-ranging feral horses and mule deer during A) winter in the Great Basin, B) winter in the Sierra Nevada, C) summer in the Great Basin, and D) summer in the Sierra Nevada study areas where we monitored diet composition and kill rates of 21 global positioning system (GPS)-collared cougars during 2012–2012. Horizontal lines indicate the mean annual kill rate for horses (black) and mule deer (gray) in each study area. We collected data from 13 cougars in the Great Basin (8 females, 5 males) and 8 GPS collared cougars (6 females, 2 males) in the Sierra Nevada, USA.

to minimize risk of injury (Knopff et al. 2010, White et al. 2011, Clark et al. 2014) or minimize energy expenditure to capture large prey (Pierce et al. 2000*b*). Our data contradict this pattern because female cougars were the primary demographic preying on larger age classes of horses in this western Great Basin ecosystem. Moreover, males and females did not differ in proportions of diets composed of horses >1 year old, which weigh between 330–420 kg (Knopff et al. 2010) and approached the estimated maximum size of prey that cougars kill (Murphy and Ruth 2009). In arid landscapes with relatively low abundance of wild ungulate prey, the reward for killing large prey may be worth the elevated risk of injury. Horse populations above carrying capacity may also be malnourished with individuals that are less risky to predators than they would be otherwise; these topics deserve further attention.

Landcover type was an important predictor of probability of horse predation. In addition to body-size disparities, it has been hypothesized that horse populations are unaffected by cougar predation because most herd management areas are considered poor cougar habitat with few cougars (NRC 2013). Cougar abundance is correlated with high-elevation forested areas with broken topography and limited viewsheds (NRC 2013). Our results suggest that cougars were more likely to kill horses in mountainous terrain at relatively high elevation but significantly less often in forested areas compared to sagebrush landscapes. Cougars were thought to limit the growth of other high-elevation horse populations where pinion-juniper woodlands were reportedly predominant (Greger and Romney 1999, Turner and Morrison 2001). Although cougars are ambush predators, forest cover is not a requirement for successful stalking (Laundré and Hernández 2003, Pierce et al. 2004, Dickson et al. 2005) and cougars at times disproportionately kill prey in areas with little tree cover. In the Great Basin of California, cougars killed mule deer more frequently in areas

of low-lying shrubs and relatively open terrain compared to cover where deer foraged (Pierce et al. 2004). Open land cover types including grasslands (Dickson et al. 2005) have been suggested to provide an advantage to stalking cougars. In Utah, USA, relatively few kills were made in the forest (Laundré and Hernández 2003) where high tree density presumably inhibited the predator's view (Laing 1988 in Laundré and Hernández 2003). In addition to cover, unmeasured terrain variables may play an important role in where cougars kill horses. Cougars often killed horses near talus slopes or in flat open areas with rocky terrain in which horses may easily lose footing and facilitate successful capture (A. A. Andreasen, University of Nevada-Reno, unpublished data).

Given the opportunistic nature of cougars and because of our observed individual variation in habitat selection (Andreasen 2014), wide variation in land cover types where prey are typically killed (Iriarte et al. 1990, Murphy and Ruth 2009), extensive home range sizes in arid environments (Stoner et al. 2018), and dispersal routes through sparsely vegetated areas (Stoner et al. 2008, Elbroch et al. 2009), we reject the hypothesis that lack of spatial overlap is a main factor limiting the effects of cougar predation on horses, particularly in the Great Basin. Our data illustrated that cougars overlap a majority of the HMAs within our study area with predation on horses recorded within or adjacent to many of those. Many Nevada HMAs and Wild Horse and Burro Territories (USFS) occur in high-elevation forests with broken terrain—characteristics that define traditional cougar habitat in the Intermountain West. We suggest that predation by cougars on horses is little studied and mapping overlap between predicted cougar occurrence and HMAs would be a good first step for future research to identify areas where cougar predation on horses may be likely to occur.

Predation can limit population growth rates, including those of novel or exotic prey (Terborgh et al. 2001, Carlsson et al. 2009). Cougar predation is thought to have limited the growth of 2 horse populations at least during some periods (Greger and Romney 1999, Turner and Morrison 2001). Relatively small ungulate populations, including horses, are more susceptible to limitation by cougar predation, particularly if additional ungulate prey are available to maintain cougar populations, despite decline of other prey species (Messier 1994, Johnson et al. 2013). The 2 horse populations noted previously were relatively small when cougars were effectively limiting growth rates (<200 horses; Greger and Romney 1999, Turner and Morrison 2001, Turner 2015)—substantially smaller than the ones studied here (e.g., Virginia Range had an estimated 1,500 horses). We also documented predation in populations of <200 horses, but we do not have the necessary data to determine how cougar predation limits or regulates those smaller populations.

Because juveniles of large-bodied ungulates are preyed on more than reproductive age classes, it has been suggested that cougars may have only weak limiting effects on large species (e.g., elk, moose, horses; Ruth and Murphy 2009). For instance, although cougars killed ≤30% of moose calves, this was thought to be primarily compensatory because those population densities likely were close to carrying capacity (Ross and Jalkotzy 1996). If cougar predation affects horse populations, it is likely through reducing survival and recruitment of young (Greger and Romney 1999, Turner and Morrison 2001), thereby reducing population growth rate. Thus, cougar predation may be additive to other sources of mortality for small populations of ungulate prey where populations are below carrying capacity, particularly where secondary prey are available (Johnson et al. 2013). In 1 instance where survival of young was highly suspected of being influenced by cougar predation, a decrease in the number of cougars resulted in increased survival of young the following year (Roelle et al. 2010).

Our results suggest that individual cougars vary in probability of preying on horses, but some individuals are capable of preying successfully on both adult horses and young. Removal of these specialist cougars that overlap small horse populations could influence subsequent growth rates of horses as found for other species with small, isolated populations such as bighorn sheep or mountain caribou (Ross et al. 1997, Ernest et al. 2002, Katnik 2002, Festa-Bianchet et al. 2006). We would suggest, however, that cougar predation is likely not a primary factor limiting growth of horse populations at range-wide scales. Currently, limited information on how predation on horses may affect smaller horse populations or other prey implies that further research is warranted.

MANAGEMENT IMPLICATIONS

Our estimates of diet composition and kill rates of cougars, including findings pertaining to the influence of season, sex of cougar, and vulnerability of horses in different age classes, can be applied to better anticipate cougar-prey dynamics where free-roaming horses occur. Results pertaining to differences in cougar kill rates of mule deer in areas where horses are available may result in a better understanding of the effects of cougar predation on mule deer populations in areas where alternative prey are available. Our results also have applications for predator management programs because removal of specialist cougars that overlap with small horse populations can influence subsequent population growth rates of horses. Moreover, population-level predator control to reduce cougar predation on native ungulates, where there is individual variation in cougar diets and specialist cougars occur, may not produce the desired outcome because removal of cougars that specialize on feral horses will not reduce predation on native species. The alternative is also true, in that leaving cougar population structure in place by limiting human-harvest of cougars in areas where individual cougars have specialized on horses, may be a useful management tool at small scales and for small horse populations, an idea worth further consideration. Cougars that specialize on feral horses may have some effect on slowing population growth of horses, especially in small populations, and may act as a form of natural population control to aid in management of feral horses. Therefore, when aiming to reduce predation on native ungulates,

predator control that does not target specific individuals, which would require monitoring of cougars prior to removal efforts to identify specialists, may result in the loss of some measure of population control of feral horses.

ACKNOWLEDGMENTS

The views and conclusions in this article represent the views solely of the authors and do not represent the position of any agency or organization. We thank S. Shea, E. Dalen, J. Willers, R. G. Seidler, K. J. Sivy, C. W. Lackey, F. L. Andreasen, L. Johnson, D. S. Thain, and D. Beronio for assisting in capturing cougars and collecting data at kill site locations. We thank C. A. Schroeder for providing mule deer estimates, and J. Axtell and M. E. Gray for helping to provide estimates of horse populations. We thank K. T. Shoemaker for helpful discussions regarding statistical analyses. We thank biologists and wardens at the NDOW for logistical support. Funding was provided by University of Nevada Reno Agricultural Experiment Station, Wildlife Conservation Society, Nevada Bighorns Unlimited—Reno chapter, Carson Valley Chukar Club, Northern Nevada Chapter of Safari Club International, Nevada Wildlife Record Book, Shepreth Wildlife Park, Nevada Wildlife Heritage Trust, and Nevada Division of State Lands-Lake Tahoe License Plate Grant. The Natural Resources and Environmental Science department, the Biology department, the Graduate Student Association, and the program in Ecology, Evolution and Conservation Biology at the University of Nevada, Reno also provided funding.

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Associate Editor: Kathryn Schoenecker.

Monitoring Feral Horse and Burro Impacts on Habitat
Sheldon National Wildlife Refuge, 2002

by Jenny Barnett, Refuge Biologist

November 2002

INTRODUCTION

Feral horse and burro populations on Sheldon National Wildlife Refuge (refuge) are increasing. Recent work by Refuge staff suggests the population is increasing at a rate of 17% per year. The Sheldon Renewable Natural Resources Management Plan of 1980 provided for maintaining a herd of 75-125 horses and a herd of 15-35 burros on the refuge. (For the remainder of this report, the term "horses" will refer to both feral horses and feral burros). Despite the fact mechanized equipment could not be used to gather horses on the refuge (helicopter authority was granted in fall 2001), gather and removal programs kept horse numbers near the management objectives through the 1980s. However, gathers ended in 1993 due to retirement of the long-term contractor and loss of funds for horse removal. Prior to 1994, funding for horse gathers came from livestock grazing receipts (6860 funds). When cattle grazing ended, so did funding for horse removal. Those funds have not been replaced. In 1999, the refuge received funding for horse gathers through the 1999 Badger Fire Burned Area Emergency Rehabilitation Plan. Almost 280 horses were removed from the Badger Mountain area since 1999, but his one-time funding source ended in October 2002. The cost of gathering horses has gone up 10-fold since 1993 due to retirement of the long-term contractor and current refuge requirements that gathered horses be fostered for life and not sold at auction. Horse removal is currently identified as the top priority project for funding in the Refuge Operations Needs System for the Sheldon-Hart Mountain National Wildlife Refuge Complex.

As horse populations grew, managers began noticing impacts and receiving complaints from the public, but no attempt was made to monitor horse impacts on wildlife habitat until 2001 when a monitoring program was started to determine the magnitude and extent of impacts across the refuge. In addition, systematic flights to track horse numbers and distribution were reinstated for the first time since 1994. In November 1993 biologists counted 237 horses in systematic flights over the refuge. The current population is estimated to be over 1000 horses and 200 burros. Data collected will also provide a baseline for future monitoring efforts and help managers prioritize areas for future gathers.

The habitat monitoring program consisted of three parts; 1) an overview of utilization in uplands in selected areas used by horses, 2) an overview of utilization on riparian areas across the refuge, and 3) intensive monitoring on selected riparian areas.

Areas known to have a relative concentration of horses were selected for upland monitoring. Monitoring was planned for subsequent years with more use areas to be added if needed. The objective of the riparian overview was to determine the extent and degree of utilization across the refuge. Each year a random set of stream reaches was selected for monitoring. The objective of the intensive riparian monitoring was to track stream reaches with moderate to severe

utilization over several years. Consistent heavy use over a number of years can damage riparian areas, therefore the intent was to monitor these reaches annually to determine if impacts continue.

This report deals primarily with data collected in 2002, the second year of the program. Some comparisons between impacts in 2001 and 2002 are made and minor changes in methodology are discussed.

METHODS

Upland:
Patterns of utilization on the uplands were mapped using the Key Forage Plant Method (BLM 1984). Three primary horse use areas were identified: Round Mountain, Fish Creek/Catnip, and Badger. Utilization was measured in July, the end of the growing season. Utilization was placed into one of 6 classes (Table 1) following Bureau of Land Management methods (BLM 1984).

Table 1. Utilization classes used for horse monitoring on Sheldon National Wildlife Refuge.

Class	Use	Description
1	No use (0-5%)	The rangeland shows no evidence of grazing use; or the rangeland has the appearance of negligible grazing.
2	Slight (6-20%)	The rangeland has the appearance of very light grazing. The key herbaceous forage plants may be topped or slightly used. Current seedstalks and young plants of key species are little disturbed.
3	Light (21-40%)	The rangeland may be topped, skimmed, or grazed in patches. The low value herbaceous plants are ungrazed and 60 to 80 percent of the number of current seedstalks of key herbaceous pants remain intact. Most young plants are undamaged.
4	Moderate (41-60%)	The rangeland appears entirely covered as uniformly as natural features and facilities will allow. Fifteen to 25 percent of the number of current seedstalks of key herbaceous species remain intact. No more than 10 percent of the number of low value herbaceous forage plants are utilized.
5	Heavy (61-80%)	The rangeland has the appearance of complete search. Key herbaceous species are almost completely utilized with less than 10 percent of the current seedstalks remaining. Shoots of rhizomatous grasses are missing. More than 10 percent of the number of low value herbaceous forage plants have been utilized.
6	Severe (81-100%)	The rangeland has a mown appearance and there are indications of repeated coverage. There is no evidence of reproduction or current seedstalks of key herbaceous species. Key herbaceous forage species are completely utilized. The remaining stubble of preferred grasses is grazed to the soil surface.

Roads within the use area were driven at a slow pace while observers surveyed key grasses and estimated utilization. Transects were run to quantify utilization. Transects were run whenever a change in utilization class was noticed or every 1 to 2 miles. Observers paced the transect taking care **not** to watch placement of the feet. Every 5 steps, utilization on the nearest plant of each key grass species in front of the observer was estimated. Ten plants of each key species were sampled at each transect.

Grasses were selected to be key species because they were widely available in the plant community in good ecological condition or they were suspected to be utilized by horses. Idaho fescue (*Festuca idahoensis*), needlegrass (*Stipa* spp.), squirreltail (*Sitanion hystrix*), basin wild-rye (*Elymus cinereus*) and bluebunch wheatgrass (*Agropyron spicatum*) were identified as potential key species. The goal was to estimate utilization on the 2 key species most prevalent on each transect. In addition to monitoring horse use from roads in primary use areas, 5 transects were run away from roads in areas refuge staff have consistently seen horses or concern about horse use has been expressed.

Riparian Overview:
Stream reaches identified by refuge biologists in 1990 for a riparian classification program were used. Streams were divided based on similar stream morphology and habitat types. For horse monitoring, reaches serve as a consistent way to break long streams into smaller sections for evaluation. Using topo maps, reaches were checked for vehicle access (within ½ of a road). Only reaches that had vehicle access were used. A sample of 20 reaches was drawn at random. Approximately ½ mile of each reach was walked in September. This was different from 2001 when reaches were walked in May, August and October. The change was made because utilization increased through summer 2001 and the ultimate management concern is the utilization levels at the end of the growing season. Observers classified utilization levels on the riparian vegetation into one of three broad categories. Utilization categories in Table 1 were combined as follows: no use/slight (classes 1-2), light/moderate (classes 3-4), and heavy/severe (classes 5-6). Notes on riparian values present, water flow (perennial, intermittent, dry), and accessability of the reach to horses were recorded. Water flow categories were defined as 1) perennial - water present throughout entire reach, 2) intermittent - water present in portions of the reach and 3) dry - no water present in reach.

Twenty springs were also sampled in 2002. They were randomly selected from all springs within ½ mile of a road. Methods were identical to those used for stream reaches. In most cases, the spring and its drainage were shorter than ½ mile, so the entire system was assessed.

Intensive Riparian:
Eight riparian reaches where refuge staff noticed moderate to heavy horse use were monitored intensively (intensive plots). Five were established last year and 3 were added this year. A

utilization cage was placed on the reach near the beginning of the growing season. The cage protected an area 1.5 m^2 from grazing and provided a reference to vegetation height without grazing. Photos were taken when the cage was placed on the stream and when stubble height data were collected. Stubble height was measured in September. Observers walked along the greenline and, every 3 steps, measured the height of the plant closest to their toe. Care was taken not to watch placement of the feet. Fifty plants were measured on each transect. Average height of vegetation within the utilization cage was estimated as well. This is different from 2001 when stubble height was estimated in 25, 10.2 x 10.2 cm frames.

In July, trend plots were established on the 8 intensive plots. Plant frequency, bare ground, and hoof prints were quantified on permanent transects. Three, 20-m transects were established near the greenline (only 2 transects were set on West Catnip Spring and 10-Mile Spring because the drainages were not long enough for 3). Transect ends were marked with rebar and GPS'd. UTM coordinates for each transect are shown in Appendix C. A tape was stretched along the transect and a sampling frame was placed at every meter, starting with 0, for 20 frames per transect. The frame was 40 x 50 cm (large frame) with a 10 x 10 cm square in one corner (small frame). Plant frequency was recorded in the small frame. To provide an index of soil displacement events (pock marks), the number of hoof prints that broke through the soil were counted in the large frame, including those partially out of the frame. Cover of vegetation and bare ground was recorded at the 4 corners of the large frame.

RESULTS and DISCUSSION

Upland:

Figures 1 through 3 show utilization pattern maps for each area. Utilization ranged from no use to light on all the use areas except 1 portion of the Badger area with moderate utilization. Utilization on the 5 transects run away from roads was classified as light (1), moderate (3), and heavy (1). Holechek et al. (1998) report that grazing intensity of moderate levels throughout the year maintained plant productivity while heavy utilization, even for only one year, harmed grasses. BLM follows a standard 50% utilization in uplands as the division between proper and improper use. However, in areas with specific resource concerns, such as sage grouse or other wildlife, BLM is increasingly managing for light use or less (T. deValois, Range Conservationist, BLM, pers.comm.).

Utilization of the uplands was generally slight and was within allowable levels using BLM standards. Utilization on riparian reaches was more of a concern. Riparian areas are likely to be severely impacted by horses before utilization on upland exceeds moderate levels. In fact, Surprise Field Office, BLM is now basing feral horse gathers on impacts to riparian areas (T. deValois, pers comm.).

Riparian

Overview:

Twenty stream reaches and 16 springs were monitored in 2002 (Figure 4). Percentage of reaches that fell into each broad use category were as follows: 33% - no to slight use, 22% - light to moderate use; 44% heavy to severe use (Table 2). Only reaches that had no access for horses or were dry had no or slight use. Springs were utilized particularly hard: 8 of the 10 that had water and horse access were used heavily to severely. Only 2 perennial stream reaches had slight use. Catnip 1-5 and Cottonwood 2-2 run through narrow, straight-sided canyons. Although there was some horse sign (trails and droppings) in the canyons, it was considerably less than most reaches and utilization in the canyons was not noticeable. Utilization was heavy to severe in adjacent, open reaches. Horses prefer open areas where they can see long distances (M. Bennett, J. Wagner, pc).

Eight stream reaches were visited in both 2001 and 2002. Utilization was similar both years, with 6 reaches (75%) classed in the same category both years (Table 3). Three of them had heavy to severe use, suggesting repeated impacts.

Intensive:

In 2002, two springs and one stream reach were added to the 5 reaches intensively monitored in 2001. Stubble heights ranged from 4 to 12 cm on the reaches and 20 to 50 cm in the cages (Table 4). Photos of the reaches, with utilization cages as a reference to use, are in Appendix 2.

Trend Plots:

In July, trend plots were established on intensive plots in order to provide baseline information. Data were collected on plant frequency, bare ground, and hoof prints. Bare ground and hoof prints, coupled with data on utilization and stubble height, can help describe the degree of horse impacts in a given year. Lower levels of bare ground and hoof prints, along with higher stubble heights mean fewer impacts. Changes in plant community composition can be tracked over the long-term using plant frequency. Increases in rushes and sedges, and decreases in forbs indicate increasing conditions while the opposite indicates decreasing condition. Percent bare ground and density of hoof prints are reported in Table 5. Plant frequency by plot is reported in Appendix C.

General Riparian Discussion:

Riparian areas are a small fraction of the habitats on the refuge but more wildlife species are associated with them than with uplands (Kauffman et al. 2001). They provide habitat for over 80% of the wildlife species in eastern Oregon (Elmore and Beschta 1987). Riparian areas provide other important functions including storing and discharging ground water (Elmore and Beschta 1987). Riparian areas on Sheldon are degraded. The Sheldon Scientific Working Group stated riparian areas were the most critical wildlife habitats on the refuge and should receive highest priority for rehabilitation and restoration. They further stated that livestock grazing was the primary cause for their poor condition and recommended no grazing by livestock, feral horses and feral burros until the habitats were restored (Davis 1995).

Overgrazing of riparian plants can have several consequences including reduced vigor or loss of the plants. This in turn can lead to compaction of floodplain soils, increased erosion, entrenchment and instability of stream banks, lowered water tables and expanded cover by upland plants (Clary and Webster 1989, Pyle and Brown 1990). Presence of healthy riparian plants such as sedges, rushes, and willows is important because these plants have strong root systems that hold soil in place during high flows. Riparian plants also trap sediment which allows bank building and channel narrowing, important aspects of riparian system recovery.

The trend plots established this year were designed to see if conditions of the riparian areas changes. Data collected this year were a baseline from which to start. An increase in bare ground and a decrease in riparian plants such as rushes and sedges indicate decreasing riparian condition while the opposite would be indicative of increasing condition. The density of hoof prints provides an index of soil disturbance, which makes the system more vulnerable to erosion. Data on percent bare ground and hoof prints should be collected every year and can be coupled with utilization and stubble height to quantify degree of impacts on an annual basis. Plant frequency data should be collected every 3 years to see if the plant community changes. Trend plots could continue to be read after horse removal to track and document riparian recovery.

Much of the material referenced in this discussion refers to proper management of livestock grazing in order to prevent damage to riparian areas. Although Sheldon has no cattle grazing, the consequences of over-grazing are the same regardless of the class of animal.

Clary and Webster (1989) present guidelines for livestock grazing geared toward protecting or improving riparian areas. They maintain that the utilization level is the most important aspect. Their recommendations include 1) utilization of herbaceous plants should not exceed 40 to 50% (moderate) during summer grazing, 2) fall use should not exceed 30% utilization (light), 3) season-long grazing should be limited to situations where animal use and distribution can be carefully controlled and stubble height requirements can be met. Season-long grazing is particularly harmful and is a primary cause of degraded riparian areas (Kinch 1989). Properly designed grazing systems also leave sufficient vegetation or provide for regrowth for maintenance of plant vigor and streambank protection (Clary and Webster 1989). Minimum stubble heights of 10 cm have been recommended by Clary and Leininger (2000) as a starting point for a riparian grazing system. Forty-four of the systems monitored this year received heavy to severe use while 22% received light or moderate use. Five of the 8 intensive plots had heavy to severe use and only 1 had adequate stubble heights in September. Feral horse use on Sheldon does not meet guidelines for riparian protection.

Results of the overview and intensive riparian monitoring suggest horse use on riparian areas continues to be too high. Distribution of feral horses is not managed and they use riparian areas season-long, the most damaging grazing regime. Heavy use at one point in time does not necessarily lead to resource damage. However, repeated heavy use does damage riparian areas (J. Hamby pc). Intensive plots were used heavily to severely both years, and only one met stubble height standards. High impacts to riparian areas are likely to continue until the horse

population is reduced. With the herd increasing at a rate of 17% per year, impacts can be expected in intensify if the population is not controlled. Intensive monitoring on these same reaches should continue. Trend plots should be reread to determine trend in heavily used riparian areas. Overview monitoring of randomly selected reaches should also continue to give managers a better picture of the pattern of horse use in riparian areas across the refuge and help prioritize areas for gathers.

RECOMMENDED GATHER PRIORITIES

Refuge Operations Specialist, Marla Bennett, and I met to prioritize areas for horse gather. Our top three areas are: 1) Big Spring Reservoir, 2) Catnip Reservoir/Round Mountain, and 3) Fish Creek Table. Figure 5 shows horse distribution and group size from the September 2002 flight. Figure 6 shows utilization on stream reaches and springs in September 2002.

Big Spring Reservoir is our highest priority due to use on Big Spring Creek and the poor conditions of the uplands surrounding Big Spring Reservoir. Big Spring Creek was severely used in 2001 and 2002 and has evident bank trampling. The creek is in better condition than Catnip Creek and Fish Creek, which both show signs of past heavy use. Catnip Creek and Fish Creek are downcut and dominated by *Juncus* spp. or *Eleocharis* spp. Big Spring Creek is not downcut, and the entire meadow is wetted by the high water table in the upper 3/4 mile of the creek. It is currently dominated by Nebraska sedge, which has excellent soil holding capabilities. We believe the grazing pressure should be removed from Big Spring Creek to prevent damage to the riparian system. Also, the uplands are characterized by Wyoming big sagebrush with little grass in the understory. Numerous horse trails are evident in the upland area north of the reservoir, but grass plants are lacking.

Catnip Reservoir/Round Mountain is our second priority due to horse impacts on Catnip Creek, the meadow east of Catnip Reservoir, and the uplands between Catnip Reservoir and Round Mountain. Catnip Canyon Creek is also used severely, but it shows signs of past damage. The creek downcut years ago and the wetted meadow is restricted to the area immediately adjacent to the stream channel. Large portions of the meadow east of Catnip Reservoir have already been impacted by the down cut channel. Horse trails are obvious in the uplands, especially on Round Mountain, but they support much more grass then the uplands surrounding Big Spring Reservoir and can withstand more grazing pressure.

Our third priority is Fish Creek Table, including Fish Creek. Like Catnip Creek, Fish Creek is severely utilized by horses, but shows signs of past damage due to livestock grazing. The channel is down cut and the wetted meadow restricted to the area adjacent the channel.

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Table 2. Utilization classification of 20 stream reaches and 16 springs on Sheldon National Wildlife Refuge, evaluated in September 2002.

Stream Reach	Use Class	Access		Spring	Use Class	Access
Perennial Reaches				***Water Present***		
Big Spring 1-1	5/6	Y		Bateman	1/2	N (fenced)
Catnip 1-5	1/2	Y?		Beebe	5/6	Y
Catnip (South) 2-1	3/4	Y		Cold	3/4	Y
Catnip (South) 2-2	5/6	Y		Corral	5/6	Y
Catnip (South) 2-4	5/6	Y		Cottonwood	5/6	Y
Catnip (North) 3-1	5/6	Y		Five-mile	5/6	Y
Cottonwood 2-2	1/2	Y?		Mud	5/6	Y
Cottonwood 3-3	5/6	Y		Murdock	5/6	Y
Cottonwood 4-4	5/6	Y		Warm	1/2	N
Hell 3-7	3/4	Y		West Catnip	5/6	Y
Hell 4-8	3/4	Y		West Rock	1/2	N (fenced)
Horse Canyon 4-11	3/4	Y		West Trough	5/6	Y
Intermittent Reaches				Willow	1/2	Y
Big Spring 3-5	1/2	N		***Dry Springs***		
Catnip Canyon 5-3	5/6	Y		Badger Flat	1/2	Y
Catnip Canyon 5-5	5/6	Y		Harriman Camp	1/2	Y
Horse Canyon 4-8	3/4	Y		Last Chance	1/2	Y
Thousand 1-2	1/2	N				
Virgin 2-7	3/4	Y				
Dry Reaches						
Virgin 1-2	3/4	Y				
Virgin 1-3	1/2	Y				

Table 3. Comparison of utilization levels on stream reaches monitored October 2001 and September 2002, Sheldon National Wildlife Refuge.

	Utilization Class			Utilization Class	
Reach	2001	2002	Reach	2001	2002
Big Spring 1-1	5/6	5/6	Hell 3-7	3/4	3/4
Catnip (South) 2-1	3/4	3/4	Catnip Canyon 5-5	5/6	5/6
Catnip (South) 2-2	5/6	3/4	Horse Canyon 4-8	3/4	3/4
Catnip (South) 2-4	5/6	5/6	Virgin 1-2	3/4	1/2

Table 4. Stubble height of riparian vegetation on intensively monitored stream reaches and springs, Sheldon NWR, September 2002.

	2002			2001		
Reach	**Avg Stubble Ht (cm)**	**Caged Veg Ht (cm)**	**Use Class**	Avg Stubble Ht (cm)	Caged Veg Ht (cm)	Use Class
Big Spring 1-1	**4**	**35**	**5/6**	5	>30	5/6
Fish Creek 2-2	**7**	**29**	**5/6**	5	20	5/6
Hell Creek 3-7	**12**	**43**	**3/4**	8	>30	3/4
Catnip Canyon 5-3	**6**	**24**	**5/6**	3	11	5/6
West Catnip Spring	**5**	**44**	**5/6**	3	15	56
Horse Canyon Spring	**9**	**27**	**3/4**	n/a	n/a	n/a
Jackass Drainage	**6**	**20**	**3/4**	n/a	n/a	n/a
10-Mile Spring	**4**	**50**	**5/6**	n/a	n/a	n/a

Table 5. Percent bare ground and density of hoof prints from 8 intensive riparian plots, July 2002, Sheldon National Wildlife Refuge.

Reach	Horse Hoof Prints per m^2	% Bare Ground
Big Spring 1-1	2.8	9
Catnip Canyon 5-3	1.9	20
Fish Creek 2-2	5.9	24
Horse Canyon Spring	0.7	15
Jackass Drainage	1.5	3
North Hell 3-7	2.0	2
Ten-mile Spring	8.0	36
West Catnip Spring	3.9	23

Figure 1. Horse Utilization in Uplands on Round Mountain Area, Sheldon National Wildlife Refuge, July 2002.

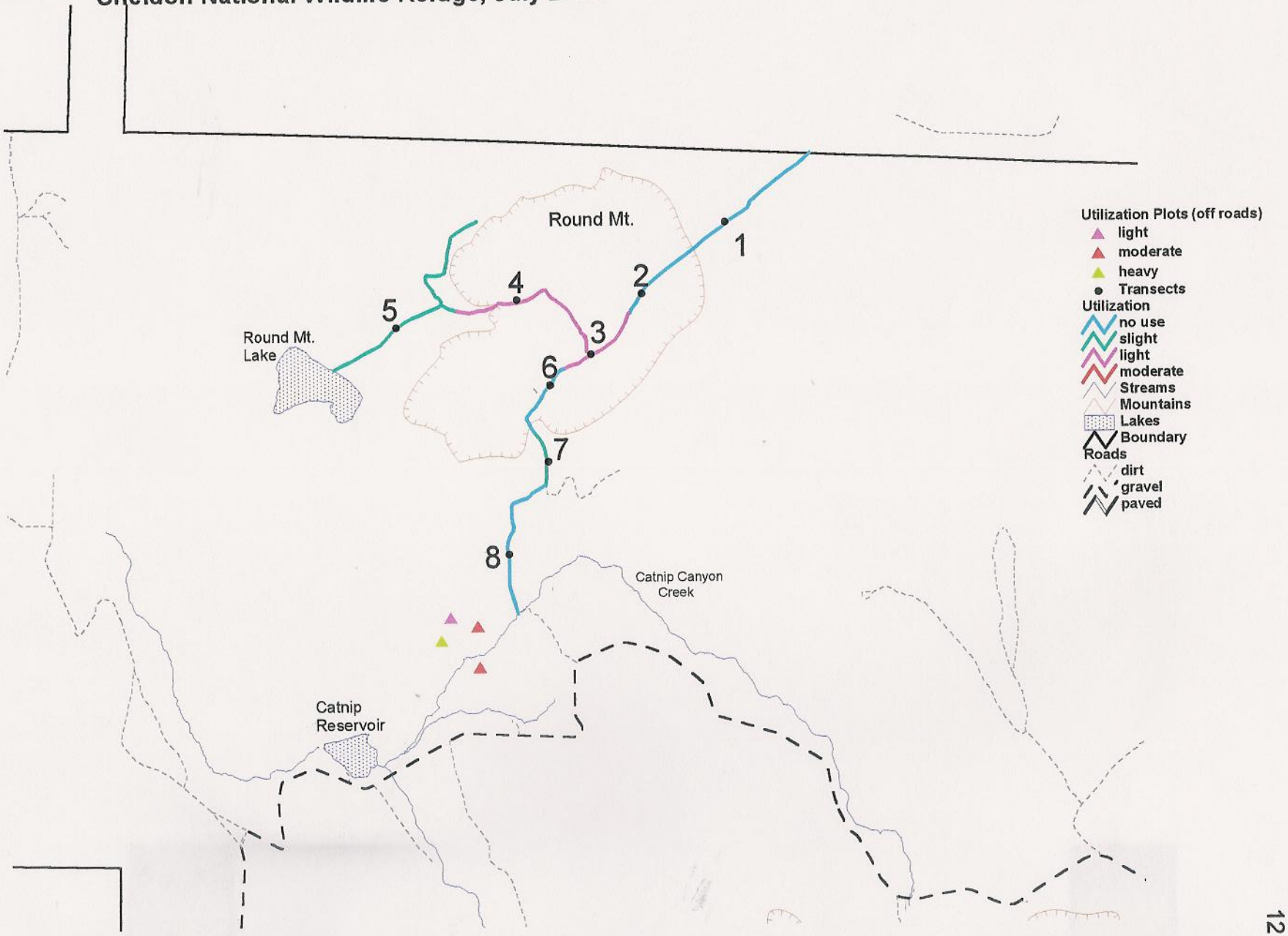


Figure 2. Horse Utilization in Uplands in the Fish Creek/Catnip Mountain Area, Sheldon National Wildlife Refuge, July 2002.

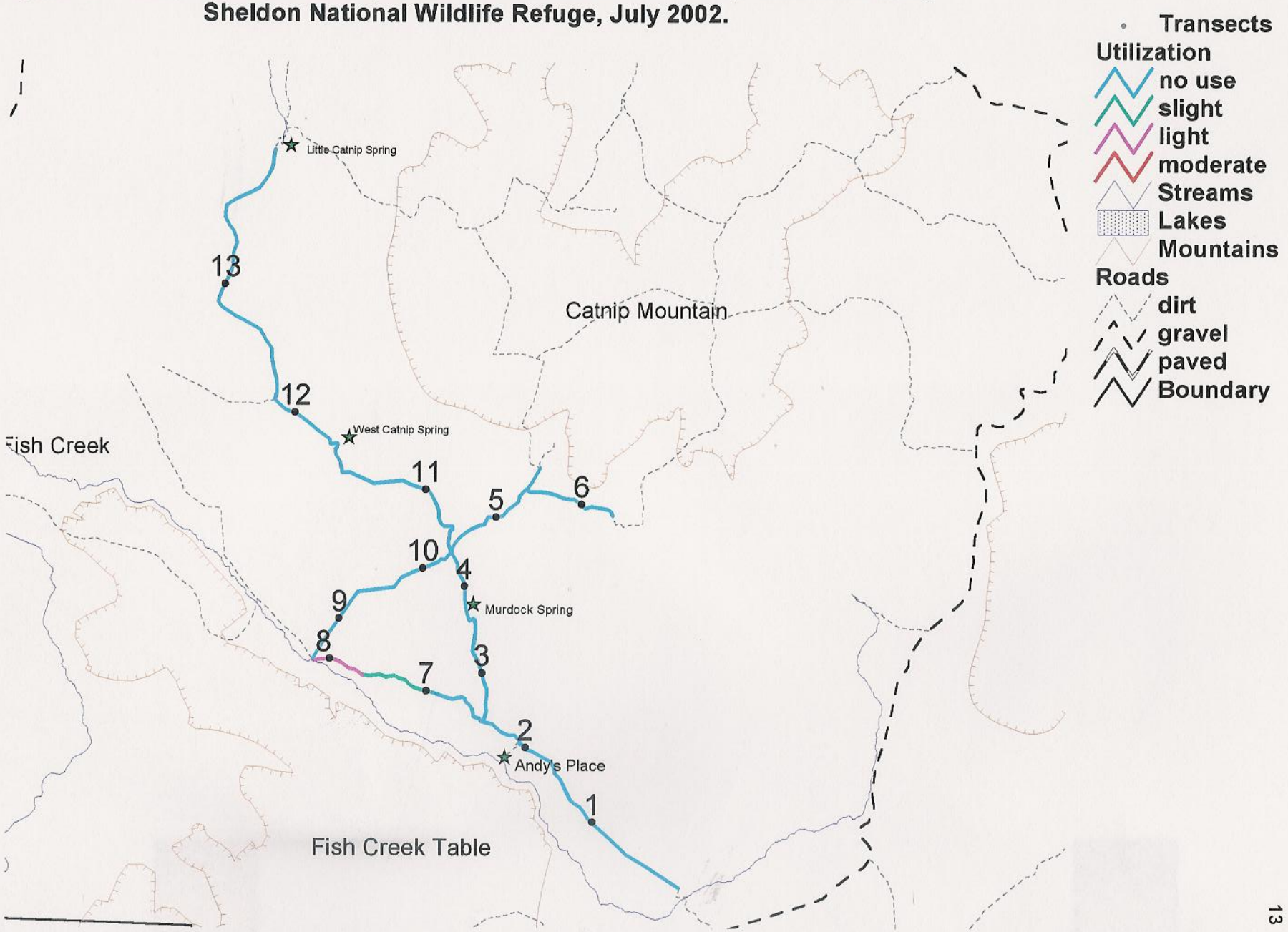


Figure 3. Horse Utilization in Uplands of Badger Area, Sheldon National Wildlife Refuge, July 2002

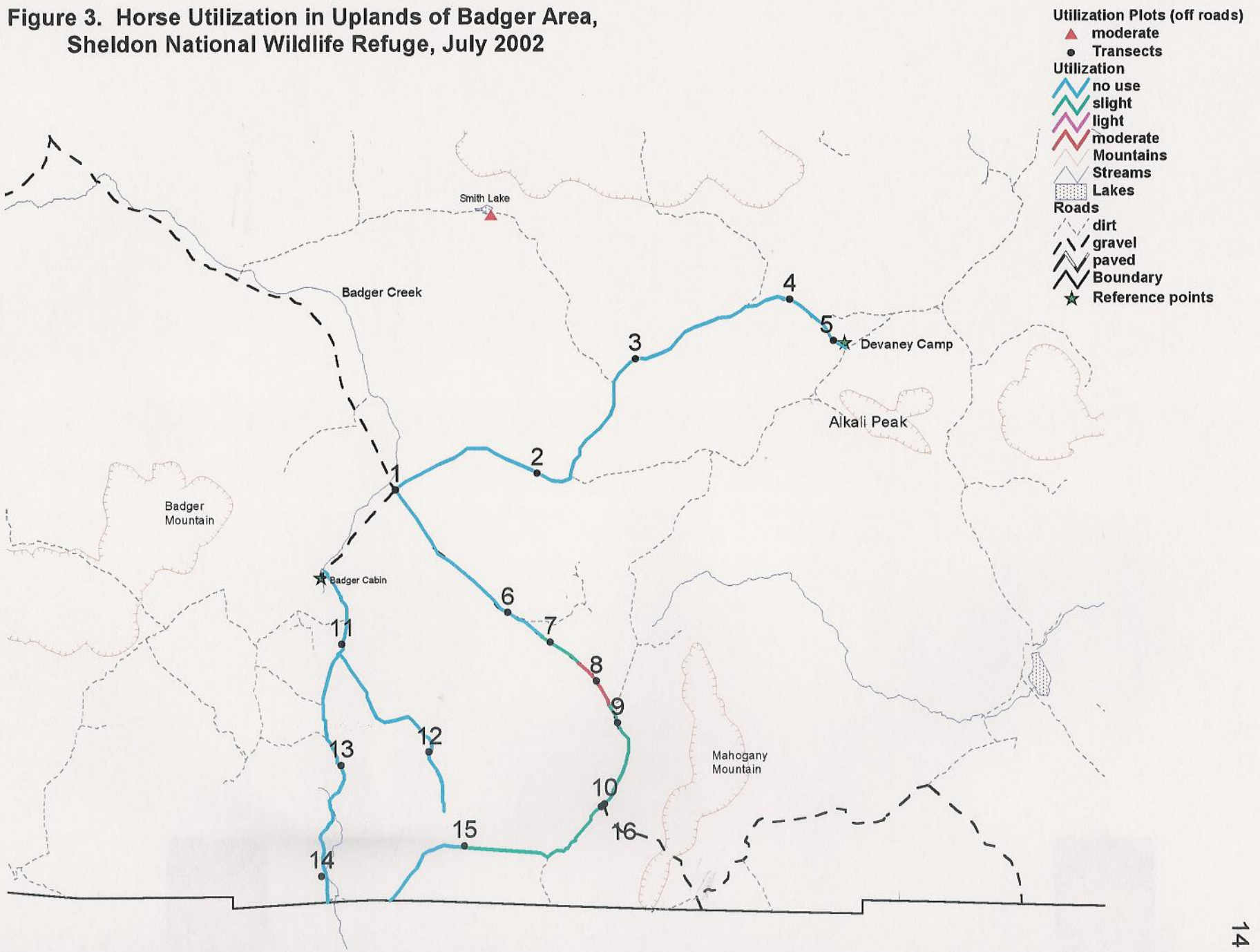


Figure 4. Location of Intensive Plots and Stream Reaches and Springs Monitored in Riparian Overview, September 2002, Sheldon National Wildlife Refuge.

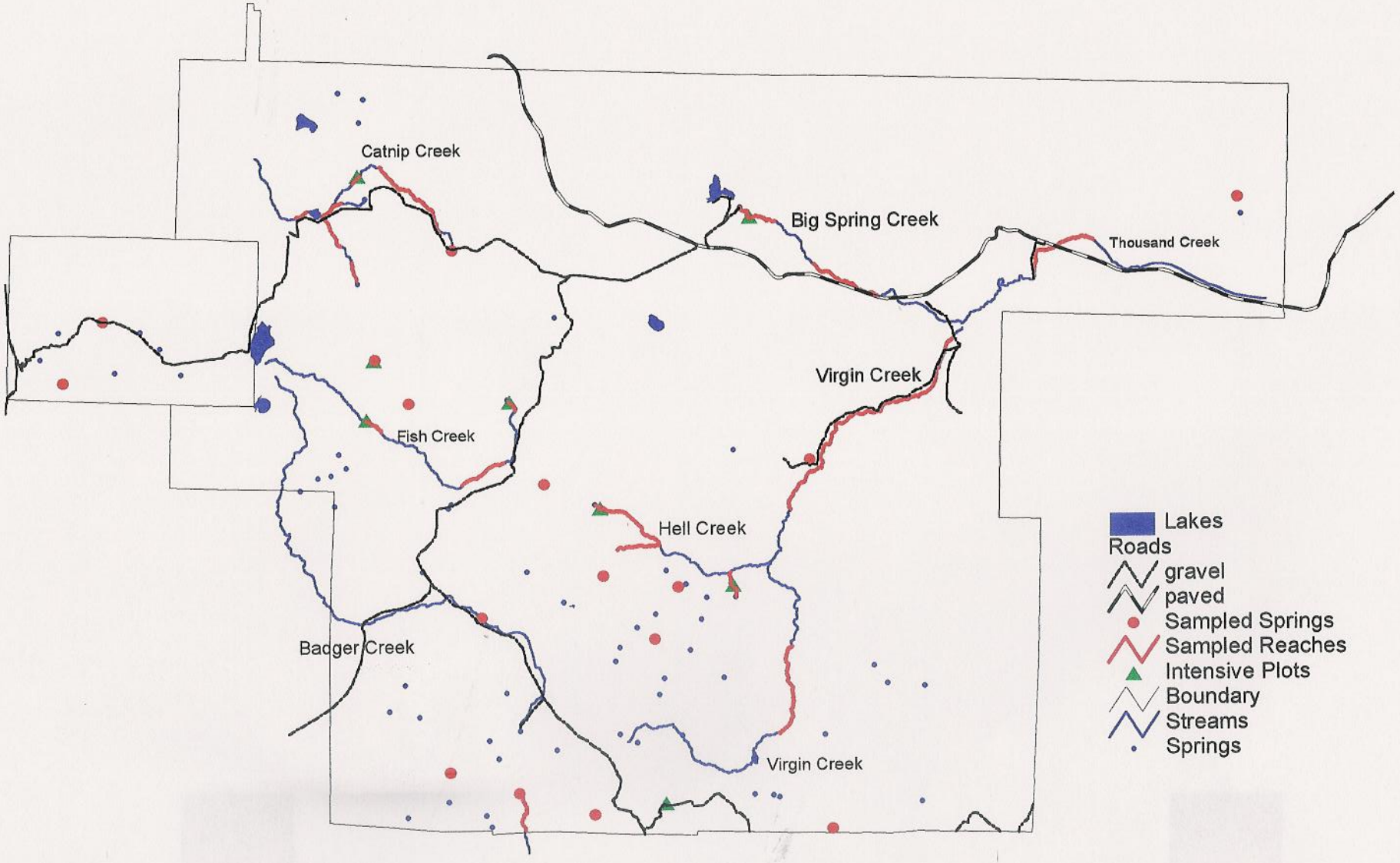


Figure 5. Location and Size of Feral Horse Groups Seen During Systematic Flight, September 2002, Sheldon National Wildlife Refuge

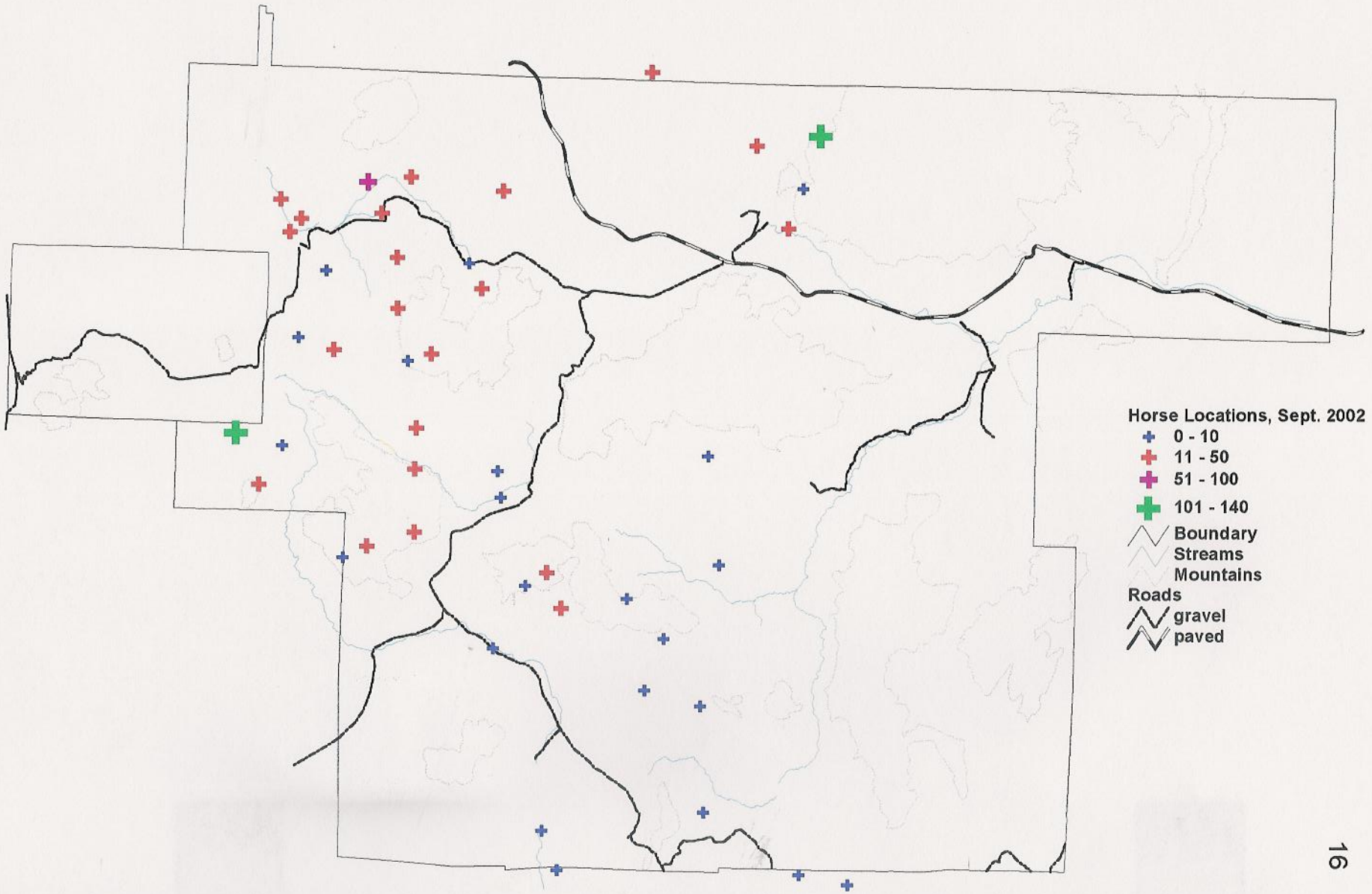
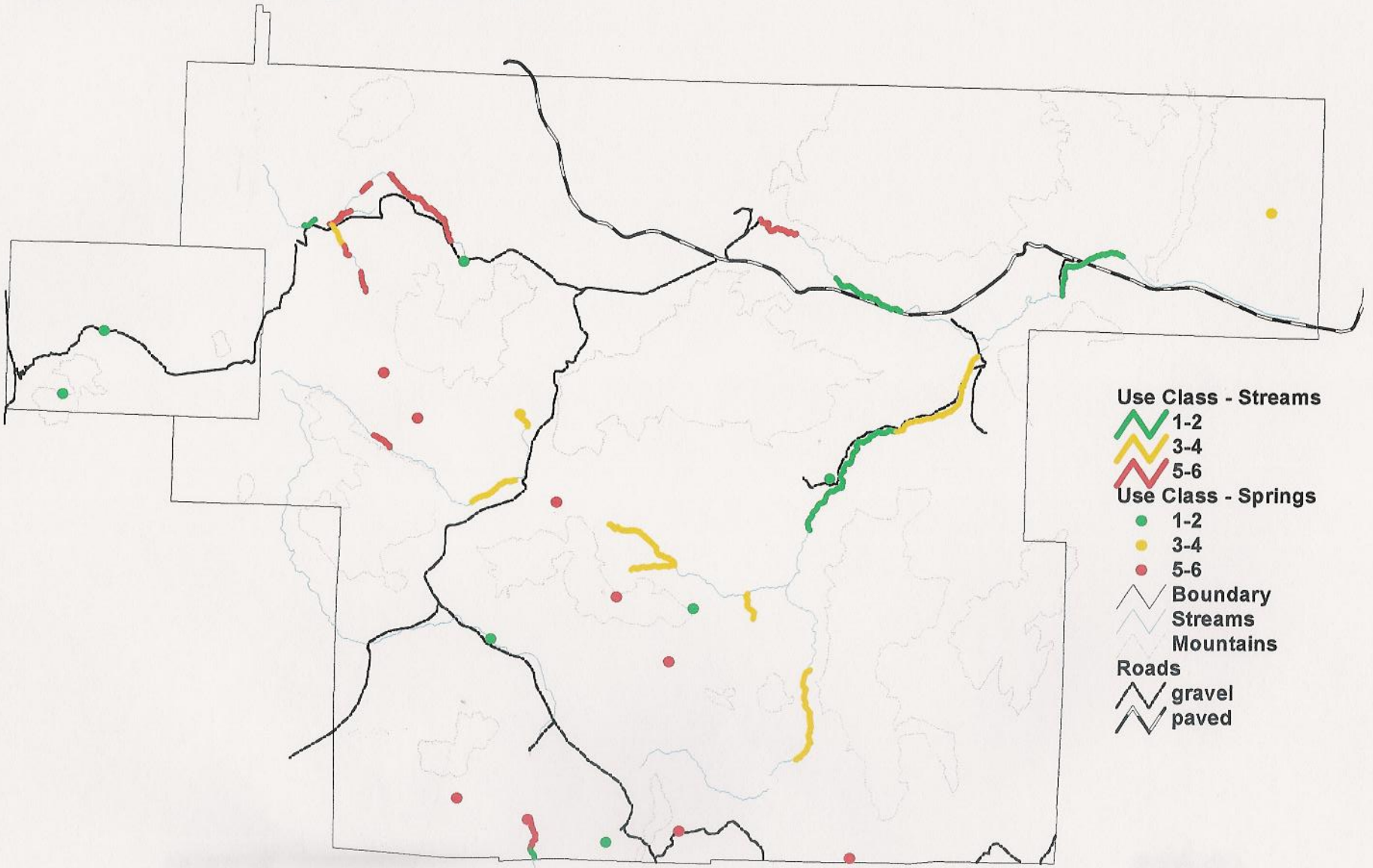


Figure 6. Feral Horse Utilization on Springs and Stream Reaches, Sheldon National Wildlife Refuge, September 2002.



Appendix A. Utilization transects run on three horse use areas, Round Mountain, Catnip, and Badger, and 5 selected transects on Sheldon National Wildlife Refuge, July 2001.

Fish Creek/Catnip Mountain Area

Transect	Sihy[a]	Stip	Agsp	Elci
1	2	2	–	--
2	2	2	2	--
3	2	4	–	–
4	2	4	–	--
5	2	2	2	--
6	2	2	–	--
7	7	–	–	15
8	–	–	–	27
9	2	2	–	--
10	–	2	–	--
11	2	2	–	--
12	2	2	–	--
13	2	2	–	–

Round Mountain Area

Transect	Sihy	Stip	Fest	Elci
1	2	–	–	--
2	2	4	–	--
3	22	–	38	--
4	5	–	24	--
5	2	10	–	--
6	5	4	–	--
7	–	–	–	19
8	4	2	–	–

[a]Key to plant abbreviations:
Agsp = *Agropyron spicatum*, Elci = Elymus cinereus, Fest = *Festuca* spp., Poa = *Poa* spp.
Sihy = *Sitanion hystrix*, Stip = *Stipa* spp.

Badger Area

Transect	Sihy	Stip	Agsp	Fest	Elci	Poa
1	2	2	–	–	–	–
2	2	2	–	–	–	–
3	4	–	4	–	–	–
4	2	2	–	–	–	–
5	2	2	–	–	–	–
6	2	2	–	–	–	–
7	16	–	–	18	–	–
8	44	–	–	–	58	39
9	15	–	–	18	–	–
10	8	2	–	–	–	–
11	2	2	–	–	–	–
12	2	4	–	–	–	–
13	2	5	–	–	–	–
14	–	2	–	–	–	–
15	7	5	–	–	–	–

Catnip Reservoir Area

Transect	Sihy	Stip	Unk Grass
1	21	–	–
2	–	–	64
3	50	41	–
4	37	43	–

Smith Lake Area

Transect	Sihy	Fest
1	44	54

Appendix B. Photographs of utilization cages on intensive riparian plots, Sheldon National Wildlife Refuge, 2002.

Figure B1. Big Spring Creek 1-1. Photo taken April 29, 2002, when utilization cage was placed on reach.



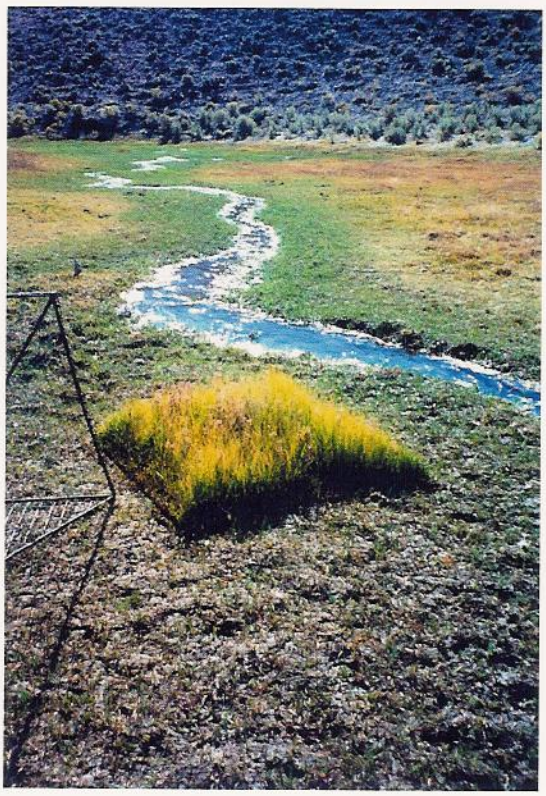


Figure B2. Big Spring Creek 1-1. Photo taken September 20, 2002, when stubble height transect was read.

Figure B3. Catnip Canyon 5-3. Photo taken April 29, 2002 when utilization cage was placed on reach.



Figure B4. Catnip Canyon 5-3. Photo taken Sept. 12, 2002 when stubble height transect was read.



Figure B5. Fish Creek 2-2. Photo taken May 7, 2002 when utilization cage was placed on reach.



Figure B6. Fish Creek 2-2. Photo taken Sept. 13, 2002 when stubble height transect was read.



Figure B7. Horse Canyon Spring Photo taken 13 September 2002, when stubble height transect was read.



Figure B8. Jackass Drainage. Photo taken July 12, 2002 when utilization cage was placed on reach.



Figure B9. Jackass Drainage. Photo taken Sept. 20, 2002 when stubble height transect was read.



Figure B10. North Hell 3-7. Photo taken May 7, 2002 when utilization cage was placed on reach.



Figure B11. North Hell 3-7. Photo taken Sept. 13, 2002 when stubble height transect was read.



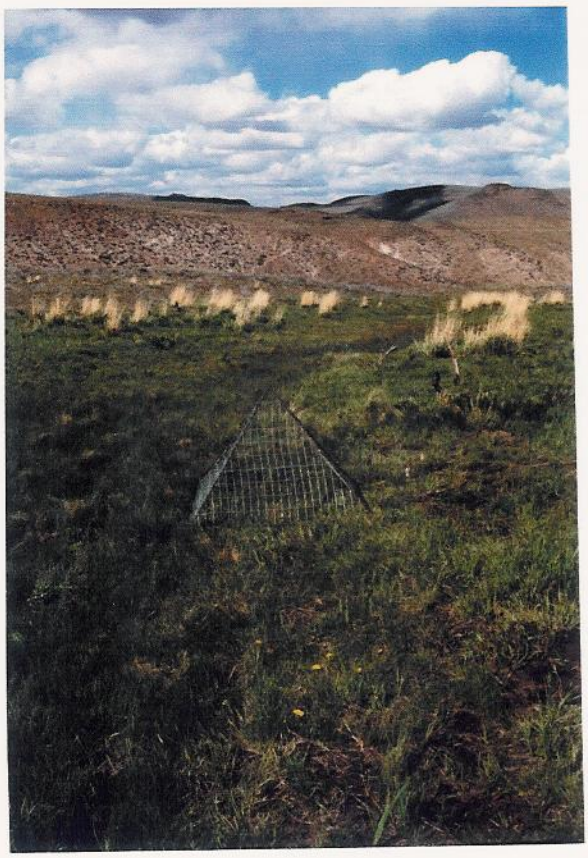


Figure B12. Ten-mile Spring. Photo taken May 22, 2002 when utilization cage was placed on reach.

Figure B13. Ten-mile Spring. Photo taken Sept 22, 2002 when stubble height transect was read.



Figure B14. West Catnip Spring. Photo taken May 7, 2002, when utilization cage was placed on reach.



Figure B15. West Catnip Spring. Photo taken Sept. 13, 2002, when stubble height transect was read.



Appendix C. Location and percent frequency of plants on riparian trend transects, intensive plots, Sheldon National Wildlife Refuge, July 2002.

Table A1. Locations of trend transects on intensive riparian plots, established for monitoring feral horse impacts, Sheldon National Wildlife Refuge, July 2002.

	Transect 1		Transect 2		Transect 3	
	Beg	End	Beg	End	Beg	End
Big Spring Creek 1-1	4642720 N 321487 E	4642706 N 321500 E	4642707 N 321499 E	4642701 N 321518 E	4642694 N 321530 E	4642698 N 321550 E
Catnip Canyon Creek. 5-3	4645181 N 298532 E	4645250 N 298521 E	4645246 N 298517 E	4645227 N 298510 E	4645227 N 298510 E	4645218 N 298489 E
Fish Creek 2-2	4630952 N 298970 E	4630952 N 298950 E	4630958 N 298940 E	4630970 N 298926 E	4630970 N 298926 E	4630983 N 298912 E
Jackass Drainage	4621131 N 320399 E	4621152 N 320400 E	4621152 N 320400 E	4621169 N 320389 E	4621129 N 320409 E	4621157 N 320402 E
Horse Canyon Spring	4631955 N 307333 E	4631946 N 307349 E	4631946 N 307349 E	4631937 N 307367 E	4631937 N 307367 E	4631926 N 307387 E
North Hell Creek 3-7	4625709 N 312622 E	4625692 N 312634 E	4625692 N 312634 E	4625667 N 312637 E	4625667 N 312637 E	4625656 N 342654 E
Ten-mile Spring	4608392 N 316376 E	4608409 N 316385 E	4608410 N 316386 E	4608428 N 316396 E	n/a	n/a
West Catnip Spring	4634427 N 299410 E	4634413 N 299396 E	4634413 N 299396 E	4634407 N 299376 E	n/a	n/a

Table C2. Percent frequency of plants on trend transects on intensive riparian plots, Sheldon National Wildlife Refuge, July 20002.

		Big Spring Creek 1-1	Catnip Canyon Creek 5-3	Fish Creek 2-2	Jackass Drainage	Horse Canyon Spring	N. Hell Creek 3-7	10-Mile Spring	West Catnip Spring
Sedges/Rushes	Carex nebrascensis	65		20	25	17	67	8	
	Carex spp.	55		40	2	18	37	2	35
	Eleocharis spp.	18				2			
	Juncus spp.	7			92	60			
	Juncus/Eleocharis[a]		85	87		17	22	60	52
Grasses	Agrostis spp.	13							
	Hordeum spp.	2		2	5	2			2
	Poa spp.	3		2	10	17	5		5
	unk grass[b]	27	62	7	42	23	10	8	42
Forbs	Achillea millefolium	3	12	5	5			5	10
	Agoseris spp.				3				
	Aster spp.			25	3				
	Iris missouriensis						2		
	Mimulus spp.				2	3	18		28
	Potentilla spp.	2	13	2					
	Ranunculus spp.	3	28		2				2
	Taraxacum officinale	2	28	5	12				2
	Trifolium spp.			7	13			5	
	Unk forb	35	8		15	2	2	45	

[a]Most trend plots were heavily grazed. Juncus/Eleocharis class was used when no seed-heads remained for identification.

[b] Most trend plots were heavily grazed. Gasses were classified as unknown when no seed-head remained for identification.

Environmental Management (2015) 55:930–942
DOI 10.1007/s00267-014-0436-2

Restoration of Riparian Areas Following the Removal of Cattle in the Northwestern Great Basin

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Received: 14 September 2014 / Accepted: 16 December 2014 / Published online: 19 February 2015
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Abstract We assessed the effects of the elimination of livestock in riparian systems at Hart Mountain National Antelope Refuge in southeastern Oregon, 23 years after the removal of cattle grazing, using 64 photos taken before grazing was removed compared with later retake photos. Two methods were used for this assessment: (1) a qualitative visual method comparing seven cover types and processes and (2) a new quantitative method of inserting digital line transects into photos. Results indicated that channel widths and eroding banks decreased in 64 and 73 % of sites, respectively. We found a 90 % decrease in the amount of bare soil ($P < 0.001$) and a 63 % decrease in exposed channel ($P < 0.001$) as well as a significant increase in the cover of grasses/sedges/forbs (15 % increase, $P = 0.037$), rushes (389 % increase, $P = 0.014$), and willow (388 % increase, $P < 0.001$). We also assessed the accuracy of the new method of inserting digital line transects into photo pairs. An overall accuracy of 91 % (kappa 83 %) suggests that digital line transects can be a useful tool for quantifying vegetation cover from photos. Our results indicate that the removal of cattle can result in dramatic changes in riparian vegetation, even in semi-arid landscapes and without replanting or other active restoration efforts.

Keywords Riparian · Grazing · Cattle · Repeat photography · Passive restoration · Hart Mountain

Electronic supplementary material The online version of this article (doi:10.1007/s00267-014-0436-2) contains supplementary material showing the 64 photo pairs, which is available to authorized users.

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Introduction

Livestock grazing is permitted on nearly one million square kilometers of public land in the 11 western states of the US, including nearly 80 % of BLM land and 60 % of US Forest Service land (Beschta et al. 2013). Cattle tend to congregate in riparian areas due to easy access to water, lush forage, and favorable terrain (Kovalchik and Elmore 1992). This concentration of cattle in riparian areas makes these systems particularly susceptible to the effects of livestock (Fleischner 1994; Belsky et al. 1999; Donahue 1999). The effects of livestock grazing on ecosystems are numerous, and effects on riparian systems in particular have been the subject of much study. Hydrology, plant and animal species composition, and soil characteristics can all be dramatically altered with the presence of cattle (Kauffman et al. 1983; Read et al. 2011).

Cattle grazing can indirectly cause a significant decrease in bird species abundance and diversity, largely by removing shrubs that are important habitat for many bird species (Taylor 1986). Altered stream cover, water depth, and bank stability due to cattle grazing can all affect fish populations, and have been shown to lead to declines in salmonids (Knapp and Matthews 1996). Cattle grazing can accelerate stream bank erosion, causing streams to become shallower and wider, which can result in higher water

temperatures (Kauffman et al. 1983). Other water quality issues that can result from the presence of cattle include pollution from excrement and increased sedimentation from trampled banks (Chaney et al. 1993). Decreases in both the density and height of woody plants have been documented with grazing activity (Kovalchik and Elmore 1992; Green and Kauffman 1995) along with increases in exotic species (Hayes and Holl 2003). Although grazing can sometimes lead to greater species richness and diversity, this often occurs due to the introduction of invasive species and the suppression of vegetation cover (Green and Kauffman 1995; Hayes and Holl 2003). Other documented effects of cattle include loss of native biodiversity, interruption of nutrient cycling, and destruction of biotic soil crusts (Kauffman and Krueger 1984; Skovlin 1984; Fleischner 1994; Trimble and Mendel 1995).

Cattle grazing can exacerbate effects of climate change. Ecosystems stressed by grazing activity may be less resistant to temperature and moisture changes, compared to ecosystems that have had time to recover from such anthropogenic stress factors (Beschta et al. 2013). Removing grazing pressure and allowing systems to undergo a process of passive restoration represent an important management option for enhancing ecosystem resilience and resistance to climate change effects.

With grazing ubiquitous across much of the western US, it is important to understand not only the effects of grazing, but also how ecosystems change with the removal of cattle both in the short and long term (Floyd et al. 2003). Two years after grazing was stopped along portions of Meadow Creek in northeastern Oregon, shrub cover increased by 50 %, and black cottonwood (*Populus trichocarpa*), alder (*Alnus* spp.), and willow (*Salix* spp.) greatly increased in crown-volume (Case 1995; Kauffman et al. 1995). Herbaceous vegetation density increased 4–6 times in riparian areas of the San Pedro River in Arizona, and 42 of 61 bird species increased in abundance when cattle were removed (Krueper et al. 2003). Ecologically important biological soil crusts also increased within a few decades after cattle removal (Read et al. 2011).

There can be dramatic results from passive restoration following the removal of cattle from a system. Plant communities may rapidly switch from disturbance-resistant ruderal grasses to hydrophytic plant communities in riparian areas after the removal of grazing (Hough-Snee et al. 2013). Twelve years after the removal of cattle from Hart Mountain National Antelope Refuge in southeastern Oregon, there was a 64 % increase in the number of medium-diameter aspen in sampled riparian areas (Earnst et al. 2012). Forb and mesic shrub cover increased by 68 and 29 %, respectively, in the riparian aspen stands of the refuge, and sagebrush cover decreased by 24 %. With the increase in riparian vegetation, bird abundance increased by 33 % (Earnst et al. 2012). These examples provide evidence of the potential of passive restoration to redress cattle impacts. Active restoration methods such as plantings or stream channel stabilization may sometimes be needed to restore riparian damage caused by cattle grazing (Booth et al. 2012); however, passive restoration processes alone may be sufficient to restore ecosystem functions in many cases (Kauffman et al. 1995).

Photographs have long been an important tool for detecting ecosystem change (Hart and Laycock 1996). Studies have used repeat photography to understand both the merits and deleterious effects of grazing (Elmore and Beschta 1987; Anderson et al. 1990; Reid et al. 1991; Chaney et al. 1993). While photos have been useful for illustrating ecological change qualitatively, less work has been done on extracting quantitative data from photos. Quantitative studies have included use of indices of visual obstruction to gage willow clump densities (Boyd and Svejcar 2005), detection of species change using geographic information systems (GIS) with pixel color and object recognition (Michel et al. 2010), and measurement of vegetation heights in historical photos based on known heights in retake photos (Ripple and Beschta 2006). Matching camera type and focal lengths with repeat photography is not critically important, as long as the retake photo was captured at the same location as the historical photo (Hall 2002). This allows for the opportunity for historical photos to be used for analysis via repeat photography even when the photos were not initially intended for this purpose. Here we investigate new methods to study ecosystem change using photos.

The objectives of this study were to (1) use repeat photography to illustrate riparian vegetation change over time following the cessation of cattle grazing at Hart Mountain National Antelope Refuge, Oregon; (2) use image analysis to quantitatively measure the amount of change in vegetation cover, as well as the change in cover type; (3) compare vegetation cover at sites with active management treatments versus those with only cattle removal; and (4) assess the accuracy of inserting digital lines into photos to measure vegetation change. We hypothesized that passive restoration (cattle removal without additional vegetation management) would result in changes in riparian vegetation cover, bare soil, eroding stream banks, and exposed stream channels. This study may provide insights that could guide similar restoration efforts in other areas of the western US.

Study Area

The study was conducted at Hart Mountain National Antelope Refuge (see Fig. 1 for location) which is administered by the U.S. Fish and Wildlife Service (USFWS) and

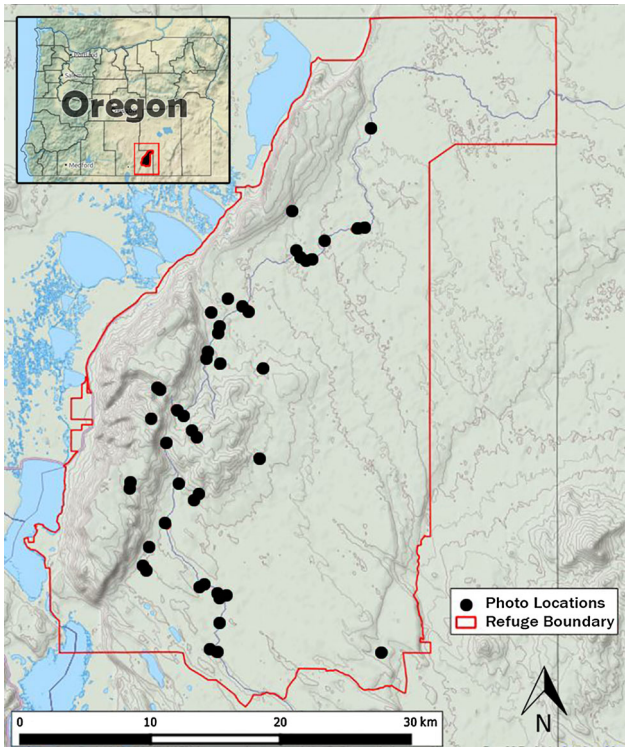


Fig. 1 Hart Mountain National Antelope Refuge is located in Oregon. The majority of riparian areas in the refuge are located in the western half of the refuge. The 64 photo plots were well distributed along a north–south axis but were limited to riparian areas that historical photos captured. Background map ©OpenStreetMap contributors http://www.openstreetmap.org/copyright

encompasses 1,095 km^2 of high desert in the Northern Basin and Range Ecoregion in southeastern Oregon (Omernik 1987). The refuge was established in 1936 for the protection of pronghorn (*Antilocapra americana*). Over time, the refuge has broadened its management goals to include conservation and restoration of wildlife and native ecosystems. Cattle grazing was long thought to be part of a strategy for meeting these goals. For example, the 1970 management plan for the refuge designated grazing as the "primary means by which vegetation would be managed" under the assumption that light to moderate grazing on 1–2-year intervals would improve the vigor and quality of forage, and improve pronghorn habitat. However, grazing along valley bottoms and riparian areas continued to be relatively heavy throughout the refuge, with many areas never given time to recover from grazing effects (USFWS 1994). By the 1990 s, cattle grazing was deemed incompatible with new management goals focused on restoring the refuge and all cattle were removed from the refuge as of 1991 (USFWS 1994). There was occasional trespass of cattle and feral horses on the refuge since cattle were officially removed, but their use of our study sites was extremely low compared to allotment cattle prior to 1991. Also, prescribed fire (sometimes with mowing) was used on some sites to remove litter, invigorate willows and remove sagebrush, and in some areas willow cuttings were planted (personal communication, Gail Collins).

Four wild ungulate species are found at Hart Mountain. Summer populations of pronghorn were estimated at < 500 animals during the 1970 s. This number increased to 1,000–2,000 animals after cattle removal, and numbers were recently estimated at 2,000–3,500 animals (Beschta et al. 2014). Other ungulates at Hart Mountain include mule deer (*Odocoileus hemionus*; $< 1{,}000$), small numbers of elk (*Cervus elaphus*; 15–20 individuals), and bighorn sheep (*Ovis canadensis*) (Beschta et al. 2014).

Climate at the refuge includes hot dry summers and cold winters with most precipitation as snow (USFWS 1994). Average precipitation ranges from 15 to 20 cm on the western foot of the mountain to 30–45 cm of precipitation at higher elevations. There are over 242 km of perennial and intermittent streams within the refuge but riparian areas comprise less than 1 % of the total land area. Approximately one half of the stream reaches on the refuge (113 km) are inhabited by fish except during periods of drought when adequate water is not available. In 1994, only 13 % of the streams were characterized as being in good condition with 73 % of riparian areas characterized as either poor or very poor condition. Cattle grazing was identified as the leading cause of stream and riparian degradation at Hart Mountain (USFWS 1994).

Common tree and shrub species in the refuge include quaking aspen (*Populus tremuloides*) and willows (*Salix* spp.) in riparian areas, with western juniper (*Juniper occidentalis*) and scattered pockets of mountain mahogany (*Cercocarpus ledifolius*) in upland areas. Rabbitbrush (*Chrysothamnus* sp.), low sagebrush (*Artemisia arbuscula*), Wyoming big sagebrush (*Artemisia tridentata*) and silver sagebrush (*Artemisia cana*) are ubiquitous across the refuge. Common riparian herbaceous vegetation includes several rushes (*Juncus* spp.), spikerushes (*Eleocharis* spp.), and bullrushes (*Scirpus* spp.). Common grasses in the refuge include saltgrass (*Distichlis spicata*), bluegrass (*Poa* sp.), and ryegrasses (*Lolium* spp.). California false hellebore (*Veratrum californicum*) is common in some riparian areas. Invasive grasses such as cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) are present in scattered patches across the refuge.

Methods

Grazing reports were summarized to determine the amount of cattle grazing on the refuge between 1972 and 1990. Animal unit months (AUM) for each year were calculated by multiplying the number of animals by the number of

months of grazing. Average monthly Palmer Drought Severity Index (PDSI) (Alley 1984) was calculated for each year from 1972 to 2013 to account for possible changes in climate fluctuations (annual moisture and temperature) during the study period. A two-sample *t* test (unequal variances) was used to compare mean PDSI between the 10-year period leading up to the removal of cattle (1981–1990) and the 10-year period preceding this study (2003–2012). Data for monthly PDSI were obtained from the Western Regional Climate Center for the Oregon-Closed Basin hydrologic unit, which includes all of the study area (WRCC 2014).

Photos of riparian areas within the refuge taken in the period 1984–1991 were collected from Hart Mountain National Antelope Refuge (hereafter, historical photos). Of this initial set, sites for 110 photos were relocated and photographed again in 2013 and 2014 (hereafter, retake photos). Photo locations included Rock Creek, Poker Jim Spring, Willow Creek, Paiute Creek, Bond Creek, Cold Creek, North Fork DeGarmo Creek, South Fork DeGarmo Creek, Stockade Creek, Guano Creek, Deer Creek, Warner Creek/Big Flat Wetlands, Goat Creek, and Warner Ponds. Retake photos were taken during the same season as historical photos. Sixty-four of the 110 photo sites were used for analysis (Fig. 1). Forty-six photo pairs were eliminated for one of three reasons: (1) multiple photos of the same geomorphic feature, (2) the photos did not have a clear foreground focus and were instead a broader landscape view, or (3) photo location could not be accurately determined using the original photo.

Stream measurements were taken of the active channel width and depth at 34 sites, where the stream channel was clearly visible in the photo. Heights of the five tallest willows within 50 m of the photo retake location were recorded if present. Percent height change was calculated for individual willow clumps when they could be identified in both the historical and retake photos.

Historical photos and retakes were registered together using photo-processing software (Adobe Photoshop CS6). Photos were matched by overlaying a semi-transparent copy of each retake photo on top of the historical photo and aligning features such as individual trees, rocks, and land contours. Retake photos were cropped as necessary to match the field of view of the cameras used to take historical photos.

Two methods were used to assess change between photo pairs. First, a qualitative visual site assessment was used to evaluate change between the historical and retake photos. Categories included willow cover, sagebrush cover, aspen recruitment, amount of bare soil, exposed channel, eroding banks, and channel width. We determined if each category had increased, decreased, had no visible change, could not be assessed, or was not applicable (Fig. 2). Second, a digital line intercept method was developed to measure change between photo pairs. Line transects were digitally inserted into each photo pair, parallel to the base of the photo. The transect was first placed in the historical photo at the location where there was the best view of the riparian vegetation and stream channel (Fig. 3). The transect was then placed in the same location in the retake photo. Each pixel on the transect was assigned one of seven categories: bare soil, exposed channel, willow, grasses/sedges/forbs (G/S/F), rushes, sagebrush, or "other". The "other" class was comprised of rare elements that appeared in less than five digital transects (e.g., aspen, mosses, juniper) or had little potential to change (e.g., rocks). If a section of the line had more than one class present (e.g., bare soil and G/S/F), the section was identified by the predominant class.

Accuracy of the digital line intercept method was assessed with field data. A tape transect was placed and photographed in the field at approximately the same position as the digital line transect in the photo. Categories of ground cover were recorded along these transects in the field. Four points were placed at equal intervals on each transect, and using the field data, the cover type was determined at each of the points. These points served as "ground truth" and were compared to the categories assigned to the points using only the photographs. Estimates of accuracy for each category were obtained. In the rare occurrence that a foreground shrub obscured the tape transect at a sample point, the site was not used for this assessment. A classification error matrix was generated and the overall accuracy level and Cohen's kappa statistic were determined (Lillesand et al. 2004). The kappa statistic accounts for probability of agreement through random chance.

Distances were measured along the tape transects in the retake photos and used to measure the length of digital transects. Images were then standardized by resizing so 1 pixel equaled 5 cm on the ground in each photo. Percent transect occupied by each cover type was calculated for each photo. A paired two-sample *t* test (two-tailed, 95 % confidence level) was used to compare percentage of digital transect occupied by each cover type in the historical and retake photos. Sample size varied depending on the number of paired transects in which the cover type occurred in either the historical or retake photo.

A raster calculator (QGIS Development Team 2014) was used to assess change in cover types between historical and retake photos. Each pixel was assigned a value of 1–11 (depending on cover category) in the retake images and the same number multiplied by 100 for the corresponding category in the historical photo. The matched pixels of the two transects were then added together and the sum indicated the beginning and ending cover category for that pixel. These values were then expressed as percentages of



Fig. 2 An example of comparing two photos using the visual site assessment method in Barnhardy Meadow. Willows have increased. Aspen are present in the photo, but due to the willow obstruction, it is unclear if the level of recruitment has changed. Bare soil has decreased, eroding banks have decreased, channel width has decreased, and amount of exposed channel decreased. Photo credits: 1990-Hart Mountain National Antelope Refuge, 2013-Jonathan Batchelor

transect length. For example, bare soil was given a value of 1 in the retake and 100 in the historical photo; G/S/F was given a value of 6 in the retake and 600 in the historical. A value of 101 indicated bare soil stayed bare soil, 106 indicated bare soil became G/S/F, 601 indicated G/S/F became bare soil, and 606 indicated G/S/F stayed G/S/F.

We compared sites that were likely treated with prescribed fire or willow plantings to those sites that did not have any active management. With visual assessment data, we compared change over time for willow and sagebrush. With line intercept data, we used a two-sample t test (unequal variances) to check for significant differences in percent cover in the retake photos of willow, sagebrush, and herbaceous vegetation (G/S/F). We were unable to assess the effects of mowing because of low sample size ($n = 5$).

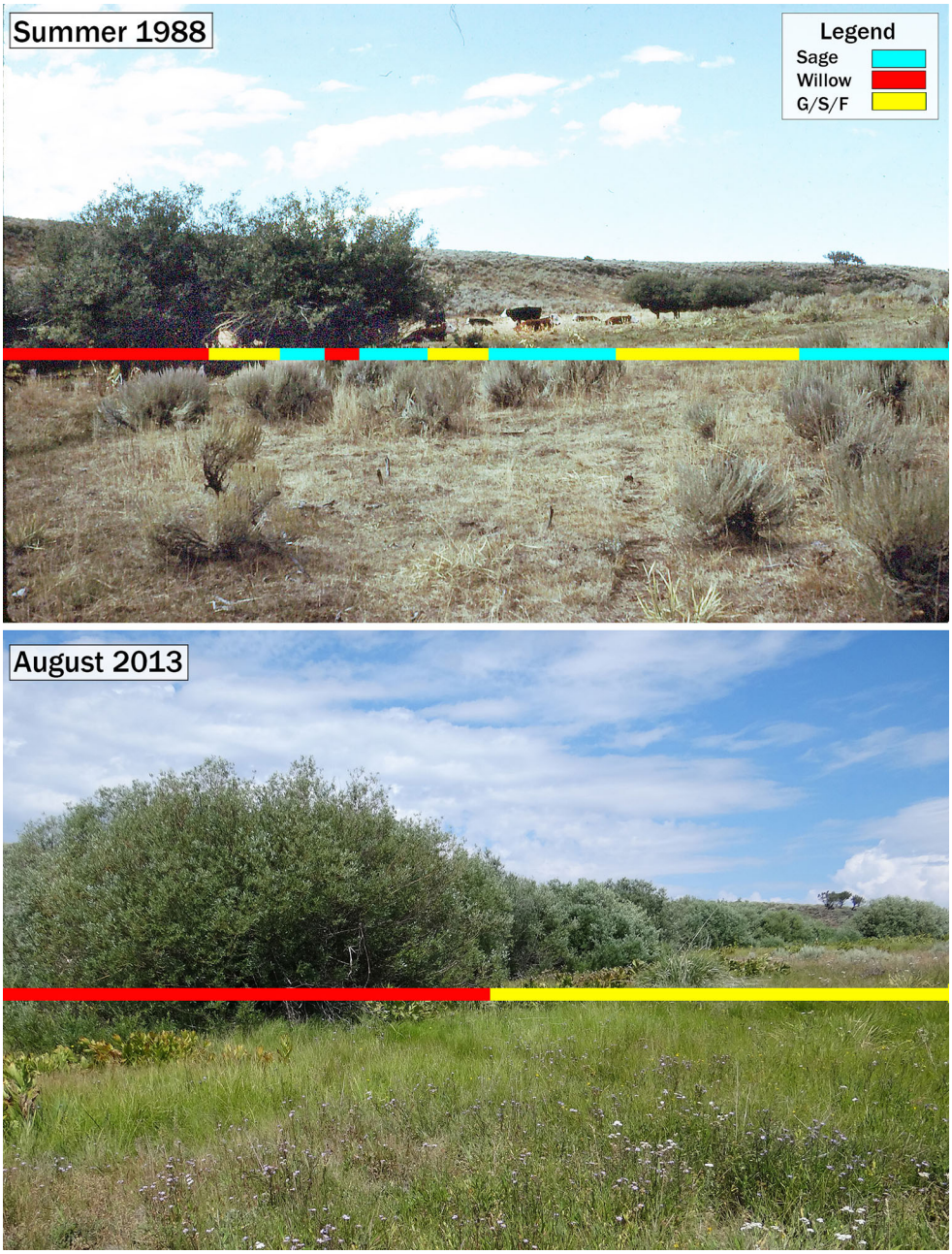


Fig. 3 Photo pair demonstrating the digital line intercept method on Stockade Creek, with a color key showing the categories identified on the transect. Transects were placed in both photos in the same location and classified by cover category. The location of the transect on the ground is affected by the oblique view from the camera, but the method is still valid as we compared two photos of the same site, taken at the same oblique angle. Photo credits: 1988-Steve Herman, 2013-Jonathan Batchelor

Results

Annual AUMs averaged 13,400 on Hart Mountain Refuge between 1972 and 1989 and dropped to 3,049 in 1990, the final year in which cattle were allowed to graze (Fig. 4). The refuge was subdivided into grazing allotments with differing grazing levels, and grazing was relatively high at all historical photo sites except two. Mean PDSI was 1.87 for the 10-year period 1981–1990, and 0.18 for 2003–2012, with no significant difference between these time periods ($P = 0.25$).

Field Measurements

Mean width/depth ratio for the 34 stream reaches measured in 2013 and 2014 was 5.0 (SD 3.9, range 0.7–20.0). One or

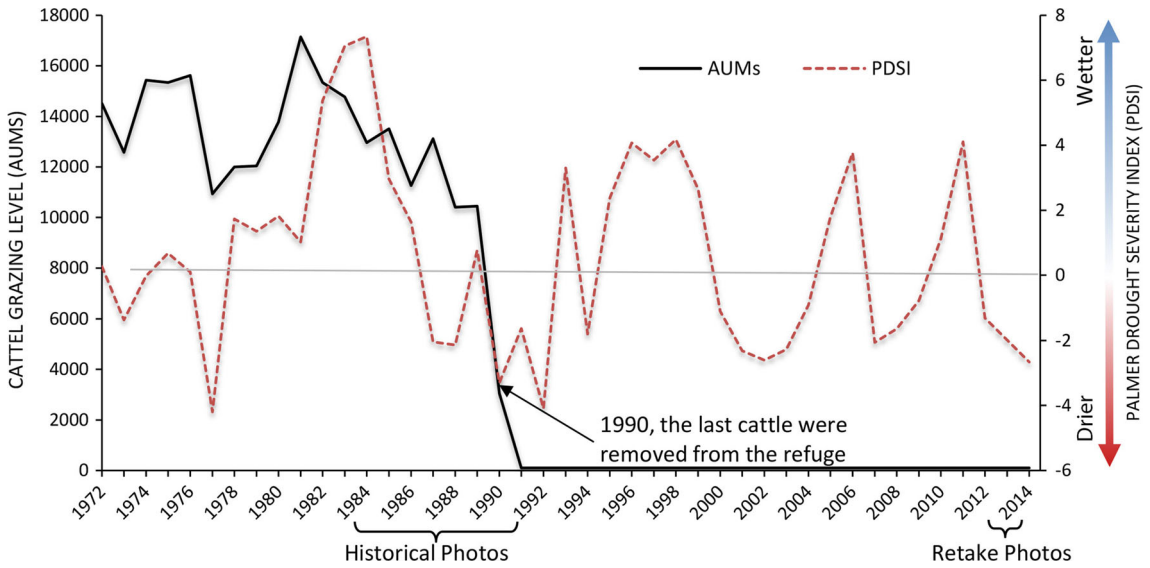


Fig. 4 Animal unit months (AUMs) permitted on the refuge since 1972 on the left axis with the Palmer Drought Severity Index for the Oregon-closed basin hydrologic unit on the *right axis*. The PDSI value for the years when the historical photos were taken range from 7.35 in 1984 to −3.31 in 1990

more individual willow clumps were identified at 12 sites in both the historical and retake photos. Of these 12 sites, seven had an increase in willow heights, averaging ~ 200 % with increases up to 300 % in some sites. Willow heights measured at retake sites averaged 3.3 m (range 0.8–6.0, $n = 30$). Five sites showed little change in willow height. However, these willows had a mushroom shape in the historic photos (Fig. 2, top photo) indicating heavy browsing pressure at the base of the plants, with growth occurring at heights above the reach of cattle (Painter and Ripple 2012). In the retake photos, these willows had full shapes with no evidence of constriction by browsing.

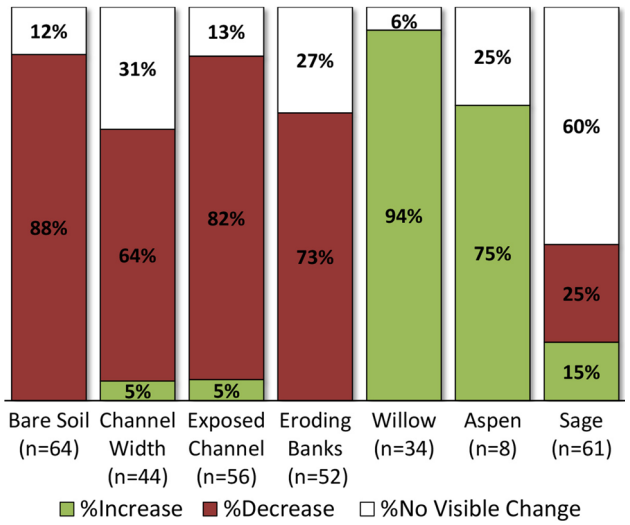


Fig. 5 *Bar graph* illustrating the visual site assessment results. Percentages are of the number of sites where a change was assessed, and not a measure of the amount of change. Sample size (n) differed because the visual site assessment was limited to photo pairs in which the category was visible in at least one of the photos

Visual Site Assessment

Overall, the amount of bare soil, exposed channels, channel widths, and eroding banks decreased since cattle removal. In 52 historical photos that showed stream banks, 73 % of the banks were eroding, while in the retake photos, 13 % were eroding (Fig. 5). Of these 52 pairs, stream banks appeared to have less erosion in 38 (73 %) of the retake photos. The remaining 14 (27 %) appeared to have no change. No site had an increase in bare soil or eroding banks. Two sites showed an increase in channel width and three sites showed an increase in exposed channel. Both willow and aspen had increased dramatically in the retake photos. Only eight sites had an unobstructed view of aspen regeneration that allowed for assessment of understory aspen change. Of these eight sites, the two that did not have an increase in aspen recruitment had a decadent aspen stand in the historical photo and the trees had died by the time of the retake photo without new recruitment. Sagebrush was the most variable in response with 25 % of sites increasing and 15 % decreasing in amount. Two sites were in areas that historically had very low grazing activity, and these had little visible change in the retake photos.

Digital Line Intercept

In both historical and retake photos, G/S/F had the highest percentage of transect length (Fig. 6). In the historical

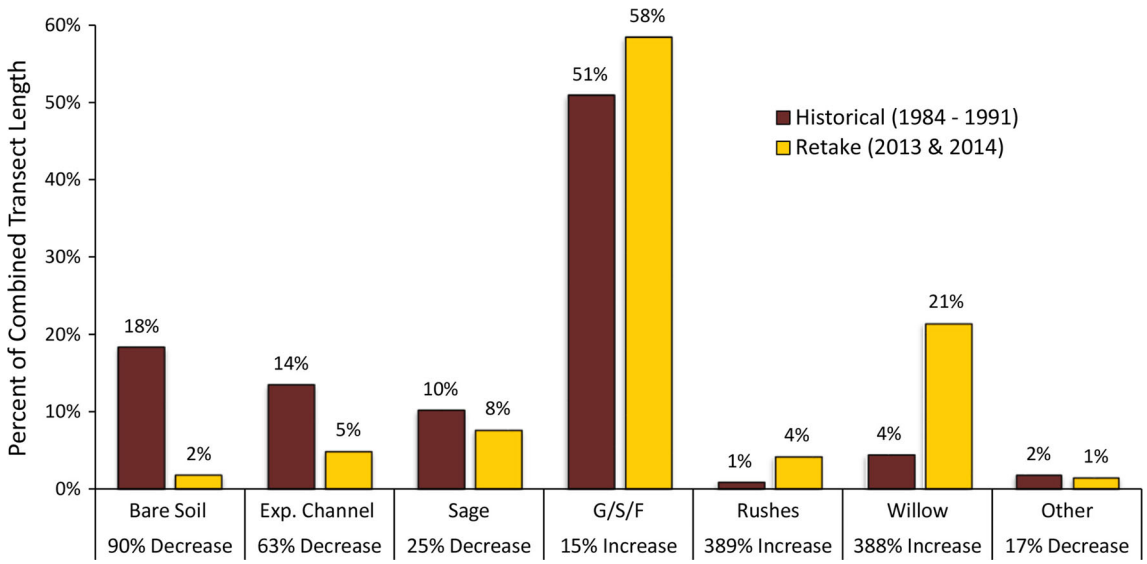


Fig. 6 Percentage of combined digital transect length occupied by each category. The total length of all transects combined was 465.4 m

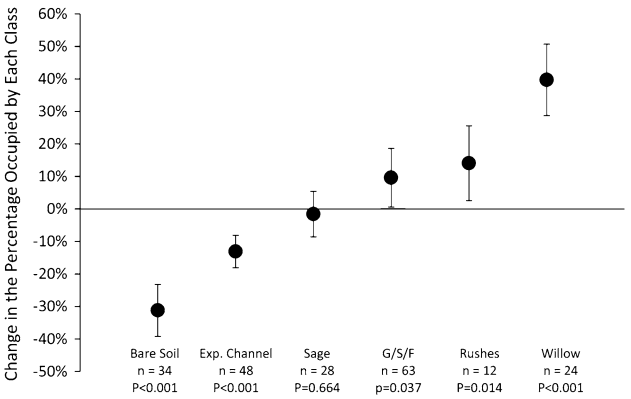


Fig. 7 The mean difference between the percentages of each class in the historical photo compared to the retake, using a paired *t* test with the digital transect percentage for each category calculated for each site individually. Ecosystem recovery is indicated by negative values for bare soil, exposed channel, and sagebrush, and by positive values for G/S/F, rushes, and willow. For example, the percentage of bare soil present in the historical photos decreased on average by about 30 % compared to the retakes. *Error bars* show 95 % confidence intervals. Sample size (*n*) is the number of transect pairs where the category was present. Values were not calculated for the "other" classification as this class is comprised of multiple biotic and abiotic elements

photos, bare soil was the second highest percentage, while in the retake photos willow was the second most dominant cover type. There was a significant decrease over time in amount of bare soil and exposed channel and a significant increase in willow ($P < 0.001$; Fig. 7). The amount of G/S/F ($P = 0.037$) and rushes ($P = 0.014$) also increased significantly. There was no significant difference in sagebrush cover ($P = 0.67$).

Through summing the category lengths from all historical photo transects, we found that the most common categories were G/S/F, willow, exposed channel, and sagebrush. G/S/F accounted for 51 % of the historical combined transect (Table 1). Within this category, 66 % remained G/S/F in the retake photos, and 24 % became willow. Only 6 % of what was bare soil remained as bare soil, while 65 % changed to G/S/F and 13 % became willow. Of the 13 % historical digital transects identified as exposed channel, 18 % remained exposed channel, while 49 % became G/S/F, 15 % became rushes, and 12 % became willow in the retake photos. Almost half (47 %) of what was sagebrush became G/S/F.

A total of 240 points were selected to assess the accuracy of the digital line intercept method for 60 photographed tape transects. Sixteen points were eliminated due to visual obstruction leaving 224 points for the assessment. The overall accuracy level was 91 % with a kappa statistic of 83 % (Table 2). Highest level of accuracy was for the willow category with (100 %). Bare soil and rushes had the lowest level of accuracy with 60 and 64 %, respectively.

Comparing Active Versus Passive Management

Using visual assessment, willow cover increased in 94 % ($n = 16$) of the sites that had burned and 94 % ($n = 18$) of the sites without fire, while sagebrush decreased at 28 % of the sites that burned ($n = 29$) and decreased at 22 % of the sites that did not burn ($n = 32$). Also, willow cover increased in 100 % of the sites that were planted ($n = 13$) and 90 % of sites not planted ($n = 21$). Two additional sites that were planted had no willows visible in either the historical or retake photos.

Table 1 Results of change from historical photos to retake photos

Historical category	Total length	What historical categories changed to in retakes						
		G/S/F	Bare soil	Exp. channel	Sage	Willow	Rushes	Other
Grasses/ sedges/ forbes	51 % (237 m)	66 % (157.8 m)	1 % (1.8 m)	2 % (4.2 m)	3 % (6.3 m)	24 % (58.2 m)	3 % (6.7 m)	1 % (2 m)
Bare soil	18 % (85.35 m)	65 % (55.9 m)	6 % (4.8 m)	7 % (5.7 m)	5 % (4.1 m)	13 % (11.5 m)	3 % (2.6 m)	1 % (0.85 m)
Exposed channel	13 % (62.85 m)	49 % (30.9 m)	1 % (0.55 m)	18 % (11.4 m)	4 % (2.3 m)	12 % (7.45 m)	15 % (9.8 m)	1 % (0.45 m)
Sage	10 % (47.4 m)	47 % (22.36 m)	0 %	0 %	43 % (20.25 m)	5 % (2.45 m)	1 % (0.5 m)	4 % (2.1 m)
Willow	4 % (20.5 m)	12 % (2.4 m)	0 %	0 %	5 % (1.05 m)	83 % (17.05 m)	0 %	0 %
Rushes	1 % (4 m)	26 % (1 m)	0 %	30 % (1.2 m)	11 % (0.45 m)	11 % (0.45 m)	22 % (0.9 m)	0 %
Other	2 % (8.3 m)	31 % (2.6 m)	0 %	6 % (0.5 m)	11 % (0.9 m)	39 % (3.2 m)	0 %	13 % (1.1 m)

The total length column is the length of each category in the historical photos, which was calculated by adding up the category lengths from all photos transects

Table 2 Classification error matrix for classification data of photos compared to field observations

Predicted class (on image)	Observed class (in field)							Total
	Bare soil	Exp. channel	Sage	G/S/F	Rushes	Willow	Other	
Bare soil	**3**	–	–	2	–	–	–	5
Exp. channel	–	**17**	–	1	–	–	–	18
Sage	1	1	**6**	3	–	–	–	11
G/S/F	–	2	1	**153**	5	–	1	162
Rushes	1	1	–	2	**9**	–	–	13
Willow	–	–	–	–	–	**12**	–	12
Other	–	–	–	–	–	–	**3**	3
Total	5	21	7	161	14	12	4	224
Accuracy 91 %								
Kappa 83 %								

Bold values in the diagonal represent correctly classified categories

Based on line transect data, there was no significant difference ($P = 0.67$) in willow cover between sites that were burned ($n = 10$) versus not burned ($n = 14$). There was a significant reduction ($P = 0.03$) in sagebrush cover at sites that had burned ($n = 7$) versus those without fire ($n = 15$). We also found no significant difference ($P = 0.28$) in the percent cover of herbaceous vegetation (G/S/F) between sites that were burned ($n = 30$) and not burned ($n = 30$). There was no significant difference ($P = 0.42$) in willow cover between sites with willow plantings ($n = 9$) compared to those that were not planted ($n = 15$).

Discussion

Consistent with our hypothesis and evident in the chronosequence of paired photos, marked changes were observed in riparian areas 23 years after cattle grazing ceased at Hart Mountain (see all 64 photo pairs in online supplementary material). These changes included a decrease in stream channel width, an increase in woody riparian vegetation, and a reduction in eroding stream banks. Almost all sites had a decrease in the amount of bare soil present (Fig. 5), and bare soil decreased by 90 % overall, changing primarily to grasses, sedges, and forbs, or to willow (Table 1). The width/depth ratio of streams varied widely but the visual assessment indicated an overall decrease in stream width, and the current average width/depth ratio of 5.0 appears to be much less than the historical value. Our results further suggest that the resurgence of riparian vegetation was not the result of any change in climate given that the years preceding when the historical photos were taken (1984–1991) were generally less drought-stressed than the years preceding photo retakes

(Fig. 4). Our comparisons of active versus passive management activities suggest that, at least in some circumstances, active restoration practices such as burning or the planting of willow are not necessary for the recovery of riparian willows after the removal of cattle.

The extent to which passive restoration has facilitated vegetation recovery at Hart Mountain speaks to the capacity for riparian systems to recover without further intervention (e.g., riparian plantings) (Fig. 8). Our results are similar to the pattern of passive restoration observed elsewhere when cattle were removed (Elmore and Beschta 1987; Kovalchik and Elmore 1992; Booth et al. 2012). With willows still absent along many of our study stream reaches 23 years after the removal of cattle, we speculate that the riparian recovery is still in the early stages. This situation may be similar to what was found in Yellowstone National Park 15 years after wolf reintroduction which was also in the early stages of recovery after reduced herbivory by wild ungulates (Ripple and Beschta 2012). It may take significantly longer for more extensive woody plant establishment (Floyd et al. 2003), but as the recovery proceeds, we expect additional cascading effects with increases in the diversity and populations of birds, mammals, other taxa, and overall riparian biodiversity (Earnst et al. 2012; Ripple and Beschta 2012).

The most dramatic changes between the historical and retake images were the widespread reestablishment of willow and the increased presence of rushes. Overall, rushes and willow both increased almost fourfold (Fig. 6). In many historical photos, rushes were nearly or entirely absent at sites where rushes were present in the retakes. Willow may be an important indicator of overall riparian health for some systems (Booth et al. 2012). Willows help reduce stream temperatures (Zoellick 2004; White and Rahel 2008) and protect stream banks against erosion (Vincent et al. 2009). The strong increase in willow cover observed in this study suggests that riparian systems at Hart Mountain are more stable, provide better habitat for many species, and are more resistant to erosion than when cattle were present.

Many willows observed in retake photos were not evident in historic photos. In addition to a limited amount of planting, willow establishment appears to be the result of two different mechanisms. The first is colonization of willow via seeds or woody segments from upstream sources. The second was through resprouting of existing willows that had found partial refugia inside incised stream banks. Incised stream banks can protect willows from grazing by creating refuges where short willows can persist. Once the grazing pressure has been removed, protected plants may rapidly grow taller. Both short and tall willows in historical photos exhibited a hedged or constricted shape resulting from repeated browsing (Painter and Ripple 2012), but in retake photos willows generally showed vigorous growth with no evidence of suppression by browsing.

A succession from bare soil to herbaceous vegetation to woody plants was observed following the removal of cattle. While there was only a modest increase in the amount of grasses, sedges, and forbs, 24 % (55.9 m of total transect length) of what was grasses, sedges, and forbs became willow and 65 % (58.2 m of total transect length) of what was bare soil became grasses, sedges, and forbs. This shows that as grasses, sedges, and forbs were establishing in the bare soil, willows were establishing in the grasses, sedges, and forbs at an almost equal amount (Table 1). Dobkin et al. (1998) found an exception to the succession that we describe for the majority of our sites. In a Guano Creek exclosure, they found a lack of willows after more than 30 years without cattle grazing, likely due to the establishment of a dense sedge community. We also found a reduction in the amount of sagebrush in riparian areas. This decrease in sagebrush could be indicative of an increase in the saturation zone providing more water for streamside vegetation. This could be due to bank stabilization and a resulting rise in the local water table possibly because of gains in flood-water detention storage and increases in baseflow (Beschta et al. 2013).

We observed a noticeable increase in aspen recruitment at the majority of sites where the understory of an aspen grove was visible. Other studies of aspen recruitment at Hart Mountain have also shown an increase in young aspen since the removal of cattle (Earnst et al. 2012; Beschta et al. 2014). The current state of most aspen groves observed at Hart Mountain is a decadent overstory dying out, with a new mid-story coming up, having been released from browsing pressure (Beschta et al. 2014). However, some aspen stands in historical photos have disappeared with only dead aspen littering the ground marking where there once was an aspen stand. Aspen are able to persist in a suppressed state without recruitment for a limited time until there is total stand mortality (Fitzgerald and Bailey 1984; Bartos and Campbell 1998).

The combination of the visual site assessment and the digital line intercept methods used for this study provided information that was synergistic, in that the combination of qualitative assessment and quantitative data allowed for site categorizations that would not have been possible if using only one type of data. The visual site assessment allowed for broad categorization of general riparian recovery trends. This method was fast, simple, and especially useful for showing general changes in the channel, bare soil, and willow cover. The digital line intercepts allowed for the detection of change in category type. This method detected what each category type changed into and would be useful if trying to quantify succession or disturbance patterns.

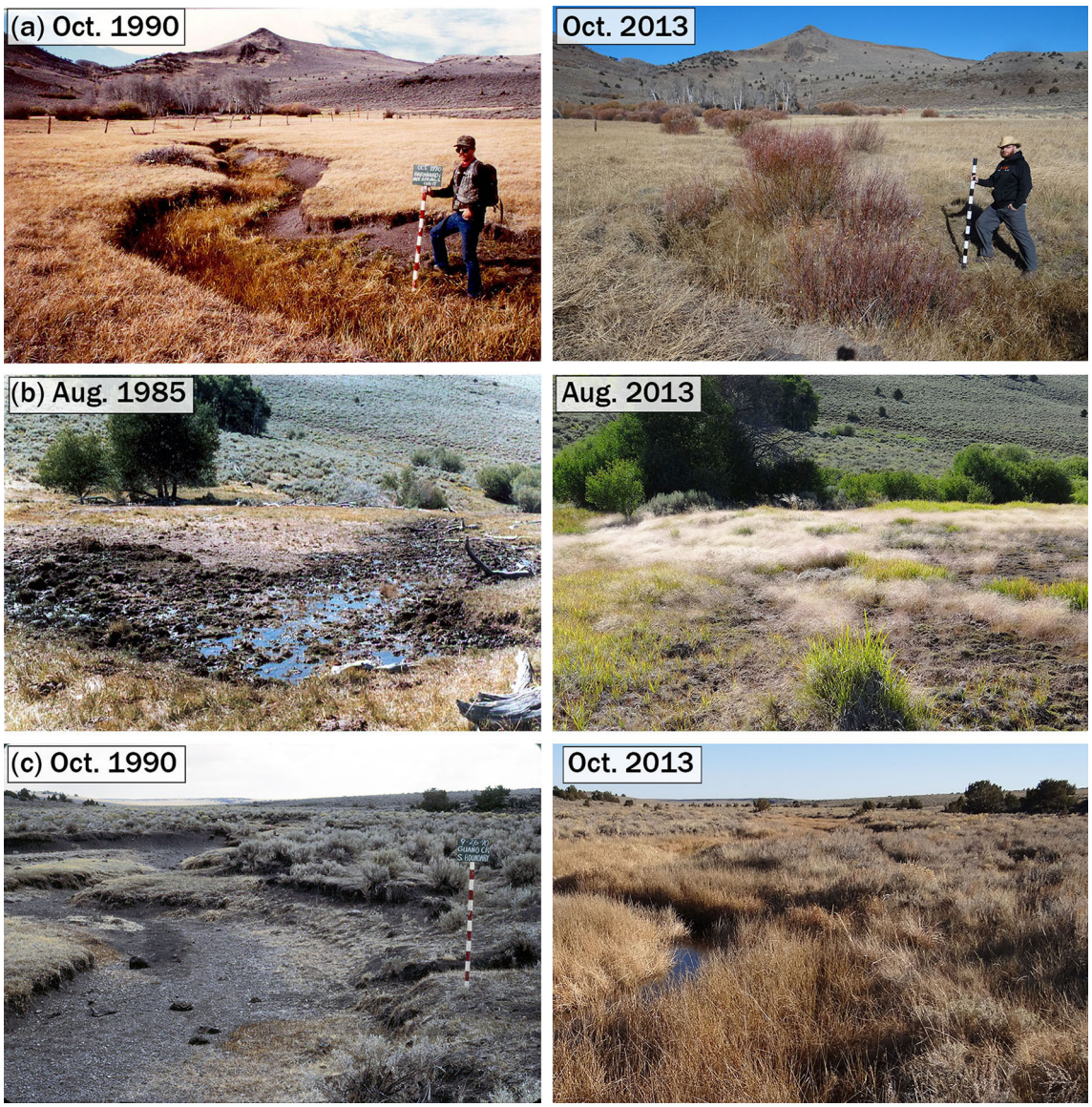


Fig. 8 Historical (*left*) and retake (*right*) photo pairs demonstrating the dramatic change that has happened at Hart Mountain and some of the mechanics of how cattle degraded the system and how the system is recovering. **a** Barnhardy meadow where the stream bed was eroding and willow nearly absent. The retake shows the stabilizing of the stream banks, narrowing of the active channel, and resurgence of willow. **b** Headwaters of Cold Creek where a seep had been trampled into a mud pit. In the retake, mosses and grasses have established in the seep, and aspen and willow have increased in the background. **c** Guano Creek at the southern border of the refuge. A dramatic increase in rushes and riparian vegetation is evident, as well as the stabilization of the stream banks and narrowing of the stream channel. Photo credits: images on *left*-Hart Mountain National Antelope Refuge, images on *right*-Jonathan Bachelor

There are inherent difficulties in trying to replicate photo locations of historical photos that were not intended for use as repeat photography stations. Given the nearly impossible task of trying to find the exact location of a historical photo, it should be assumed that there is some error in the alignment of photo pairs. However, the digital line intercept method showed the succession from bare soil to herbaceous species to willow, and had a high level of accuracy (91 %) in categorization of ground cover types. Accuracy was the lowest for categories similar in appearance (grasses, sedges, and forbs compared to rushes) and categories easily obscured (bare soil), but there is great potential to refine this process by using marked photopoints with marked transects on the ground. With new technologies such as ground-based LiDAR providing spatially explicit data, coupling this ability with photo retakes and other remote sensing applications could provide a level of change detection previously not possible.

In conclusion, this study at Hart Mountain National Antelope Refuge provides insight into how riparian systems in sagebrush/bunchgrass ecosystems of the Great Basin can respond to the cessation of livestock grazing. Fourfold increases in willow and rushes, with bare soil decreasing to a tenth of what it was during the period of cattle grazing, show just how much a system can change within only two decades of cattle removal. Hart Mountain presents a unique opportunity to assess passive restoration as a means to rehabilitate a landscape after decades of cattle grazing. The results are promising, and similar on sites with passive versus active restoration treatments such as burning or planting. Simply removing cattle from areas may be all that is required to restore many degraded riparian areas in the American West.

Acknowledgments We thank those who provided helpful discussions or assistance on this project including Jeff Mackey, Keely Lopez, Schyler Reis, Ariel Muldoon, Bill Pyle, Steve Herman, and Boone Kauffman. We also thank Robert Beschta and David Dobkin for reviewing an early draft, and two anonymous reviewers. Gail Collins kindly provided refuge data and background information for this study. Partial funding was provided to WJR by the Greater Hart-Sheldon Conservation Fund and Wilburforce Foundation, and to TMW by the Bureau of Land Management, Oregon State Office, and the U.S. Forest Service, Pacific Northwest Research Station.

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Journal of Arid Environments 59 (2004) 271–297

Journal of Arid Environments

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Community- and landscape-level responses of reptiles and small mammals to feral-horse grazing in the Great Basin

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Received 22 April 2003; received in revised form 29 August 2003; accepted 5 December 2003

Abstract

We investigated species- and community-level responses of squamate reptiles and granivorous small mammals to feral-horse grazing in two elevational strata across nine mountain ranges of the western Great Basin, USA. Although mammal species richness did not differ between horse-occupied and horse-removed sites, occupied sites possessed less community completeness (biotic integrity) and 1.1–7.4 times greater deer mice (*Peromyscus maniculatus*) than removed sites. In opposite fashion, horse-removed sites possessed greater reptile species richness and tended towards greater abundance for seven of nine species, yet unequal species pools across sites dictated that community completeness did not differ statistically between horse-removed and -occupied sites.
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Keywords: Granivorous small mammals; Great Basin; Feral-horse grazing; *Equus caballus*; Species pools; Reptiles; *Peromyscus maniculatus*; Sagebrush

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0140-1963/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2003.12.008

1. Introduction

As understanding of the natural environment continues to improve, ecological investigation and management move toward broader spatial scales. Although ecosystem management is rapidly becoming the dominant paradigm for investigating, managing, and monitoring ecological resources, our ability to characterize landscapes and predict landscape-level responses to single or interacting disturbances remains limited. This limitation results from a paucity of broadly collected data, an incomplete understanding of higher-order interactions, and a lack of knowledge of how diverse ecosystem components respond to disturbance (Franklin, 1993; Christensen et al., 1996).

Past studies of grazing disturbance have investigated effects of various grazing regimes on plants much more frequently than on any other ecosystem component, except perhaps soils. Studies investigating only the responses of vegetation can provide insight into the direct interaction between plant and herbivore (e.g. coevolution, effects of grazing intensity or timing on the interaction), but cannot predict responses of other taxa to grazing processes such as nutrient redistribution and soil trampling. Therefore, comprehensive understanding of ecosystem responses to large-mammal herbivory remains illusive. Although some grazing-impact studies (e.g. Bock et al., 1984; Heske and Campbell, 1991) have included larger numbers of variables, they often suffer from lack of replication and compare sites in relatively close proximity to each other (Brown and McDonald, 1995). Grazing studies such as these have provided insights into site-specific changes in various components of ecosystems, understanding as to the role of grazing intensity, duration and timing, and have investigated mechanisms of change. Though small-scale investigations allow for a high degree of experimental control, they may have questionable generality, particularly if sites are not representative of conditions or habitat types dominant on the landscape. Thus, although intensive multi-variable studies are increasing in frequency and have clarified many interactions, they may not represent spatially widespread relationships among grazers and other ecosystem components.

We investigated the grazing ecology of feral horses (*Equus caballus*) in the western Great Basin at a landscape scale using a diverse collection of ecosystem components. Because comparing replicates across broad spatial scales encompasses large amounts of environmental variability, we developed response variables that are less influenced by local conditions and applicable across all sites. We tested the null hypothesis that within relatively narrow elevational strata, sites experiencing horse grazing did not differ in their mammal and reptile faunas from ecologically similar sites from which horses had been removed 10–14 years earlier.

Ancestral horses had been absent from North America for at least 13,000 years (Grayson, 1989) when domestic horses (*E. caballus*) were brought to the southwestern United States by Spanish conquistadors near the end of the 16th century (Zarn et al., 1977; Wagner, 1983). Over time, these once-domesticated horses gave rise to populations of feral horses throughout much of western North America. In recent decades, much controversy has developed concerning the role of feral horses in ecosystems of western North America. The controversy has prompted

federal legislation (the Wild Free-Roaming Horse and Burro Act of 1971) designed to protect feral horses as well as continuing calls for the complete removal of feral horses from western rangeland. At present, land managers are charged with controlling the growth of horse populations and maintaining the biotic integrity of rangeland. A crucial part of the latter mandate is to acquire knowledge of the ways in which grazing by feral horses affects the composition (e.g. species diversity) and functioning of ecosystems. Due to differences in species habitat use, mode of digestion, diet, evolutionary history, and morphology, it is inappropriate to assume that effects of grazing by feral horses are similar in nature or in magnitude to effects of grazing observed for other introduced or native species (Beever, 2003). Furthermore, although numerous studies on grazing ecology of domestic horses have been published (e.g. Reiner and Urness, 1982; Menard et al., 2002), extrapolating these results to free-roaming populations may be problematic, particularly with respect to behavior.

One important indirect effect of grazing on ecosystems may be that imposed on small-mammal communities. Mammals perform a variety of ecological functions in semi-arid ecosystems, including seed dispersal, seed predation, and herbivory, as well as soil perturbation and aeration (Brown and Harney, 1993). Consequently, changes to mammal communities may also indirectly affect the plant community. Furthermore, mammals comprise a significant portion of the vertebrate biomass in sagebrush communities and may thus exhibit the greatest response to horse grazing. Changes in mammalian communities have been interpreted to indicate deterioration or simplification in many ecosystems (Carothers et al., 1976; Reynolds and Trost, 1980; Martell, 1983; Medin and Clary, 1989). In this study, we tested for an effect of feral-horse grazing on abundance of individual mammal species as well as on evenness and completeness of small-mammal communities. Evenness may be defined as the degree to which the total number of individuals is distributed evenly among all species (as in Simpson's index), and completeness defined as the proportion of the full complement of species that might occur historically or in the absence of disturbance.

In addition to small mammals, desert squamates (lizards, snakes, and amphisbaenids) occupy a broad diversity of trophic and habitat niches. Species in the Great Basin include insectivores, carnivores, and near-omnivores. Many of these species serve as important links between lower and higher trophic levels (Stebbins, 1985). Because of these links to other ecosystem components such as plants, invertebrates, and soils, loss of squamate diversity or large decreases in abundance may further simplify ecosystems. Although domestic cattle and sheep can affect the abundances of several lizard and snake species (Busack and Bury, 1974; Szaro et al., 1985; Jones, 1988), it remains unknown how the unique grazing ecology of feral horses affects reptile abundance and diversity. Presumably, grazing by feral horses can lead to soil compaction, decreases in prey abundance, and decreases in vegetative cover, all of which may affect the abundances and diversity of reptile species. The present study represents a preliminary investigation of the relationship between feral-horse grazing and the abundances and species richness of reptiles.

2. Methods

2.1. Study area: the Great Basin

The Great Basin has been used as a model system to test predictions of ecological theory (e.g. Johnson, 1975; Brown, 1978; Lawlor, 1998), because of its unique combination of physiography and climate. Within broad life zones (Merriam, 1890; Hall, 1995), mountain ranges of the Basin can be used as experimental replicates to test ecological hypotheses across broad spatial scales. The Great Basin currently has the highest percentage of its area as public land of any ecoregion in the contiguous United States, and thus it represents an important reservoir for biodiversity (Newmark, 1995).

Most biogeographic studies of the Great Basin have focused on small montane areas, which are relatively unaffected by human disturbance, as a result of their isolation and climatic harshness. In contrast, the sagebrush steppe, shrublands, and grasslands that dominate the Intermountain western United States are considered by some to comprise some of North America's most critically endangered ecosystems (Noss et al., 1995). By these authors' estimates, the sagebrush-steppe ecosystem of the Great Basin has been degraded across 98% of its original extent since European settlement, due primarily to livestock grazing. Although their potential role in landscape alteration has rarely been investigated, feral horses are also a common herbivore on the Great Basin landscape. For example, in Nevada, the state central to the Great Basin, management areas for feral horses occupy nearly 30% of the land area (Anonymous, 1997).

2.2. Selection of study sites

Because our broad sampling domain encompassed large amounts of environmental heterogeneity, we used seven criteria to try to achieve ecological similarity between horse-occupied sites and sites from which resident and immigrant horses had been removed for 10–14 years as a result of conflicts with railroad and private-property interests. We selected only sites that were: (1) on east-facing ($\pm 45^{\circ}$) slopes; (2) of low ($<40\%$) slope gradient; (3) at elevations loosely corresponding to high-elevation (2000–2300 m) and low-elevation (1350–1700 m) sagebrush zones in the western Great Basin; (4) dominated by sagebrush (*Artemisia tridentata*); (5) within 1 km of a dirt road (for small-mammal trapping accessibility); (6) relatively unused by cattle in the past two decades; and (7) had no evidence of recent (<15 yr) fire within or adjacent to the plot. By using these seven criteria, we were able to limit the effects that unmeasured confounding variables might have on our response variables, by tightening the study domain within the large geographic area. With these criteria, 10 horse-removed and 9 horse-occupied sites were selected (Fig. 1, Appendix A). For our horse-occupied sites, we chose areas where horses had been found during BLM aerial censuses of the previous 3 to 8 years. This meant that our horse-occupied sites did not necessarily represent the mean condition of their

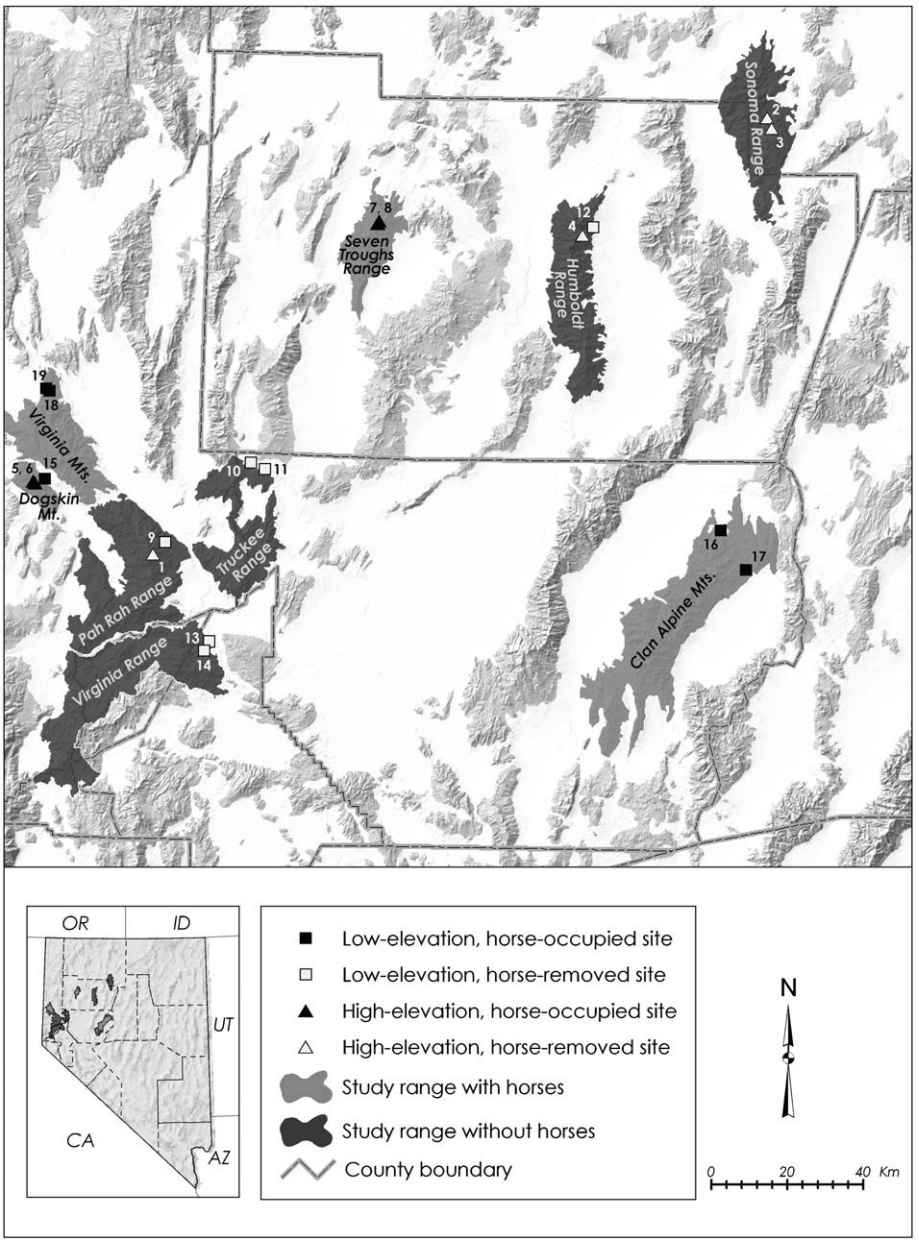


Fig. 1. Location of 19 study sites, stratified into high- (2000–2286 m) and low-elevation (1340–1700 m) sagebrush zones in nine mountain ranges of the western and central Great Basin of western North America. Reno, NV occurs in the lower left corner of the larger map.

respective herd management areas (HMAs); however, we sought to compare sites that received at least periodic use by free-roaming horses to horse-removed sites.

Because we were constrained by the seven selection criteria, our specific sites (135 m × 135 m each) did not reflect extreme grazing intensities; in every horse-occupied HMA, we observed one to several areas that had received notably more horse use than our selected sites. The BLM maintains data on horse densities only at the level of the HMA; thus, we can only state that horse densities for the HMAs in which our sites were located ranged from 0.005 to 0.015 horses/ha (Anonymous, 1997). At the finest spatial scale, we located sites (Appendix A) within homogeneous areas of vegetation (Daubenmire, 1959) distant from streams, because use by horses and other ungulates can be anomalously high near water sources in semi-arid ecosystems (Crane et al., 1997; Beever and Brussard, 2000).

The distribution of feral horses in western North America is organized into 209 BLM-administered HMAs, which occupy 14.2 million ha of land across ten western states (unpublished data, BLM). In addition, another 109 BLM "herd areas" totaling 27.5 million ha contained horses when the Wild Free-Roaming Horse and Burro Act was passed in 1971, but are not currently managed for horses. US Forest Service-administered herd areas occupy an additional 1.1 million ha of land in the western United States (Anonymous, 1997). Boundaries for these HMAs were delineated according to location of horses at the time the (1971) Act was passed. Horse-occupied sites were located in HMAs that exhibited horse densities ranking among the top half (21 of 42) of HMAs in central and western portions of northern Nevada in 1997. Across all our sites, the size of HMAs ranged from 3077 to 178,920 ha, and mean size (±1 SE) was 61,756 ± 20,613 ha. Given that horse removals were based on socio-political rather than biological criteria, and that horse-removed and horse-occupied sites were relatively interspersed across the landscape, we did not expect a priori confounding differences in sites of the treatment groups.

This was confirmed in comparisons between horse-occupied and horse-excluded sites of abiotic variables ($n = 10$) analysed both individually in two-way ANOVAs and collectively in reciprocal-averaging analyses (Beever, 1999; Beever et al., 2003). Horse-removed and horse-occupied sites did not differ significantly in their elevation, aspect, mean slope gradient, average annual precipitation, mean annual temperature, precipitation during either year of sampling, cover of bedrock, production (lb/ac), available water capacity, erosion Factors K and T, or frost-free days/yr, nor in any of their qualitative soil properties (Beever, 1999; Beever et al., 2003). This lack of difference provides additional evidence that any differences in vegetation, animal, and soil response variables would be due to presence of horses rather than abiotic parameters.

In practice, the most difficult site-selection criterion to satisfy was finding areas not grazed by cattle. In addition to using BLM allotment data, we performed fecal counts at all sites to find areas that had received significantly less recent use by cattle than by horses. For both horse-removed and horse-occupied sites, we spent a day or more per HMA in areas identified as appropriate by managers to find two sites that met all selection criteria. We could census no more than two sites at one time, and we could find only two or three sites in each HMA that met all of our selection criteria.

If three potential sites existed, the site with the highest cattle use (i.e. lowest ratio of # horse defecations/# cattle defecations) was avoided.

2.3. Field sampling

We sampled each of our response variables during May through August in both 1997 and 1998, except that reptiles were sampled only in 1998.

At each site, we established a 10×10 grid of Sherman small-mammal live traps (one trap/station) with 15 m between traps and lines, and trapped for three consecutive nights with a bait mixture of millet, milo, and sunflower seeds. This 1.82-ha grid delineated the boundaries of the site for all other sampling methods. For each individual captured, we recorded the species, mass, sex, and reproductive status. Next, each individual was marked near the shoulders on the dorsal side with a permanent-dye pen (using a blue pen on the right side on day 1 and a red pen on the left on day 2), and released. These markings were intended to last only a few days, and identified animals that had been previously captured. We suspended trapping when significant rain was predicted overnight. To assess the efficacy of our trapping duration in detecting target species, we trapped for extended duration at one low- and one high-elevation site in 1998.

During 1998, we recorded sightings of all squamate reptiles at or immediately adjacent to ($\leqslant$20 m from) the trapping grid at each site during sampling of our other indices (e.g. incidental captures in small-mammal traps). Although these surveys did not occur along transects designed exclusively for reptiles, the search effort for these encounter surveys was roughly equivalent across sites because we spent approximately the same amount of time at each 2.4-ha (including 20-m buffers) site. Furthermore, $>95\%$ of our search effort at each site occurred along the small-mammal trap lines, providing consistent search coverage across sites. We recorded abundance of each species; an individual was only counted if it was observed simultaneously with previously recorded conspecifics or if it was found >30 m from other sightings. We advocate use of more intensive field methods (e.g. mark-recapture techniques) in future studies of reptilian response to horse grazing, especially for investigating abundance of individual reptile species.

To investigate potential mechanisms by which small mammals and reptiles might be affected by the presence of horses (if influence were in fact detected), we also measured soil and vegetation attributes at sites. We measured soil-surface hardness using a handheld manual penetrometer (Soiltest, Inc., Chicago, IL) by depressing the 6.4-mm diameter tip 1 cm into the soil (Bradford et al., 1986; USDA, 1993) in shrub interspaces at 25 locations per site. To characterize structure, cover, diversity, and composition of vegetation, we used four 50-m line-intercept transects (Bonham, 1989), one located randomly in each quadrant of the trapping grid. Complete description of vegetation and soil sampling methods occur in Beever et al. (2003).

At each site, we assessed relative intensity of recent use by cattle, horses, and all native ungulates by tallying fecal piles within 2 m of an imaginary line drawn along the rows of the trapping grid, which produced a $4\,\text{m} \times 1485\,\text{m}$ undulating strip transect. To avoid over-counting instances when an individual engaged in

continuous defecation while moving, we excluded cattle defecations <8 cm in diameter and horse defecations having three or fewer pellets.

2.4. Analyses

2.4.1. Description of derived variables

We combined data from 1997 and 1998 to get cumulative measures of richness for plant species and small-mammal communities. We calculated Simpson's and Berger-Parker diversity indices for plants and small mammals using equations presented in Magurran (1988). More complete definitions of the shrub-continuity and soil-hardness variables, as well as variables used in calculating the diversity indices, appear in Beever (1999).

Because we investigated horse disturbance across a broad area and to allow appropriate comparisons across all sites, our response variables had to be more generic than variables often used to detect disturbance at smaller scales. For example, to account for variability in microhabitat and geographic location among our sites, we created a community variable to assess richness of the small-mammal faunas across sites, whose potential species pool varied among sites. Realized richness of rodents (RRR) at each site represents the arcsine-transformed ratio of small-mammal species captured to the total number of species possibly occurring at a site [arcsin (♯spp. captured/♯spp. possible)]. This hypothetical list of possible species was created using geographic and elevational distributions of mammals in Nevada (Hall, 1995). These lists only included nocturnal rodent species that could fit in a small ($8 \times 8 \times 25$ cm) Sherman trap and persist in sagebrush habitats distant from streams. Additionally, a species was included only if appropriate microhabitat was present at a site (for all intrinsic, non-dynamic habitat properties of sites) or potentially occurred at the site (for site properties that could be affected by horses; e.g. soil-surface properties).

We created two versions of the variable, an "inclusive RRR" and a "restrictive RRR." The more restrictive version of RRR included only granivores, and excluded all habitat specialists that did not have equal chance of occurrence at all sites (such as *Neotoma lepida*, *Peromyscus crinitus*, *P. truei*, etc.) because their habitat was present within only some of our sites. In contrast, the inclusive RRR variable included all of the restrictive RRR species, plus non-granivorous nocturnal mammals (such as microtines and *Onychomys* spp.) and habitat specialists. However, these extra species were included as potential fauna for inclusive RRR only when they were captured at a site.

As we did for rodents, we investigated treatment effects on completeness of squamate communities across a broad spatial domain by comparing realized richness of detectable squamates (RRDS) at sites. Given that distribution of reptiles in the Great Basin is less well known than for mammals, we supplemented the comprehensive treatment of herpetofauna in Nevada (Linsdale, 1940) with a commonly used field guide (Stebbins, 1985) and sampling by other authors near our study region (Espinoza and Tracy, 1999; St. John, 2002) to ascertain whether sites fell within a species' geographical range. Secondly, we used these references,

supplemented with museum specimens and other unpublished records (archived at the Biological Resources Research Center, Univ. of Nevada, Reno) to determine elevational boundaries for species. Elevational ranges from areas closer in latitude to our sites (e.g. Espinoza and Tracy, 1999) were given priority over elevational ranges for a species' entire range (Stebbins, 1985). The third filter considered whether appropriate microhabitat existed within the 2.4-ha area at sites (rocky outcrops for *Crotaphytus bicinctores*, sandy gravelly soils for *P. platyrhinos*). We used this filter for both restrictive and inclusive RRDS because only 9 species could potentially be used in the inclusive version, and we did not want to reduce this pool further.

As for mammals, we again created restrictive and inclusive lists of RRDS at sites. The more restrictive variable included only (subsets of) the 9 lizard species that could be detected in the course of other work at sites, without extensive searches targeted specifically for reptiles. In contrast, the more inclusive list included other squamate species as potential species at sites, but only when they were observed at the site. We added these species in this manner because they are not easily detectable without targeted searches at sites, which are difficult to standardize across sites—an important consideration when assessing treatment effects. Our relatively poor understanding of reptile distributions also led us to be conservative in removing potential species from the species pool at each site—we included in the restrictive variable even species that were only marginally possible at sites.

These variables resemble those developed independently by Cam et al. (2000), who investigated relative species richness and community completeness in birds of the US mid-Atlantic region. They concluded that the existence of regionally different species pools mandates a flexible specification of the "reference community" in broad-scale management and conservation investigations.

Because deer mice (*P. maniculatus*) have frequently been found to be insensitive to or thrive under disturbance, we sought to compare their relative importance in the small-mammal community at horse-occupied and -removed sites (in addition to simply comparing their abundance). For tests involving the rank abundance of deer mice (*P. maniculatus*) within mammal communities at sites, we ranked inclusive RRR species according to the number of individuals trapped, with the most abundant species receiving a ranking of 1. Although deer mice have been captured at nearly all elevations and habitat types in northern Nevada, we excluded all sites ($n = 3$) at which deer mice were not caught in either year. This effectively made our assessments of effects of horse presence on deer mouse dominance more conservative, because all three sites were horse-excluded sites; assuming that deer mice were present at these sites would give them the rank of least abundance at each site. At sites in which deer mice were caught in one of the two years, we assigned a rank of

$$[1 + (\text{number of inclusive RRR species captured})]$$

to deer mice for the year in which they were not caught, thereby assuming that their densities were lower than all other species captured that year. We compared ranks between horse-occupied and horse-removed sites in separate analyses for high- and low-elevation sites using Mann–Whitney U tests (Sokal and Rohlf, 1995).

2.4.2. Comparing horse-occupied and horse-removed areas: analytical techniques

Because we performed tests on numerous permutations of diversity indices, we evaluated significance of these tests using sequential Bonferroni corrections (Sokal and Rohlf, 1995). In contrast, because tests for other variables addressed fundamentally different questions (e.g. effects due to direct vs. indirect mechanisms), and because we wished to be cautious to avoid Type II errors (for a disturbance agent whose effect on vertebrates has not previously been investigated) we did not employ such corrections for other response variables. For comparisons of response variables, we performed two-way analyses of variance (ANOVAs) using horse density and elevation as binary categorical variables, and probabilities in Table 1 refer to effects of horses across all sites when stratified by elevation. We used Bartlett's test of homogeneity of variances to identify significant heteroscedasticity or severely non-normal distributions (Sokal and Rohlf, 1995).

When needed, arcsine (for all percentage variables), logarithmic, or square-root transformations were used to achieve homoscedasticity, normality, and additivity of treatment effects (Sokal and Rohlf, 1995). For logarithmic transformations with zero values, we added 1 to the value of all sites before transforming the data for count variables and 0.1 to all sites for variables with lower values (i.e. diversity indices and soil hardness) (Sokal and Rohlf, 1995). For comparing abundances of single mammal species, to avoid bias resulting from false zeroes we only included sites that possessed appropriate habitat for that species, following species descriptions in Hall (1995) and our inclusive lists of potential species. Statistical analyses were performed using StatView versions 4.02 and 5.0 (SAS, 1998). Unless otherwise noted, we used an alpha level of 0.05 to determine significance for all statistical tests.

3. Results

3.1. Fecal counts

Standardized fecal counts revealed that horses were the dominant feral grazer at our sites in recent years, as the ratio of horse defecations/cattle defecations across years at all horse-occupied sites exhibited a geometric mean of 10.4:1. Furthermore, fecal counts suggested that intensity of cattle grazing did not differ between horse-grazed and horse-removed sites during 1997 ($p = 0.71$) or 1998 ($p = 0.60$). Pellet counts of other ungulates (primarily mule deer, *Odocoileus hemionus*, and pronghorn antelope, *Antilocapra americana*) also did not differ between horse-occupied and horse-removed areas (two-way ANOVAs, both $p > 0.20$) (Beever et al., 2003).

3.2. Small mammals

We observed several trends in composition of small-mammal communities with respect to horse presence or absence. Data from both 1997 and 1998 showed that

Table 1
Means ± 1 SE for small-mammal and reptile response variables at 19 sites in the western Great Basin, USA, during 1997 and 1998 for each treatment-elevation category

	1997					1998				
Elevation	High		Low		Probability	High		Low		Probability
Horse presence	Removed	Occupied	Removed	Occupied		Removed	Occupied	Removed	Occupied	
Small mammals										
Total number of individuals captured/site	39.8 ± 10.3	68.5 ± 17.0	36.0 ± 13.5	26.4 ± 6.6	0.44	30.8 ± 4.6	31.3 ± 3.9	32.0 ± 7.0	50.8 ± 15.3	0.43[a]
Total number of species captured/site	4.5 ± 0.5	5.5 ± 0.3	6.5 ± 1.7	3.8 ± 1.0	0.42[b]	4.5 ± 0.9	4.0 ± 0.4	5.7 ± 1.1	4.8 ± 1.1	0.51
Realized richness of granivorous rodents (inclusive)	60.0 ± 11.5	53.1 ± 4.3	75.6 ± 12.2	36.9 ± 8.3	0.032	50.0 ± 5.8	33.5 ± 4.1	68.7 ± 11.4	40.9 ± 9.8	0.042
Realized richness of granivorous rodents (restricted)	60.0 ± 11.5	53.1 ± 4.3	73.6 ± 12.3	33.6 ± 8.9	0.032	50.0 ± 5.8	33.5 ± 4.1	67.8 ± 11.1	37.6 ± 9.3	0.032
Cumulative (1997 + 1998) inclusive RRGR						65.8 ± 10.0	56.7 ± 2.6	85.3 ± 8.7	52.2 ± 4.9	0.01
Cumulative (1997 + 1998) restricted RRGR						65.0 ± 9.6	56.7 ± 2.6	81.9 ± 9.5	47.7 ± 5.1	0.012
# Individuals of deer mice per site	14.5 ± 2.5	31.0 ± 6.3	2.3 ± 1.9	8.6 ± 1.2	0.017	14.3 ± 3.1	15.0 ± 2.7	3.3 ± 2.2	24.4 ± 8.8	0.007[a,c]
Percent of (inclusive RCR) as deer mice	45.4 ± 12.7	48.1 ± 6.9	4.3 ± 2.6	23.2 ± 13.2	0.40	59.3 ± 12.9	58.4 ± 10.7	8.6 ± 5.2	58.8 ± 13.9	0.019[c]
Rank of deer mice, high sites	1.5 ± 0.3	1.0 ± 0.0			0.25	1.25 ± 0.3	1.25 ± 0.3			0.99
Rank of deer mice, low sites			3.5 ± 0.5	1.7 ± 0.3	0.037			2.5 ± 0.9	1.6 ± 0.4	0.37
Squamate reptiles										
Mean # squamate species per site								4.8 ± 0.2	2.2 ± 0.9	0.01
Mean # squamate individuals per site								10.7 ± 1.1	5.0 ± 3.0	0.09
Community completeness of reptiles (restricted)								45.3 ± 6.1	26.7 ± 11.3	0.13
Community completeness of reptiles (inclusive)								52.5 ± 3.8	28.1 ± 12.1	0.07

All percentages are reported as proportions of 100%, but were arcsine-transformed before being analysed. Probability refers to p-value of the test of the effect of presence of horses on response variables, as measured by two-way ANOVAs with elevation as a binary cofactor (except for reptile variables, for which only low-elevation sites were analysed with a 1-way ANOVA). Deer mice = *Peromyscus maniculatus*.

[a] Log_{10}-transformed data.

[b] Square-root transformed data.

[c] Significant interaction; presence of horses only significant among low-elevation sites.

[#] Bonferroni–Dunn post hoc tests showed effect of horse presence was significant ($p < 0.050$) as a main effect.

horse-removed areas contained a greater proportion of the species potentially present at each site (restrictive RRR and inclusive RRR, $p<0.05$; Table 1). In addition, in spite of a number of interannual differences in species composition at sites (Table 2), captures pooled across years showed the same pattern (Table 1). In addition, of 21 species (including 14 nocturnal granivorous rodents) captured in 1997, eight species (including six rodents) were captured exclusively at horse-removed sites (Table 2). In contrast, no species were captured exclusively at horse-occupied sites during 1997. Of 20 species (including 13 nocturnal granivorous rodents) captured in 1998, five species (including four rodents) were captured exclusively at horse-removed sites (Table 2). In contrast, only two species were captured in 1998 exclusively at horse-occupied sites, and both were single incidental captures (a shrew and a skunk).

Most individual species did not significantly differ in capture rates between horse-occupied and horse-removed sites, often due to low capture rates per species. The most notable exception was that deer mice were much more abundant at horse-occupied sites than at horse-removed sites in both 1997 (all sites, $p = 0.017$; Tables 1 and 2) and 1998 (low-elevation sites, $p = 0.032$; Beever, 1999). Among low-elevation sites, we captured 3.4 and 7.4 times more individuals at horse-occupied sites than at horse-removed sites in 1997 and 1998, respectively, and 1.1–2.1 times more deer mice at horse-occupied versus horse-removed sites among high-elevation sites (Tables 1 and 2). In 1998 but not significantly so in 1997, deer mice occupied greater proportions of the community of inclusive RRR species at sites with horses than at horse-removed sites (Table 1).

We observed a number of less robust trends in small mammals that may have ecological and management significance, especially if corroborated by subsequent investigations. When considering sites appropriate for the species (Hall, 1995), sagebrush voles (*L. curtatus*) exhibited significantly higher abundances at horse-grazed areas in 1997 ($F_{1,5} = 7.66$, $p = 0.040$). However, this difference was driven by high capture rates at both sites in one horse-occupied HMA. During 1998, Merriam's kangaroo rats (*Dipodomys merriami*) were less abundant at low-elevation sites receiving horse grazing than at horse-removed sites ($F = 6.63$, df $= 1.8$, $p = 0.033$). Several other species were caught more frequently at horse-removed sites, including western harvest mice (*Reithrodontomys megalotis*), white-tailed antelope ground squirrels (*Ammospermophilus leucurus*), and, during 1998 only, long-tailed voles (*Microtus longicaudus*) and Merriam's kangaroo rats, although low capture rates obscured the robustness of these trends (Table 2). In contrast, several species exhibited non-significant trends towards greater abundance at horse-disturbed sites, including pinyon mice (*P. truei*) in 1998 and Ord's (*D. ordii*) and Panamint (*D. panamintinus*) kangaroo rats in 1997 (Table 2). At our 19 sites, the presence of horses did not significantly affect the total number of mammal individuals (of all species) captured at a site, nor any of the diversity indices in either year. All comparisons of diversity indices were not significant after we performed Bonferroni corrections for multiple tests of the same question (Table 3).

Table 2
Numbers of individuals of 17 non-incidental and 2 incidental mammal species captured across all sites in each year, summed within treatment-elevation categories

Year	Treatment-covariate category (number of sites)	*Perognathus longimembris*	*P. parvus*	*Chaetodipus formosus*	*Microdipodops megacephalus*	*Dipodomys panamintinus*	*D. ordii*	*D. microps**	*D. merriami*	*Onychomys leucogaster**	*O. torridus**	*Reithrodontomys megalotis*	*Peromyscus crinitus**	*P. maniculatus*	*P. truei**	*Neotoma lepida**	*Microtus longicaudus**	*Lemmiscus curtatus**	*Ammospermophilus leucurus*	*Tamias* sp.
1997	High, excluded (4)	0	55	0	0	0	0	0	0	0	0	3	0	59	0	0	1	4	0	32
	High, horses (4)	0	52	0	0	3	4	0	0	0	0	1	0	126	0	0	1	32	0	52
	Low, excluded (4)	19	43	17	3	5	3	1	1	4	1	5	3	9	0	2	0	0	7	1
	Low, horses (5)	0	42	21	0	18	4	0	1	0	0	4	0	38	0	1	0	2	3	0
1997	Total	19	192	38	3	26	11	1	2	4	1	13	3	232	0	3	2	38	10	85
1998	High, excluded (4)	0	35	0	0	0	0	0	0	0	0	0	1	57	0	0	5	0	0	19
	High, horses (4)	0	44	0	0	0	2	0	0	0	0	0	0	60	0	0	1	0	0	16
	Low, excluded (6)	7	66	30	0	6	8	0	63	0	0	8	0	20	2	1	0	1	23	1
	Low, horses (5)	0	34	50	0	5	2	0	1	0	0	2	0	122	26	0	0	1	7	0
1998	Total	7	179	80	0	11	12	0	64	0	0	10	1	259	28	1	6	2	30	36

Note: In addition to the last two species (*A. leucurus* and *Tamias* sp.), 22 individuals of 6 species not listed (*Sorex* sp., *Mustela frenata*, *Spilogale gracilis*, *Spermophilus lateralis*, *Thomomys talpoides*, and *Sylvilagus nuttalli*) were captured incidentally across both years. Captures from these 8 incidental species were included only in calculations of number of individuals per site.
Species with an "*" were included in inclusive RCR, but not in restricted RCR. The sequence and scientific names of species follow Hall (1995).

Table 3
Numbers of individuals observed for each of 14 squamate species during 1998 surveys at 19 study sites in Nevada, USA

Site number	Mountain range	Elevation (m)	*Gambelia wislizenii*	*Crotaphytus bicinctores*	*Cnemidophorus tigris*	*Callisaurus draconoides*	*Phrynosoma platyrhinos*	*Sceloporus graciosus*	*S. occidentalis*	*S. magister*	*Uta stansburiana*	*Eumeces skiltonianus*	*Coluber constrictor*	*Pituophis melanoleucus*	*Salvadora hexalepis*	*Crotalus viridis*	Total species richness	Total number of individuals per site
1	Pah Rah range	2134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Sonoma range	2164	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	2
3	Sonoma range	2118	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
4	Humboldt range	2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Dogskin mountain	2060	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1	6
6	Dogskin mountain	2200	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	2
7	Seven Troughs range	2225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Seven Troughs range	2286	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	3
9	Pah Rah range	1500	3	0	2	0	0	0	0	0	0	1	0	1	1	0	5	8
10	Truckee range	1540	2	0	3	0	4	4	0	0	1	0	0	0	0	0	5	14
11	Truckee range	1500	2	0	5	0	2	0	0	0	2	0	0	0	0	0	4	11
12	Humboldt range	1433	0	0	2	0	0	0	1	2	0	0	1	0	1	0	5	7
13	Virginia range	1500	3	0	0	1	0	4	0	0	3	1	0	0	0	0	5	12
14	Virginia range	1400	1	0	0	0	1	0	3	0	6	0	0	0	0	1	5	12
15	Dogskin mountain	1646	1	0	7	0	0	0	3	5	0	0	0	0	0	0	4	16
16	Clan alpine mountains	1340	1	1	1	0	0	0	0	0	0	0	0	0	0	0	3	3
17	Clan alpine mountains	1700	2	0	1	0	2	0	0	0	0	0	0	0	0	1	4	6
18	Virginia mountains	1646	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	Virginia mountains	1554	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
# of low-elevation sites at which present		8	1	7	1	4	2	3	2	4	2	1	1	2	3			
Total # individuals of this species (low-elev. sites)		15	1	21	1	9	8	7	7	12	2	1	1	2	2			
Average # of individuals per potential (low-elevation) horse-removed site		1.83	0.00	2.00	0.20	1.17	1.33	0.67	0.33	2.00								
Average # of individuals per potential (low-elevation) horse-occupied site		0.80	0.25	1.80	0.00	0.40	0.00	0.60	1.25	0.00								

The 5 leftmost spp. were used for inclusive but not restrictive richness estimates.

3.3. Squamate reptiles

We encountered reptiles at 14 of 19 sites during our four days at each site in 1998. Sites at high elevations averaged only 1.75 individuals per site and had at most one species (either *Sceloporus* sp. or *Crotalus viridis*; site numbers 1–8, Table 3). Consequently, we focused our analyses for these ectotherms on the lower-elevation sites that had greater abundances of individuals and species. Among low-elevation sites, horse-removed sites exhibited higher absolute species richness (Mann–Whitney U-test, $Z = -2.556$, $n = 11$, $p = 0.01$) than did horse-occupied sites. When different potential species pools were accounted for on the basis of geographic range, elevation, and microhabitat, however, low-elevation horse-removed sites did not possess more complete reptile assemblages than did horse-occupied sites ($F_{1,9} = 2.8$, $p = 0.13$; Table 1). Six of the seven snakes captured or observed occurred at horse-removed sites, as did both occurrences of skinks (Table 3). Even though 7 of the 8 low-elevation incidental records were from horse-removed sites, the inclusive version of RRDS remained statistically indistinguishable between horse-occupied and horse-removed sites at low elevation ($F_{1,9} = 4.2$, $p = 0.071$; Table 1).

In terms of total abundance of reptiles, we counted twice as many individuals at horse-removed sites (10.7 per site) than at horse-occupied sites (5.0 per site) (Table 1). In terms of observed abundance of individual reptile species, all five of the most common species (ranked either by number of sites at which detected or abundance across all sites) were more abundant at horse-removed sites (Table 3). These species included *Gambelia wislizenii*, *Cnemidophorus tigris*, *Phrynosoma platyrhinos*, *Sceloporus graciosus*, and *Uta stansburiana*. Two of the remaining species (*Callisaurus draconoides* and *S. occidentalis*) were slightly more abundant at horse-removed sites they could potentially inhabit, whereas *S. magister* and *C. bicinctores* appeared more abundant at potentially habitable horse-occupied sites (Table 3).

4. Discussion

Large mammalian herbivores exert numerous influences on landscapes they inhabit, including trampling and disturbance of soils, altering nutrient distribution, selective consumption of plant material, and trampling of vegetation (Archer and Smeins, 1991; Augustine and McNaughton, 1998). As a result, these animals can modify ecosystems by creating spatial heterogeneity, modulating successional processes, and controlling the switching of ecosystems between alternative states (Hobbs, 1996). The effects that large herbivores impose upon a given ecosystem will depend upon many factors, including the plant-animal coevolutionary history, soil development, climate, recent weather, frequency and seasonality of the grazing, effects of other sympatric species, and often most importantly, animal density (Milchunas et al., 1988). As a result of the non-uniform patterns of habitat use by horses (as for other native ungulates; see references in Hobbs, 1996), the magnitude

of grazing impacts will vary widely across the landscape, from areas minimally affected to areas used heavily (Pastor et al., 1997).

Detecting effects of different grazing intensities on discontinuously distributed vertebrates across broad spatial domains necessarily requires a more sophisticated response variable than simple species richness. Reptiles and granivorous small mammals should relate quite differently to the disturbance processes of a large-bodied grazer (e.g. nutrient redistribution, trampling of soils and vegetation), given their distinct physiological and life history traits. Not surprisingly, incorporation of geographic range, elevation, and microhabitat constraints on potential species pools reversed the apparent effect of horses on both reptiles and small mammals, but in opposite directions (in terms of significance) for the two guilds. Furthermore, this reversal of treatment effect occurred whether we used a more restrictive guild of species that our standardized sampling methodology was designed for or a more inclusive guild of species that were incidentally detected.

For small mammals, although simple species richness suggested that horse-occupied and horse-removed sites were faunally similar, RRR was significantly greater at horse-removed sites in both years. Discrepancies between tests of species richness versus guild completeness (also known as biotic integrity) may arise from variability in the true species pools across sites or from our estimation of species pools at sites. For mammals, species pools were not equivalent between horse-occupied and -removed sites for two reasons. First, our study area was bisected by the Lahontan trough, which contains a unique set of species within its extent and demarcates the geographic range of several other small-mammal species. Second, horse-removed sites at lower elevation averaged nearly 100 m lower, falling in some cases below the lower elevational limit of various species. In exact opposite fashion, although species richness of reptiles was statistically greater at low-elevation horse-occupied sites, community completeness at low-elevation sites was statistically indistinguishable between horse-occupied and horse-removed sites. This loss of significance stemmed from the larger species pools of reptiles at horse-removed sites, which in turn were partly caused by the lower elevation and position of horse-removed (relative to horse-occupied) sites at low elevation.

4.1. Small mammals

Few species of small mammals exhibited significant differences in abundance between horse-occupied and horse-removed sites. This lack of difference was often due to low capture numbers, which led to low statistical power to detect significant differences in abundance. For example, we predicted that western harvest mice would be caught at lower abundances at sites with horses because these mice forage and nest usually in areas of grasses (Hoffmeister, 1986; Hall, 1995), the major dietary item of horses. Although the trend in harvest mice was observed during both years and across elevational strata (Table 2), it was never statistically significant, even though grass cover was significantly lower at horse-occupied sites in both years

(Appendix B). The lack of individual species differences may also have been due to the broad geographical range across which our sampling areas occurred and the consequent heterogeneity in our sites.

This heterogeneity prompted us to devise a generic metric of guild richness, RRR, which suggested that horse-occupied sites had more depauperate granivorous rodent faunas in both 1997 and 1998. We found more depauperate communities at horse-occupied sites even though we captured more total individuals at horse-occupied sites (due mostly to deer mice) during both years. If, contrary to advice of Cam et al. (2000), one ignores differences in potential species pools across sites and simply analyses total species richness of mammals at sites, we see that species richness was not statistically different between horse-occupied and horse-removed sites (in a two-way ANOVA with elevation). This was true in both 1997 and 1998 using the pool of restrictive RRR species, inclusive RRR species, or all mammals ($p > 0.42$; Table 1). If species pools truly did not vary across sites, one could employ a method similar to that developed by Solow (1993) to detect altered community structure for our data. However, that randomization test re-assigns individuals to the treatments on the assumption that species pools are equivalent among sites, which is difficult to substantiate for our large domain. Independent of the RRR analyses, importance of biogeographic influence on richness was further suggested by evidence from stepwise regressions of species richness, using the three measures of richness from the previous sentence. In those regressions, no variable entered the model (for any measure) in 1997 nor for the all-species measure in 1998, even though at least one variable entered the model for every other plant and mammal response variable in both years (Beever, 1999). The small-mammal regressions used elevation, presence of horses, site exposure, available water capacity, precipitation, and mean annual number of frost-free days as predictors. Whether the site was exposed or sheltered was the only variable that entered the other two models in 1998.

We chose to perform this research in the summer, when the highest percentage of the lizard and small-mammal faunas is detectable via trapping or observation. Although most of our sites are sufficiently remote to be accessible only during a few months per year, greater understanding of responses of granivorous small mammals to horse grazing could be obtained by trapping across seasons. Consequently, our conclusions are strictly valid only for summer assemblages.

Higher total abundance of mammals at our horse-occupied sites agrees with findings that rodent and lagomorph densities may increase in moderately degraded rangelands, as these densities can correlate with large amounts of eroded ground, high dicot diversity, and low grass cover (Fogden, 1978; Archer and Smeins, 1991; Kerley, 1992). The point has been made, especially within individual species, that density (or abundance) of any mammal is not necessarily an accurate reflection of habitat quality (Van Horne, 1983). Nonetheless, we have observed alteration in mammals at the level of communities (not species), and our evidence of environmental alteration suggested by small mammals is supported by parallel evidence from vegetation, soils, squamates, and ants (Appendix B).

Although it is difficult to ascertain mechanisms by which small-mammal communities apparently became more depauperate without manipulative

experiments or data sufficient for path analyses, some observations may shed insight. Given that the vast majority of the small mammals we captured are fossorial and spend most or all daylight hours underground, it is not surprising that several desert rodent granivores are known to be sensitive to soil characteristics such as surface hardness (e.g. Hoover et al., 1977; Hoffmeister, 1986). Increased hardness could increase energy expenditures for digging mammals or simply reduce the area available for burrowing activity. Data from 1998, when soil sampling occurred at more sites than in 1997, suggest that the completeness of the fundamental granivorous guild (=restrictive RRR) was closely associated with soil-surface hardness across 18 sites ($r = -0.57$, $p = 0.01$). The more complete guild that included habitat specialists (=inclusive RRR) was also associated with hardness, but less strongly ($r = -0.51$, $p = 0.03$). Correlation in 1997 was even stronger ($r = -0.70$ and -0.73, respectively), even though hardness was sampled only at 8 sites. Although some granivorous mammals are strongly influenced by characteristics of the sympatric vegetation, community richness of mammals was not associated strongly with sites' shrub cover, plant species richness, continuity of the shrub mosaic, or total vegetative cover. Restrictive (but not inclusive) RRR was marginally correlated with grass cover at sites ($r = 0.45$, $p = 0.051$).

The deer mouse, perhaps the most abundant, widely distributed, and eurytopic species of mammal in both Nevada (Hall, 1995) and North America (Hall, 1981), was captured more frequently at horse-occupied sites during both 1997 and 1998. Other authors have found deer mice to be insensitive to various types of disturbance, and even to flourish in conditions of environmental or disturbance-imposed harshness (e.g. Martell, 1983; Songer et al., 1997). Interestingly, differences between horse-occupied and horse-removed sites were greater at high elevations in 1997, but greater at low elevations in 1998. This shift in abundance of deer mice from high to low elevations accounted for most of the reversal in trend in total number of animals captured at high and low elevations between 1997 and 1998.

Not only were deer mice more abundant at sites with horses, but they also played a more significant role in community dynamics of small mammals at horse-occupied sites. Although the percentage of the community occupied by deer mice was generally not correlated ($r < 0.50$) with realized guild richness (inclusive RRR), this percentage as deer mice was higher at horse-occupied sites in 1998. Similarly, using a conservative approach to compare the rank in the community of abundance of deer mice, deer mice occupied lower ranks at horse-occupied sites at low elevations in 1997. If sites at which no deer mice were captured are assigned values of deer mouse rank one greater than the number of inclusive RRR species caught at the site that year, then deer mice at low-elevation, horse-occupied sites exhibited significantly lower ranks than did mice at horse-removed sites again in 1998 ($U = 4.5$, $U' = 25.5$, tied $Z = -1.981$, tied $p = 0.048$). In summary, the deer mouse may exert greater influence on community dynamics at sites experiencing grazing by horses. In a comparison of small mammals in the Mojave desert scrub and riparian vegetative communities on one 2.2-ha control site versus one site heavily utilized by burros directly across the Colorado River, Carothers et al. (1976) similarly found that *Peromyscus* spp. averaged 97.5% of all individuals captured on the 'impact' site, but

only 59.3% on the control site. Increased abundance and dominance of deer mice may be cause for concern in areas of rapid human expansion such as the western Great Basin, because deer mice are the primary known vector for the Sin Nombre hantavirus and up to 60% of individuals in Great Basin populations can carry antibodies for the virus (Boone et al., 1998).

Although sagebrush voles exhibited significantly greater abundances at high-elevation horse-occupied sites in 1997, we caught only two individuals across all sites in 1998, one from each treatment group. Such interannual population fluctuations are not uncommon for arvicolines (=microtines; Krebs et al., 1973; Hall, 1981; Hoffmeister, 1986). The difference in 1997 was largely due to high numbers of captures at both sites in the Seven Troughs Range, which exhibited higher percent cover of sagebrush than did any other high-elevation, horse-occupied site. At these sites in 1997, we captured only one individual from a non-incidental species other than Great Basin pocket mice (*Perognathus parvus*) or deer mice, suggesting that, at least in some years, the sagebrush vole may be occupying empty (i.e. vacated) niche space. Significantly higher numbers of Merriam's kangaroo rats observed at horse-removed sites in 1998 agrees with Heske and Campbell's (1991) exclosure work in Arizona that found significantly lower numbers of these rats in areas grazed by cattle. Because of the inconsistency of trends in Merriam's kangaroo rats and sagebrush voles and because of the lack of broad replication to support these possibilities, however, we suggest them as avenues for further research.

Several species appeared to be relatively insensitive to disturbance imposed by feral horses, including Great Basin pocket mice, long-tailed pocket mice (*Chaetodipus formosus*), Panamint kangaroo rats, and chipmunks (*Tamias* sp.) (Table 2). Other species that appeared to be insensitive to horse disturbance, from anecdotal observation, included the desert woodrat *Neotoma lepida* (because horses will not disturb its large and impassable dwelling), as well as black-tailed jackrabbits (*Lepus californicus*) and cottontails (*Sylvilagus* sp.). Several other authors have found lagomorphs to flourish under disturbance created by grazing (Fogden, 1978; Kerley, 1992).

We attempted to use our data to empirically test the utility of diversity indices for characterizing Great Basin communities, however, they provided the least insight of all our response variables. Diversity indices did not differ consistently or significantly between horse-occupied and horse-removed sites, and values varied greatly between indices (e.g. Simpson's versus log-series), between years, and between species inclusion rules (all species, inclusive RRR species, and restrictive RRR species). Although Magurran (1988) provides a means to assess comparison of diversity and evenness between two sites, she does not describe procedures for comparing sites from replicated treatments. Although diversity indices are theoretically appealing, assumptions related to underlying distributions of species abundances and other factors are probably rarely met in Great Basin mammal communities. Furthermore, diversity indices lose particular information such as species identities, are heavily dependent on sample size, and are less frequently accepted among ecologists (Noss, 1990).

4.2. Squamate reptiles

Our finding of lower absolute squamate species diversity and a trend toward lower abundance of many reptile species at horse-grazed sites agrees with other studies of reptiles experiencing disturbance. In the Mojave Desert of California, Busack and Bury (1974) found lizard abundance to be two times higher and biomass to be 3.7 times higher at an ungrazed site than at an area grazed by domestic sheep. In a study stratified by vegetation types in Arizona, Jones (1981, 1988) reported greater diversity and abundance of lizards in ungrazed sites in four of five vegetation types. Similarly, Szaro et al. (1985) reported the wandering garter snake (*Thamnophis elegans vagrans*) to be five times more abundant in ungrazed sites in New Mexico. Lower encounters of horned lizards at horse-occupied sites is consistent with the 3.5 to 8 times lower abundance of ant mounds at those sites at low elevations (Appendix B).

If disturbance is maintained at a moderate or low level, however, it is possible that some species of lizards may benefit from patchiness in vegetation created by grazing herbivores (Dean and Milton, 1991). For example, the common zebra-tailed lizard (*Callisaurus draconoides*) and Great Basin whiptail lizard (*Cnemidophorus tigris tigris*) generally inhabit more open areas to utilize their rapid locomotion (Stebbins, 1985). Although horse-removed sites had a slightly higher average number of whiptail lizards than did horse-occupied sites (2.0 versus 1.8 individuals per site), the site with the greatest number of individuals was a horse-occupied site with the highest amount of non-horse disturbance among low-elevation sites. This coincidence is by no means conclusive, however, and we suggest this as an avenue for further research.

4.3. Alternative explanations

Our research at the landscape scale is mensurative rather than manipulative (*sensu* Hurlbert, 1984); thus, we cannot rule out alternative mechanisms as possible causes of observed differences. The most plausible alternative explanation to horses being the cause of the vegetative (and, consequently, vertebrate) differences we observed is that horses simply choose to traverse areas that have less vegetative cover. It is not difficult to imagine horses, or any other large herbivore, choosing areas with lower shrub cover, because traveling through dense shrub cover would require either taking a more sinuous path or encountering resistance or risk of abrasion. If one considers all differences we observed at the landscape scale (Beever, 1999), however, the possibility that horses simultaneously select areas that have harder soils, fewer ant mounds, greater cover of forbs, lower abundance of reptiles, and more depauperate floral and mammal communities becomes less plausible.

Because cattle grazing is so ubiquitous in the Great Basin and the West, and because cattle may comprise up to 23 times more animal unit months (AUMs) in the western United States (Wagner, 1983), it is tempting to suspect that effects of horse grazing are confounded by either past or current livestock grazing. It is likely, if not certain, that at least one of either cattle (*Bos taurus*) or domestic sheep (*Ovis ovis*)

used many of the ranges we studied in both the distant and more recent past. Accurate records do not exist for the mountain ranges in our study; thus, it is not possible to assess the validity of this possibility. However, it is unlikely, given the interspersed spatial arrangement of our sites in two-dimensional space, that these effects would have been differentially distributed across currently horse-occupied and horse-removed sites. Sites from which horses have been removed were largely selected based on ownership and other socio-political considerations. Consequently, a priori differences due to effects of other feral grazers seem unlikely. This conclusion was supported by fecal counts that indexed recent use. These counts demonstrated an average of 10.4 times greater recent use of horse-occupied sites by horses compared to cattle, and approximately equal intensity of both recent livestock grazing and native ungulate use between horse-occupied and horse-removed sites.

Numerous ecosystem properties that may affect small mammals and reptiles, particularly vegetation and soil attributes, commonly vary significantly with a site's exposure (i.e. sheltered vs. exposed) and position on the slope (upper, middle, or lower). To assess whether our results were confounded either by a site's position on a slope or its level of exposure, we performed two-way ANOVAs of each response variable against position and exposure. After selecting all of our sites, we noticed that the two treatment groups in 1997 did not possess equivalent proportions of sites in exposed versus sheltered areas. This bias occurred because we had difficulty finding sheltered sites used by horses that were not also used by cattle. Therefore, to avoid confounding the effects of exposure and horse grazing, horse-occupied sites added in 1998 were placed in exposed areas. Given this and the fact that the two-way ANOVAs for all our response variables showed stronger response to exposure than to position, we additionally tested the effect of exposure on response variables as a main effect, and as a second factor in two-way ANOVAs with each of elevation and horse presence to identify significant interactions. No reptile or small-mammal response variable was significantly predicted by either position or exposure in either year (all $p > 0.05$) in any of these ANOVAs.

4.4. Reliability of methods

To assess the ability of our methods to consistently capture the dynamics of our targeted ecosystem components, we used a number of techniques. To assess the reliability of our three-day trapping strategy to estimate true community composition of small mammals at sites, we used species accumulation curves produced by extended-duration trapping (6 nights per site) at a pre-selected high- and low-elevation site in 1998. Of 54 individuals captured beyond Day 3 at both sites, only one individual (captured on Day 4) represented a new species, an incidentally captured folivore (chisel-toothed kangaroo rat, *D. microps*). We observed a similar pattern across all sites during our 3-day trapping periods, as the third night of trapping produced no new species at $\geqslant 65\%$ of our sites in both 1997 and 1998. This last fact, combined with the fact that species pools were small (as low as four species, and <10 species for both taxa at all but one site for mammals), gave us confidence in the adequacy of our sampling and led us to elect

not to use individual-based rarefaction (*sensu* Gotelli and Colwell, 2001) to compare richness between treatments. Because total number of individual mammals was higher at horse-occupied sites, however, individual-based rarefaction would presumably increase the difference in community completeness between treatments.

Lack of interannual correlation in our small-mammal variables contrasted with the significant interannual correlation we observed in our other variables (Beever, 1999), and reflects endogenous cyclical and irregular population fluxes of Great Basin mammals (Hoffmeister, 1986; Hall, 1995). This variation in small mammals suggests that longer-term data sets and generic variables such as RRR are preferable when investigating effects of horses on native mammals. The robustness of our results across years in spite of significant interannual variation suggests that climatic variations did not eclipse effects imposed by horses on semi-arid ecosystems, contrary to findings from research on feral horses in two grassland national parks (Detling, 1998).

4.5. Future research

Given the 42.8 million ha of land dedicated to herd areas in the United States, it is important to understand how free-roaming horses affect the biotic landscape. From the perspective of experimental design, the top priority for future analyses of synecology of horse grazing should be the incorporation of manipulative experiments of horse density (such as horse removals or exclosures, additions of horses to experimental areas, and before-after contrasts; Underwood, 1994). In addition, because feral horses appear to exhibit different watering behavior than do cattle in arid systems (Pellegrini, 1971), more studies at springs and other watering areas may help elucidate priorities for future protection efforts in riparian and spring areas (e.g. Beever and Brussard, 2000). In the Great Basin, likely focal species for these studies include shrews (*Sorex* spp. and others), *Reithrodontomys megalotis* (a grass specialist), and *Microtus* species, particularly *M. montanus* (a meadow specialist). Because we did not capture and tag reptile individuals, we recommend further investigation of the relationship between horse grazing and reptile abundance using field methods focused exclusively on reptiles. In this vein, apparent responses to horse grazing in abundance of active, rapid predators such as common zebra-tailed lizards and Great Basin whiptail lizards would be of particular interest. Investigations of other taxa as response variables (e.g. other invertebrates, avifauna, carnivorous mammals) may further clarify mechanisms by which horses induce alterations in arid systems, and may aid in devising a more comprehensive monitoring strategy.

Acknowledgements

We thank J. Axtell, J. Gianola, and T. Seley of the Bureau of Land Management for help with site selection. K. Geluso assisted with construction of small-mammal potential faunas and with preparation of mammal specimens for the museum

Appendix A. Physiographic and habitat characteristics of 19 study sites in the Great Basin of western North America (sampled 1997–1998)

Site number[a]	Mountain range	Site name	Elevation (m)	Average slope (%)[b]	Aspect	Position on slope	Exposure[c]	Non-horse disturbance[d]	Average percent bedrock[e]	Mean soil hardness (kg/cm^2)	Cumulative (97–98) site richness, plants
High-elevation, horse-excluded											
1	Pah Rah range	Virginia Peak	2134	25	ENE	Upper	0	1	3.22	0.072	46
2	Sonoma range	Lake valley hillside	2164	40	NE	Middle	1	2	0.09	0.75	37
3	Sonoma range	Cabin	2118	25	ENE	Lower	0	3	3.99	0.92	33
4	Humboldt range	Pflum Creek Mine	2000	20	NE	Middle	0	3	0.68	0.193	56
High-elevation, horse-occupied											
5	Dogskin mountain	Dry Valley Creek saddle	2060	20	E	Upper	1	2	4.57	0.453	35
6	Dogskin mountain	Dry Valley Creek peak	2200	30	NE	Upper	1	2	1.00	1.414	37
7	Seven Troughs range	Side road with junipers	2225	20	E	Upper	1	2	1.78	1.999	27
8	Seven Troughs range	High saddle	2286	25	E	Middle	1	2	0.11	1.767	25
Low-elevation, horse-excluded											
9	Pah Rah range	Bigmouth Canyon	1500	15	E	Lower	0	3	0.05	0.132	28
10	Truckee range	Jeep trail	1540	5	NE	Lower	1	1	0.13	0.138	22
11	Truckee range	Sage Hen Creek	1500	10	NE	Lower	0	3	0.41	0.173	29
12	Humboldt range	Low side valley	1433	25	SE	Middle	0	3	0	N/A[f]	24
13	Virginia range	Fernley view	1400	5	ENE	Lower	1	2	0	0.062	1998 only
14	Virginia range	Homogeneous valley	1500	5	ENE	Middle	0	3	0	0.019	1998 only
Low-elevation, horse-occupied											
15	Dogskin mountain	Winnemucca Valley spur	1646	25	NE	Middle	0	4	3.44	0.93	26
16	Clan alpine mountains	Dixie Valley vista	1340	10	NE	Middle	0	1	0.66	2.913	17
17	Clan alpine mountains	Shoshone Pass	1700	15	E	Middle	1	1	0.02	1.667	19
18	Virginia mountains	Juniper saddle	1646	20	E	Middle	1	1	0.59	2.462	27
19	Virginia mountains	Juniper Basin	1554	25	ESE	Middle	0	2	0.76	1.173	23

[a]See Fig. 1 for location of site in Nevada.
[b]Obtained using a handheld clinometer, averaged across the entire sampling area.
[c]Subjective classification of exposure, after Wentworth (1976). 0 = site somewhat protected by adjacent slopes, 1 = site on open slope, unsheltered by adjacent slopes.
[d]Subjective classification of disturbance by humans and livestock, after Wentworth (1976). 1 = apparently undisturbed, 2 = slight disturbance, 3 = moderate, 4 = heavy, 5 = severe
[e]Average from eight line intercept transects, four performed during each of 1997 and 1998.
[f]This site could not be sampled for soil-surface hardness using our standardized criteria.

Appendix B. Means ± 1 SE for several plant, soil and ant response variables at sites in the western Great Basin, USA, during 1997 and 1998

	1997					1998				
Elevation	High		Low		Probability	High		Low		Probability
Horse presence	Removed	Occupied	Removed	Occupied		Removed	Occupied	Removed	Occupied	
Vegetation characteristics										
Percent cover grasses	5.8 ± 1.2	2.0 ± 0.3	3.2 ± 1.3	1.7 ± 0.9	0.034	12.6 ± 1.7	4.5 ± 1.2	6.7 ± 2.2	3.6 ± 1.2	0.011
Percent cover forbs	4.1 ± 1.7	12.9 ± 3.2	2.2 ± 1.1	1.5 ± 0.3	0.042[b]	14.3 ± 2.7	22.7 ± 4.4	2.6 ± 1.5	1.4 ± 0.3	0.28
Percent cover shrubs	51.1 ± 0.9	32.7 ± 5.4	26.3 ± 3.8	24.9 ± 3.7	0.027	53.1 ± 4.0	27.8 ± 2.9	28.9 ± 2.8	23.3 ± 2.3	0.0002
Total percent cover (Grasses + Forbs + Shrubs)	61.1 ± 2.2	47.5 ± 4.6	31.7 ± 4.4	28.1 ± 4.3	0.062[#]	80.0 ± 5.1	55.0 ± 6.3	38.2 ± 4.9	28.2 ± 2.8	0.003
Total percent cover (G + F + S + trees)	61.1 ± 2.2	47.5 ± 4.6	32.9 ± 5.0	28.1 ± 4.3	0.051[#]	82.5 ± 5.1	55.0 ± 6.3	38.4 ± 4.8	28.2 ± 2.8	0.001
Site species richness	20.8 ± 1.3	18.0 ± 1.2	14.8 ± 0.8	12.4 ± 1.0	0.036	39.0 ± 4.1	27.0 ± 1.7	22.3 ± 2.0	18.6 ± 1.7	0.006
Interannual site species richness	43.0 ± 5.1	31.0 ± 2.9	25.8 ± 1.7	22.4 ± 1.9	0.028					
% cover sagebrush shrubs	34.4 ± 4.2	16.6 ± 4.6	23.4 ± 6.0	19.9 ± 3.5	0.22	32.0 ± 3.8	14.8 ± 2.7	20.3 ± 4.3	18.5 ± 2.7	0.039
Average of 4 longest shrub tape lengths	1.7 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.1 ± 0.1	0.003	1.5 ± 0.0	1.0 ± 0.1	1.2 ± 0.1	1.0 ± 0.1	<0.0001[b]
# of cheatgrass stems per transect	34.1 ± 22.8	54.9 ± 27.2	289.3 ± 76.5	197.4 ± 61.1	0.52	39.3 ± 14.2	103.4 ± 55.8	266.9 ± 46.0	419.5 ± 126.8	0.32[c]
Soil surface compaction (penetration resistance)										
Mean soil harness (MPa)	0.2 ± 0.1	0.6 ± 0.0	0.2 ± 0.1	0.9	0.007	0.5 ± 0.2	1.4 ± 0.3	0.1 ± 0.0	1.8 ± 0.4	<0.0001[a]
Ant mounds										
Mean total # of ant mounds per site	8.0 ± 4.6	2.0 ± 1.0	1.7 ± 0.9	0.2 ± 0.2	0.089[#,a]	17.3 ± 9.4	7.8 ± 1.9	7.8 ± 2.3	2.2 ± 1.5	0.036[a]

All percentages are reported as proportions of 100%, but were arcsine-transformed before being analysed. Probability refers to *p*-value of the test of the effect of presence of horses on several types of response variables at 19 sites, as measured by two-way ANOVAs with elevation as a binary cofactor. Cheatgrass = *Bromus tectorum*; Sagebrush = *Artemisia tridentata*.

[a]Log_{10}-transformed data.

[b]Significant interaction; presence of horses only significant among high-elevation sites.

[c]Significant interaction; presence of horses only significant among low-elevation sites.

[#]Bonferroni–Dunn post hoc tests showed effect of horse presence was significant ($p \leqslant 0.050$) as a main effect.

collection at the University of Nevada. We thank N. Wendel, D. Watterson, and especially J. Landmesser for field assistance. M. Beck, M. Bogan, K. Geluso, S. Jenkins, W. Longland, J.M. Reed, J. Veech, F. Wagner, and two anonymous reviewers all provided critical reviews of earlier manuscript drafts. Logistic and financial support at the University of Nevada was provided by the Biological Resources Research Center, the Department of Biology, and the Program in Ecology, Evolution, and Conservation Biology. Bob Elston of the BRRC created Fig. 1. At the University of Nevada, the Nevada Agricultural Experiment Station, Center for Environmental Arts and Humanities, College of Agriculture, Department of Biology, Nevada Biodiversity Research and Conservation Initiative, and Graduate Student Association all provided financial assistance to EAB, as did the Kosciusczko Foundation and the American Museum of Natural History.

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Journal of Arid Environments 66 (2006) 96–112

Journal of Arid Environments

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Effects of feral horses in Great Basin landscapes on soils and ants: Direct and indirect mechanisms

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Received 19 January 2005; received in revised form 11 November 2005; accepted 14 November 2005
Available online 27 December 2005

Abstract

We compared soil-surface penetration resistance and abundance of ant mounds at 12 western Great Basin sites (composed of 19 plots) either grazed by feral horses (*Equus caballus*) or having had horses removed for the last 10–14 years. Across this broad spatial domain (3.03 million ha), we minimized confounding due to abiotic factors by selecting horse-occupied and horse-removed sites with similar aspect, slope, fire history, grazing pressure by cattle (minimal to none), and dominant vegetation (*Artemisia tridentata*). During both 1997 and 1998, we found 2.2–8.4 times greater abundance of ant mounds and 3.0–15.4 times lower penetration resistance in soil surfaces at horse-removed sites. In 1998, thatched *Formica* ant mounds, which existed predominately at high elevations, were 3.3 times more abundant at horse-removed sites, although abundance varied widely among sites within treatments. Several types of analyses suggested that horses rather than environmental variability were the primary source of treatment differences we observed in ecosystem components. Tests of several predictions suggest that alterations occurred through not only direct effects, but also indirect effects and potentially feedback loops. Free-roaming horses as well as domestic grazers should be considered in conservation planning and land management in the Great Basin, an ecoregion that represents both an outstanding conservation opportunity and challenge. Published by Elsevier Ltd.

Keywords: *Equus caballus*; *Formica*; *Pogonomyrmex*; Nevada; Disturbance; Conservation

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0140-1963/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.jaridenv.2005.11.006

1. Introduction

Grazing animals may affect ecosystem properties and processes directly (e.g., by foliage consumption or soil-surface trampling), indirectly (e.g., alteration of ant communities due to herbivore-induced reduction of plant cover), or through a feedback loop. Although the ecological literature is replete with reports of direct effects of a particular land use or type of disturbance on one or more response variables, less commonly is there explicit quantitative consideration of the indirect effects and feedbacks that may modify or modulate the disturbance's influence.

We measured penetration resistance of soil surfaces and density of ant mounds in areas with and without feral horses (*Equus caballus*) in order to test the overarching hypothesis that the presence of horses fundamentally changes key soil properties, and to increase our understanding of the potential importance of soil–plant–animal feedbacks in this ecosystem. Free-roaming horses in western North America move widely both daily (e.g., to and from water sources) and seasonally (e.g., to higher elevations in hottest months), and use some portions of the landscape more intensively than others at both local (e.g., wallows, communal defecation sites) and landscape scales (e.g., meadows, springs in otherwise arid regions). In addition to testing whether sites experiencing horse grazing differed in penetration resistance and ant-mound abundance from ecologically similar sites from which feral horses had been removed 10–14 years earlier, we used regression and correlational analyses to test whether relationships predicted by different mechanisms of change (e.g., direct and indirect effects) were operating. To our knowledge, this is the first investigation of ecological effects of feral horses on either soil properties or ants, and one of relatively few ecoregional-scale investigations of the ecological consequences of grazing by large ungulates in North America.

1.1. Direct effects

Horses have been shown to have direct effects on vegetation characteristics in semi-arid ecosystems (Reiner and Urness, 1982; Fahnestock and Detling, 1999; Gerhardt and Detling, 2000), and cattle in semi-arid ecosystems can directly affect soil properties, including bulk density, through trampling (Weltz et al., 1989; review in Lull, 1959). We predicted that horses would have similar effects on soil compaction, namely: (a) horse-occupied sites would exhibit higher mean penetration resistance than would horse-removed sites; and (b) resistance would increase across plots with increasing numbers of horse defecations, a surrogate of recent grazing intensity.

Large-bodied, broad-hoofed animals may reduce density of ant mounds directly by trampling. We predicted that: (a) some recently trampled mounds would be encountered during our field surveys; and (b) the number of defecations at plots should be negatively correlated with density of ant mounds.

1.2. Indirect effects

In intertidal marsh communities, free-roaming horses have been shown to exert a variety of indirect effects on diversity and abundance of crabs, birds, and fishes, through their effects on the dominant vegetation (Levin et al., 2002). In semi-arid communities, most indirect effects of ungulates are associated with removal of plant biomass or with

the combination of biomass removal and direct effects of trampling on soil structure (Thurow, 1991). Preferential removal of one or more plant species can contribute to shifts in plant community composition (Hobbs, 1996; Augustine and McNaughton, 1998). Due to the very different physical and chemical effects of different plant species on soils and the fact that a species shift is generally more persistent than the removal of plant biomass, changes in species composition in response to grazing can have dramatic impacts on infiltration (Thurow, 1991). Herbivore-induced reduction in vegetative cover at semi-arid sites can affect soils through at least three mechanisms: (a) reduction of soil organic-matter inputs; (b) reduction in shading of soils, and consequent increase in soil-surface temperatures; and (c) reduction of precipitation interception by above-ground plants, resulting in greater erosion. We predicted that, if horses were affecting penetration resistance through their effects on vegetative cover, total cover at plots would inversely predict resistance after recent grazing intensity (# horse defecations) and soil texture (%clay) were accounted for (i.e., as 'forced' variables in a stepwise regression).

Ants play pivotal roles in semi-arid ecosystems, acting as seed consumers, seed dispersers, soil manipulators, generalized herbivores, and most commonly, scavengers (Rosenberg et al., 1986; Petal, 1991; Andersen and Sparling, 1997; MacMahon et al., 2000). In addition to the potential direct effect of ungulates on ant mounds mentioned above, herbivores may thus reduce ant-mound densities indirectly by removing vegetation, which is used by ants in Great Basin ecosystems for both nesting material and nutrition. In addition to trampling and consumption of plant biomass, grazing animals can also affect the ratios and spatial distribution of nutrients available to plants through their patterns of urination and defecation. We predicted that either shrub cover or total cover at plots would predict ant-mound abundance after recent grazing intensity (# horse defecations) was accounted for (i.e., as a 'forced' variable in a stepwise regression). Additionally, we predicted that an index of continuity of the shrub canopy would correlate positively with abundance of ant mounds.

1.3. Objectives

Feral horses are a common herbivore on the Great Basin landscape, yet their potential role in landscape alteration has rarely been investigated. Management areas for feral horses occupy 29% of the land area of Nevada (Anonymous, 1997), the state central to the Great Basin, plus portions of all states that comprise the Basin. The objective of this study was to enhance our understanding of the direct and indirect effects of feral horses on ecosystem structure and function. Other reports (Gerhardt and Detling, 2000; Beever et al., 2003) have described vegetation differences associated with feral horses. In this study, we specifically sought to quantify differences in soil-surface penetration resistance and ant-mound density in horse-grazed and ungrazed areas, and to use a variety of analytical approaches together with a literature review to investigate how these differences may be directly and indirectly associated with feral horses. To ensure that the results of our study were not related to the idiosyncrasies of a particular site, we replicated our plots in ranges across an area of 3.03 million ha. Based on our analyses and the literature review, we developed a conceptual model (Fig. 1) to describe our current understanding of the relationship between feral horse impacts on these two properties, and more general ecosystem functions.

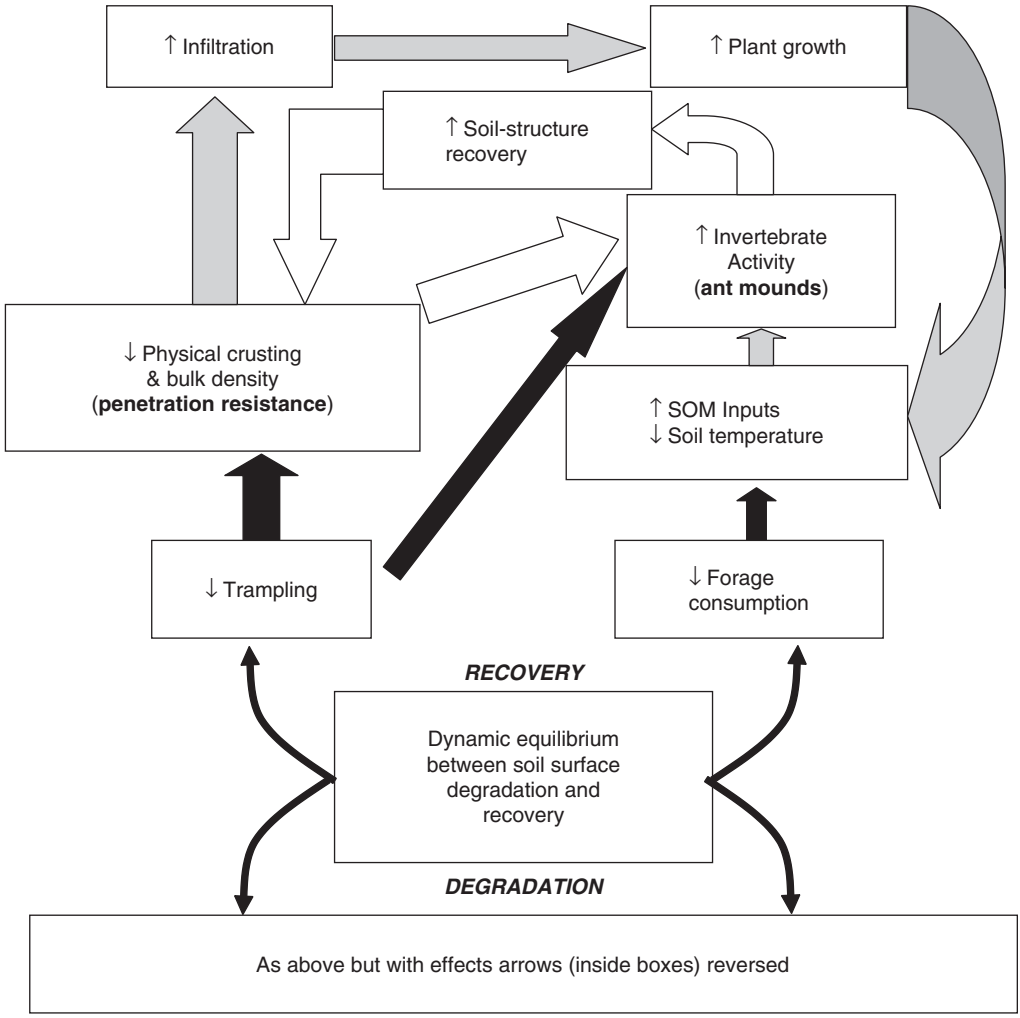


Fig. 1. Diagram illustrating connections between horse grazing (and trampling) and various ecosystem properties and processes, for pathways of both degradation and recovery. Black arrows represent direct effects of horses, gray arrows indicate indirect effects, and white arrows indicate potential feedback loops.

2. Methods

2.1. Selection of study sites

Management areas administered by the Bureau of Land Management for free-roaming horses include 318 herd-management areas (hereafter, HMAs) and 41.7 million ha across 10 US states, although 109 HMAs totaling 27.5 million ha are not currently managed for horses (BLM, *unpublished data*). Horse herd sizes may increase >20% annually in the Great Basin; consequently, periodic horse removals (roundups) are implemented to limit ecosystem degradation due to overgrazing. Seven criteria were used to try to achieve

ecological similarity between horse-occupied plots and plots from which all resident and immigrant horses had been removed for 10–14 years. To minimize confounding factors, we selected only plots that were: (1) on east-facing slopes; (2) of low slope gradient; (3) at elevations loosely corresponding to high-elevation (2000–2300 m) and low-elevation (1350–1700 m) sagebrush zones in the western Great Basin; (4) dominated by sagebrush (*Artemisia tridentata*); (5) relatively unused by cattle in the past two decades; and (6) had no evidence of recent fire within or adjacent to the plot (Beever and Brussard, 2004). With these criteria, 10 horse-removed and 9 horse-occupied plots were selected within nine mountain ranges (Appendices A and B and Fig. 2). Given that locations of horse removals were selected on socio-political (specifically, railroad-owned jurisdiction) rather than biological criteria, and that horse-removed and horse-occupied sites were relatively interspersed across the landscape, we did not expect a priori confounding differences in sites of the treatment groups (Beever and Brussard, 2004).

In practice, the most difficult criterion to satisfy was finding plots not grazed by cattle. In addition to using BLM stocking-rate data, we performed fecal counts at all sites to find areas that had received significantly less recent use by cattle than by horses. At the finest spatial scale, we located plots so as to avoid obvious ecotones and plant-community shifts, which represented <5–10% of the sagebrush-dominated areas within our HMAs. Plots were also located at least 1.5 km from perennial streams, because use by both horses and cattle can be anomalously high near water sources in semi-arid ecosystems (Crane et al., 1997; see Beever and Brussard (2004) for more details on site selection).

2.2. Field sampling

We sampled each of our response variables (mean penetration resistance, ant-mound abundance, and thatched-mound abundance at sites; see Beever (1999) for vegetation response variables) from May through August in both 1997 and 1998. Each plot consisted of a 135 m × 135 m (1.82-ha)^2, defined by a 10×10 grid of sampling stations with 15 m between both columns and rows. We added the soil and ant components to our sampling protocol in the middle of the 1997 season; therefore, we have soil penetration resistance data for only eight sites and ant data for only 14 sites in 1997. In 1998, however, we sampled ant mounds at all 19 plots and penetration resistance at 18 plots (Table 1).

2.2.1. Soil sampling

We measured soil-surface penetration resistance using a handheld pocket penetrometer (Soiltest, Inc., Chicago, IL, USA) by depressing the 6.4-mm diameter tip 1 cm into the soil at a constant rate (Bradford et al., 1986; US Department of Agriculture, 1993). Values of penetration resistance exhibited great variability in preliminary sampling; therefore, we adopted a two-tiered sampling strategy that involved taking 250 soil subsample measurements at each plot. At every fourth sampling station ($100/4 = 25$ locations), 10 subsamples were taken in areas not under vegetative canopy but within a 1-m diameter circle at a randomly selected cardinal direction from the center point. The 1-m diameter circle was enlarged if the original circle did not contain areas of open soil. One low-elevation, horse-removed site could not be sampled because areas with exposed soil could not be found near most sampling stations. Values of penetration resistance ranged from 0 to an instrument-imposed maximum of 4.7 kg/cm^2. Sampling locations were offset by two sampling stations from 1997 locations for sampling in 1998. Precipitation and resulting soil

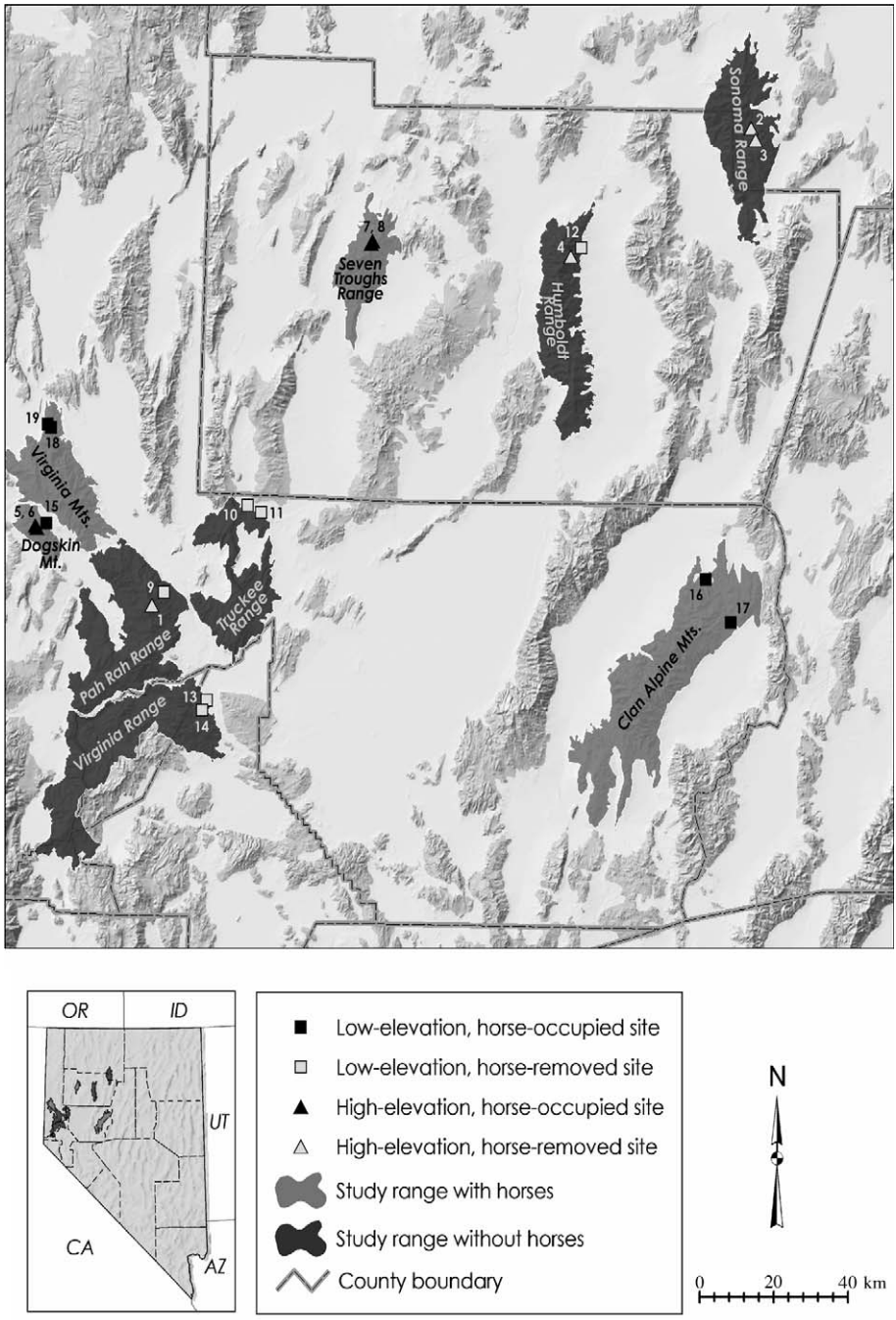


Fig. 2. Location of 19 study 'sites' (i.e., plots), stratified into high-elevation (2000–2286 m) and low-elevation (1340–1700 m) sagebrush zones in mountain ranges of the western Great Basin of North America. Site labels refer to "Site number" in Appendix A. Plots of the same treatment and elevational stratum within the same range were treated as subsamples for analyses.

Table 1
Means ± 1 SE for our response variables at 12 sites in the western Great Basin, USA, during 1997 and 1998 for each treatment-elevation category

	1997					1998				
Elevation	High		Low		Probability	High		Low		Probability
Horse presence *N*: #sites (# plots)	Removed 3 (4)	Occupied 2 (4)	Removed 3 (4)	Occupied 3 (5)		Removed 3 (4)	Occupied 2 (4)	Removed 4 (6)	Occupied 3 (5)	
Soil-surface compaction (penetration resistance)										
Mean soil harness (MPa)	0.2 ± 0.1	0.5	0.2 ± 0.1	0.9	0.026[a]	0.4 ± 0.2	1.4 ± 0.5	0.1 + 0.0	1.7 ± 0.4	0.0027[b]
ANT mounds										
Mean total # of ant mounds per site	8.7 ± 5.4	2.0	1.7 ± 0.9	0.2 ± 0.2	0.09[b]	21.8 ± 13.3	7.8 ± 0.3	7.3 ± 1.9	3.2 ± 2.5	0.09
Mean # thatched mounds per high site						18.8 ± 12.3	5.0 ± 0.9			0.25

Probability refers to *p*-value of the test of the effect of presence of horses on response variables, as measured by two-way ANOVAs with elevation as a binary cofactor. Tests considered 'sites' as replicates, and averaged values from plots to obtain a site value.

[a]Due to small *N* (total sites sampled = 8) and non-significant effect of elevation on resistance both years, this test reflects a one-way ANOVA.

[b]Log_{10}—transformed data.

moisture can temporarily change the surface characteristics of soils as a result of cohesive and adhesive forces (USDA, 1993). Consequently, we sampled sites only when they had received no precipitation during the previous 48 h. Typical of the Great Basin during summer, high soil-surface evaporation at our sites ensured that the top 2 cm of the soil was effectively air-dry at the time of sampling. We chose to measure penetration resistance of soil surfaces rather than bulk density for one biological reason and one practical reason. Biologically, conditions on the soil surface will affect many more biotic and abiotic processes in Fig. 1 (e.g., seed germination, water capture vs. runoff) than will bulk density at far-belowground horizons. Logistically, we sought to use a sampling instrument that might feasibly be implemented by land managers in a time- and cost-effective manner, yet still provide robust information.

2.2.2. Ant mounds

We tallied above-ground ant mounds by counting mounds in a 4-m wide corridor (2 m on each side) located along the row-by-row path through the sample-station grid (1485 m length). Mounds fell into two categories: thatched mounds (produced by *Formica* ants, often at high elevations) and pebble mounds (usually constructed by *Pogonomyrmex* ants). Mounds were tallied by type in 1998 but not during 1997. Although we performed tests on mound *abundance* (occasionally transformed), given that all censuses occurred within a 4×1485 m area, abundance translates directly to mound *density*. To begin to assess composition of ant communities at plots, we collected individuals ($n \geqslant 7$) from two different mounds encountered during sampling at each site during 1998. If both types of mounds were present at a plot, we collected ants from a mound of each type. *Formica* ants were identified to species group and *Pogonomyrmex* ants to species using Wheeler and Wheeler (1986).

2.2.3. Fecal counts

Scanning the same area used to census ant mounds, we counted the number of fecal piles from cattle, horses, and other ungulates in the 4 m wide corridor along trap lines in the sampling-station grid (following Beever and Brussard, 2004). Communally used defecation sites (often termed 'stud piles'), which can exceed 20 m^2 in extent, were each assigned a value of 7 defecations, reflecting the average ratio of fecal material in stud piles vs. individual defecations that we observed anecdotally across hundreds of stud piles. Horses appeared to be the dominant ungulate grazer at our sites in recent years, as the geometric mean of ratios of horse defecations/cattle defecations across years at all horse-occupied plots was 10.4:1 (Beever et al., 2003). Fecal counts further suggested that intensity of neither cattle grazing nor browsing by other ungulates (primarily *Odocoileus hemionus* and *Antilocapra americana*) differed between horse-occupied and -removed sites during 1997 or 1998 ($p > 0.20$; Beever et al., 2003).

2.3. Analyses

We used a conservative approach and considered plots within the same mountain range and elevational stratum as subsamples and averaged values from the two plots to produce a 'site' value. This approach is conservative for the following reasons: (1) replicate plots within the same range and elevational stratum were separated from each other by up to 12.3 km; (2) replicate plots in horse-occupied sites are overridingly used by different bands

of horses; (3) many of the replicate plots in horse-removed sites were de-stocked at different times; (4) reciprocal averaging analyses (also known as correspondence analyses) showed that same-range plots were less similar to each other than to plots in other ranges for 4 of 5 previously analysed datasets (Beever et al., 2003), and (5) ant mound density at plots within the same range were consistently less similar to each other than to other plots in the same treatment-elevation category. We considered all plots as replicates when using number of defecations (rather than the binary horse-treatment variable) in regressions and correlations to understand the mechanisms underlying ecosystem alteration.

We calculated means for penetration resistance at each plot using the 25 subsample means, and used the overall site mean for testing of treatment effects. For analyses of treatment effects on response variables, we performed two-way ANOVAs using horse density and elevation as binary categorical variables (i.e., main effects); probabilities in Table 1 refer to the main effect of horse presence across all sites when stratified by elevation. We used Bartlett's test of homogeneity of variances to identify significant heteroscedasticity or severely non-normal distributions (Sokal and Rohlf, 1995). When needed, logarithmic transformations were used to achieve homoscedasticity, normality, and additivity of treatment effects (Sokal and Rohlf, 1995). Since the variables undergoing logarithmic transformations had some zero values, we added 1 to the value of all sites before transforming the ant-mound data (a count variable), and 0.1 to all sites before transforming the penetration-resistance data (Sokal and Rohlf, 1995). To determine inter-annual variability in our response variables, we compared values of selected variables at each plot between 1997 and 1998 using paired t-tests. We used correlation coefficients to determine whether the relative values of response variables across sites persisted between years (a desirable characteristic for indicators of disturbance) and employed Fisher's R-to-z transformation to test whether correlations were significantly different from zero. Statistical analyses were performed using StatView versions 4.02 and 5.0 (SAS Institute Inc., 1998). We performed fewer tests on 1997 data for penetration resistance, due to our lower sample size that year ($n = 8$ plots).

We compared numerous abiotic variables between horse-occupied and horse-removed sites, to test the assumption that any differences in ant and soil response variables were due to presence of horses rather than abiotic parameters. These variables included some that we measured at plots, and some generated by precipitation models (Daly et al., 1994) or published and unpublished soil surveys from Natural Resources Conservation Service (NRCS) (Appendix C). Using two-way ANOVAs, unpaired t-tests, and Mann–Whitney tests, we found that no variable was significantly different between horse-removed and horse-occupied sites in individual analyses, nor were the two types of sites distinguishable in multi-variate analyses of all uncorrelated physical site attributes (Beever et al., 2003; Beever and Brussard, 2004). Furthermore, by digging four soil pits per plot, we found that horse-removed and -occupied sites also did not differ systematically in their soil color, structure, consistence, or effervescence (Beever et al., 2003). Perhaps most important to penetration resistance, we compared soil texture across sites, using the four pits/plot. Horse-removed and -occupied sites again did not differ significantly in any soil particle-size fraction, including clay or gravel ($p > 0.10$). Textural characterizations were performed using the hydrometer method (BYU Soil Analysis Lab, Provo, UT, USA) on four samples (depth 0–20 cm) per plot.

Finally, we used pre-planned stepwise regression analyses with forward selection (yet backward-looking to remove variables from the model whose F-value fell below 3.996) on

both abundance of ant mounds and penetration resistance. Variables used to explain penetration resistance, in the order they were entered initially into the analysis, included average %clay, available water capacity, USLE soil erodibility factor (K), and horse presence. For ant mounds, variables included precipitation, K, horse presence, elevation (in m), and mean slope gradient of sites. These stepwise models sought to confirm our ANOVA results and ensure that an abiotic variable (rather than the presence of horses) was not obviously driving variability in response variables that differed significantly between horse-occupied and -removed sites. We also performed simple- and multiple-linear regressions to investigate contributory mechanisms of change, following our predictions above.

3. Results

3.1. Direct effects

Penetration resistance of soil surfaces was significantly higher at sites with horses in both 1997 ($F_{1,4} = 11.9, p = 0.026$) and 1998 ($F_{1,7} = 20.4, p = 0.003$; Table 1). In 1998, horse-occupied sites exhibited 15.4 times higher penetration resistance than did horse-removed sites at low elevations and 3.8 times higher penetration resistance at high elevations. Evidence of a direct effect of horses on penetration resistance was best illustrated by a strong correlation in 1998 (the year of more extensive soil sampling) of average penetration resistance and total number of horse defecations ($r = 0.69, n = 18, p = 0.001$; Fig. 3a). This correlation was apparent both among high-elevation plots ($r = 0.71, n = 8, p = 0.05$) and among low-elevation plots ($r = 0.77, n = 10, p = 0.0065$). Corroborating the strength of the direct effect was the result of the stepwise regression in 1998 on penetration resistance. Among the four variables considered (see Section 2.3), presence of horses was the only variable to enter the model, regardless of whether plots or sites were treated as replicates (using number of horse defecations or categorical horse presence, respectively, to analyse horse effects). Data from 1997 provided a weaker test of the mechanism, as only seven sampled sites had all NRCS data available; however, %clay and the presence of horses were the strongest determinants of penetration resistance among those sites.

Across years and elevational strata, ant mounds occurred in greater abundance at horse-removed sites than at horse-occupied sites. Ant mounds occurred 2.2–4.0 times more densely at horse-removed than at horse-occupied sites at high elevation, and 3.6–8.4 times more densely at horse-removed sites at low elevation. Although there was high variability within the high-elevation horse-removed category, horse-removed sites tended to have a greater number of ant mounds in both 1997 and 1998 ($p = 0.09$; Table 1). Across both years, we observed few mounds that appeared to have been recently trampled by horses. In 1998 among high-elevation sites, whereas thatch mounds were 3.8 times more abundant at horse-removed than at horse-occupied sites, pebble mounds were nearly equivalent in their density at horse-removed (3.0 mounds/5940 m^2 strip transect) and horse-occupied sites (2.8 mounds/5940 m^2). Total number of horse defecations at plots was poorly related inversely to abundance of ant mounds in both years, and defecations accounted for only 6–9% of the variation in mound abundance in both 1997 ($r = -0.23, n = 14, p = 0.42$) and 1998 ($r = -0.30, n = 18, p = 0.23$; Fig. 3b). Furthermore, no variable entered the stepwise model for abundance of ant mounds at sites in either year, although presence of horses was

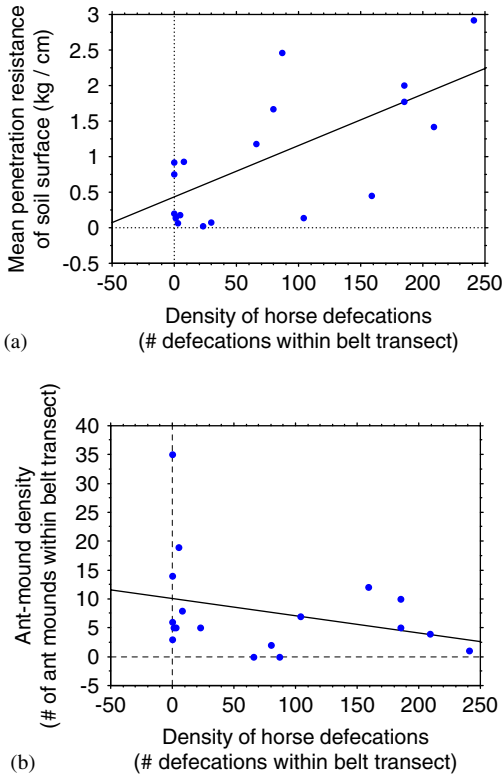


Fig. 3. (a) Mean penetration resistance at plots regressed linearly against the density of horse defecations observed within a standardized belt transect ($1485 \times 4\,\text{m} = 5940\,\text{m}^2$) at each plot, 1998 data. Regression equation: Y (in kg/cm^2) $= 0.434 + 0.007$*(#defecations) $+ \varepsilon$; $r^2 = 0.467$. (b) Mean number of ant mounds encountered within the ($1485 \times 4\,\text{m}$) 5490-m^2 belt transect at each plot, regressed linearly against the density of horse defecations observed within that plot's belt transect, 1998 data. Regression equation: Y (in # of mounds) $= 0.434 + 0.007$*(#defecations) $+ \varepsilon$; $r^2 = 0.092$.

the strongest predictor of abundance out of all predictor variables (ranked by partial correlation and corresponding F-value).

3.2. Indirect effects

When number of horse defecations and %clay were forced in a stepwise model for penetration resistance at plots in 1998, total cover at plots did not enter the stepwise regression ($r_{\text{partial}} = -0.137$; $F = 0.3$). Nonetheless, the two forced variables accounted for much of the variability in resistance, and the regression model (with only the two forced variables) strongly predicted resistance ($F = 10.7; p = 0.001$). In contrast, only 6–9% of the variability in mound abundance was accounted for by our stepwise models in 1997 and 1998 ($0.7 < F < 1.6; p > 0.20$), and neither cover of shrubs nor total cover of vegetation entered the model once recent horse-grazing intensity was accounted for. However, our index of the continuity of the shrub canopy—the average of the four longest shrub

interceptions across all four 50-m line-intercept transects at a plot—which was significantly lower at horse-occupied compared to horse-removed sites in both years (Beever, in revision), was positively correlated with abundance of ant mounds across plots in both 1997 ($r = 0.57, n = 14, p = 0.03$) and 1998 ($r = 0.42, n = 18, p = 0.09$).

3.3. Inter-annual variability

Although the number of ant mounds at a plot was highly correlated between years ($p < 0.0001$), we encountered about 5.2 more mounds per plot during 1998 than in 1997 ($t_{12} = 3.34, p = 0.006$). Counts for all fecal types generally exhibited strong correlation between years ($p < 0.03$), and were generally not statistically different between years. Finally, mean sampling date of plots occurred approximately 28 days earlier in 1998 ($t_{16} = -3.12, p = 0.007$).

4. Discussion

E. caballus has inhabited North America for only the past 400 years, after an absence of all equids from the Great Basin for at least 13,200 years (Grayson, 1989). Thus, horses should be considered ecologically as part of a novel disturbance regime in the Great Basin (rather than as a native species), and their effects should be considered along with those of domestic livestock when planning for conservation of Great Basin landscapes (Beever, 2003). As a result of the non-uniform patterns of habitat use by horses (as for other ungulates; see references in Hobbs, 1996), the magnitude of grazing impacts will vary widely across the landscape, from areas minimally affected to areas used heavily (Beever, 2003). In our research, we observed notable differences in ant mounds and soil-surface penetration resistance between sites grazed by horses and sites from which horses had been removed for 10–14 years, when comparing sites at the landscape scale. Results of our analyses suggest that these apparent ecosystem alterations are likely due to a combination of direct and indirect effects (Fig. 1). Our analyses and a literature review also suggest the potential importance of feedback loops.

4.1. Direct effects

4.1.1. Soils

Of all ecosystem components measured at sites, penetration resistance was the variable that differed most strongly between horse-occupied and -removed sites. Although it is possible to have trampling without herbivory, it is not possible to have herbivory without concomitant soil trampling. Our predictions for two tests of direct effects of horses on penetration resistance were confirmed in both cases. First, soil surfaces at horse-occupied sites exhibited significantly higher penetration resistance than did those at horse-removed sites, in both 1997 and 1998 (Table 1). Second, resistance was clearly and positively related to number of horse defecations across sites in 1998 ($r = 0.69, p = 0.001$), when soil sampling was most extensive.

Soil compaction has been found to increase linearly with increasing livestock grazing intensity in fields of Kentucky bluegrass (Alderfer and Robinson, 1947; Bryant et al., 1972), in riparian zones (Orr, 1960; Kauffman and Krueger, 1984), and at areas with silty clay soil (Rauzi and Hanson, 1966). In Colorado grasslands, finer-textured soils are the

most likely to exhibit increases in soil compaction due to grazing (Van Haveren, 1983). Alderfer and Robinson (1947) found that grazing on clay and sandy loams resulted in compaction of only the top 5 cm of soil, but density of soil in this horizon increased from 1.09 g/cm^3 on ungrazed sites to 1.51 g/cm^3 on lightly grazed sites, and 1.54–1.91 g/cm^3 on heavily grazed sites. This is consistent with our results, which showed significant compaction of the soil surface of our loamy soils (averages at sites ranged from 13.3% to 29.0% clay. In addition, increases in bulk density have been experimentally demonstrated for domestic cattle in New Mexico after as little as one month of grazing (Weltz et al., 1989). Significantly higher penetration resistance at horse-occupied sites raises concern, because alterations of the soil environment can affect a wide variety of ecosystem processes (Fig. 1; Thurow, 1991).

4.1.2. Ant mounds

We found greater abundance of ant mounds at horse-removed as compared to horse-occupied sites in both 1997 and 1998, with 2.2–4.0 times more mounds at high-elevation sites, and 3.6–8.4 times more mounds at low-elevation sites (Table 1). Greater abundance of ant mounds at horse-removed sites is particularly interesting, given that several factors would seem to suggest that numbers should be higher at horse-occupied sites, where: (a) the greater amount of open space should mean more substrate for mound-building activities, especially for *Pogonomyrmex* species; and (b) reduced vegetative cover should favor warmer microclimates, the latter of which would allow for longer activity periods (especially at high-elevation sites), both seasonally and diurnally (Crist and Williams, 1999). In spite of this coarse-level difference (i.e., horse-occupied vs. -removed sites) in mound abundance, there was less support ($p > 0.20$) for a linear relationship between horse-grazing *intensity* (as measured by defecation counts) and ant-mound abundance (compared to the horse intensity–soil relationship).

Several possible explanations could account for our inability to find recently trampled mounds at horse-occupied sites. First, horses may avoid pebble and thatch ant mounds in semi-arid mountain ranges, particularly the latter, given that *Formica* ants sting. Alternatively, horses may indeed trample mounds, but ants rebuild their mounds quickly enough that we rarely observed trampled mounds. Finally, horses may trample mounds, but such trampled mounds may be quickly abandoned, and without regular maintenance, are obliterated by wind, rain, or activity of other animals.

Although we did not comprehensively investigate species richness of ants at sites, our finding of greater species richness per site across pooled horse-removed versus horse-occupied sites (Appendix D) is consistent with findings of some previous research on ants. Suarez et al. (1998) found reduced species richness of native ants as habitat fragmentation increased, generally caused by the presence of the exotic Argentine ant (*Iridomyrmex humilis*). While other authors have also found decreased species richness of ants at sites disturbed by grazing animals (e.g., Majer, 1985; Majer and Beeston, 1996; Andersen and Sparling, 1997; Nash et al., 1998), a number of other studies found no negative effects of grazing (e.g., Heske and Campbell, 1991; Whitford et al., 1999).

Alternative explanations for our results (e.g., differences in historical or current livestock grazing between horse-removed and -occupied sites, confounding by site properties such as exposure and position on the slope) were reviewed by Beever and Brussard (2004) in their research on small mammals and reptiles at these sites. In brief, analyses overwhelmingly

failed to support these alternative explanations as drivers of the differences in penetration resistance and ant-mound abundance we observed between horse-removed and -occupied plots.

4.2. Indirect effects and potential feedbacks

Research on soil-surface penetration resistance and ant mounds (as depicted by our conceptual model in Fig. 1) suggests that in semi-arid ecosystems, alteration of the vegetative canopy may be one of the stronger pathways by which grazers indirectly affect soil surfaces and ant mounds. Indeed, horse-occupied sites in this study had significantly lower abundance and cover of grasses, lower shrub cover, lower total vegetative cover, lower species richness at the site level, and a less continuous shrub canopy, compared to horse-removed sites (Beever, 1999; Beever, unpublished data). Greater vegetative cover can: provide more extensive shading for soils to retain greater soil moisture; reduce soil erosion by intercepting more incident precipitation and reducing surface wind velocities; and provide greater organic-matter inputs to soils, which in turn alter both chemistry and physical properties of soils (Fig. 1).

Furthermore, Van de Koppel et al. (1997) attributed catastrophic shifts in vegetation reported by several other authors to deterioration of soil conditions and reduction of standing biomass. In the two focal examples of van de Koppel et al. (1997), irreversible changes in the vegetative mosaic were attributed to increased herbivory. Other authors (e.g., Archer and Smeins, 1991; Belsky and Blumenthal, 1997) have similarly related herbivore-induced alterations in soil properties and vegetation, through various pathways. USDA (1993) reported that numerous plant species experience physical root restriction when penetration resistance is greater than 1.0 MPa. In our sampling in 1998, up to 23 (92%) of 25 sampling stations at horse-occupied sites had at least two subsamples with resistance above that threshold, and the value was exceeded at a minimum of 10 sampling stations. This is a minimum estimate of average resistance, because our instrument for sampling penetration resistance had a maximum value of $4.7\,kg/cm^2$.

Our results also support indirect effects on ant abundance associated with changes in vegetative cover and the potential existence of feedbacks as shown in Fig. 1. We found a positive (though weak) correlation between ant mound abundance and total vegetative cover across all sites in both 1997 and 1998. Stronger correlation between these two variables has been observed by other researchers, however (Sneva, 1979; Andersen, 1991; Andersen and Sparling, 1997). Furthermore, mound abundance correlated quite strongly with an index of shrub-canopy continuity in both 1997 ($r = 0.57, p = 0.03$) and 1998 ($r = 0.42, p = 0.09$), suggesting that small-scale *pattern* in vegetation cover may influence abundance more than simply the *quantity* of cover. The discrepancy between the strength of these last two types of correlations is consistent with findings of other investigators of ants. For example, Bestelmeyer and Wiens (1996) found that community diversity of ants in Argentina varied with respect to both season (wet vs. dry) and scale of analysis. After analyzing low-level aerial photographs of ant distributions, Crist and Wiens (1996) suggested that ant distributions are influenced both by fine-scale determinants such as neighborhood interactions and by broad-scale factors such as grazing, topography, and soils.

5. Conclusions

Previous research demonstrated that free-roaming horses can alter aspects of vegetation, granivorous small mammals, and reptiles in Great Basin mountain ranges (Beever, 1999; Beever and Brussard, 2004). This, in addition to the findings presented here that horse-occupied sites have more compacted soil surfaces and lower abundances of ant mounds, suggest that horses as well as domestic livestock need to be considered in conservation planning in semi-arid ecosystems. For example, given that horses use steeper and higher-elevation locations than do cattle, addition of horses to landscapes means that non-native herbivory and trampling occurs across a greater percentage of the physiographically heterogeneous Great Basin than if only domestic stock were present (Beever, 2003). Several lines of evidence also suggest that efforts of conservation researchers and land managers alike would be more effective if both direct and indirect disturbance effects were considered. The relative importance of different types of effects needs to be further quantified with manipulative experiments.

Acknowledgments

We thank J. Axtell, J. Gianola, and T. Seley of the Bureau of Land Management for help with site selection. J. Knight, State Entomologist of the Nevada Department of Agriculture, identified ant samples and provided useful insights about ants. J. Fisher of the NRCS assisted with soil data and interpretation. B. Elston created Fig. 2. We thank N. Wendel, D. Watterson, and especially J. Landmesser for field assistance. B. Bestelmeyer, F. Wagner, J. Reed, T. Wojtowicz, and P. Brussard all provided critical reviews of earlier manuscript drafts. At the University of Nevada, the Nevada Agricultural Experiment Station, Biological Resources Research Center, Center for Environmental Arts and Humanities, College of Agriculture, Department of Biology, Nevada Biodiversity Research and Conservation Initiative, and Graduate Student Association all provided financial assistance to EAB, as did the Kosciusczko Foundation and the American Museum of Natural History.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at: doi:10.1016/j.jaridenv.2005.11.006.

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CHAPTER FOURTEEN

Influences of Free-Roaming Equids on Sagebrush Ecosystems, with a Focus on Greater Sage-Grouse

Erik A. Beever and Cameron L. Aldridge

Abstract. Free-roaming equids (horses [*Equus caballus*] and burros [*E. asinus*]) in the United States were introduced to North America at the end of the 15th century, and have unique management status among ungulates. Legislation demands that these animals are neither hunted nor actively managed with fences and rotation among pastures, but instead constitute an integral part of the natural system of the public lands. Past research has elaborated that free-roaming horses can exert notable direct influences in sagebrush (*Artemisia* spp.) communities on structure and composition of vegetation and soils, as well as indirect influences on numerous animal groups whose abundance collectively may indicate the ecological integrity of such communities. Alterations to vegetation attributes and invertebrates can most directly affect fitness of Greater Sage-Grouse (*Centrocercus urophasianus*) and other sagebrush-obligate species; alterations of soils and other ecosystem properties may also indirectly affect these species. Across 3.03 million ha of the western Great Basin, horse-occupied sites exhibited lower grass, shrub, and overall plant cover; higher cover of unpalatable forbs and abundance of cheatgrass; 2.2–10.0 times lower densities of ant mounds; and 2.9–17.4 times greater penetration resistance in soil surfaces, compared to sites from which horses had been removed for 10–14 years. As is true for all herbivores, equid effects on ecosystems vary markedly with elevation, stocking density, and season and duration of use. However, they may be especially pronounced in periods of drought, which are forecasted to occur with increasing frequency in the southwestern United States under climate change, and when they interact synergistically with livestock-grazing effects. Equids' use of sagebrush landscapes will have different ecological consequences than will livestock grazing, at both local and landscape scales. Spatially, the addition of horses to sagebrush landscapes means more of the landscape receives use by nonnative grazers than if domestic cattle alone were present. In spite of recent advances in ecological understanding of equid synecology, much remains to be learned. Life-history characteristics of Greater Sage-Grouse and other sagebrush-obligate species suggest the great value in evaluating equid effects more broadly than through a horses-vs.-livestock perspective, and in monitoring ecosystem components such as soil-surface hardness

Beever, E. A., and C. L. Aldridge. 2011. Influences of free-roaming equids on sagebrush ecosystems, with a focus on Greater Sage-Grouse. Pp. 273–290 *in* S. T. Knick and J. W. Connelly (editors). Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, CA.

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and ant-mound density that have ecological and management relevance yet for which data are relatively inexpensive to collect.

Key Words: burros, *Centrocercus urophasianus,* direct and indirect effects, *Equus asinus*, *Equus caballus,* grazing, horses, sagebrush, sage-grouse.

Efecto de los Équidos de Vida Libre en los Ecosistemas de *Artemisia* spp., con Énfasis en el Greater Sage-Grouse

Resumen. Équidos de movimiento libre en los Estados Unidos (caballos [*Equus caballus*] y burros [*E. asinus*]) fueron introducidos a Norteamérica a fines del siglo XVI, y ellos han tenido un manejo único entre los ungulados. La legislación requiere que estos animales no sean cazados, ni manejados con cercas, ni tampoco dejados en un tipo de pastoreo rotacional pero en vez éstos constituyen una parte esencial del sistema natural de tierras públicas. Investigaciones previas han demostrado que estos caballos de movimiento libre pueden tener influencias directas sobre la estructura y composición de los suelos y vegetación en comunidades dominadas por *Artemisia* spp., así como también influencias indirectas en varios grupos de animales en donde su abundancia colectiva puede indicar la integridad ecológica de estas comunidades. Alteraciones a las características de la vegetación e invertebrados pueden afectar en forma directa al éxito reproductivo del Greater Sage-Grouse (*Centrocercus urophasianus*) y de otras especies obligadamente relacionadas a comunidades de *Artemisia* spp. También alteraciones a los suelos y a otras propiedades del ecosistema pueden afectar indirectamente a estas especies. Dentro de 3,030,00 hectáreas de la Gran Cuenca Occidental, áreas ocupadas por caballos han exhibido una menor cobertura de gramíneas, arbustos, y vegetación en general; una mayor cobertura de hierbas no comestibles y mayor abundancia de la gramínea exótica *Bromus tectorum*; una reducción de entre 2.2 a 10 veces en la densidad de los nidos de hormigas en montículo; y un aumento de entre 2.9 y 17.4 veces en los niveles de resistencia a la penetración de la superficie en los suelos, todo esto si se compara con áreas en donde caballos han sido removidos por períodos de entre 10 a 14 años. Así como sucede con todos los herbívoros, los efectos de los équidos en ecosistemas varían de acuerdo a la densidad del ganado, duración y estación de pastoreo, y la elevación en el sitio. Sin embargo, estos efectos pueden ser especialmente dramáticos durante períodos de sequía, los cuales son previstos que ocurrirán en una mayor frecuencia en el suroeste de los Estados Unidos debido al cambio climático, y más aun cuando éstos interaccionan sinergísticamente con los efectos del pastoreo de la ganadería. El uso del paisaje en comunidades de *Artemisia* spp. por équidos tendrá consecuencias ecológicas muy distintas a las del pastoreo por medio del uso de ganado tanto a nivel local y del paisaje. En términos espaciales, la introducción de caballos a estos ecosistemas dominados por *Artemisia* significa que una mayor proporción de este ecosistema sea usado por herbívoros no nativos si este mismo fuese únicamente usado por el ganado doméstico. A pesar de los avances recientes en el entendimiento ecológico de la sinecología de équidos, todavía queda mucho que aprender. Las características naturales del *C. urophasianus* y de otras especies en estas comunidades sugieren que pueden ser de gran valor: 1) la evaluación del efecto de los caballos y que ésta debe ser tomada en forma más amplia que la simple perspectiva caballos vs. ganadería, y 2) el monitoreo de componentes del ecosistema tales como la dureza en la superficie de los suelos y la densidad de los nidos de hormigas en montículo, los cuales tienen relevancia ecológica y de manejo ya que la colección de datos es relativamente de bajo costo y factible de implementar en el campo.

Palabras Clave: Artemisia, burros, caballos, *Centrocercus urophasianus,* efectos directos e indirectos, *Equus asinus*, *Equus caballus*, pastoreo, sage-grouse.

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Sagebrush (*Artemisia* spp.) habitats have undergone significant change during the last century because of conversion, degradation, and fragmentation (Knick et al. 2003, Connelly et al. 2004). Remaining sagebrush habitats continue to be threatened by direct loss of habitat due to agricultural conversion (West and Young 2000, Connelly et al. 2004), degradation or loss from energy exploration and extraction (Braun et al. 2002, Knick et al. 2003, Lyon and Anderson 2003, Aldridge and Boyce 2007), invasions of exotic plants (Knick et al. 2003, Connelly et al. 2004), intensive grazing practices (Beck and Mitchell 2000, Hayes and Holl 2003, Crawford et al. 2004), fire (Connelly et al. 2000c, 2004), and climate change (Neilson et al. 2005). Grazing is often implicated in reducing sagebrush habitat quality (Beck and Mitchell 2000, Hayes and Holl 2003, Crawford et al. 2004) resulting in consequences for sagebrush-obligate species; however, these effects are rarely addressed quantitatively. This is due to the difficulties in accounting for legacy effects related to past management (Beever et al. 2006, Rowe 2007) and developing defined experimental treatments integrated with management actions that allow for testing of hypotheses within an adaptive-management framework (Aldridge et al. 2004).

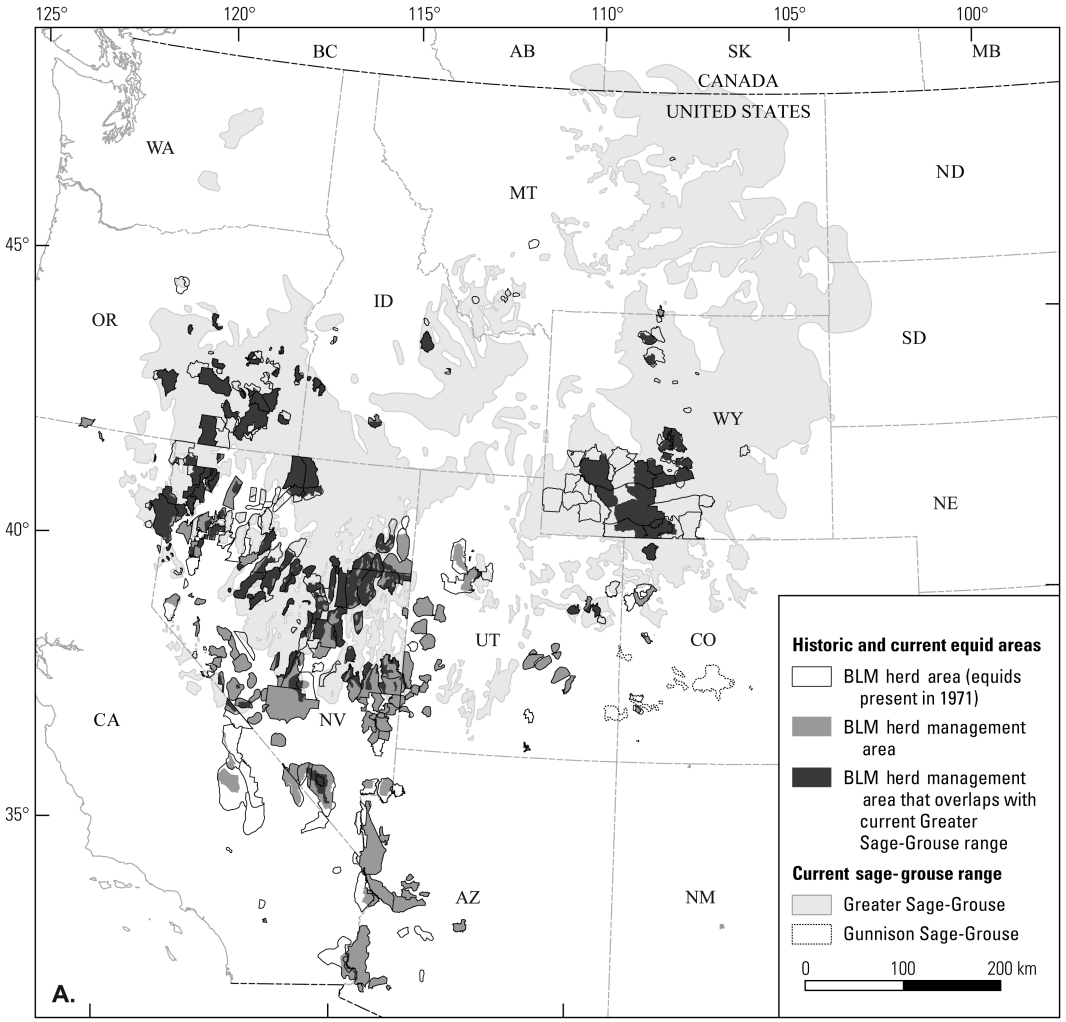


Figure 14.1. A) Distribution of Bureau of Land Management (BLM) free-roaming equid herd areas (equids historically present) and herd management areas (equids currently present), as well as B) U.S. Forest Service (USFS) wild horse and burro territories (equids currently present) across western North America. The current distributions (Schroeder et al. 2004) for both Greater Sage-Grouse and Gunnison Sage-Grouse are shown to illustrate the spatial overlap of equid landscape use with sage-grouse. Spatial data for equid ranges were compiled from state and local BLM and USFS offices.

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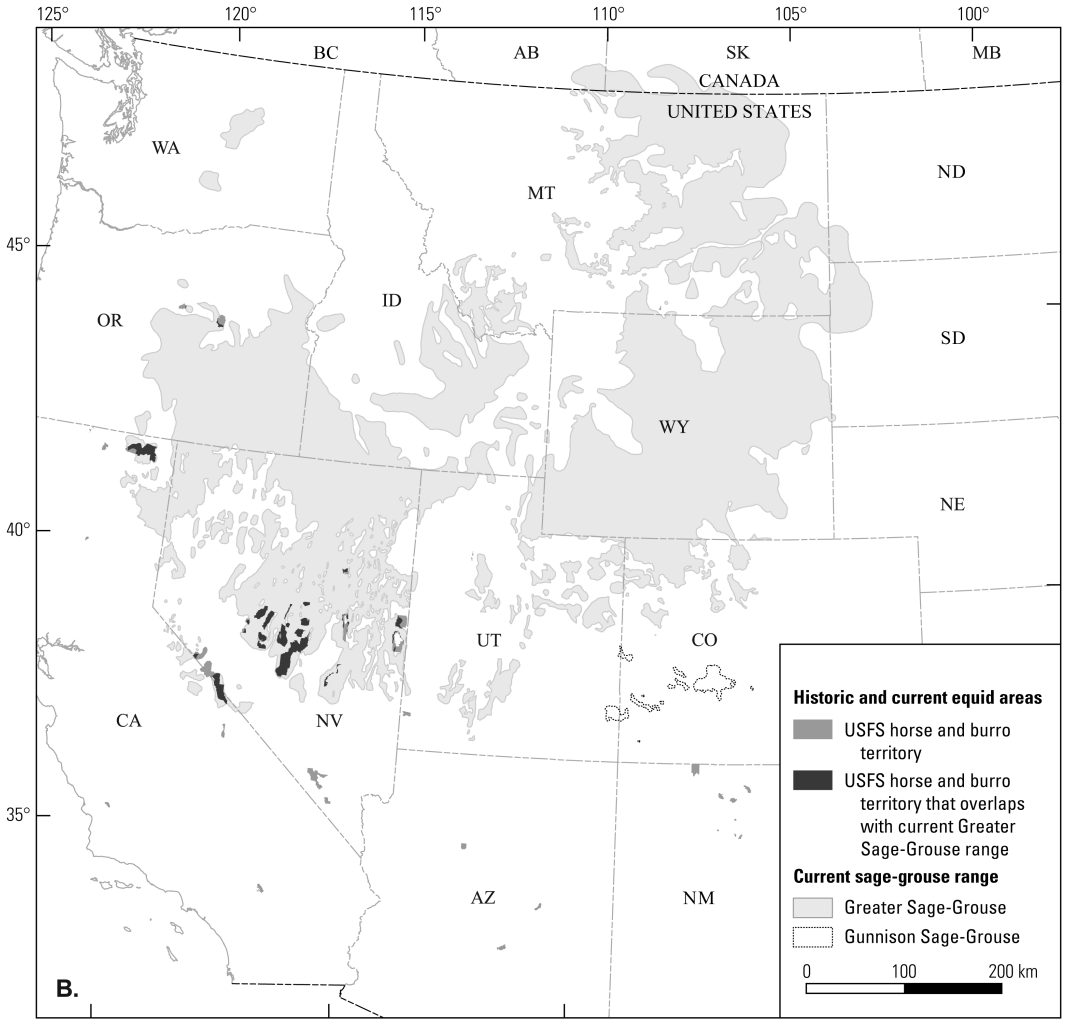


Figure 14.1. B. (*continued*)

Furthermore, relatively little consideration has been given to understanding links between the effects that free-roaming equids (hereafter, equids refer to horses [*Equus caballus*] and burros [*E. asinus*] in western North America; see distribution in Fig. 14.1) may have on sagebrush ecosystems and sagebrush-obligate species that these systems support.

Many wildlife species have been negatively affected by changes to sagebrush ecosystems. For example, many sagebrush-obligate birds have experienced population declines and range contractions over the past 40 years (Sauer et al. 2003, Connelly et al. 2004). Most monitored populations of Greater Sage-Grouse (*Centrocercus urophasianus*), for instance, have declined by ~2% or more per year since 1965 (Connelly and Braun 1997, Braun 1998, Connelly et al. 2004). Greater Sage-Grouse use a diversity of habitats across life stages and encompass annual home ranges as large as 2,975 km^2 (Connelly et al. 2004). Large tracts of contiguous sagebrush habitat are required for their persistence (Aldridge et al. 2008), although heterogeneity within those patches may also be important (Aldridge and Boyce 2007).

A larger body of knowledge exists on Greater Sage-Grouse habitat requirements at local scales (Connelly et al. 2000c, Crawford et al. 2004, Hagen et al. 2007) compared to landscape-scale understanding (Connelly et al., this volume, chapter 4). Greater Sage-Grouse require habitat patches with extensive cover of sagebrush during breeding and nesting (15–25% cover), brood-rearing (10–25%), and winter (10–30%) (Connelly et al. 2000c, Hagen et al. 2007). In addition to the vegetation structure that Greater Sage-Grouse require from woody plants, grass cover is important for nest concealment and

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as escape cover, and increased grass cover results in increased nest success (Connelly et al. 2000c, Crawford et al. 2004, Aldridge 2005, Hagen et al. 2007). Forb-rich mesic areas constitute important habitats during summer and brood-rearing; these areas provide forbs and insects as food resources that are required for chick survival (Johnson and Boyce 1990, Drut et al. 1994b, Sveum et al. 1998a). Greater Sage-Grouse exhibit strong selection for greater cover (i.e., 14–40%) and greater diversity of forbs (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994a, Sveum et al. 1998a).

Free-roaming equids within these sagebrush ecosystems, as is true for all large-bodied herbivores, can alter ecosystem components directly through any of several processes, including selective plant consumption, trampling of plants and surface soil horizons, and spatial redistribution of nutrients via ingestion and subsequent excretion (Fig. 14.2; Beever et al. 2003, Beever and Herrick 2006). These

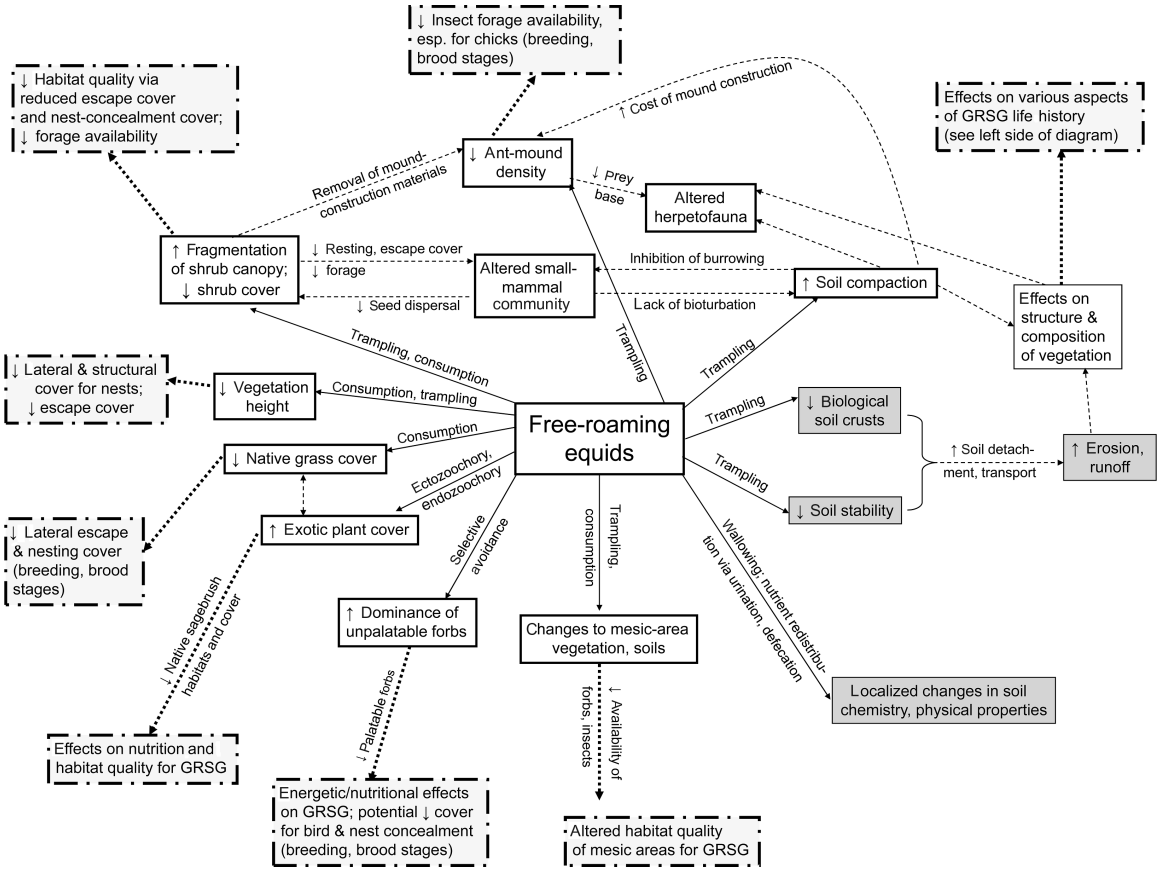


Figure 14.2. Conceptual model of relationships between free-roaming equids (center) and various aspects of sagebrush communities (inner ring of boxes) and, in turn, between those aspects and life-history characteristics of Greater Sage-Grouse (GRSG) (outer ring of boxes: dash-dot border). Direct effects of equids are denoted by solid lines, whereas potential ecological cascades and indirect effects are denoted with dashed lines. Unless otherwise noted, alterations to habitat may affect Greater Sage-Grouse fitness during multiple important life stages, including at winter, brood-rearing, and breeding and nesting habitats. Thick inner boxes denote that horse-occupied sites have been found to differ significantly from horse-removed sites for these aspects of ecosystems (see text). Labels along arrows describe the likely mechanisms underlying these relationships. Arrows inside the boxes can be interpreted as increased or decreased. Equid influences likely interact with other drivers in their relationships with ecosystem components; such drivers include rapid climate change, wildfire and prescribed fire, western juniper dominance, off-highway vehicle use, native and domestic ungulates, other herbivores, and pests and disease invasions. For model clarity, potentially beneficial effects of free-roaming equids (e.g., reduction of site vulnerability to catastrophic fires due to brief removal of fine fuels, increase of pore spaces via chipping of soils at low equid densities, and creation of germination sites for new plants) were not included graphically. Note that whereas the relationships of equids to ecosystem components and the relationships of Greater Sage-Grouse to various habitat conditions have both been documented in some systems, the entire link of equids to Greater Sage-Grouse has not been demonstrated experimentally to date.

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processes all occur at local through landscape scales, and thus can have relevance for life processes of Greater Sage-Grouse and other sagebrush-obligate species. Equids' rubbing against plant parts and creation of wallows are two examples of these disturbance processes at local scales. In addition to exerting these direct effects, equids can also affect sagebrush-inhabiting vertebrates indirectly through their influences on structure, composition, and chemistry of vegetation, as well as on the structure and local chemistry of soils (Beever and Herrick 2006, Beever et al. 2008). In turn, effects on vegetation can affect its value as hiding cover for terrestrial species. Collectively, these influences on both vegetation and soils can alter the competitive interactions among plants, alter soil-erosion patterns, create niches for colonizing or ruderal (early-successional, often disturbance-tolerant) species, and create feedback loops (Hobbs 1996, Beever and Herrick 2006) that could ultimately reduce the functionality of habitats for sagebrush-obligate species such as sage-grouse (includes Greater Sage-Grouse and Gunnison Sage-Grouse [*Centrocercus minimus*]).

Greater Sage-Grouse currently occupy ~668,412 km^2 of habitat across 11 states and two Canadian provinces, roughly 56% of their historic pre-settlement range in North America (Schroeder et al. 2004: Fig. 1). Based on extents of Bureau of Land Management (BLM) wild horse and burro herd areas (HAs) and herd management areas (HMAs), and United States Forest Service (USFS) wild horse and burro territories, we estimate that during at least some of the years since the establishment of the Wild Free-Roaming Horses and Burros Act of 1971, these equids have occupied 366,690 km^2 of semiarid ecosystems in western North America (Table 14.1). Areas that have been managed for horses and/or burros from 1971 to 2007 constitute ~18% (119,703 km^2) of the currently occupied Greater Sage-Grouse range. This estimate excludes dispersal and extra-limital movements by equids (i.e., outside of management areas), which are difficult to quantify but may be widespread; considering these would appreciably increase the percentage of Greater Sage-Grouse habitats affected by equid grazing. About 12% (78,380 km^2) of the current range of Greater Sage-Grouse is now managed for free-roaming equids (Table 14.1). Thus, there may be unmeasured consequences for a significant portion of sage-grouse habitat throughout the species' range because of the aforementioned ways in which free-roaming equids can directly or indirectly impact sagebrush habitats.

Our goal is to critically consider the relationship between free-roaming equids and sage-grouse, focusing on Greater Sage-Grouse. Our objectives were to (1) synthesize the alterations to sagebrush and other communities that equids have been shown to exert in past research and (2) interpret these findings in view of the current body of knowledge of life-history and conservation requirements of Greater Sage-Grouse, as they pertain to continued persistence of the species.

A HISTORICAL REVIEW OF EQUID DYNAMICS IN NORTH AMERICA

Understanding relationships between free-roaming equids and sagebrush-obligate species such as sage-grouse requires a review over evolutionary and historical time. During the Eocene, equids (specifically, *Hyracotherium*) arose and began to diversify in North America (Simpson 1951, Zarn et al. 1977). Wild horses have occupied a variety of habitats worldwide throughout their evolutionary existence, but have generally favored cooler, more mesic habitats (e.g., grassland, open forest, and tundra), in contrast to the dry-steppe and desert habitats of burros and zebras such as *Equus burchellii* (Bennett 1992). After their long history in North America, however, horses were extirpated from the continent between 10,500 and >13,200 years ago, hypothesized to have resulted from overhunting by primitive peoples, climatic influences, or both (Martin 1984, Bennett and Hoffmann 1999). Equids were absent from North America until the end of the 15th century, when horses and burros were introduced by Spanish conquistadors into what is now the southwestern United States. Free-roaming horses spread rapidly across the Intermountain West, and populations reportedly peaked in the United States at 2,000,000–7,000,000 animals in the late 1700s to early 1800s (Ryden 1978, Thomas 1979). However, competing interests dictated that horses were captured in increasing numbers, a process that was accelerated by passage of the Taylor Grazing Act of 1934. These interests included using horses as saddle animals, breeding stock, or both; selling horses entrepreneurially for profit; and reducing suspected competition with livestock grazing. By 1934, numbers of free-roaming horses were reduced to ~150,000 animals (Thomas 1979).

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TABLE 14.1

Area (km²) affected by free-roaming equids across western United States, by individual states overlapping the current range of Greater Sage-Grouse.

State[a]	BLM herd area[b]	BLM herd management area[c, d]	USFS wild horse and burro territories[d]	Area historically occupied by free-roaming equids[e]		Current area occupied by free-roaming equids	
				Within western North America	Within Greater Sage-Grouse current range	Within western North America	Within Greater Sage-Grouse current range
Arizona	14,722	12,480	303	27,505	—	12,783	—
California	28,184	9,787	2,640	40,611	8,720	12,427	6,981
Colorado	2,973	1,638	—	4,611	816	1,638	634
Idaho	1,933	1,692	—	3,625	1,594	1,692	1,440
Montana[f]	905	150	18	1,073	362	168	8
New Mexico	512	116	641	1,269	—	757	—
Nevada	1,788	70,716	6,881	169,384	48,281	77,596	38,229
Oregon[f]	17,584	11,991	414	29,990	16,904	12,405	11,775
Utah	15,885	11,482	133	27,501	1,870	11,616	1,023
Wyoming	41,795	19,326	—	61,121	41,156	19,326	19,290
Totals	216,282	139,378	11,029	366,690	119,703	150,408	78,380

SOURCE: Spatial data for equid ranges were compiled from a variety of state and local BLM and USFS offices; current area and equid numbers represent data as of 2007.

[a] Indicates state that administers the federal land (not all land area reported is within the boundary of that state).

[b] BLM wild herd areas represent areas historically occupied by free-roaming equids, but that are not currently managed to contain horses, unless currently contained within a BLM herd management area.

[c] BLM herd management areas are contained within BLM herd areas.

[d] BLM herd management areas and USFS wild horse and burro territories both historically were, and currently are, occupied by free-roaming equids.

[e] During at least some period between 1971–2007.

[f] Equid areas managed by the BLM within South Dakota and North Dakota are administered by Montana; areas in the state of Washington are administered by Oregon. Numbers are inclusive within those states.

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Given burros' value to both Native Americans and Euro-Americans as work animals and as food after their introduction to western North America, burros probably did not become feral until the 19th century, likely the result of their escaping from loose confinement or being deliberately released and not rounded up (McKnight 1958, Carothers et al. 1976, Wagner 1983). Based on mail-survey and field estimates, McKnight (1958) reported that feral burros occurred in 10 western states in 1957. Burro movements overlap sage-grouse habitats in multiple areas across the southwestern United States, and although the overlap is less extensive than is the overlap with horse habitats, burros tend to spend more time in lower-elevation habitats, as do sage-grouse. Free-roaming burros are descended from the African wild ass (*Equus africanus*) native to northeastern Africa, and are more abundant in the warmer deserts south of the sagebrush distribution. Historically, horses have outnumbered burros in the historic range of Greater Sage-Grouse by 50 to 1 to well over 80 to 1. In addition, much of the scientific literature on burros in the western United States (1) comes from study areas outside the historic range of Greater Sage-Grouse; (2) focuses on potential competition between burros and bighorn sheep (*Ovis canadensis*), and only indirectly considers effects of burros on other ecosystem components; and (3) occurs in proceedings and other gray literature not subject to the same level of scrutiny as other peer-reviewed sources (McKnight 1958, Carothers et al. 1976, Wagner 1983). We thus focus most of the remaining discussion on free-roaming horses and direct comparatively little attention to burros.

Legislative and Legal Mandates That Affect the Equid-Sagebrush Ecosystem Relationship

The legislation that established management policies for equids in western North America (Wild Free-Roaming Horses and Burros Act of 1971) deemed free-roaming equids an integral part of the natural system of public lands. Horse numbers rose sharply after enactment of the 1971 act that afforded horses and burros strong protection on BLM and USFS lands (Wagner 1983, United States Departments of Agriculture and the Interior 1997c). In the absence of any widespread, effective predator (but see Turner and Morrison 2001, Jeffress and Roush 2010 for a localized exception—mountain lions [*Felis concolor*]) and removal of any population constraint due to aridity because of human development of remote water sources such as guzzlers, humans became the strongest force regulating size of horse populations (Tables 14.2, 14.3). The Federal Land Policy and Management Act of 1976 and the Public Rangelands Improvement Act (PRIA) of 1978 amended the 1971 act and required record

TABLE 14.2

Criteria used by wild horse managers to set population goals reported in survey questionnaire from six states, administered in 1999.

Managers may have used more than one technique in Herd Management Areas (HMAs).

Technique used	No. of HMAs using technique	% of HMAs using technique
Grazing levels	31	55
Forage consumption rates	28	50
AUMs	16	29
Birth rates	3	5
Trend studies	3	5
Court order	2	4
Multiple-use decision (MUD)	2	4
Water availability	1	2
Genetics/N_e	1	2

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TABLE 14.3

Removal strategies used by managers in six states to maintain population numbers of wild horses, reported in survey questionnaires in 1999.

Some Herd Management Areas (HMAs) use more than one strategy.

Removal strategy	No. of HMAs using technique	% of HMAs using technique
Selective by age	48	86
Selective by phenotype	13	23
Emergency removal due to drought, mortality, or both	6	11
Entire harems removed	2	4
Contraception	2	4
No removals conducted	2	4
Selective by breeding needs	1	2
Nuisance animals only	1	2
Ranchers remove without legal authorization	1	2

SOURCE: K. A. Schoenecker (unpubl. data).

keeping of equid population sizes and distribution; required removal of excess animals from public lands once excess was identified, as well as disposition of animals through adoption; and allowed use of helicopters for capture and removals (Boyles 1986). The Public Rangelands Improvement Act also required research on the interrelationships with wildlife, water, and forage resources, and analysis of what constitutes "excess" animals. Currently, free-roaming equids have a unique management status in North America (Beever 2003). They must be managed according to the 1971 act at the minimal feasible level; thus, many free-roaming herds of horses and burros are neither fenced nor rotated among grazing areas. The act also stipulates that, in contrast to other wild ungulates, hunting of horses or burros is not permitted. Free-roaming horses on other jurisdictions—national wildlife refuges and national parks—are not governed by the same legislation as are lands administered by the BLM or the USFS. Collectively, these evolutionary, cultural, and management histories have set the stage for critically considering the current relationship of equids to Greater Sage-Grouse and other wildlife species dependent on sagebrush habitats.

REVIEW OF PAST RESEARCH

Overview

Influences of large-bodied herbivores on sage-grouse and other sagebrush obligates can occur directly, indirectly, and via feedback loops (Fig. 14.2). Equids can directly affect these by disturbance of lekking behavior and trampling of nests or altricial young, but these interactions have not been investigated. However, direct interactions have been anecdotally observed in the field for other native and nonnative herbivores, such as nest trampling and nest abandonment due to cattle activity $<$30 cm from the nest (C. L. Aldridge, unpubl. data). We thus discuss studies of equids' effects on each of several components of sagebrush ecosystems and relate those effects to requirements of sagebrush-obligate species, focusing on Greater Sage-Grouse. The magnitude of grazing impacts will vary widely across the landscape, from areas minimally affected to areas used heavily (Coughenour 1999, Beever 2003), because of the nonuniform patterns of habitat use by horses and other ungulates (Hobbs 1996). However, the potential exists for these impacts to have consequences for Greater Sage-Grouse populations range-wide, given the

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broad distribution of equids within the range of Greater Sage-Grouse (Fig. 14.1).

Possible Effects of Equids on Plants Within Sagebrush Ecosystems

Horse diets may contain >95% grasses in some seasons (Hubbard and Hansen 1976, Hanley and Hanley 1982, McInnis 1985). It is thus not surprising that across nine mountain ranges of the western Great Basin, horse-removed sites averaged 1.9–2.9 times more grass cover and significantly higher grass density than did horse-occupied sites in years that received 104–120% of the long-term average of precipitation (Beever et al. 2003, 2008). As was true for most other vegetative variables in that study, the magnitude of difference in grass cover and density was most pronounced on the more-productive and species-rich high-elevation sites (Beever et al. 2008). Grasses were similarly heavily used in Utah pastures grazed moderately by domestic horses, regardless of their phenology and thus fiber content (Reiner and Urness 1982).

Grass cover is important for Greater Sage-Grouse throughout the year (Crawford et al. 2004, Hagen et al. 2007). Grass provides escape cover and is particularly important for concealing nests, which are often in heterogeneous sagebrush habitats (Aldridge and Boyce 2007) that have greater residual and live cover of tall grasses (Sveum et al. 1998b, Connelly et al. 2004, Crawford et al. 2004, Hagen et al. 2007). Thus, removal of tall-grass cover in horse-occupied sites could negatively impact quality of habitat for Greater Sage-Grouse (Fig. 14.2).

Sites where horses were removed across the western Great Basin exhibited 1.1–1.9 times greater shrub cover than did horse-occupied sites ($P > 0.027$), although stem density of shrubs did not differ between the two types of sites ($P > 0.60$) (Beever et al. 2003, 2008). In particular, cover of sagebrush (*Artemisia* spp.) among high-elevation sites was 1.47–1.57 times higher at horse-removed than horse-occupied sites, but the difference among all sites was statistically significant ($P < 0.05$) in only the wetter of two years (Beever et al. 2008). This trend in sagebrush cover occurred in spite of a lack of difference in the stem count of sagebrush between the two types of sites (Beever et al. 2008). Horse-occupied sites also had a more fragmented shrub canopy, thought to be due to the combined effects of trampling, rubbing, and consumption by horses. Specifically, randomly placed 50-m transects within horse-removed sites had significantly longer maximum intercepts of shrubs than did similar transects within horse-occupied sites (Beever et al. 2008). The relatively minor contribution of consumption to reductions in shrub cover was suggested by two studies from the Great Basin: (1) a study of the effects of domestic horses at different grazing intensities in northern Utah, which found that utilization of shrubs was usually ≤4.2% (Reiner and Urness 1982), and (2) a study of food-resource partitioning among five sympatric ungulates in northeastern California and northwestern Nevada, which found that horse diets included an average of only 5.0% (range 1.0–11.8%) of browse—shrubs and trees combined—across seasons (Hanley and Hanley 1982).

Loss of sagebrush cover can directly affect food resources for Greater Sage-Grouse, given that they consume sagebrush throughout the year (Patterson 1952; Connelly et al. 2000c, 2004). In addition, loss of sagebrush and other shrubs could directly reduce the quantity and quality of nesting and winter habitat. Reduction in escape cover can result in increased predation pressure on both nests and birds (Connelly et al. 1991, Schroeder and Baydack 2001), which could be exacerbated in the presence of free-roaming equids.

Domestic horses in heavy-grazing regimes in Utah pastures primarily consumed grasses, but consumption of grass was increasingly replaced by forb consumption as duration of grazing lengthened. However, rates of forage removal per animal were lower than in moderately grazed pastures. The authors hypothesized that this diet-switching may have been due to the increased search time for preferred species, lower intake, or more frequent animal interactions (Reiner and Urness 1982). Horse diets in the northwestern portion of the Great Basin contained an average of only 5.5% forbs across seasons (range 2.1–9.4%; Hanley and Hanley 1982).

Sites across the western Great Basin occupied by free-roaming horses at higher elevations possessed greater cover and abundance of grazing-tolerant and unpalatable (to ungulate grazers) forbs such as mules' ears (*Wyethia* spp.) and lupine (*Lupinus* spp.) than did horse-removed sites (Beever et al. 2008), which Ruthven (2007) also reported for sites grazed by domestic livestock in south Texas. These forbs are not food items ingested by Greater Sage-Grouse. This trend was generally true for all forbs

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combined, but was inconsistently and less strongly so than for other plant metrics. Furthermore, information-theoretic analyses suggested that variability in forb cover and frequency more strongly reflected precipitation, year, elevation, and site effects than the presence of horses (Beever et al. 2008). In spite of their greater (unpalatable) forb cover, horse-occupied sites were more depauperate floristically, averaging 4–12 fewer plant species per site; differences primarily reflected herbaceous species, particularly forbs (Beever et al. 2003). These site-level differences in plant species richness were evidenced in spite of a lack of statistical difference in average number of plants intercepted per transect, underscoring the greater heterogeneity within horse-removed sites (Beever et al. 2008) with which many vertebrates in sagebrush ecoregions are associated (Aldridge and Boyce 2007).

Cheatgrass (*Bromus tectorum*) tends to be more abundant at horse-occupied than horse-removed sites (1.6–2.6 times greater abundance; Beever et al. 2003, 2008). Dung piles of feral horses in montane natural grasslands of Argentina act as invasion windows for exotic plants: an invasive thistle was consistently associated with dung piles, and nonnative plant cover in abandoned dung piles was higher than in control plots (Loydi and Zalba 2009). From field-collected fecal samples in two research rangeland areas of the interior northwestern United States and subsequent studies of seed germination in greenhouses, Bartuszevige and Endress (2008) estimated that nonnative ungulates (domestic cattle) disperse 1,200,000 germinable exotic seeds/km^2—about two orders of magnitude greater than that estimated for the native ungulates in the same area (elk [*Cervus elaphus*] and mule deer [*Odocoileus hemionus*]). Invasion of cheatgrass into lower-elevation, xeric sites and alteration of fire frequencies result in reduced plant diversity and habitat structure (Connelly et al. 2004, Crawford et al. 2004). Herbaceous components of the system are lost, resulting in reduced food resources for sage-grouse, and fire frequency is increased, directly eliminating native forbs, shrubs, and perennial grasses within sagebrush habitats (d'Antonio and Vitousek 1992, Miller et al. 1994, Crawford et al. 2004). All of these ecological cascades reduce habitat suitability for sage-grouse (Fig. 14.2; Connelly et al. 2004). Given the drastic changes in stable-state dynamics and management alternatives when cheatgrass invasions occur, possible changes to sagebrush ecosystems as a result of the presence of wild horses—changes in vulnerability or resilience of communities to fire, mechanisms of spread or increase in nonnative plant density—may merit more consideration in light of concerns over the viability of Greater Sage-Grouse populations and other sagebrush-obligate bird species.

Within horse-occupied areas of the western Great Basin, transects adjacent to horse trails had less grass and shrub cover, equivalent or higher forb cover (primarily unpalatable species), and lower species richness than did randomly selected transects within the same site (Beever et al. 2008). That horse grazing affected ecosystem components similarly at both local and landscape scales is important because reports of home-range size in horses vary from 0.9 km^2 on Sable Island, Nova Scotia, to 303 km^2 in Wyoming (Pellegrini 1971, Welsh 1975, Green and Green 1977). We expect the most appropriate scale for analyses of interactions between equids and sage-grouse (or other species dependent on sagebrush habitats) will vary greatly across the geographic range of these sagebrush-associated species.

Insights from the Great Plains

Many of the longest-term and most intensive studies of free-roaming horses have occurred in the far northeastern corner of the current geographical extent of horses in the United States. The Pryor Mountain Wild Horse Range at the Montana-Wyoming border (Fig. 14.1) makes up $<$0.5% of the total extent of HMAs. Paleoevidence, coevolutionary arguments, and recent data all suggest that ecosystem response to equid grazing should be fundamentally different in grasslands and steppes of the Great Plains than in the lower-productivity communities of the Great Basin (Mack and Thompson 1982, Milchunas and Lauenroth 1993, Wilsey et al. 1997, Grayson 2006). Thus, extrapolating results from Pryor Mountain studies across the domain of free-roaming horses in North America should generally be avoided. However, long-term research in the Pryor Mountains suggests horse-grazing impacts on vegetation may vary by year (largely due to interannual variability in precipitation, especially precipitation during the growing season), short-term and especially long-term grazing history, life-form and species of plant, and, most commonly, site elevation and soil type (Coughenour 1999, Gerhardt and Detling 2000).

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Insights from Research in Mesic Systems

Within sagebrush landscapes, streams and springs receive disproportionately heavy use by horses (Fig. 14.2; Crane et al. 1997, Beever and Brussard 2000). The extent to which these resources are negatively affected depends on timing, duration, and intensity of equid grazing; spring density in the area; and productivity and resilience of the habitats and soils adjacent to the water (Beever and Brussard 2000). Degradation of spring-associated resources in steeper terrain and higher-elevation areas by equids is of particular concern, given that these springs would less likely be accessible if domestic cattle were the only grazer in the area (Ganskopp and Vavra 1986, 1987; Beever 2003).

Research on ecosystem response to free-roaming horses in more mesic habitats such as salt marshes, oligotrophic bogs, pastures, and peatlands has a longer history and greater spatial replication at a global scale, but may contribute in only a limited manner to ecologists' understanding of grazing dynamics in semiarid landscapes and sagebrush communities. These ecosystems often have horses present in only limited numbers and over a limited area, and their response to horse grazing is likely to be fundamentally different from that expected in upland areas of semiarid ecosystems where thresholds and nonlinear dynamics dominate (Mack and Thompson 1982, Laycock 1991).

However, these studies may reveal how areas with wetted or hydric soils will respond to horse grazing, such as at springs and margins of riparian areas in the western United States; what plant attributes, portions of the plant community, or areas on the landscape may be particularly vulnerable to effects of horse grazing; and the mechanisms by which indirect effects are brought about by horse grazing. Collectively, these limitations in extrapolating results from other ecoregions to the Intermountain West, combined with the importance of springs and seeps for Greater Sage-Grouse and other sagebrush-obligate species, highlight equid relationships with mesic areas as a fruitful avenue for future research on conservation implications.

Possible Effects of Equids on Soils in Sagebrush Ecosystems

Soil hardness at horse-occupied sites averaged 2.9 times greater than at horse-removed high-elevation sites in the western Great Basin, and 17.4 times greater among low-elevation sites (Beever et al. 2003, Beever and Herrick 2006). Strong within-year correlations ($r = 0.69$, $P = 0.001$) in these studies between average soil-surface penetration resistance and the number of horse defecations at each site suggested a direct effect of horses on penetration resistance (Beever and Herrick 2006). The correlation was stronger within each of the two elevational strata, including the low-elevation ($r = 0.77$) and high-elevation plots ($r = 0.71$). Alterations of soil properties such as bulk density, thickness of surface horizons, and soil chemistry have been implicated in catastrophic degradation of vegetation, invasion of exotic plant species, and desertification (Thurow 1991, van de Koppel et al. 1997), all of which could reduce habitat availability and quality for Greater Sage-Grouse across all life stages (Fig. 14.2).

These alterations have been demonstrated for domestic-livestock grazing via compaction, hoof action and consequent erosion, and redistribution of nutrients such as nitrogen (Archer and Smeins 1991, van de Koppel et al. 1997). Surface soils are involved with numerous biotic and abiotic pathways (Thurow 1991, Belsky and Blumenthal 1997, Beever and Herrick 2006). Consequently, further work on equid-soil relationships would increase ecological understanding and identify implications of and identify management strategies to minimize the influences of free-roaming equids on sagebrush habitats and, thus, on Greater Sage-Grouse populations. For example, two questions that have management significance are to what depths do increases in penetration resistance extend below the soil surface, and what factors (e.g., soil texture or percent clays, consistence, and strength of effervescence) most strongly modify these relationships and pathways?

Whole-Community Perspectives in Analyzing Effects of Equid Grazing

The question of whether horse-occupied and horse-removed sites differ across a broad region in a community or whole ecosystem sense needs to be addressed, in addition to examining grazing effects on individual ecosystem components. Beever et al. (2003) investigated the relative performance of five different data sets, all collected or estimated for long-term abiotic properties across the same 19 sites and two years of field

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work, in detecting disturbance by free-roaming horses. Horse-occupied and horse-removed sites could not be clearly discriminated in multivariate ordination space using cover of key plant species consumed by horses (and measured by BLM horse specialists in horse-effects monitoring), cover or frequency of all plant species, or a full suite of abiotic site characteristics (Fig. 2 in Beever et al. 2003).

In contrast, the two types of sites were clearly distinguished by a suite of variables that were sensitive to grazing disturbance in prior ecological research. These diverse grazing-sensitive ecosystem attributes included density of ant (Formicidae) mounds, penetration resistance of the soil surface, percentage of hypothetically possible granivorous small mammals that were actually trapped, species richness of plants, grass cover, forb cover, shrub cover, and abundance of cheatgrass (Beever et al. 2003). This may be important for Greater Sage-Grouse and other sagebrush-obligate species because although neither cover of the species that free-roaming horses eat nor abiotic site properties differed between horse-removed and horse-occupied sites in a collective (multivariate) sense, community-level differences between the two types of sites clearly existed (Beever et al. 2003). These differences may be important to differing degrees, depending on the species, but effects of these ecosystem alterations have not been addressed for Greater Sage-Grouse. Greater Sage-Grouse have been shown to choose more complex vegetation structure (Crawford et al. 2004, Aldridge 2005). Changes at the community level could result in a reduction in visual obstruction barriers for Greater Sage-Grouse and increase predation on nests and individual birds (Martin 1993, Schroeder and Baydack 2001, Crawford et al. 2004, Aldridge 2005).

Habitat-Use Patterns by Equids and Potential Synergies with Livestock-Grazing Effects

One of the more important challenges in interpreting equids' role in the ecological integrity of sagebrush communities for the future of sage-grouse and other species of concern involves understanding how equids' effects are distributed across the landscape. Spatially explicit quantitative assessment of habitat-use patterns does not translate directly into equivalent understanding of how shorter- and longer-term grazing effects are distributed across semiarid landscapes. This is because of the differential vulnerability of various soil types and plant communities to equid grazing. However, habitat-use analyses provide a foundation that can be focused with emerging scientific information.

Several authors have noted particularly heavy use of the more mesic portions of semiarid landscapes—meadows, grasslands, springs, and riparian zones—by free-roaming horses, especially during the warmest, driest portions of the year (Feist 1971, Pellegrini 1971, Ganskopp and Vavra 1986). Beever and Brussard (2000) concluded local spring density was one of the strongest factors explaining differences in magnitude of impacts at springs across multiple mountain ranges. McKnight (1958) reported that feral burros may remain at watering locations for several hours, and roll and defecate in the water.

Mesic habitats are important for Greater Sage-Grouse survival, providing an abundance of forbs and insects as food resources from pre-laying in early spring (Crawford et al. 2004) through brood-rearing and into the fall (Klebenow and Gray 1968, Drut et al. 1994b, Sveum et al. 1998a, Aldridge 2005). Loss of productive mesic habitats can result in low productivity for Greater Sage-Grouse, which has been linked to population declines throughout the species' range (Connelly et al. 2004, Aldridge and Boyce 2007). Heavy use of these sites by equids could increase conflicts and reduce the availability and quality of important Greater Sage-Grouse habitats. Especially in arid and semiarid ecosystems, springs and riparian ecosystems are of paramount importance to maintaining regional biodiversity because of their facultative or obligate use by ≥70% of a region's species (Naiman et al. 1992). The extent to which free-roaming equids in sagebrush communities directly or indirectly alter the availability of insects important to Greater Sage-Grouse broods at these mesic sites is currently unknown.

Most ungulate species are known to move in response to local and seasonal shifts in distribution of forage abundance, availability, and nutrient quality (Talbot and Talbot 1963, Kitchen 1974). Horses in many of the Great Basin HMAs (Fig. 14.1) tend to move to higher elevations from late spring until early fall, and descend to lower habitats during colder months, when snow may persist at higher elevations (Pellegrini 1971, McInnis 1985). Seasonal shifts in habitat use by Greater Sage-Grouse occur during the late brood-rearing period (July and August) and are driven by the availability of forbs,

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which are required by chicks and adults (Patterson 1952, Klebenow and Gray 1968, Peterson 1970). Similar to the shift in habitat use by equids, Greater Sage-Grouse often move to higher-elevation mountain-shrub communities, spatially tracking the phenology of plant communities to ensure access to more mesic habitats with forbs throughout summer (Fischer et al. 1996a, Connelly et al. 2004). The seasonality of equids' use of the landscape may have important implications for Greater Sage-Grouse habitats and populations, given the varying requirements of Greater Sage-Grouse throughout the year.

Horses use plant communities and landscapes differently than do cattle and native ungulates, across both time and space. Within seasons, horses often segregate by elevation from cattle by using steeper slopes and occupying higher-elevation habitats (Pellegrini 1971; Ganskopp and Vavra 1986, 1987). Both cattle and horses most commonly used the sagebrush-grass vegetation type when averaged across the year in the Red Desert of Wyoming, but peak use by horses occurred in fall and winter, whereas use by cattle peaked in summer and fall (Miller 1980). Horses also spend considerably less time at watering locations than do cattle (Meeker 1979, Ganskopp and Vavra 1986) and range farther from watering sources throughout the year (up to 49.2 km in eastern Nevada; Feist 1971, Pellegrini 1971, Welsh 1975, Green and Green 1977). Horses graze an average of six hours per day longer than cows (Arnold and Dudzinski 1978, Rittenhouse et al. 1982, Duncan et al. 1990) and consume 20–65% more forage than would a cow of equivalent body mass because of their cecal digestion and rapid passage rate of food (Hanley 1982, Wagner 1983, Duncan et al. 1990, Menard et al. 2002). Horses can crop vegetation closer to the ground than can other ungulates due to their sensitive, flexible lips and possession of both upper and lower incisors (Stoddart et al. 1975, Symanski 1994). This cropping sometimes delays the recovery of plants (Symanski 1994, Menard et al. 2002). Furthermore, native ungulates such as mule deer and pronghorn (*Antilocapra americana*) can range farther from water than can horses, are browsers, and have much smaller body mass and hoof area relative to horses (Symanski 1994).

Taken collectively, these broader-scale differences in grazing ecology indicate that a larger proportion of the landscape experiences nonnative grazing when horses and cattle are present sympatrically, compared to when only cattle are present (Symanski 1994, Beever 2003). Domestic livestock consume an estimated 7,100,000 animal-unit months (AUMs) of forage annually (Table 14.4) within the current range of Greater Sage-Grouse. We estimate that free-roaming equids consume an additional 315,000–433,000 AUMs annually within the current range of sage-grouse (Table 14.4). It is unknown whether effects of cattle grazing, horse grazing, and native-ungulate browsing are synergistic or simply additive. However, the significance of the aforementioned differences is underscored by the importance that both patch dynamics and landscape patterns have been shown to have for several species, including Greater Sage-Grouse, which use the landscape at multiple spatial scales (Connelly et al. 2004, Aldridge 2005, Aldridge and Boyce 2007). The peak spatial overlap in use of sagebrush habitat with sage-grouse may thus occur during the breeding or late brood-rearing periods.

In addition to these contemporary additive or synergistic effects, large-mammal researchers and managers often struggle to separate the legacies of past mismanagement or poor implementation of livestock grazing strategies (especially during 1890–1920) from effects of current disturbances (Foster et al. 2003, Rowe 2007). Domestic livestock grazing is nearly ubiquitous across public lands of western North America, and the ratio of livestock to equid AUMs in this region averaged 23 to 1 in 1982 (Wagner 1983). However, within Nevada—the state with over half of the continent's free-roaming equids—this ratio averaged only 4.8 to 1 livestock-to-equid AUMs in 1982, and varied from 23 to 1 in the Elko BLM District to 2 to 1 in the Las Vegas BLM District (Wagner 1983).

FUTURE APPROACHES TO INVESTIGATE EQUID–SAGE-GROUSE RELATIONSHIPS

Several methods can quantitatively assess the influence of equids on the biotic integrity of sagebrush communities within the historic range of sage-grouse. The most informative for managers and perhaps most powerful statistically would be to regress an index of biotic integrity (Angermeier and Karr 1986) obtained from remotely sensed data against equid density using points from across the region. Unfortunately, this approach is currently untenable for several reasons. First, although the use of light detection and ranging (LiDAR) and satellite-based imagery to remotely

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TABLE 14.4

Animal unit months (AUMs) permitted for domestic livestock and free-roaming equids by state, across the current distribution of Greater Sage-Grouse within the United States.

Domestic livestock and equid estimates are based on BLM-administered lands within the current range of Greater Sage-Grouse.

State	Domestic livestock AUMs (2007)[a]	Range of equid AUMs[b]	
		Lower (1.2 times)	Higher (1.65 times)
California	150,228	30,874	42,451
Colorado	326,393	5,875	8,078
Idaho	855,131	10,541	14,494
Montana	1,334,208	2,218	3,049
North Dakota	9,268	0	0
Nevada	1,436,771	159,869	219,820
Oregon	866,194	29,722	40,867
South Dakota	36,958	0	0
Utah	261,075	19,224	26,433
Washington	10,307	0	0
Wyoming	1,894,034	56,693	77,953
Totals	7,118,989	315,014	433,145

[a] Livestock estimates are based on 2007 allocations, as summarized by the BLM Rangeland Administration System, http://www.blm.gov/ras/, 24 October 2009.

[b] Permitted AUMs does not necessarily mean all AUMs were used, but the BLM system does not track used AUMs. Range of AUMs used by equids was estimated using numbers obtained from the National Wild Horse and Burro Program (http://www.wildhorseandburro.blm.gov/statistics/2007/index.htm, 24 October 2009), assuming 12 mo of use at 1.2–1.65 times greater forage consumption for equids (both horses and burros) compared to cattle (Hanley 1982, Wagner 1983, Menard et al. 2002).

map and monitor habitats across large landscapes is developing rapidly, indices that would be meaningful for Greater Sage-Grouse and other sagebrush obligates are not yet broadly available at sufficiently fine resolution to permit quantitative analysis.

Second, it is unclear whether maximum equid density or average density within AUMs would be a more logical predictor of current sagebrush conditions (Ellison 1960, van de Koppel et al. 1997). Third, except in the Pryor Mountain Wild Horse Range in Montana, the finest scale for which equid density estimates are available is the entire HMA, which is often an entire mountain range(s). This is critical because, as evidenced by the example that ~40% of the Pryor Mountain Wild Horse Range was unsuitable for horse grazing due to steep topography or large extents of rock or bare ground (Fahnestock and Detling 1999b), estimates of entire HMA equid density can be off by a factor of at least 1.7. This error factor for any given location could be even higher, because the conservative assumption that every remaining "suitable" location is grazed at the same intensity is clearly not true.

Fourth, high increase rates observed in populations of wild horses (to >20% annually; Eberhardt et al. 1982) indicate that the number of horses in a given fall or spring census period will not necessarily correspond either to the population size in the management unit at a given time in the future or to an average number of AUMs on the landscape during the entire year. This would only be problematic if error magnitudes were distributed nonrandomly, but this seems feasible (e.g., higher error in larger populations). Fifth, differences in precision of equid censuses across the sagebrush

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range due to differences in aircraft, observer experience, tree cover that reduces animal detectability, and other factors would reduce the power of the analysis (Caughley 1974, Ohmart et al. 1978).

Finally, and perhaps most seriously, the way in which equid, cattle, sheep, and native-ungulate AUMs are allocated to HMAs would confound the analysis if lower levels of equid AUMs are correspondingly or randomly replaced by increased cattle AUMs. Livestock grazing intensity could be incorporated as a covariate, but intensity is known only at the spatially coarse level of allotments, and historical records of density are not widely available, thus crippling this potential analysis.

A second analytical approach would compare a metric of sagebrush biotic integrity—such as cover of sagebrush from remotely sensed data—in management areas with and without equids. In addition to the aforementioned lack of alternative indicators, a problem for this analysis is the fact that because HMAs often correspond to entire mountain ranges, lower sagebrush cover within an HMA may be a consequence of that range's vicariance history rather than a reflection of greater disturbance. A new challenge created by this approach is that HMAs where equids have been removed are not allocated in a random, dispersed manner, but instead are driven by sociopolitical concerns (e.g., conflicts with railroad property rights). Thus, equid-removed herd areas are at times spatially clumped, a hindrance to landscape-scale analyses.

This second approach circumvents the second through fifth problems in the first analytical approach, but with the sixth, effects of other ungulates would remain—a serious confounding factor. Horse specialists realize it is difficult to separate effects of other sympatric ungulates, such as domestic livestock and native ungulates such as mule deer, elk, and pronghorn, from equid effects.

A final analytical approach would involve assessment of the possible direct interactions between equids and Greater Sage-Grouse or other sagebrush-obligate species. In this approach, radio transmitters placed on individuals of both grouse and equids would provide the raw data needed to develop habitat-selection maps for both species. In turn, these maps would indicate the factors driving habitat selection for the two taxa in regions where they are sympatric and allow investigation of overlap of use for the two species in different seasons that correspond to critical life-stages for Greater Sage-Grouse.

CONCLUSIONS

Conservation challenges posed by sage-grouse and other sagebrush-obligate species provide a timely impetus to consider the role free-roaming equids might play in ecoregional-scale conservation strategies. From a practical standpoint, such challenges may be an avenue by which the limiting horses versus cows debate that has dominated discussions and popular perception of equid management for decades may be broadened to include other resource values. Free-roaming burros and especially horses are undeniably charismatic and enigmatic, and have been used to symbolize power, freedom, wildness, and toughness. Given the multiple stresses that interact to influence ecosystem dynamics across western North America, however, the benefits these nonnative herbivores provide for various publics within society must be weighed against actual and potential ecological costs.

As with any large-bodied herbivore, the magnitude and permanence of impact that free-roaming horses and burros will have on sagebrush ecosystems depend upon a host of factors, including the plant-animal coevolutionary history, soil development, climate, recent weather, effects of other sympatric herbivores, site elevation, amount of recent and long-term precipitation, and the seasonality, duration, and intensity of grazing (Milchunas et al. 1988, Fahnestock and Detling 1999a, Beever et al. 2008). In turn, intensity of landscape use by equids is influenced by a host of biotic factors, including vegetation and soil types, vegetation physiognomy, proximity to water, presence and recency of wildfire, spatial and temporal distribution of plant defenses against herbivory, behavior of conspecifics or competitors, and past, current, and future nutritional states of animals, among other factors. Abiotic factors such as elevation, aspect and slope, snow depth, thermoregulatory constraints, and proximity to roads and other disturbances also affect habitat use of free-roaming equids.

Equid-induced changes in sagebrush and other communities that may most strongly affect sagebrush-obligate birds and have been observed to date include reduction in grass abundance and cover, alterations to the structure and composition

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of the shrub mosaic (e.g., lower cover and greater fragmentation of shrubs, and lower sagebrush cover), increases in compaction in surface soil horizons, and increased dominance of forbs unpalatable to livestock and Greater Sage-Grouse (Fig. 14.2). Collectively, these effects represent a nontrivial contribution to ecosystem integrity across the sagebrush range. All of these ecosystem alterations may increase the vulnerability of Greater Sage-Grouse and other species to predation, parasites, or disease; increase energetic costs and stress levels required to locate suitable habitat or resources; and negatively affect nest success, chick survival, or other aspects of fitness and survival, all of which could ultimately affect the viability of some populations.

CONSERVATION IMPLICATIONS

Multidisciplinary teams of managers and researchers comprising leading experts on various aspects of equid biology have long considered investigation of grazing impacts to be of highest priority (Blaisdell and Thomas 1977, Kitchen et al. 1977, Zarn et al. 1977, Wagner et al. 1980, Singer 2004), but understanding how feral horses may affect the nonungulate components of sagebrush ecosystems is only beginning (Crane et al. 1997, Fahnestock 1998, Peterson 1999, Beever and Brussard 2004, Beever and Herrick 2006). Recent research suggests that equid use of a landscape can indirectly affect a wide array of taxa in a community through numerous pathways (Fig. 14.2) (Levin et al. 2002). For example, compared to ecologically similar horse-removed sites in the western Great Basin, horse-occupied sites differ in numerous aspects of ecosystem structure, such as lower shrub cover, higher compaction of soil surfaces, and a more fragmented shrub canopy, composition (e.g., lower grass cover, lower total vegetative cover, lower plant species richness), and function (e.g., lower density of ant mounds). In spite of the increasing attention in recent research to synecological relationships of equid grazing in arid and semiarid landscapes of western North America, many basic questions remain unanswered.

Nearly all of the research on equids in western North America has been performed at spatially limited scales due to the advantages in terms of logistics, costs, and research design. Unfortunately, these focused investigations are difficult to amalgamate into a landscape- or regional-level understanding of equid biology. This is especially true given that horse behavior can be plastic across ecoregional scales (Bennett and Hoffmann 1999). Furthermore, most studies have usually used only two treatment levels for equid grazing—present and absent. If, instead, investigators were to select equid-occupied sites across a range of grazing intensities, this would allow clarification of the shape of the dose-response curves of various ecosystem indicators. This has importance for monitoring, because monitored indicators should ideally be sufficiently sensitive to grazing disturbance to act as early-warning indicators of system degradation.

Results from past research across 3,030,000 ha of the western Great Basin may help in forecasting how Greater Sage-Grouse and other sagebrush-obligate species may be affected by free-roaming equids. For example, community completeness may be lower in horse-grazed than in horse-free areas (e.g., for granivorous small mammals) as a result of the absence of rarer species from horse-grazed sites (Beever and Brussard 2004). In that work, community completeness was defined as the percentage of species detected during a standardized trapping effort, compared to the full suite of species predicted to exist at a site given the elevation, geographic location, and microhabitats of the site. Differences in grass cover are likely to have a biologically meaningful effect for some grass-specialist animals, as was illustrated by two to four times higher capture rates of the western harvest mouse (*Reithrodontomys megalotis*) at horse-removed compared to horse-occupied sites (Beever and Brussard 2004). Equid-influenced areas may be more dominated by disturbance-tolerant generalists like deer mice (*Peromyscus maniculatus*) and species that specialize in open areas without vegetation, such as western whiptails (*Cnemidophorus tigris*) (Beever and Brussard 2004). Greater density of ant mounds at horse-free sites than at horse-occupied sites suggests that at least a portion of the invertebrate community is more robust at horse-removed sites, and may also reflect differences in level of ecological function (Beever and Herrick 2006). Collectively, these responses not only illustrate the types of community restructuring that can occur in areas heavily influenced by equids, but also suggest indicators and mechanisms that may be important for further investigating equids'

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effects on Greater Sage-Grouse and other sagebrush-obligate species.

Given current knowledge, however, and the fact that recovery can be protracted and uncertain in arid and semiarid ecosystems within the geographic range of Greater Sage-Grouse—due to their low-productivity, event-driven, threshold state-and-transition dynamics (Laycock 1991, Tausch et al. 1993)—several conservation considerations appear warranted. First, arid land health and ecosystem integrity are important considerations for long-term conservation of sagebrush systems, along with minimum viable population sizes and other genetic concerns for free-roaming equid populations. Long-term conservation objectives should consider the appropriate management levels of horses and burros that can be maintained (Tables 14.2, 14.3) because free-roaming equids can influence the structure and function of sagebrush ecosystems. Fencing and rotational grazing can be used to limit spatial and temporal effects of domestic livestock grazing, but few options outside of controlling population levels are available to land managers for managing horse and burro distributions and grazing effects. Consequently, the primary mechanisms for managing equids will center on approaches that reduce herd levels or limit population growth.

Second, it remains important within this context to have explicit management goals to justify and reinforce decisions of where and how many free-roaming equids will occupy public lands. Third, extensive research into immunocontraception as a potential method to limit equid populations should be accompanied by synecological investigations that not only support adaptive management of equid herds but also provide insights into additional ecological indicators of grazing disturbance as it relates to ecosystem integrity. Finally, herd reductions during drought periods that managing agencies currently use may be important in sustaining sagebrush ecosystems during ecological stresses. Such emergency reductions not only avoid the pronounced grazing-induced ecosystem degradation that can accompany drought (Jardine and Forsling 1922, Archer and Smeins 1991) but also avoid conditions that can be stressful or lethal for equids.

ACKNOWLEDGMENTS

Previous versions of the manuscript were read by F. H. Wagner, S. T. Knick, C. E. Braun, and two anonymous reviewers. This manuscript benefited from fruitful discussions with numerous BLM horse specialists; many are cited in the text, but others include T. M. Pogacnik, J. M. Gianola, G. McFadden, and T. J. Seley. T. J. Assal compiled tabular and spatial data on BLM and USFS wild horse and burro data.

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Western North American Naturalist 60(3), © 2000, pp. 236–254

EXAMINING ECOLOGICAL CONSEQUENCES OF FERAL HORSE GRAZING USING EXCLOSURES

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ABSTRACT.—Although feral horses have inhabited western North America since the end of the 16th century, relatively little synecological research has been conducted to quantitatively characterize how they interact with ecosystem components. Because feral horses exhibit watering behavior markedly different from that of domestic cattle, it is particularly important to evaluate response of ecosystem elements near water sources to horse use. To assess this response, we performed live-trapping of small mammals and 2-tiered vegetative sampling in 2 mountain ranges in central Nevada in the interior Great Basin, USA. At low elevations, plots around horse-excluded springs exhibited notably greater plant species richness, percent cover, and abundance of grasses and shrubs, as well as more small mammal burrow entrances than plots at horse-grazed springs. At high elevations, meadows protected from grazing exhibited maximum vegetation heights 2.8 times greater than vegetation grazed by horses only and 4.5 times greater than vegetation grazed by horses and cattle. Species richness in quadrats was most different between the horse-and-cattle-grazed meadow and its ungrazed counterpart, suggesting the possibility of synergistic effects of horse and cattle grazing in the same location. This study, the first in the Great Basin to investigate quantitatively ecosystem consequences of feral horse use with exclosures, represents a preliminary step in identifying factors that determine the magnitude of horse grazing impacts.

Key words: exclosures, feral horses, Equus caballus, *vegetative comparisons, Great Basin.*

Researchers have long known that the magnitude of cattle impacts near springs is greatest at the spring itself and decreases asymptotically with increasing distance from the spring (Wooton 1916, Jardine and Forsling 1922, Valentine 1947). Furthermore, cattle in arid regions often spend a disproportionate amount of time in riparian areas (Roath and Krueger 1982, Van Vuren 1982), where forage, water, and shade are initially abundant. As reviewed by Szaro (1991), domestic livestock have been shown to have notable consequences on bird (Mosconi and Hutto 1982, Taylor 1986), lizard (Jones 1981), and plant (Cannon and Knopf 1984) communities in western riparian systems.

Behavioral studies of feral horses in western North America have shown that horses visit watering locations daily, usually during crepuscular hours (Pellegrini 1971, Meeker 1979, Ganskopp and Vavra 1986). However, in contrast to domestic cattle, horses often travel greater distances from water and spend less total time at springs or other watering areas (Meeker 1979, Denniston et al. 1982, McInnis 1985). Thus, due to their distinct watering behavior, it remains unclear to what extent horses may modify areas around springs. In spite of the urging of Kitchen et al. (1977:56) over 2 decades ago that "studies of wild horse impacts on watersheds (and other water sources) need to be conducted," few data have been gathered to date to examine this question.

Although a number of behavioral, physiological, and dietary studies have been done on domestic horses, extrapolating these results to feral populations of horses is problematic, particularly with respect to behavior. For example, large pastures grazed by domestic horses exhibited a pattern of areas of short, grazed grass mixed with areas of tall, ungrazed grass in which horses generally defecated (Ödberg and Francis-Smith 1977). In contrast, at least in semiarid systems, concentrations of feces ("stud piles") are made by feral horses in areas frequently traveled by horses that generally are sparsely vegetated or devoid of vegetation (Pellegrini 1971, Berger 1986, personal observation). One study has most directly examined the ecological consequences of domestic horse use in the semiarid Great Basin. In this enclosure study in northern Utah, forage consumption per-animal-mass decreased under heaviest stocking density, and all horse-grazed pastures exhibited increased production of bitterbrush,

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Purshia tridentata (Reiner and Urness 1982). Although the study highlighted horse utilization of various species and the response of *P. tridentata* to 2 levels of horse grazing, no community dynamics, such as species richness or long-term recovery trends, were investigated.

Exclosures

In past studies researchers have employed exclosures to study effects of herbivory by insects (Reader 1992), jackrabbits (Rice and Westoby 1978), small mammals (Brown and Heske 1990), domestic sheep (Laycock 1967, Rice and Westoby 1978), and, most commonly, domestic cattle (McLean and Tisdale 1972, Heske and Campbell 1991, several studies reviewed by Fleischner 1994). When investigating changes over time or comparing plots with and without herbivory, using exclosures allows manipulation of levels of herbivory across small spatial scales and separation of grazing effects from differences due to environmental or microsite variables.

Use of exclosures to investigate effects of feral horse herbivory in western North America has been done in the Pryor Mountain Wild Horse Range in Montana and Wyoming (Detling 1998, Fahnestock 1998, Fahnestock and Detling 1999). Fahnestock and Detling (1999) indirectly investigated effects of horse grazing. They simulated herbivory in long-term (>20 yr) horse exclosures using 2 × 2 factorial designs of defoliation and irrigation at a low-elevation site and defoliation and fertilization at a high-elevation site. Although they concluded (Fahnestock and Detling 1999:269) that "dominant graminoids in the Pryor Mountains are able to withstand fairly heavy levels of defoliation through compensatory growth" (depending upon water availability), their study removed from the natural herbivory process the effects of trampling and consequent soil compaction, which can be substantial (Butler 1995, Belsky and Blumenthal 1997). When comparing vegetation inside and outside 4 exclosures (2 in montane grasslands and 2 in low-elevation grassland sites) in the same vicinity, they found that effects of horse grazing were often overshadowed by between-site or interannual variation, probably due to precipitation differences (Detling 1998, Fahnestock 1998). Because they found significant effects of grazing removal only for biomass and percent cover of 1 or 2 dominant grass species, they concluded that either low-elevation exclosures were not in place long enough for vegetative differences to accrue or horse densities were low enough to avoid major changes in grassland vegetation (Detling 1998). Because vegetation in grasslands may respond more favorably to large mammal herbivory than in arid and semiarid deserts such as the Great Basin (Bartolome 1993, Patten 1993), it is crucial to assess the influence of horses in the Great Basin. To our knowledge, this study represents the 1st investigation of the effects of grazing by feral horses using exclosures in the hydrographic Great Basin.

In practice, numerous factors complicate the use of exclosures to study consequences of grazing by feral mammals. Few exclosures in the Great Basin are large enough to contain core areas relatively free from edge effects. Consequently, small mammal species that may in fact be impacted by horse grazing may not exhibit different abundances inside compared with outside exclosures, simply because exclosure sizes are not significantly larger than their home ranges (e.g., Heske and Campbell 1991). Similarly, exotic plants, especially wind-dispersed species, may be able to invade such small areas from seed sources outside the exclosure. Furthermore, most exclosures either have been recently constructed or have not had an uninterrupted span of no grazing. Exclosures often are knocked down or breached over time, and monitoring and maintenance of exclosures, especially in remote areas, is usually infrequent. As a result, such exclosures provide an imperfect representation of long-term removal of grazing pressure. Additionally, because there is little agreement on how grazing intensity outside the exclosure is characterized (e.g., "heavy," "moderate"), it is difficult to compare results across studies (Fleischner 1994). Finally, even within broad environmental strata, exclosures are generally not well replicated, limiting investigators to conclusions that may have low external validity at larger scales.

Another suite of problems arises when one attempts to use exclosures to investigate effects of feral horse grazing. Generally, exclosures are not located in areas in which horses are the only grazers in the system. Rather, across much of its current range in western North America, *Equus caballus* is sympatric with some combination of cattle, pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*),

or, less frequently, bighorn sheep (*Ovis canadensis*), feral burros (*Equus asinus*), or elk (*Cervus elaphus*). Fortunately, data from state and federal management agencies suggest that spatial overlap of feral horses with bighorn sheep, burros, and elk is minimal (BLM 1996, Anonymous 1997). Even when sympatric, feral horses may use somewhat different slopes than bighorn sheep and, to a lesser extent, mule deer (Ganskopp and Vavra 1987). Furthermore, dietary studies of sympatric deer, antelope, and feral horses in the western United States have shown that deer and antelope diets overlap only marginally with feral horse diets, usually exhibiting 0–20% similarity (Hubbard and Hansen 1976, Meeker 1979, Hanley and Hanley 1982, McInnis 1985), although Vavra and Sneva (1978) observed overlaps of 20–37% during a drought year in eastern Oregon. In contrast, however, diet items of feral horses may share 60–80% similarity with diet items of sympatric cattle, depending on season, location, and other factors (Hubbard and Hansen 1976, Vavra and Sneva 1978, Hanley 1982, Krysl et al. 1984). Because of this lack of dietary niche differentiation, it is impossible to separate grazing effects of cattle and horses when both species forage in the same area, even if at different times of year. This is especially problematic because there are few areas in the Great Basin that remain ungrazed by cattle for extended time periods and even fewer areas that experience horse grazing but not cattle grazing.

A further complication for studying effects of feral horse grazing is that horse-excluded areas are neither randomly selected nor evenly interspersed within areas used by horses. Rather, herd areas in which horses are removed almost always comprise entire mountain ranges, and these areas were selected for sociopolitical, rather than biological, reasons. Specifically, horse-excluded areas generally correspond to private landholdings, often of railroad companies. This spatial arrangement of horse and non-horse areas prevents small-scale comparisons between areas that would have higher levels of ecological similarity. Thus, although wild horse and burro herd areas occupy 18.9 million acres of land in Nevada alone (Anonymous 1997), there are currently extremely few opportunities for even small-scale manipulative experimental studies of equid grazing.

Spring Areas

We chose spring and meadow areas to investigate consequences of horse grazing for several reasons. First, most of the few long-standing exclosures in the Great Basin have been constructed by management agencies near springs. Second, although the Great Basin is a biogeographic region characterized by relatively low primary productivity (Cronquist et al. 1972, Grier et al. 1992, Grayson 1998), springs and other riparian areas are oases of higher productivity, especially if not overly disturbed. Because they receive continuous water and nutrient inputs, undisturbed high-productivity areas provide a useful benchmark of diversity against which to compare horse-occupied areas. Third, particularly in arid and semiarid regions, spring and riparian areas are used obligately by many taxa, far more than the number predicted by their areal extent (Gregory et al. 1991, Szaro 1991, Naiman et al. 1992). Thus, these areas may play crucial roles in maintaining diversity at landscape or regional scales, as up to 70% of a region's vertebrate species may use riparian corridors in a significant way during their lifetime (Raedeke 1989). Numerous bird species, for example, are obligate users of riparian areas (Gaines 1977, Ohmart and Anderson 1986). Fourth, because of the Great Basin's dissected topography and resulting isolation and local adaptation, springs often contain rare endemic taxa, such as fishes (LaRivers 1962, Deacon 1979), ostracods (Külköylüoğlu and Vinyard 2000), springsnails (Hershler and Sada 1987, Hamlin 1996), and other invertebrates.

We investigated several measures of vegetative and small mammal communities at high- (Seven Troughs Range) and low-elevation (Clan Alpine Mountains) sites to compare ecologically similar areas that were either grazed or ungrazed by feral horses. We investigated the null hypothesis that feral horses exerted no significant effects on the structure or composition of vegetation and small mammal communities near springs and in meadows.

METHODS

Low-elevation Study Sites: Clan Alpine Mountains

During October 1998 we examined 4 plots (springs A, B, C, and D; 2 ungrazed, 2 grazed

by feral horses) with areas between 553 and 581 m^2, in Shoshone Creek canyon, Clan Alpine Mountains, Churchill County, west central Nevada (Fig. 1A). The Clan Alpine Mountains occupy an area of 1149 km^2 and range in elevation from 1166 to 3047 m (BRRC 1998). All plots were on east-facing slopes of low (≤15%) gradient, dominated by sagebrush–salt scrub habitats. *Artemisia tridentata, Sarcobatus vermiculatus, Chrysothamnus nauseosus, Grayia spinosa,* and *Atriplex confertifolia* were the dominant shrubs. The 2 grazed plots were grazed only by horses during the previous 15–20 yr, and the 2 ungrazed plots had had horses excluded for either 4 or 8 yr.

Soils near the spring A study area are very fine sandy loams dominated by Duric Natrargids and Typic Torriorthents, are moderately to strongly alkaline, and have a slightly hard, very friable consistence (Natural Resources Conservation Service unpublished soil surveys, February 1999). Soils near springs B, C, and D are very stony or very gravelly loams, are dominated by Lithic Xerollic Haplargids and Lithic Torriorthents, are moderately alkaline, and the top 10 cm has a soft, very friable consistence (Natural Resources Conservation Service unpublished soil surveys, February 1999).

Shoshone Creek canyon has been actively managed since 1983 by the Bureau of Land Management to exclude domestic livestock, but feral horses have occupied portions of the canyon for several decades (J. Axtell, Carson City District wild horse and burro manager, BLM, personal communication). Exclosures were constructed in 1990 (Living Legend Spring 2, "spring C") and 1994 (Living Legend Spring 1, "spring D"), both at an elevation of 1500 m. We used exclosure dimensions and orientations to delineate plots at grazed springs. Spring B is located 110 m WNW from the exclosure surrounding springs C and D, at the east-facing base of a steeply sloping ridge peninsula. Another horse-grazed spring (spring A) is located 6.8 km southeast of the exclosure springs at an elevation of 1325 m. These exclosures excluded horses but not other herbivores (e.g., *Odocoileus hemionus, Antilocapra americana, Lepus californicus,* and *Sylvilagus auduboni*). Aerial censuses in the spring of 1998 found 1076 feral horses in the Clan Alpine Herd Management Area (HMA). This area occupies 130,637 ha, 99% of which is under BLM jurisdiction (Anonymous 1997, J. Axtell personal communication).

Because exclosures in this HMA (including those in this study) are relatively small and thus subject to significant edge effects, we did not perform small mammal trapping inside or outside exclosures. Instead, as a crude estimate of small mammal activity, we tallied within each plot the number of visible entrances of mammal burrows.

Using a hierarchical sampling scheme, we assessed vegetation in plots. Across the entire area of each plot, an exhaustive search was conducted for all shrub, forb, and grass species, and individuals were counted for all shrub and most grass and forb species. Individuals were defined by stems for shrubs and forbs, and by spatial separation from other such individuals in grasses. We were unable to identify several specimens to species (Appendix), but they were clearly distinguishable as different species (A. Tiehm personal communication). Total percent vegetative cover (live + standing dead) was visually estimated for each plot, and these estimates were verified by comparing them to the average of percent cover values from 1-m^2 quadrats (described below). For the most abundant species that could not feasibly be counted exhaustively, we estimated the number of individuals to the nearest 10. Similarly, because grasses were ubiquitous in exclosure plots, the total number of grasses in each exclosure plot was estimated by extrapolating the average estimates of grass abundance in all 7 quadrats (see below) across the entire area of the plot. This final method of estimation was not necessary for grazed plots because grasses were much less numerous and could be tallied comprehensively.

At the quadrat level, we threw a 1-m^2, PVC-constructed square from the plot center to 7 random locations within the plot. Within each quadrat, we recorded percent cover and count of each species following Wentworth (1976, 1981), as well as species richness, total vegetative percent cover, and maximum height of vegetation across the quadrat. For all forb and grass species, samples were collected as herbarium specimens and deposited in the University of Nevada–Reno Herbarium. Species were identified using Cronquist et al. (1972), but taxonomy presented here follows Hickman (1993).

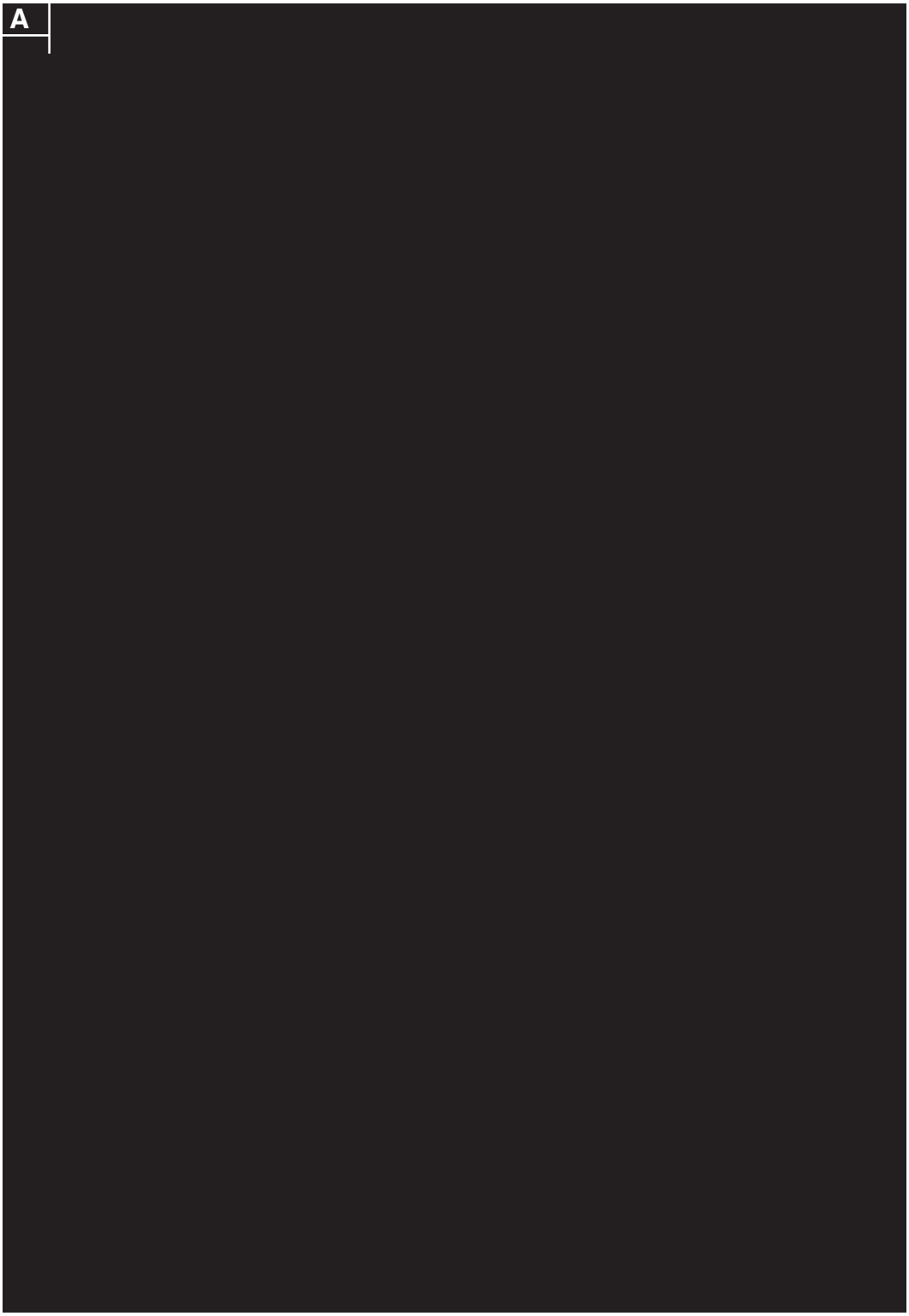
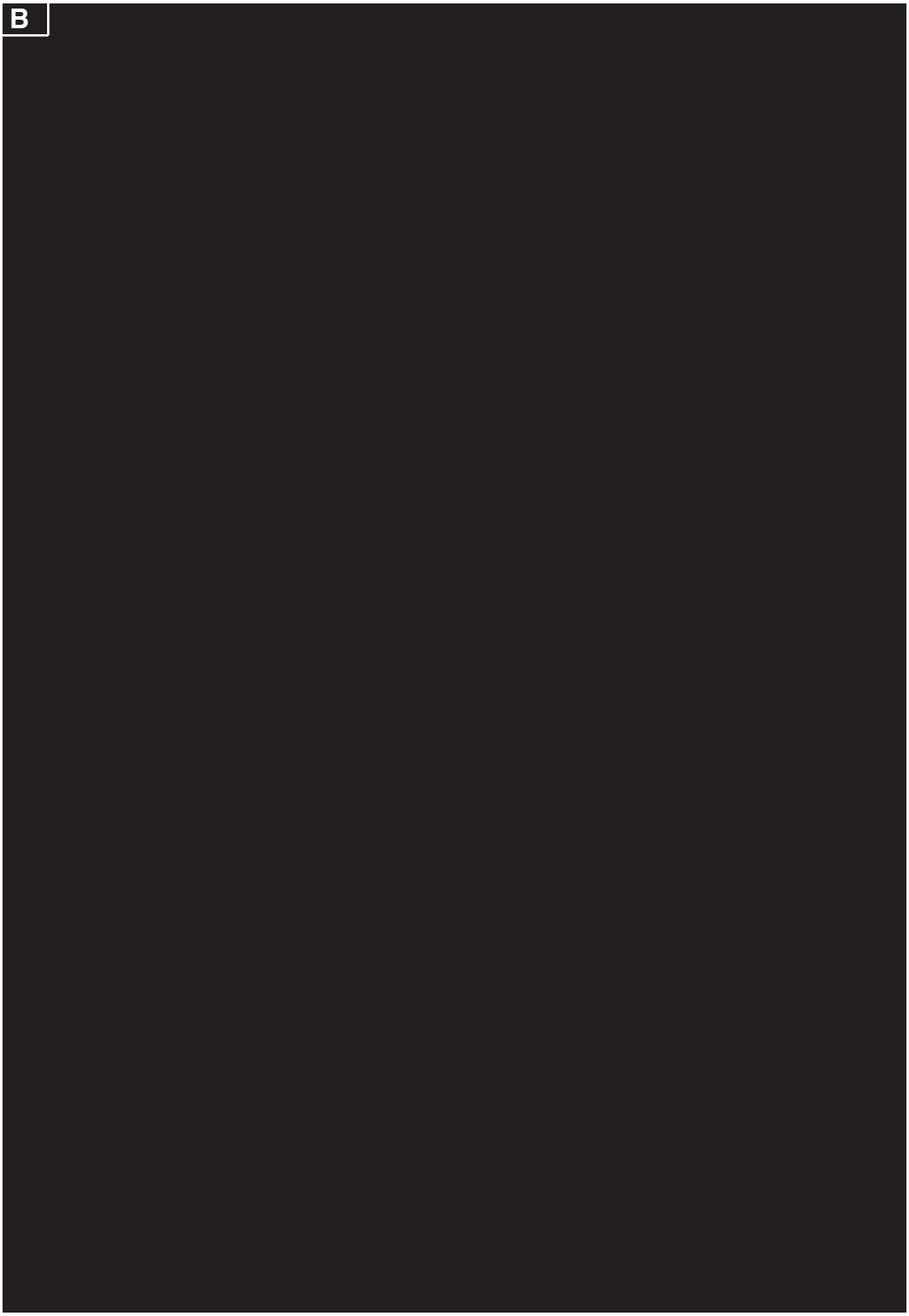


Fig. 1. Location of study plots within State of Nevada (i); within a relief map of the respective mountain range (ii); and as a small-scale schematic (iii). A, Clan Alpine Mountains; B, Seven Troughs Range.


B

High-elevation Study Site: Seven Troughs Range

During July 1998 we examined plots at a 50.6-ha exclosure above Cow Creek, Seven Troughs Range, Pershing County, Nevada. The Seven Troughs Range occupies an area of 335 km^2 and ranges in elevation from 1278 to 2373 m (BRRC 1998). All plots were on areas of low (<15%) slope gradient. Vegetation in this portion of the mountain range is a mixture of big sagebrush (*A. tridentata*) and low sagebrush (*A. arbuscula*) scrub habitats, with rushes (Juncaceae, especially *Juncus* spp.), sedges (Cyperaceae), and other meadow species dominating mesic areas. Although the exclosure does not contain a permanent spring with definable boundaries, standing water arises from within the exclosure, and the area in and around the exclosure is markedly more mesic than surrounding vegetation.

Soils near the study areas are very gravelly loams dominated by Aridic and Lithic Argixerolls, are neutral to slightly alkaline, and the surface horizon is very friable with a soft to slightly hard consistence (Natural Resources Conservation Service unpublished surveys, February 1999). According to aerial counts performed in 1995, approximately 292 feral horses occupied 59,859 ha of land in the Seven Troughs HMA, 88% of which is under BLM jurisdiction (Anonymous 1997).

The roughly square-shaped exclosure, elevation 2125 m, features barbed-wire construction, probably preventing herbivory only by cattle and horses. We focused our investigations on 3 paired plots, each 15 × 15 m (Fig. 1B). For all 3 pairs, 1 plot was located inside the exclosure, and its partner was located outside the exclosure. In selecting paired plots, we strove to maximize similarity of habitat, homogeneity within each plot, and equivalence with the other member of the pair.

The paired sites in Figure 1B represent the only paired locations that were similar in habitat and internally homogeneous. Pair #1 sites were separated by about 6–8 m by a rarely traveled road and were located in a meadow that is mostly dry in the summer. We found approximately equal numbers of horse and cattle defecations in the grazed plot of pair #1. Pair #2 sites were both located in dry meadows, but were separated by about 0.8 km. As demonstrated by their similar species lists (Appendix), both sites were relatively mesic. In the grazed plot we found only horse dung, suggesting exclusive horse grazing. Our observations are in accord with observations of agency biologists that cattle rarely frequent the upper meadow area, but instead tend to stay near an artificial reservoir 0.5 km below the exclosure. Although we did not explicitly tally dung piles, the site appeared to experience a moderate level of horse grazing, as compared with other horse-occupied meadow areas we have studied in central Nevada. Pair #3 consisted of sagebrush (*A. tridentata*)-dominated sites, separated by about 20 m by a dirt road and intervening habitat. Scat evidence suggested the grazed plot was used exclusively by cattle at a light to moderate intensity. Because horses often prefer areas with good visibility, tall vegetation in the plot likely discouraged horse use of the area.

Each of the 6 plots contained a 4 × 4 trapping grid for small mammals, with traps separated by 5 m. Small mammals were trapped for 3 consecutive nights (18–20 July 1998) on all 6 plots using Sherman live-traps (8 × 8 × 25 cm) baited with mixed wild bird seed. Additionally, for the meadow plots (pairs #1, #2), we measured vegetation height 25 cm away from each trap station in the 4 cardinal directions. At each of these 4 points, we measured the tallest plant within 3 cm of an erect meter stick. At both the grazed and ungrazed plot in pairs #1 and #2, we randomly selected 4 of 9 possible 5 × 5-m quadrats in which to measure species richness and maximum vegetation height. Maximum height of vegetation was used instead of average height because it better reflects both the degree of homogenization of vegetative structure produced by grazing and the amount of heterogeneity occurring at small scales and because it could be measured with greater precision.

Data Analysis

For sampling in the Clan Alpine Mountains, we considered plots as independent replicates and treated 1-m^2 quadrats as subsamples nested within plots. Thus, each of the 2 ungrazed and 2 grazed springs and their associated plot areas were treated as experimental units. Because of the small sample size ($n = 2$ per treatment), we simply make descriptive comparisons using springs A, B, C, and D and do not employ inferential statistics for Clan Alpine data.

For the Seven Troughs Range, because pairs differed with respect to habitat and nature of grazing, each of the sampled quadrats and vegetation height averages at each trap station was treated as a replicate for within-pair comparisons, and samples were not pooled across pairs (Wester 1992). To compare vegetation heights in grazed and ungrazed plots, we performed single-factor ANOVAs in Statview v5.0 (SAS Institute, Cary, NC). In cases of significant heteroscedasticity (assessed using Bartlett's test), we compared groups using a nonparametric Mann-Whitney U test (Sokal and Rohlf 1995). Because species richness was measured in only 4 quadrats per plot, richness was compared using unpaired *t* tests, except in the case of significant heteroscedasticity, when a Mann-Whitney U test was used. Statistical comparisons do not explicitly test for treatment effects, but rather describe variability in, and the magnitude of, difference between paired plots.

Because we could not assign grazing treatments to the plots, we tested for the presence of unknown directed gradients spanning the length of adjacent grids that could confound comparisons of vegetation height. If such a gradient were to exist perpendicular to the fence, a monotonically decreasing or increasing trend would most likely be evident in average height of stations within each row. Alternatively, if the difference were due to grazing pressure, a stepped function should be observed, with the step occurring at the fence. Values of vegetation height were compared among the 8 rows using Fisher's PLSD tests.

RESULTS

At both the high-elevation (Seven Troughs) and low-elevation (Clan Alpine) sites, we observed striking differences in the structure, composition, and character of vegetation inside compared with that outside the exclosures (Figs. 2A–E). Similarly, notable differences were observed in relative burrow density of small mammals between horse-grazed locations and horse-excluded plots at low elevations. At high



Fig. 2. Examples of enclosure and grazed plots in the Clan Alpine Mountains and Seven Troughs Range, Nevada: A, spring A, horse-grazed plot, Clan Alpine Mountains; B and C, spring C, exclosure plot, Clan Alpine Mountains; D, spring D, exclosure plot, Clan Alpine Mountains; E, fence line at grazed and exclosure plots, pair #1, Seven Troughs Range.



Fig. 2. Continued. B and C, spring C, exclosure plot, Clan Alpine Mountains.





Fig. 2. Continued. D, spring D, exclosure plot, Clan Alpine Mountains; E, fence line at grazed and exclosure plots, pair #1, Seven Troughs Range.



TABLE 1. Vegetative characteristics of 4 plots at springs, Clan Alpine Mountains, Nevada, 1998.

	Plot-level surveys				
	No. burrows	Total percent cover	Species richness[c] (S,F,G)	No. shrubs	No. grasses
Spring A[a]	1	~10–15	5 (1,2,2)	18	210
Spring B[a]	5	~5–8	10 (1,6,3)	30	52
Spring C[b]	22	~92–95	25 (3,13,9)	242	~386,000
Spring D[b]	15	~85–90	24 (3,12,9)	77	~176,000

	Quadrat means[d]			
	Species richness	Grass SR	Percent cover	Maximum height
Spring A	0.7 ± 0.4	0.3 ± 0.2	10.0 ± 5.9	12.8 ± 7.8
Spring B	1.3 ± 0.4	0.6 ± 0.2		
Spring C	6.3 ± 0.9	2.6 ± 0.6	91.4 ± 4.7	106.5 ± 32.8
Spring D	5.4 ± 0.5	2.4 ± 0.5	82.1 ± 11.4	53.1 ± 9.4

[a]Grazed almost exclusively by horses for last 15 yr.
[b]Living Legend Spring exclosure plots, constructed by BLM in 1990 (spring C) and 1994 (spring D).
[c]Species richness, all species combined, then separated into classes (**S**hrub, **F**orb, **G**rass and grasslike species).
[d]All values ± 1 $s_{\bar{x}}$. $N = 7$ quadrats per plot. See text for methods.

elevations there were some differences between identities and relative abundance of species inside versus outside the large exclosure.

Clan Alpine Mountains

At the plot level, areas around horse-excluded springs had approximately 6–18 times greater vegetative cover than horse-grazed areas (Table 1). We observed no plant species along the water's edge at spring B and only 2 *S. vermiculatus* shrubs beside spring A (Fig. 2A), which contrasts strongly with the increased plant richness found at the aquatic-terrestrial boundary inside the exclosures (Figs. 2B–D). In general, the only vegetation that remained in spring A plot was vegetation that was sheltered from trampling by large rocks, man-made structures (e.g., fencing), or steep slopes (Fig. 2A). Furthermore, many plants in both grazed plots were senescent, stunted in height, and without inflorescences. Horse-excluded areas exhibited 3.3 times greater total species richness than did horse-grazed plots (mean = 24.5 versus 7.5 species; Table 1, Appendix). Although at least 4 shrub species were found within 1 km of each grazed plot, no grazed plot contained more than 1 species of shrub (Appendix). There were 6.7 times as many individual shrubs (mean = 160 vs. 24) in plots protected from horse grazing as in horse-grazed plots (Table 1). We estimate that the number of grasses in the exclosure plots was 3 orders of magnitude greater than the number observed in grazed plots (mean = ca 281,000 vs. 131; Table 1). Thirteen of 14 randomly located 1-m^2 quadrats in grazed areas contained between zero and 2 species (mean = 1.0 species · $quadrat^{-1}$), yet all subsamples in exclosures contained between 3 and 10 species (mean = 5.9 species). In all cases, averages of percent cover estimates from 1-m^2 quadrats were within 3% of estimates of cover across plots (3rd and 9th columns in Table 1).

Exclosure plots near springs on average had 6 times more small mammal burrow entrances than did horse-grazed plots (mean = 18.5 vs. 3 burrows per plot; Table 1). In addition to tallying burrow entrances, we also observed pocket gopher (*Thomomys* sp.) tunnels in both spring C and spring D plots, but not in either of the horse-grazed plots.

Seven Troughs Range

Meadows protected from grazing exhibited maximum vegetation heights 2.8 times greater than vegetation grazed by horses only (pair #2) and 4.5 times greater than vegetation grazed by horses and cattle (pair #1, Fig. 2E; $Z = -4.82$, $P < 0.0001$ for each pair). Although mean heights of vegetation around trap stations were similar between the 2 meadow sites

inside the exclosure, the site outside the exclosure grazed by both cattle and horses exhibited a mean height more than 40% lower (8.8 cm vs. 15.1 cm) than that observed in the meadow grazed exclusively by horses. In post-hoc Fisher's PLSD analyses of the 8 trapping rows at both pair #1 and pair #2 plots, none of the row vegetation heights were significantly different within plots on either side of the fence ($n = 12$ comparisons per pair, $P > 0.05$), but all 32 possible cross-fence comparisons (16 per pair) demonstrated significant ($P < 0.03$) differences.

Species richness in the 4 randomly selected 25-m^2 quadrats was lowest in the area grazed by both horses and cattle (pair #1; mean = 9.5 species per plot). Species richness averaged 61% (5.8 species per plot) higher in ungrazed quadrats in pair #1 ($Z = -2.31$, $P = 0.021$), but only 13% (1.7 species per plot) higher in ungrazed exclosure quadrats in pair #2 ($t = 0.88$, df = 6, $P = 0.41$).

During live-mammal trapping for 3 consecutive nights at 6 plots (288 total trap-nights), we captured 21 individuals of 4 rodent species and had 13 recaptures (Table 2). Meadow pairs exhibited higher species richness and higher capture rates in ungrazed grids, but the sagebrush pair exhibited higher species richness and abundance of small mammals in the grazed grid (Table 2). No animals were captured in the grazed plot in pair #1, and the plot located in the exclosure core (pair #2) exhibited greatest species richness and number of individuals captured (Table 2).

DISCUSSION

To date, feral horse research in North America has been largely autecological, focusing on aspects of behavior, reproductive biology, movement patterns, and dietary ecology. Although these studies provide valuable information, they apply only indirectly to the relationships that horses maintain with other ecosystem elements. This is one of few studies to investigate quantitatively the ecological consequences of feral horse grazing in western North America, and the first to examine small mammal response to horse grazing. Results from the Clan Alpine Mountains show that, even when horse numbers within herd areas are <10% above appropriate management levels established by the BLM, strong differences in vegetation and qualitative differences in small mammal activity can be observed between horse-excluded and horse-occupied areas. Although comparisons for individual species

TABLE 2. Results of small mammal trapping and summary of vegetation sampling, Seven Troughs Range.

	Vegetative height[a] (cm)	Quadrat diversity[b] (species)	Mammal species captured[c]	No. males captured	No. females captured
PAIR #1[d]					
Grazed plot	8.8 ± 0.6**	9.5 ± 0.3*	None	0	0
Ungrazed plot	40.0 ± 2.6**	15.3 ± 1.5*	*Peromyscus maniculatus*	1	0
PAIR #2[e]					
Grazed plot	15.1 ± 1.2**	12.8 ± 1.6	*Peromyscus maniculatus*	4	1
			Microtus longicaudus	0	1
Ungrazed plot	42.7 ± 3.5**	14.5 ± 1.2	*Peromyscus maniculatus*	4	2
			Microtus longicaudus	1	0
			Lemmiscus curtatus	1	0
			Tamias sp.	1	0
PAIR #3[f]					
Grazed plot			*Tamias* sp.	1	0
			Peromyscus maniculatus	3	0
Ungrazed plot			*Tamias* sp.	1	0

[a]Mean ± 1 $s_{\bar{x}}$ of 16 trap stations per plot, $n = 4$ subsamples per trap station.
[b]Mean ± 1 $s_{\bar{x}}$ of vegetation within 25-m^2 quadrats, $n = 4$ quadrats per plot.
[c]Trapping occurred in 4 × 4 grids for 3 consecutive nights within each plot.
[d]Meadow habitat plots, separated (ca 8 m) by a narrow road. Grazed plot was grazed by both cattle and horses.
[e]Meadow habitat plots, separated by 0.8 km. Grazed plot was grazed exclusively by horses.
[f]Sagebrush (*Artemisia tridentata*) -dominated plots, separated by a narrow road. Grazed plot was grazed primarily by cattle.
*$P \leq 0.05$ for within-pair difference.
**$P \leq 0.001$ for within-pair difference.

are not presented here, strong treatment differences in percent cover and abundance were observed for nearly all plant species at Clan Alpine springs. For both Seven Troughs ($4.88 \cdot 10^{-3}$ horses $\cdot$ ha^{-1}) and the Clan Alpine ($8.24 \cdot 10^{-3}$ horses $\cdot$ ha^{-1}) HMAs, horse density was much lower than the density of 0.1 animal $\cdot$ ha^{-1} reported for feral donkeys over hundreds of square kilometers in northern Australia (Graham et al. 1982, Bayliss 1985). Although our studies lack extensive replication, we have observed differences in 2 mountain ranges, at high and low elevations, and in salt scrub, meadow, and spring habitats. Contribution of cattle to observed differences was not zero, but we chose areas that minimized this contribution as much as possible without logistically difficult large-scale manipulations.

The specific biology of horses (Hafez et al. 1969, Feist and McCullough 1975, Janis 1976, Berger 1986) suggests that there will be both similarities and differences in the factors that determine consequences of herbivory by horses and other mammals. For example, in this study, local spring density and habitat type may influence the frequency or intensity of use of an area and, consequently, the magnitude of grazing effects. More specifically, the more dramatic impacts at Clan Alpine grazed sites may be due in part to a lower spring density in that range compared with the Seven Troughs Range or to the lower productivity (and in some cases, lower resilience) of salt scrub habitat.

Edge Effects

Because none of the Clan Alpine plots had a radius greater than 15 m, it is safe to assume that the exclosure was effectively all "edge" habitat, at least as experienced by small mammals (Wilcove et al. 1985, Laurance and Bierregaard 1997). The much lower species richness and overall abundance of mammals captured in exclosure plots #1 and #3 may have resulted from their proximity to the edge of the exclosure as compared with the centrally located plot #2. In contrast, greatest species richness in exclosure grid #2 suggests that in landscapes of heterogeneous land use, large exclosures may act as habitat refugia for small mammal populations, preventing local extirpation of species (especially widely fluctuating arcivolines) via subsequent recolonization (Amaranthus et al. 1994, Perry and Amaranthus 1997). Edge effects were also observed for plants, supported by the presence of at least 3 exotic plant species at spring C and 4 species at spring D in the Clan Alpine Mountains. Similarly, in the Seven Troughs Range, plot #2, located over 30 m from any edge, is the only plot in which no exotic species were detected. Ideal experimental design would employ large, replicated exclosures located amidst a matrix of habitat similar to that found in the exclosures.

Equivalence of Grazed and Ungrazed Plots

We considered all plots around springs in the Clan Alpine range to be equivalent except for the treatment variable, because they are all located in the same canyon and habitat type. Furthermore, all plots have the same aspect, approximately the same flow rate, and differ at most by 175 m elevation. Inasmuch as we did not determine mammal species composition at grazed and ungrazed springs at the Clan Alpine plots, it is possible that differences in burrow abundance were due to the presence of species with differing burrowing tendencies (Hall 1946). This is unlikely, however, because of the similarities of the plots and because species that could most seriously confound the analysis (*Microtus* spp., *Lemmiscus curtatus*) do not occur at these low elevations in central Nevada (Hall 1946). In the Seven Troughs Range, the larger exclosure size allowed us to minimize confounding effects of unmeasured covariates by employing a matched pairs design. In 2 of 3 pairs, plots were located within 20 m of one another. The 3rd pair was separated by 0.8 km, but no closer habitat match existed.

Although in our experience no grazed plot represents an extreme example of horse grazing effects in the Great Basin, grazed Clan Alpine plots represent areas receiving heavier than average horse use, particularly spring A. Crane et al. (1997) similarly found that feral horses in south central Wyoming preferentially selected streamside, bog, meadow, as well as mountain sagebrush habitats. In contrast, our experience suggests that the Seven Troughs plots represent areas receiving moderate use by horses, in comparison to other Great Basin herd areas. It is important to exercise caution when comparing effects of grazing by horses alone with effects of grazing by horses and cattle (i.e., when evaluating possible synergistic effects). Because we were not

able to control total grazing intensity at grazed sites, it is possible that lower vegetation height and species richness in the pair #1 grazed plot reflects a higher combined grazing intensity. Further research may elucidate whether horse grazing and cattle grazing combine in an additive, multiplicative, or some other fashion.

Other large herbivores in the Clan Alpine and Seven Troughs ranges (pronghorn, mule deer) also may have contributed to the degradation we observed. Meeker (1979) and Berger (1985) found horses to be dominant among native Great Basin ungulates in social interactions, particularly at spring areas. As such, horses can induce alterations in the spatial and temporal dimensions of habitat use by sympatric native ungulates (Meeker 1979, Ganskopp and Vavra 1987, Coates and Schemnitz 1994). However, neither deer nor antelope were observed at our plots during 14 d of observation during the summers of 1997 and 1998, although we observed horses almost daily during our research there. Due to the nature of exclosure construction, both of these species (as well as other herbivores such as *Lepus californicus* and *Sylvilagus audubonii*) could access all plots. Thus, these species should not have contributed to differences observed between grazed and exclosure plots. Studies that quantify influences of all herbivores in a given system may provide insight into how effects of diverse consumers interact.

Finally, the legacy of past grazing impacts (domestic sheep or cattle, particularly between 1890 and 1920) may confound differences currently observed. This is nearly impossible to assess quantitatively because historical records of grazing from that time can rarely be found today. When such records do exist, they are almost universally qualitative, and there may have been incentive to underreport stocking rates purposefully (D. Aicher, rangeland management specialist, USDA-FS, personal communication). Historical grazing impacts should not pose a problem, however, because it is unlikely that such grazers would have differentially used either set of plots (i.e., the grazed or ungrazed plots) to the exclusion of others.

Recommendations for Future Research

Numerous authors (e.g., Szaro 1991, Bartolome 1993) have highlighted the need for longer-term studies of herbivory that encompass natural stochastic variability in environmental factors such as precipitation and temperature. We echo this call and recommend collection of data across seasons and years. Precipitation data from weather stations near 9 mountain ranges (Beever et al. in review) indicate that precipitation in western Nevada during 1998 was 120% of the 1961–1990 average. Because other authors (Jardine and Forsling 1922, Detling 1998) and horse managers in the region (T. Seley and J. Axtell, BLM, personal communication) have suggested that effects of grazing are magnified during drier years, our estimation of grazing effects in a single growing season should be conservative with respect to temporal variation. Observed treatment effects of this study are valid only for the areas we investigated. Future studies could achieve greater experimental rigor (through replication and experimental manipulation of treatment level) if performed on large private landholdings or if the BLM could accommodate more exclosure studies for feral horses.

Because our experiment is mensurative rather than manipulative, it is less robust than a double-translocation study with controls (Hurlbert 1984, Underwood 1997). In cases where plots are not randomly assigned to different treatments (i.e., grazed or ungrazed), and when researchers do not have data from before and after imposition of the treatment for both control and experimental plots, it is not possible to attribute observed differences unequivocally to the effect of the treatment. However, we have shown that grazed and ungrazed plots do not systematically differ for many of the environmental variables (e.g., habitat type, aspect, elevation, and soil type) most likely to affect our response variables. Furthermore, especially in the adjacent pairs of plots in the Seven Troughs Range, if another environmental variable were confounding our results, it would be expected to produce a graded change in response variables along a spatial axis. However, we have shown that vegetation height, for example, instead exhibits a stepped function, with differences occurring only across the fence line (Fig. 3).

ACKNOWLEDGMENTS

Information we use from the University of Nevada, Biological Resources Research Center

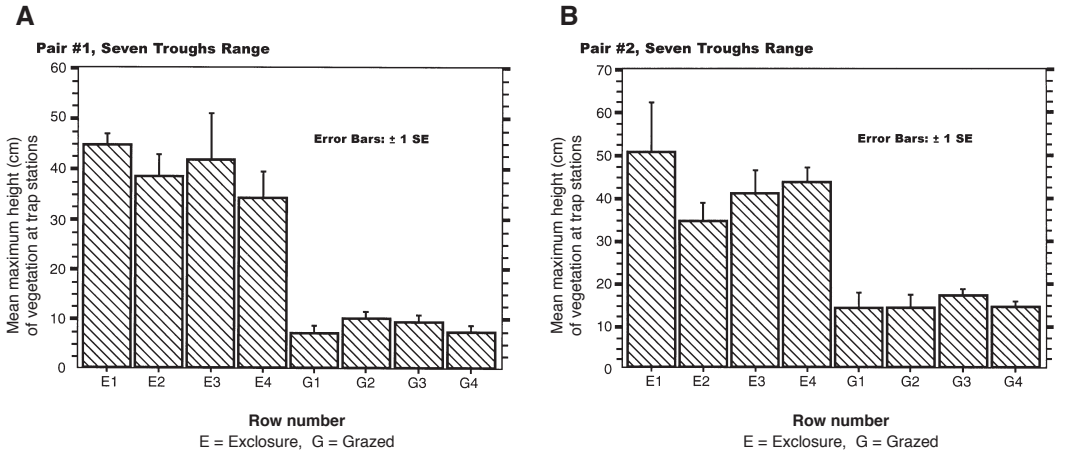


Fig. 3. Maximum height of vegetation (cm ± 1 $s_{\bar{x}}$) at trap stations by row for 2 pairs of meadow plots, Seven Troughs Range. Height at each trap station represents mean of 4 subsamples. Means for each row are obtained by considering each trap station ($n = 4$ per row) as replicates: A, pair #1, grazed rows received use by both horses and cattle; B, pair #2, grazed rows received use by horses only.

website (BRRC 1998) was originally created using U.S. Geological Survey digital elevation model GIS coverages. This publication was made possible by financial assistance provided to EAB from the Kosciuszko Foundation, a Theodore Roosevelt grant from the American Museum of Natural History, and the Nevada Biodiversity Initiative. At the University of Nevada–Reno, the Nevada Agricultural Experimental Station, College of Agriculture, Biology Department, Center for Environmental Arts and Humanities, and Biological Resources Research Center also provided funding to EAB. We extend special thanks to A. Tiehm of the Northern Nevada Native Plant Society for assistance with plant identification, to J. Fisher of the Natural Resources Conservation Service in Reno for soils information, and to J. Gianola, J. Axtell, and T. Seley, horse management biologists from the Carson City and Winnemucca BLM district offices, for assistance in locating large, long-standing exclosures. S. Jenkins, K. Geluso, and B. Longland commented on earlier drafts of this manuscript.

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Received 21 July 1999
Accepted 24 January 2000

APPENDIX. Identification and frequency of species encountered in quadrats used for diversity measures, Seven Troughs Range, Nevada, USA. Horizontal lines separate shrubs, forbs, and grasses in each grid. Taxonomy and life forms follow Hickman (1993).

Pair 2: Exclosure grid	N^a
Artemisia arbuscula [Asteraceae]	1
Epilobium brachycarpum [Onagraceae]	4
Epilobium ciliatum [Onagraceae]	1
Iva axillaris robustior [Asteraceae]	4
Limosella aquatica [Scrophulariaceae]	1
Mimulus guttatus [Scrophulariaceae]	3
Penstemon rydbergii oreocharis [Scrophulariaceae]	1
Plagiobothrys cusickii [Boraginaceae]	1
Polygonum polygaloides kellogii [Polygonaceae]	1
Potentilla gracilis elmeri [Rosaceae]	4
**Tragopogon pratensis* [Asteraceae]	3
Unidentified forb B	4
Unidentified forb C	4
Unidentified forb H	4
Unidentified forb I	2
Unidentified forb J	1
Unidentified forb K	2
**Bromus tectorum* [Poaceae]	1
Carex douglasii [Cyperaceae]	3
Elymus elymoides [Poaceae]	2
Juncus balticus [Juncaceae]	4
Juncus bufonius [Juncaceae]	3
Leymus cinereus [Poaceae]	1
Muhlenbergia richardsonis [Poaceae]	3
Unidentified Poaceae A	4
[b]TOTAL: 25 spp. (0,1,16,8)	62

Pair 2: Grazed grid	N^a
Artemisia arbuscula [Asteraceae]	1
Chrysothamnus viscidiflorus [Asteraceae]	1
Iva axillaris robustior [Asteraceae]	4
Navarretia breweri [Polemoniaceae]	1
+* *Polygonum arenastrum* [Polygonaceae]	2
Potentilla gracilis elmeri [Rosaceae]	2
Unidentified forb B	4
Unidentified forb C	4
Unidentified forb H	3
Unidentified forb I	2
**Bromus tectorum* [Poaceae]	1
Carex douglasii [Cyperaceae]	3
Elymus elymoides [Poaceae]	1
Juncus balticus [Juncaceae]	4
Juncus bufonius [Juncaceae]	3
Poa sandbergii [Poaceae]	3
[b]TOTAL: 16 spp. (0,2,8,6)	39

Pair 3: Exclosure grid	N^a
Juniperus osteosperma [Cupressaceae]	1
Artemisia arbuscula [Asteraceae]	4
Artemisia tridentata [Asteraceae]	2
Achillea millefolium [Asteraceae]	1
Epilobium brachycarpum [Onagraceae]	3
Epilobium ciliatum [Onagraceae]	2
Gnaphalium palustre [Asteraceae]	4
Iva axillaris robustior [Asteraceae]	4
Limosella aquatica [Scrophulariaceae]	1
Mimulus floribundis [Scrophulariaceae]	1
Mimulus guttatus [Scrophulariaceae]	2
Penstemon rydbergii oreocharis [Scrophulariaceae]	2
Potentilla gracilis elmeri [Rosaceae]	1
Unidentified forb A	1
Unidentified forb B	2

Pair 3: Grazed grid	N^a
Juniperus osteosperma [Cupressaceae]	1
Artemisia arbuscula [Asteraceae]	4
Artemisia tridentata [Asteraceae]	1
Crepis intermedia [Asteraceae]	1
Epilobium brachycarpum [Onagraceae]	1
Eriogonum umbellatum [Polygonaceae]	2
Gnaphalium palustre [Asteraceae]	1
Iva axillaris robustior [Asteraceae]	3
Lupinus argenteus [Fabaceae]	2
Navarretia breweri [Polemoniaceae]	3
Potentilla gracilis elmeri [Rosaceae]	4
Perideridia bolanderi [Apiaceae]	1
**Tragopogon pratensis* [Asteraceae]	1
Unidentified forb B	2
Unidentified forb C	4

APPENDIX. Continued

Pair 3: Exclosure grid	N^a	Pair 3: Grazed grid	N^a
Unidentified forb C	3	Unidentified forb E	1
Unidentified forb D	1	Unidentified forb G	1
Carex douglasii [Cyperaceae]	3	*Carex douglasii* [Cyperaceae]	3
Elymus elymoides [Poaceae]	2	*Elymus elymoides* [Poaceae]	4
Juncus balticus [Juncaceae]	4	*Juncus balticus* [Juncaceae]	4
Juncus bufonius [Juncaceae]	4	*Juncus bufonius* [Juncaceae]	4
Muhlenbergia richardsonis [Poaceae]	2	Unidentified Poaceae A	2
Poa sandbergii [Poaceae]	1	Unidentified *Achnatherum* C	1
Unidentified Poaceae A	4		
Unidentified Poaceae B	2		
[b]TOTAL: 25 spp. (1,2,14,8)	57	[b]TOTAL: 23 spp. (1,2,14,6)	51

[a]Number of 5 × 5-m plots (out of 4) in which the species was found.
[b]Number of tree, shrub, forb, and grass species.
*Species not native to the Great Basin (Hickman 1993).
+Species is tolerant of trampling (Hickman 1993).

Ecological Applications, 13(1), 2003, pp. 119–136
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CHARACTERIZING GRAZING DISTURBANCE IN SEMIARID ECOSYSTEMS ACROSS BROAD SCALES, USING DIVERSE INDICES

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Abstract. Although management and conservation strategies continue to move toward broader spatial scales and consideration of many taxonomic groups simultaneously, researchers have struggled to characterize responses to disturbance at these scales. Most studies of disturbance by feral grazers investigate effects on only one or two ecosystem elements across small spatial scales, limiting their applicability to ecosystem-level management. To address this inadequacy, in 1997 and 1998 we examined disturbance created by feral horses (*Equus caballus*) in nine mountain ranges of the western Great Basin, USA, using plants, small mammals, ants, and soil compaction as indicators. Nine horse-occupied and 10 horse-removed sites were stratified into high- and low-elevation groups, and all sites at each elevation had similar vegetation type, aspect, slope gradient, and recent (≥15-yr) fire and livestock-grazing histories. Using reciprocal averaging and TWINSPAN analyses, we compared relationships among sites using five data sets: abiotic variables, percent cover by plant species, an index of abundance by plant species, 10 disturbance-sensitive response variables, and grass and shrub species considered ''key'' indicators by land managers. Although reciprocal averaging and TWINSPAN analyses of percent cover, abiotic variables, and key species suggested relationships between sites influenced largely by biogeography (i.e., mountain range), disturbance-sensitive variables clearly segregated horse-occupied and horse-removed sites. These analyses suggest that the influence of feral horses on many Great Basin ecosystem attributes is not being detected by monitoring only palatable plant species. We recommend development of an expanded monitoring strategy based not only on established vegetation measurements investigating forage consumption, but also including disturbance-sensitive variables (e.g., soil surface hardness, abundance of ant mounds) that more completely reflect the suite of effects that a large-bodied grazer may impose on mountain ecosystems, independent of vegetation differences. By providing a broader-based mechanism for detection of adverse effects, this strategy would provide management agencies with defensible data in a sociopolitical arena that has been embroiled in conflict for several decades.

Key words: *broad spatial scales; disturbance;* Equus caballus*; feral horses; grazing; Great Basin; landscape ecology; monitoring; Nevada; reciprocal averaging; semiarid ecosystems; TWINSPAN.*

INTRODUCTION

Disturbances, both natural and anthropogenic, produce changes within ecosystems that vary in spatial and temporal extent. Frequency, intensity, scale (extent), and timing (season) are all fundamental aspects of disturbance regimes (Pickett and White 1985). Recovery from disturbance in semiarid systems such as the Great Basin can be relatively slow and uncertain, or may involve systems shifting to new stable states (Laycock 1991, Tausch et al. 1993, Rietkerk and van de Koppel 1997). Several studies in western North America have reported no significant recovery of various ecosystem components after one to several decades of removal of the disturbance agent (McLean and Tisdale 1972, Rice and Westoby 1978, West et al. 1984, Heske and Campbell 1991, Knapp 1992), but other studies from the same region have found that systems experiencing removal of disturbance can exhibit significant changes over both short and long time scales (Laycock 1967, Dormaar et al. 1994, Dobkin et al. 1998, Beever and Brussard 2000). Clearly, further research on detecting disturbance in semiarid systems can help to clarify the factors that determine response to disturbance, mechanisms by which change occurs, and how effects vary across the landscape.

Ungulates are a disturbance agent that may directly influence arid ecosystems in numerous ways, including consumption of plants, redistribution of nitrogen and plant seeds via urination and defecation, trampling of vegetation, and compaction of soils (Hobbs 1996, Belsky and Blumenthal 1997). Most studies investigating effects of grazing by large mammals, especially feral horses, have been performed at sites distributed over relatively localized regions. Areas such as the Great

Manuscript received 7 November 2001; revised 12 March 2002; accepted 2 April 2002; final version received 3 June 2002. Corresponding Editor: D. P. C. Peters.

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Basin, however, are physiographically very diverse, and many potentially affected taxa exhibit high degrees of local adaptation. Furthermore, response to disturbance can depend upon attributes of the disturbance, as well as on the local coevolutionary history of the species involved in the interaction (Briske 1993, DeAngelis and Huston 1993, Noy-Meir 1993). These sources of variability may severely limit ecologists' ability to extrapolate results of ecosystem response to disturbance or release from disturbance at one or a few sites to broad-scale conclusions (Westoby 1980, Mack and Thompson 1982). Although many small-scale comparisons of acute grazing vs. no grazing have been made, effects of chronic disturbance over broad areas are not well understood. In addition, although disturbance by cattle has been investigated, feral horses are only beginning to be investigated as a disturbance agent. Previous research has found that disturbance by feral horses (*Equus caballus*) can significantly influence aspects of vegetation, small mammals, ants, and soils (Beever 1999; E. A. Beever and P. F. Brussard, *unpublished manuscript*). Given this knowledge, we used 19 sites located in nine mountain ranges of the Great Basin of the western United States to study the ability of various response variables to detect disturbance by horses across the landscape.

Research in western North America comparing grazing-disturbed areas with protected or recovering areas often focuses attention on one or two types of response variables (e.g., Medin and Clary 1989, Schulz and Leininger 1991, Rosenstock 1996). Even when investigators examine three or more response variables, disturbance effects are frequently evaluated separately for each variable. Although ecosystem management and conservation biology are moving toward more holistic management at larger scales, it is difficult to assess whether disturbance produces a broadly detectable change in semiarid ecosystems. Although results from various studies can be compared to infer how several ecosystem components might react to a single type of disturbance (e.g., Kauffman and Krueger 1984), differences in experimental conditions among studies may confound results and prevent the creation of a unified predictive model. Whereas monitoring and much research often investigate only defoliation-related effects of grazing, we attempted to quantify the effects of numerous grazing-related disturbance processes listed at the beginning of the previous paragraph.

Because of the complex environmental gradients present within the Great Basin, a repeating sequence of more than 200 distinct mountain ranges isolated by numerous valleys (Hunt 1967, Fiero 1986, Grayson 1993), it is difficult to create a monitoring scheme appropriate for assessing disturbance across broad spatial scales. As demonstrated by Brown (1971) and subsequent researchers (e.g., Lawlor 1998), even adjacent mountain range complexes may contain different collections of montane mammal species. This differentiation may be even more pronounced for plant species that have low vagility (Kartesz 1987, Charlet 1991). We therefore sought to compare the ability of different monitoring strategies to detect disturbance by feral horses amidst the clinally complex gradients of Great Basin landscapes.

In most field districts, managers are unlikely to adopt and implement assessments that are prohibitively time-intensive or costly. However, given limited agency budgets, it is important that monitoring: (1) consistently detects change; (2) is sufficiently sensitive to provide an early signal of degradation; (3) provides information across broad spatial scales; and (4) relates to the disturbance processes and mechanisms of change that may influence response variables (Noss 1990). Here we compare sites at both high and low elevations with different degrees of disturbance by feral horses. We applied two multivariate techniques, reciprocal averaging and TWINSPAN analysis, to empirical field data collected in 1997 and 1998. We tested whether horse-occupied and horse-removed sites could be discriminated across broad spatial scales using data sets of plant cover (all species or only species of management concern), abiotic variables, and a set of disturbance-sensitive variables related to vegetation, soils, small mammals, and ants.

In evaluating these alternative monitoring strategies, the objectives of our research were to: (1) determine to what extent inherent site (i.e., abiotic) differences existed between selected horse-occupied and horse-removed sites; (2) determine how the composition of plant species at semiarid sites changes across broad spatial scales; (3) ascertain whether diverse disturbance-sensitive variables detect disturbance more consistently than abiotic or strictly plant-related data sets; and (4) compare characterization of horse-occupied and horse-removed sites using commonly monitored response variables (''key'' plant species only) with characterization using other data sets.

Methods

Site selection

We collected data at 17 sites in eight mountain ranges in western and central Nevada during 1997 and 19 sites in nine ranges during 1998 (Table 1, Fig. 1). During both years, sites were stratified into high (2000–2286 m) and low (1340–1700 m) elevations (hereafter, ''strata''), corresponding roughly to the lower and upper sagebrush zones. Half of the sites in each elevational stratum had horses removed for the last 10–14 yr; feral horses had access to the remaining (''horse-occupied'') sites since at least 1971 (Table 1). Because horses were known from aerial censuses to have used horse-occupied sites during at least some seasons in some years during the 3–8 yr before our sampling, we assumed that disturbance had occurred on these sites. Two low-elevation, horse-removed sites were added in 1998.

Sampling of all response variables occurred within the boundaries of a mammal-trapping grid (area = 1.82 ha per site).

All sites were dominated by big sagebrush (*Artemisia tridentata*), east-facing, of low (<40%) slope gradient, and located within 1.0 km of a dirt road to facilitate small-mammal trapping. Because feral horses often demonstrate a tendency for heavy use of productive mesic sites (Miller 1980, Rogers 1991, Crane et al. 1997, Detling 1998), we compared sites in scrub habitat distant from streams and springs. All sites had not been burned within at least the last 15 yr, and cattle were actively excluded or stocked at low densities (T. Seley and J. Gianola, Bureau of Land Management Horse Specialists, *personal communication*). Consequently, the ratio of horse defecations : cattle defecations across years at all horse-occupied sites exhibited a geometric mean of 10.4:1. Furthermore, fecal counts suggested that intensity of recent cattle grazing did not differ between horse-grazed and horse-removed sites during 1997 ($P = 0.71$) or 1998 ($P = 0.60$). Pellet counts of other ungulates, primarily mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*), also did not differ between horse-occupied and horse-removed areas in either year ($P > 0.20$). Although accurate site-specific data on historical grazing intensities were not available, geographic interspersion of sites, combined with lack of spatial pattern in historical grazing (Young and Sparks 1985), suggested that historical livestock use was not appreciably different between treatment groups. Simultaneously satisfying all seven of these criteria restricted us to two or three sites per mountain range; of these, we selected sites with the least cattle use.

Although many grazing studies use very small-sized plots that are often paired, we argue that larger sized plots correspond more closely with scales at which large-bodied herbivores such as horses will affect ecosystems. Thus, although at the finest scale we chose sites that exhibited maximum homogeneity of big sagebrush vegetation and avoided steep slopes (after satisfying the six other selection criteria), variability in depth to bedrock, color of soils, soil texture, and to some degree, abundance of calcium carbonate varied notably across the 1.82-ha area at many sites. Consequently, variability in soil characteristics within each site and among replicates of an elevation-treatment category rivaled variability between treatments. We collected samples of the upper 20 cm of soil horizons at sites, one from each quadrant of the trapping grid, and dug soil pits to supplement information from NRCS (Natural Resources Conservation Service) soil surveys. We also used cover of dominant shrub and grass species to further clarify which soil series occurred in our plot.

Field Procedures

Vegetation

Sampling was conducted from May through August in 1997 and 1998. To characterize vegetation, we used four 50-m line-intercept transects as subsamples at each site. We measured an index of abundance (the number of individuals intersected per transect; Bonham 1989) and cover (the sum of the lengths of tape intercepted by individual plants, divided by the total transect length) for each plant species encountered (Whittaker 1973). Hereafter, we refer to this index of abundance as simply ''abundance.'' We used a random-number generator to select the mammal trap station at which to begin each transect, but forced selection of one line transect in each quadrant of the grid (Goodall 1952). From preliminary transect work, we found that four dispersed transects consistently captured variability among transects and species richness at sites.

Forbs and grasses with no evidence of current photosynthesis were excluded from measures of cover. Because dense clumping and early senescence of cheatgrass (*Bromus tectorum*) plants made it difficult to identify individuals, cheatgrass values represent the average number of stems that crossed the tape per 50-m transect.

Disturbance-sensitive response variables

We measured penetration resistance using a pocket penetrometer (Soiltest model CL-700, Evanston, Illinois, USA) that measures the pressure required to push the flat end of a 6.4 mm diameter cylindrical rod beyond a distance of 6.4 mm into the soil surface (Bradford 1986, USDA 1993). Hard soil surfaces can decrease infiltration rates, inhibit digging by burrowing mammals, limit plant establishment, and restrict root growth (USDA 1993, Belsky and Blumenthal 1997). Time constraints prevented us from measuring soil moisture and soil structure (including bulk density) directly. Instead, we measured penetration resistance at least 48 h after a precipitation event. Penetration resistance declines with increasing soil moisture and decreasing bulk density. Consequently, a reduction in penetration resistance can reflect higher infiltration, higher water-holding capacity, lower evapotranspiration in near-surface horizons, or lower bulk density. Higher infiltration, in turn, can occur as a result of changes in both soil and vegetation structure. Because penetration resistance values exhibited great variability in preliminary sampling, we adopted a two-tiered sampling strategy at each site that involved taking 10 measurements within 1 m of every fourth mammal trapping station, for a total of 250 subsampled measurements per site. Measurement locations were offset from areas sampled in previous years. All samples were taken in bare interspaces (>20 cm from shrub bases); values were discarded and another reading was taken if the penetrometer contacted a rock or shrub root. Although this disturbance variable is abiotic, it is distinguished from the data set of ''abiotic'' inherent site characteristics by being dynamic and vulnerable to trampling influences.

We trapped small mammals using a 10×10 trapping grid with a single $8 \times 8 \times 25$ cm Sherman trap (Sher-

TABLE 1. Physiographic and other characteristics of 19 study sites used to compare horse-occupied and horse-excluded areas in high- and low-elevation sagebrush habitats. Sites occurred in nine mountain ranges in the western Great Basin of North America and were sampled in 1997 and 1998.

Site no.†	Mountain range	Site name	RA tag	Horse status	Elevation (m)	Soil textural classification	Average slope (%)‡
High-elevation, horse-excluded sites							
1	Pah Rah Range	Virginia Peak	P1	absent	2134	stony loam	25
2	Sonoma Range	Lake valley hillside	S1	absent	2164	stony loam	40
3	Sonoma Range	Cabin	S2	absent	2118	stony loam	25
4	Humboldt Range	Pflum Creek Mine	H1	absent	2000	gravelly loam	20
High-elevation, horse-occupied sites							
5	Dogskin Mountain	Dry Valley Creek saddle	D1	present	2060	sandy loam	20
6	Dogskin Mountain	Dry Valley Creek peak	D2	present	2200	sandy loam	30
7	Seven Troughs Range	Side road w/junipers	G1	present	2225	sandy loam	20
8	Seven Troughs Range	High saddle	G2	present	2286	sandy loam	25
Low-elevation, horse-excluded sites							
9	Pah Rah Range	Bigmouth Canyon	P2	absent	1500	sandy loam	15
10	Truckee Range	Jeep trail	T1	absent	1540	sandy loam	5
11	Truckee Range	Sage Hen Creek	T2	absent	1500	sandy loam	10
12	Humboldt Range	Low side valley	H2	absent	1433	sandy loam	25
13	Virginia Range#	Horse Spr1:Fernley view	V1	absent	1400	sandy loam	5
14	Virginia Range#	Horse Spr2:homogen. vly	V2	absent	1500	gravelly loam	5
Low-elevation, horse-occupied sites							
15	Dogskin Mountain	Winnemucca Valley spur	D3	present	1646	sandy loam	25
16	Clan Alpine Mountains	Dixie Valley vista	C1	present	1340	stony loam	10
17	Clan Alpine Mountains	Shoshone Pass	C2	present	1700	gravelly loam	15
18	Virginia Mountains	Flanigan1: Juniper saddle	F1	present	1646	stony loam	20
19	Virginia Mountains	Flanigan2: Juniper Basin	F2	present	1554	stony loam	25

† Site numbers correspond to locations shown in Fig. 1.
‡ Obtained using a handheld clinometer, averaged across the entire sampling area.
§ Subjective classification of exposure, after Wentworth (1976): 0, site somewhat protected by adjacent slopes; 1, site on open slope, unsheltered by adjacent slopes.
‖ Subjective classification of disturbance, after Wentworth (1976); 1, apparently undisturbed; 2, slight disturbance; 3, moderate; 4, heavy; 5, severe.
¶ Average from four line-intercept transects performed during 1997 and 1998.
Site sampled in 1998 only.

man, Tallahassee, Florida, USA) at each station, with rows and columns separated by 15 m. Grids were located within homogeneous vegetation assemblages. Trapping occurred for three consecutive rainless nights at each site. We recorded species, sex, body mass (±0.2 g), trap station, and reproductive status of each animal, and whether it had been captured previously.

We counted aboveground ant mounds within 2 m of an imaginary line drawn along the rows of the trapping grid, which produced a 4 × 1485 m undulating strip transect. Although we encountered both thatched mounds (produced by *Formica*) and pebble mounds (constructed mostly by *Pogonomyrmex*), we gave a value of 1 to each mound.

Assessment of recent grazing intensity at small spatial scales: fecal counts

At each site, we assessed relative intensity of use by cattle, horses, and all native ungulates by tallying fecal piles within 2 m of the rows of the mammal-trapping grid. To avoid overcounting instances in which an animal defecated while moving across the site, cattle-produced fecal piles <8 cm in diameter and horse-produced piles with <4 pellets were not counted. Fecal counts suggested that the recent intensity of horse grazing varied little among high-elevation sites (184.5 ± 10.2 dung piles per site, mean ± 1 SE). Although one site heavily used by horses created greater variability in intensity among low-elevation sites (96.4 ± 38.8 dung piles per site), this site (C1) did not exhibit consistent differences from other low-elevation sites in RA (Fig. 2) or TWINSPAN analyses.

ANALYSIS

Data sets

We characterized sites using five types of variables. The first four, abiotic characteristics (e.g., precipitation, elevation, soil erodibility), abundance by plant species, percent cover by plant species, and percent cover of plant species sampled by horse managers, are commonly used for monitoring. The fifth type included variables that have been shown by previous research (Table 2) to respond to disturbance. We did not pool samples across years because some variables exhibited significant interannual variation (Beever 1999) and because we added two sites in 1998. For each of the

TABLE 1. Extended.

Aspect	Position on slope	Exposure§	Non-horse disturbance‖	Average percent bedrock¶	Distance to nearest same-range site (km)
ENE	upper	0	1	3.22	4.4
NE	middle	1	2	0.09	3.1
ENE	lower	0	3	3.99	3.1
NE	middle	0	3	0.68	3.4
E	upper	1	2	4.57	0.6
NE	upper	1	2	1.00	0.6
E	upper	1	2	1.78	0.8
E	middle	1	2	0.11	0.8
E	lower	0	3	0.05	4.4
NE	lower	1	1	0.13	4.1
NE	lower	0	3	0.41	4.1
SE	middle	0	3	0	3.4
ENE	lower	1	2	0	2.7
ENE	middle	0	3	0	2.7
NE	middle	0	4	3.44	2.8
NE	middle	0	1	0.66	12.3
E	middle	1	1	0.02	12.3
E	middle	1	1	0.59	1.1
ESE	middle	0	2	0.76	1.1

abiotic and disturbance data sets, we used a correlation matrix between all variables to identify multicollinearity in our variables ($r > 0.70$). In such cases, we present analyses with the abiotic or disturbance variable whose connection to response variables has been most strongly developed in previous research.

Abiotic variables: inherent site characteristics

We used data from several sources to assess the degree to which sites were distinguishable on the basis of their inherent site properties, as opposed to the more dynamic properties such as soil hardness and vegetative cover in other data sets. Because sites were not near existing weather stations, we used a PRISM model-generated 1:1 190 000 scale map based on 1961–1990 weather data to estimate average annual precipitation at each site (Daly et al. 1994). These modeled long-term averages were then multiplied by the ratio of precipitation received at the nearest weather station during 1997 or 1998 to the 30-yr average received at that station (Hungerford et al. 1989). Values for mean annual number of frost-free days, available water capacity, and erosion factors K and T (an index of susceptibility to erosion by rainfall, and the maximum rate of erosion tolerated to permit sustained crop productivity, respectively) were obtained from published and unpublished soil surveys of the Natural Resources Conservation Service (e.g., Baumer 1983, Zielinski 1994). Soil types were mixed among high- and low-elevation strata, with horse-occupied and horse-removed sites each having five sites dominated by sandy loams, three with stony loams, and one (or two) with gravelly loams (Table 1). Because most sites contained significant heterogeneity in soil properties within the 1.82-ha area, we estimated values of variables at sites using an average weighted to reflect percentage composition occupied by each of the three soil series in the association at each site. We also recorded (Table 1) the position of the site on the slope, its exposure, non-horse disturbance, and amount of exposed bedrock, following Wentworth (1976). Non-horse disturbance was a categorical estimate, from relatively undisturbed to severely disturbed, that included evidence of human and livestock use at the site (e.g., rubbish, off-road vehicle tracks, livestock defecations). Other variables included Julian date (day 1 = 1 January) of vegetation sampling, elevation in meters, and mean slope gradient measured at numerous locations within each site with a handheld clinometer. Horse-occupied and horse-removed sites did not significantly differ (two-way ANOVAs, $P > 0.05$; $0.05 < \text{power} < 0.50$) in any of their abiotic properties previously mentioned or in their depth to bedrock when each variable was analyzed individually using published NRCS, modeled, or field-collected data (Beever 1999). Horse-removed and horse-occupied sites also did not differ systematically in their soil color,

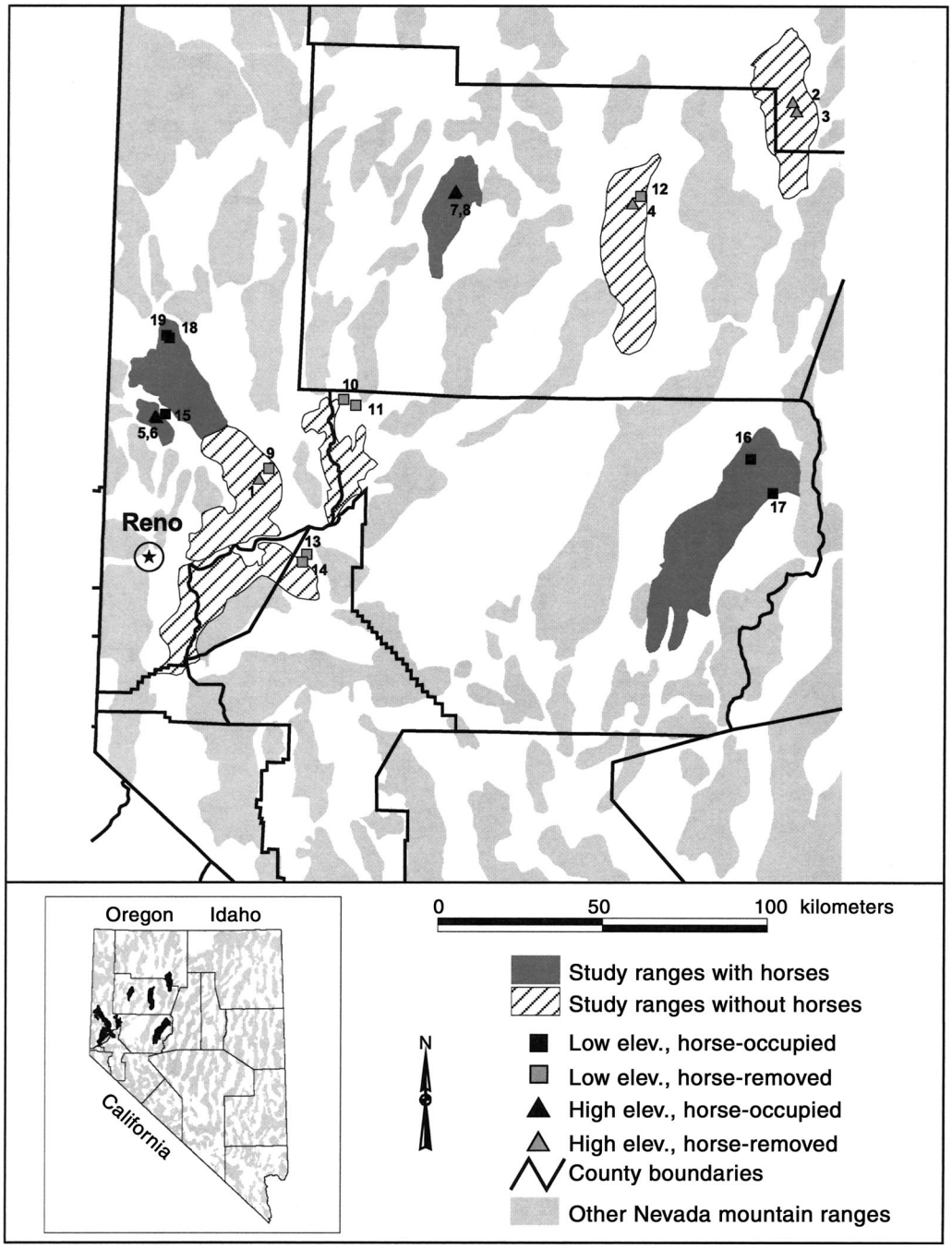


FIG. 1. Locations of 19 horse-occupied or horse-removed sites in the western Great Basin, Nevada (USA), sampled during 1997 and 1998.

permeability, structure, consistence, plasticity, or degree of calcic soils. Here we tested whether sites differed when all quantitative variables available for all sites were included.

Individual plant species data

Because most synecological research on feral horses has involved plants and because horse-monitoring strategies currently focus exclusively on vegetation, we investigated relationships among sites using three measurements of the plant community. The first measurement included site-by-site abundance data for each plant species observed in 1997 or 1998, and the second used percent cover data. Because cover has been suggested to be more important than abundance in community dynamics (Daubenmire 1959), the final clas-

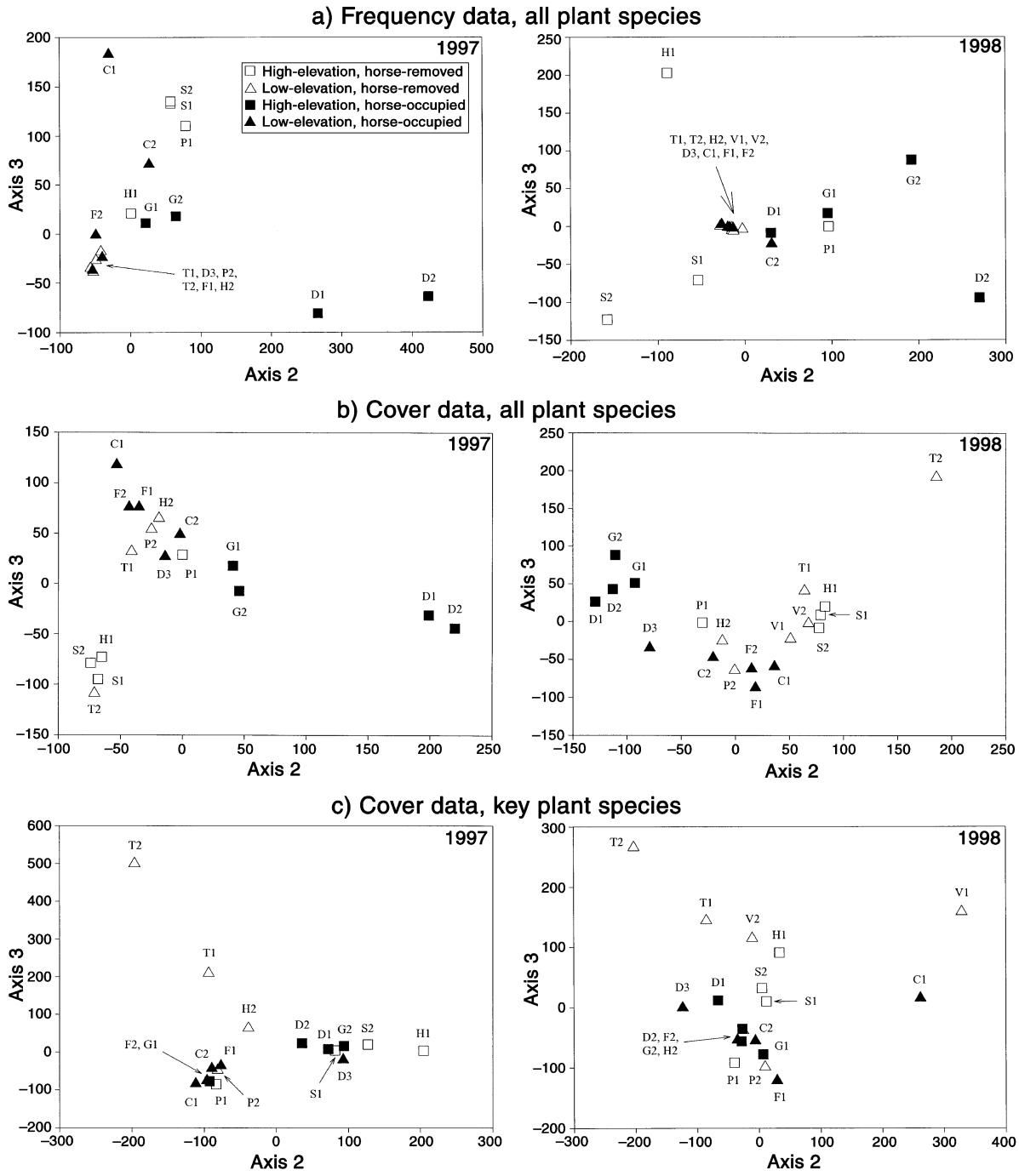


FIG. 2. Relationships between horse-removed and horse-occupied sites in two elevational strata, from reciprocal-averaging analyses with data sets composed of: (a) abundance (no. plants/transect) of all plant species; (b) percent cover of all plant species; (c) percent cover of only plant species monitored by agency managers (i.e., species dominant in horse diets from the region). All data are from sites in the western Great Basin, during summers of 1997 and 1998. The key for site ''tags'' (e.g., T2) is found in Table 1, column 4.

sification involved cover of only ''key'' grass and shrub species monitored by horse managers in the western Great Basin (listed in Appendix A). We identified species and life forms following Hickman (1993).

Disturbance variables

The final set of variables used to characterize horse-occupied and horse-removed sites was the set of 10 (of all variables measured) response variables shown pre-

TABLE 2. List of disturbance-sensitive variables used in RA and TWINSPAN analyses, accompanied by references that support their connection to disturbance, based on grazing disturbance unless noted.

Variable (units)	References
Penetration resistance [≈soil surface compaction] (MPa)	Kelly and Walker (1976), Wood et al. (1987), Weltz et al. (1989), Mahaney and Linyuan (1991), Dormaar et al. (1994), Belsky and Blumenthal (1997), van de Koppel et al. (1997)
Abundance of aboveground ant mounds in a 5940-m^2 area (unitless)	Majer (1983),‡ Rosenberg et al. (1986),‡ Andersen and Sparling (1997),‡ Suarez et al. (1998)‡
Percentage of small-mammal community (long RCR) as *P. maniculatus* (unitless)†	Martell (1983),‡ Schulz and Leininger (1991), Bich et al. (1995), Songer et al. (1997),‡ Bradley et al. (2000)
Total number of small-mammal individuals (long RCR) captured per site, three nights trapping	Reynolds and Trost (1980), Medin and Clary (1989), Heske and Campbell (1991), Rosenstock (1996), Hayward et al. (1997)
Percentage of hypothetical small-mammal species captured at a site (= long RCR; unitless)†	Reynolds and Trost (1980), Medin and Clary (1989), Dunstan and Fox (1996), Rosenstock (1996)
Species richness of plants at a site	Rummell (1951), Reynolds and Trost (1980), Brady et al. (1989), Knapp (1992),‡ Rusch and Oesterheld (1997)
Mean percent cover of grasses at a site [$n = 4$ transects] (unitless)†	Pickford (1932), Gardner (1950), Webb and Stielstra (1979), Brady et al. (1989)
Mean percent cover of forbs at a site [$n = 4$ transects] (unitless)†	Pickford (1932), Shupe and Brotherson (1985), Maschinski et al. (1997),‡ Dobkin et al. (1998), Clary (1999)
Mean percent cover of shrubs at a site [$n = 4$ transects] (unitless)†	Pickford (1932), Bock et al. (1984), Brady et al. (1989), Owens and Norton (1990)
Number of cheatgrass stems per 50-m transect [$n = 4$ transects] (unitless)	Pickford (1932), Gould (1951), Mack (1981), Pyke (1986), D'Antonio and Vitousek (1992), Knapp (1996)

† The variable was arcsine-transformed before being entered into analyses.
‡ The variable was affected by some type of disturbance other than grazing.

viously to be potentially altered by mammalian herbivory (Table 2). We arcsine-transformed all percentage variables (Sokal and Rohlf 1995). In the few cases in which a site was not sampled for a particular variable, we estimated its value either by regressing 1998 values for the variable on 1997 values or (less frequently) by using the mean of the site's treatment–elevation category from that year (Appendix B).

Values for cheatgrass (*Bromus tectorum*) abundance and percent cover of grasses, forbs, and shrubs represent averages from four 50-m line transects (Table 2). We calculated plant species richness for sites by pooling subsamples and adding any other species observed inside or within 10 m of the trapping grid. Realized community richness of small mammals reflected the percentage of nocturnal granivorous rodent species potentially present at each site (dictated by range maps, elevation, vegetation, soil type, and microhabitat) that were actually captured during trapping. We used this relative measurement (sensu Cam 2000) because the pool of mammal species that we could potentially capture varied greatly across our sites.

Reciprocal averaging (RA) and TWINSPAN analyses

All data matrices were analyzed in PC-ORD 2.0 (McCune and Mefford 1995) using RA (reciprocal averaging; Hill 1973) and TWINSPAN (Hill 1979, Gauch and Whittaker 1981) techniques. In RA, site and species ordinations are done simultaneously, with the species scores representing averages of the site scores, and reciprocally, the site ordination scores representing averages of the species ordination scores (Gauch 1982, Ludwig and Reynolds 1988). We used graphs to visually examine relationships between sites for all three axis combinations (i.e., 1–2, 1–3, and 2–3). Because elevation was the strongest determinant of many of our variables (Beever 1999) and because axis 1 carried most of the variation due to elevation, we used Axes 2 and 3 to illustrate relationships between sites after accounting for the effects of elevation.

TWINSPAN analyses traditionally have been used to classify sites and plant species simultaneously, based upon compositional similarity or distinctness. However, TWINSPAN may be used to divide a reciprocal ordination space for several types of ecological data (McCune and Mefford 1995). We used a minimum group size of three for division of sites, with a maximum of five indicators per division and 100 species in the final table. Indicator species in TWINSPAN occur at the end of the reciprocal-averaging axes and are used to further polarize the ordination (McCune and Mefford 1995). Because each abiotic and disturbance variable exhibited a unique mean and standard deviation, we used frequency histograms of values for each variable with 15–30 equivalent divisions to assign groups into five discrete categories in TWINSPAN analyses. This allowed us to calibrate diverse variables to the same scale and enter the same analysis. We used cut levels of 0, 2, 5, 10, and 20 for plant abundance analyses, cut levels of 0, 0.02, 0.05, 0.10, and 0.20 for percent cover analyses, and cut levels of 0, 1, 2, 3, and 4 for abiotic and disturbance variables. One of the most useful out-

puts of TWINSPAN analyses is the ordered two-way table (McCune and Mefford 1995), which graphically represents relationships between sites and variables.

We evaluated the effectiveness of data sets for characterizing sites with RA and TWINSPAN analyses by observing how closely results matched our design criteria, i.e., our designation of sites with respect to elevational stratum and presence of horses. Given our assumption that all horse-occupied sites had experienced at least *some* level of disturbance (by virtue of their occasional-to-frequent use by horses) compared to horse-removed sites, we assumed that horse-occupied sites should be more similar to each other than to horse-removed sites. RA analyses provided graphical representations of relationships among sites, and were evaluated by visual inspection. In TWINSPAN analyses, we compared the four collections of sites created by the first two levels of division (hereafter, ''groups'') to the grouping of sites illustrated in Table 1. An ''equal mix'' of horse-removed and horse-occupied sites meant that numbers of sites from the two treatments were exactly equal in groups with an even number of sites, and differed by one in groups containing an odd number of sites. We defined ''improvement'' of classification by the third-level TWINSPAN division as a perfect separation of a group of ≥ 3 horse-removed and horse-occupied sites that could not be explained by biogeographic (mountain range) patterns. For TWINSPAN analyses only, we measured the effects of biogeography by tallying the number of sites from the same range that occurred in the same group.

Results

In 1997, we found a total of 72 plant species at 17 sites, with an average of 15 species/site. In 1998, we recorded 182 species from 19 sites, with an average of 24 species/site. However, 78 of these 182 species were small, ephemeral forbs distinguishable as separate species, but too phenologically advanced for identification. Because we encountered many uncommon species in 1998, we analyzed these cover data with downweighting to reduce the contribution that rare species made to differentiation among sites. However, because fewer species were encountered in 1997 and downweighting of those data produced no significant change in the relationships among sites, we present 1997 cover and all ''key species'' results without downweighting (Fig. 2a–c).

RA analyses

Regardless of which combination of axes was used or whether downweighting of rare species occurred, sites were associated largely by mountain range in analyses of plant abundance data, due to range-to-range differences in species composition (Beever 1999). Across years and axis combinations, all low-elevation sites across mountain ranges appeared to be very similar (Fig. 2a), indicating a high level of floristic similarity, especially in 1998. The lone exception was the pair of Clan Alpine sites, separated from remaining low sites along axis 1 in 1997. Using 1998 data, most lower-elevation sites (depending upon axis combination) clustered so tightly that they could not be easily discriminated. Downweighting rare species slightly reduced the association of sites by mountain range, although not consistently. All three pairs of high-elevation sites were distinguishable from other sites, except for one pair in 1998 (Fig. 2a). Sites from the same mountain range (hereafter, ''pairs'') but different elevational strata never associated. Overall, horse-occupied sites were not clearly distinguishable from horse-removed sites in either year.

In both 1997 and 1998, percent cover of individual plant species segregated sites by mountain range to an even greater extent than did abundance data. Both high-elevation horse-occupied pairs of sites segregated from other sites in both years, and in 1998 one low-elevation pair of sites from each treatment type (Horse Springs HMA [Horse Management Area] and Virginia Mountains) additionally segregated from other sites (Fig. 2b, 1998 data). Analyses of percent cover data suggested greater differences between sites of different ranges than did analyses of plant abundance data in both years, especially improving the differentiation of low-elevation sites (Fig. 2a–b). Data from percent cover by plant species trailed only data from disturbance variables in their ability to separate horse-occupied and horse-removed sites along the ordination axes. Percent cover data clearly separated half (four) of the horse-removed sites from occupied sites in 1997, and all but 1–3 of the horse-removed sites in 1998 (e.g., Fig. 2b). One site (T2) with the most salt-scrub influence separated strongly from other sites in both years on all axis combinations (Fig. 2b).

Analyses of the cover of ''key'' plant species suggested that most sites were too similar to be distinguishable, and that mountain range effects explained most of the remaining variability. Across both years and all axis combinations using key plant species cover, $>50\%$ of sites clustered tightly together, suggesting no difference between horse-occupied and horse-removed sites (Fig. 2c). The Truckee Range site (T2) again separated strongly from other sites across years and axis combinations. In spite of sometimes great distance between them (Table 1), sites within the same mountain range and elevational stratum usually possessed vegetation more similar in composition to each other than to sites from other ranges (Fig. 2c).

Reciprocal averaging of 12 inherent (abiotic) site properties suggested that relationships among sites were strongly affected by elevation, slightly affected by mountain range, and were not noticeably affected by presence of horses (Fig. 3a). In contrast to characterizations using plant species, abiotic variables grouped sites less consistently by mountain range, particularly in 1998 (Fig. 3a). Abiotic variables showed

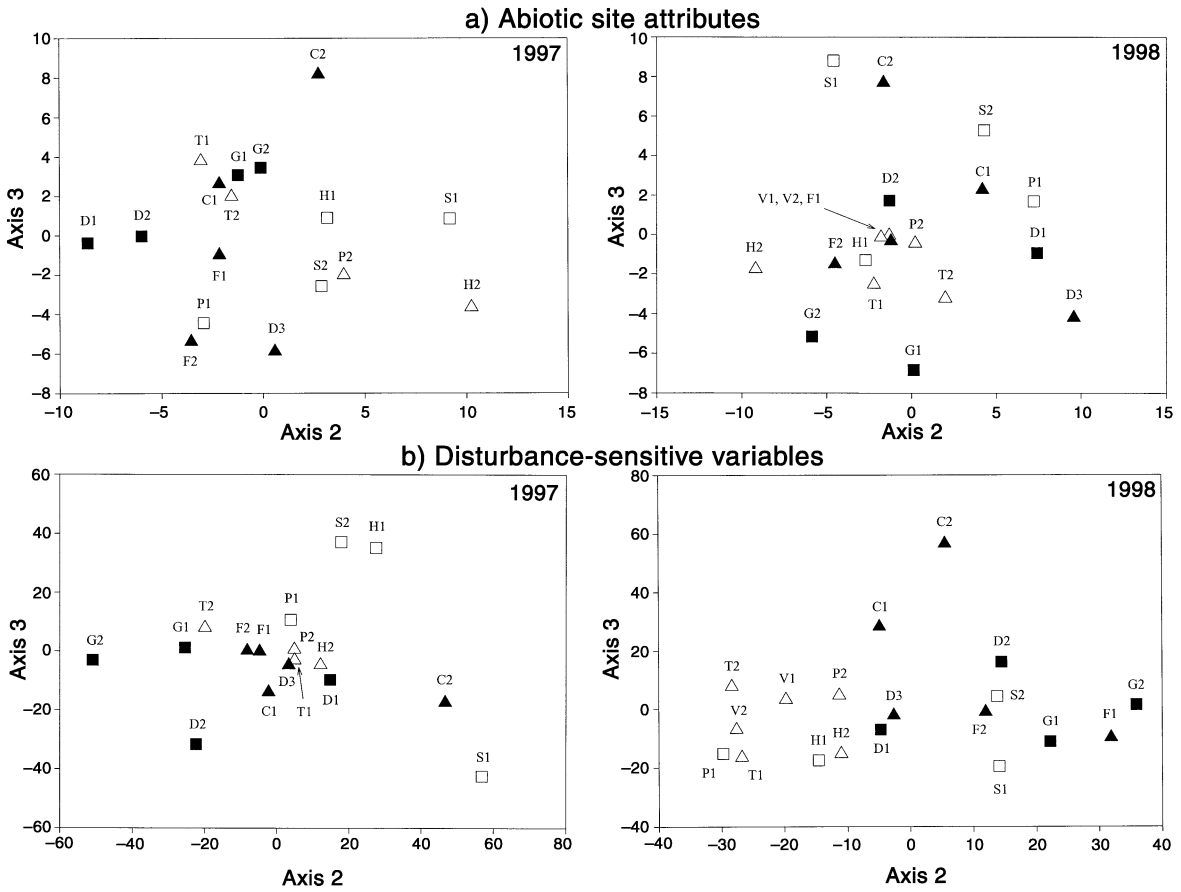


FIG. 3. Relationships between horse-removed and horse-occupied sites in two elevational strata, from reciprocal-averaging analysis with data sets composed of (a) abiotic site characteristics (e.g., precipitation, slope gradient, soil properties); and (b) disturbance-sensitive variables. Data are from sites in the western Great Basin, during the summers of 1997 and 1998. See Table 1 for site tags.

strong differences between elevational strata; high-elevation sites were separated completely from low sites along axis 1 in both years. Although some separation of high-elevation horse-removed and horse-occupied sites occurred along axis 2 in 1997 because of different Julian dates of sampling (Fig. 3a), horse-occupied sites were not distinguishable from horse-removed sites within either elevational stratum in five of six graphs across years (see Fig. 3a, 1998 data) and were not distinguishable in 1997 when Julian date was removed from the analysis.

When we analyzed sites using our 10 diverse disturbance-sensitive variables, sites segregated most strongly by presence of horses rather than by elevation stratum or mountain range (Fig. 3b). Only one of seven pairs of sites from the same range and stratum consistently segregated from other sites, suggesting little effect of biogeography. However, horse-occupied sites were clearly distinguished from horse-removed sites in both years, with the exception of one site in each year (S1, S2).

TWINSPAN analyses

Similar to RA analyses of plant abundance, the first two divisions of TWINSPAN analyses of plant abundance classified sites largely by mountain range. Analysis of 1997 data grouped five of six same-range, same-stratum pairs. All but four sites (from only two ranges) were grouped by mountain range (Table 3) in 1998. In contrast, only 12 of our 19 sites grouped according to elevation and presence of horses in 1998 (Table 3).

Using cover data for individual plant species, relationships among sites were also driven by differences in species composition at the mountain-range level, rather than by the presence or absence of horses (Table 3). Three of the first four groups in 1997 had an equal mix of horse-occupied and horse-removed sites, and the fourth group contained three horse-occupied sites and five horse-removed sites. All three mountain ranges having two high-elevation sites segregated companion sites into the same groups. Data from 1998 produced a pattern reflecting a strong biogeographic effect, with only two sites from different strata not segregating with

TABLE 3. Number of sites (out of 17 or 19) that TWINSPAN analyses grouped by mountain range and sites whose classification matched experimental design criteria (i.e., presence of horses and elevation), using five types of data sets in 1997 and 1998.

Site data†	No. sites grouped with sites of the same range	Classification accuracy‡	
		Second level of division	Third level of division
1997 (n = 17 sites)			
Abiotic variables	12	8	no improvement
Frequency, all plant spp.	10	11	no improvement
Percent cover, all plant spp.	8	7	no improvement
Percent cover, eight ''key'' plant spp.	8	9	no improvement
Disturbance variables	10	15	no improvement
1998 (n = 19 sites)			
Abiotic variables	14	12	no improvement
Frequency, all plant spp.	15	12	no improvement
Percent cover, all plant spp.	17	13	no improvement
Percent cover, 16 ''key'' plant spp.	13	10	no improvement
Disturbance variables	12	14	17

† Data were collected from sites in nine mountain ranges in the western Great Basin of North America.

‡ Defined in *Methods*, expressed as number of sites grouped according to elevation stratum and presence of horses (i.e., in agreement with the organization of Table 1).

other sites of the same range (Table 3). In contrast, the two groups containing the most sites exhibited equal mixes of horse-occupied and horse-removed sites, and only 13 sites grouped according to our experimental criteria (Table 3). Greater cover of one-sided bluegrass (*Poa secunda* ssp. *secunda*) most strongly distinguished horse-occupied from horse-removed sites at low elevations in 1998.

Cover of key plant species of management concern classified sites similarly to analyses using all plant species, although mountain range effects were somewhat reduced. In 1997, three of four TWINSPAN groups possessed an equal mix of horse-removed and horse-occupied sites, and the fourth contained two high-elevation sites from the same range. Although only nine sites grouped according to experimental criteria, biogeographic tendencies were weaker yet, as only eight sites grouped according to mountain range (Table 3). Two of the four primary TWINSPAN groups in 1998 possessed an equal mix of horse-occupied and horse-removed sites, and no more than two-thirds of sites in either of the other two groups came from one treatment group.

Analyses using inherent site (abiotic) properties also exhibited strong effects of biogeography, as all but five sites, the same in both years, fell into groups with other sites from the same range (Table 3). In contrast, TWINSPAN groups classified only eight of our 17 sites in 1997 and 12 of 19 sites in 1998 according to experimental design criteria (Table 3). Across both years, all eight groups produced by the first two divisions contained both horse-occupied and horse-removed sites, and six of these groups exhibited equal mixes of sites from the two treatment types.

In contrast to the above data sets, analyses of disturbance variables largely separated horse-occupied from horse-removed sites at both high and low elevations (Table 3). In 1997, all eight high-elevation sites and all but two low-elevation sites were separated into horse-removed and occupied groups. Horse-removed sites in 1997 were distinguished most strongly from occupied sites by greater shrub cover at high elevations and by higher numbers of ant mounds at low elevations. In 1998, two of the initial four TWINSPAN groups were composed exclusively of either low-elevation horse-occupied or horse-removed sites. The largest group contained seven of eight high-elevation sites. These seven sites segregated into horse-removed and horse-occupied groups with the third level of division (Table 3), which did not occur in any of 24 cases from other data sets of both years. In 1998, horse-occupied sites were distinguished from horse-removed sites at high elevations by sparser shrub cover, and at low elevations by greater dominance of deer mice.

When looking collectively at TWINSPAN analyses across years for plant species cover, plant species abundance, and abiotic variables, sites were not lumped in the same group as other sites from the same range in only 29% of 108 cases. About half (17 of 31) of those occurrences were sites that were each the lone site in the stratum and mountain range in which it was located (Table 1: P1, H1, P2, H2, or D3). Eight of those 17 occurrences, in turn, were instances in which Pah Rah Range sites were split into different groups. Of the remaining 14 (i.e., 31 minus 17) occurrences, eight were instances in which sites in the Clan Alpine Mountains were ordered in different groups. Thus, sites in a mountain range that were most distant geographically from other sites in the same range tended to dissociate themselves more frequently than did geographically

closer same-range sites when we used vegetative or abiotic variables to detect disturbance.

Discussion

Although effects of grazing disturbance are probably sustained at hierarchical spatial and temporal scales (Archer and Smeins 1991), most investigations of herbivory, especially herbivory by feral horses, occur at a few closely located sites using only one or two types of disturbance indicators. Although this strategy provides greater experimental control in mensurative and manipulative field experiments, findings have low external validity and, thus, low predictive ability. We have demonstrated that grazing disturbance can be detected in semiarid environments such as the Great Basin across broad spatial scales using diverse response variables, even when treatment differences in plant communities are masked by geographic differences in species composition (Fig. 4). Thus, with careful site selection and explicit consideration to avoid possible confounding factors, it is possible to broaden the experimental domain to meaningfully investigate effects of disturbance across broad spatial scales. It is important to note, however, that multivariate statistics such as reciprocal averaging and TWINSPAN have limited ability to establish cause–effect relationships, in spite of tools available to supplement these analyses and clarify their interpretation for biological systems.

Assessment of inherent site differences between horse-occupied and horse-removed sites

Abiotic inherent properties of sites showed no consistent difference between horse-occupied and horse-removed sites. For both years, TWINSPAN analyses with abiotic variables suggested that physical properties of sites more closely reflected mountain range differences than presence of horses, a result consistent with the complex gradients of natural clinal variation present in the physiographically diverse Great Basin (Fig. 4). Similarly, horse-removed and occupied sites were not distinguishable in RA analyses based on abiotic properties for either 1997 or 1998 data. Relationships reflected location (i.e., mountain range) and elevation, both perhaps influenced by local climate patterns. Because plant growth in the Great Basin is often limited by water, the result that high-elevation, horse-occupied sites exhibited lower plant species richness and lower grass and shrub cover in spite of receiving on average 16–23% greater precipitation than horse-removed sites (Beever 1999) suggests that horse-related disturbances overshadow environmental influences. Segregation of high-elevation sites from different treatments in 1997 occurred only because we sampled slightly earlier at horse-occupied sites; segregation disappeared when sampling date was removed from the analysis.

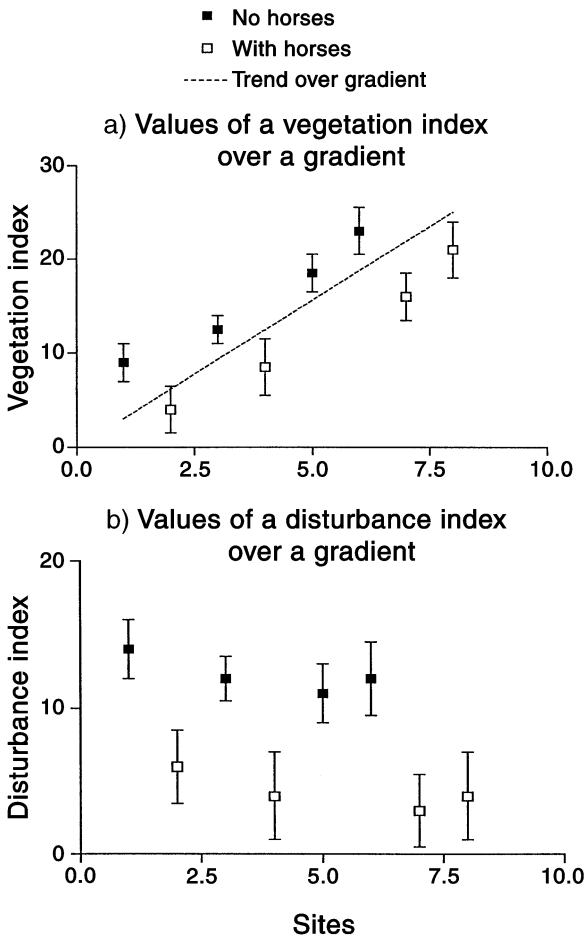


Fig. 4. Heuristic illustration of the detection of disturbance by horses on sites occurring across an environmental gradient, where pairing of sites is not sociopolitically feasible. Measurement of disturbance by a vegetation index. Even though values for horse-occupied sites are consistently below the trend line, multivariate analysis will not separate the two groups. Use of the proper disturbance index factors out the effect of the gradient (in essence, by flattening the trend line), allowing for direct assessment of the effect of horse disturbance, independent of clinal variability.

Effects of broad sampling domain on environmental assessment

The strong effect of mountain range on site relationships in both RA and TWINSPAN analyses using data sets of plant cover and abundance suggests that flora of isolated ranges in the western Great Basin possess numerous distinctive species and compositional patterns, especially in their upper sagebrush zones (Grayson 1993, Charlet 1996). Thus, monitoring strategies proposed for detecting ungulate disturbance across large spatial areas must account for patterns arising from vicariance or strong abiotic differences (Fig. 4), especially when assessing less vagile organisms in heterogeneous environments. This is best accomplished by using variables that are sufficiently generic to be

appropriate for monitoring grazing disturbance at these scales across the entire sampling domain. If they are not, then managers and experimenters should use other means to stratify by, or factor out, the dominant environmental gradients. Otherwise, much larger sample sizes are needed to achieve equivalent statistical power. We suggest that the 10 disturbance variables listed in Table 2 are examples that reflect a reasonable compromise between the ideals of: (1) capturing directly or indirectly many of the components and processes in sagebrush scrub habitats of the Great Basin, especially those that relate to grazing disturbance; and (2) being concise enough to be readily implemented by land managers.

Just as samples from different ranges provided investigation of broad-scale effects of disturbance, comparing relationships among same-range sites separated by varying amounts of elevation and distance allowed investigation of the effects of elevational clines. If elevation strongly influences variables in our data sets, then TWINSPAN analyses should associate sites with other same-range sites least frequently for mountain ranges having sites separated by the greatest amount of elevation. We indeed observed greater difference in floral composition and abiotic characteristics within and between elevation categories in the Clan Alpine and Pah Rah ranges, respectively, than for other ranges. Clan Alpine sites were separated by 360 m elevation, more than 2.5 times greater separation than any other same-range pair of sites in the same elevational stratum (Table 1). Perhaps also contributing to greater heterogeneity was the fact that Clan Alpine sites are horizontally separated by 12.7 km, far greater than for sites in any other range. Similarly, comparing ranges that had a site in each elevational stratum, Pah Rah sites were elevationally separated more than were Humboldt sites (Table 1). Not surprisingly, Pah Rah sites segregated in different groups twice as often as did Humboldt Range sites. These patterns of differences suggest that although grazing may be meaningfully monitored across broad spatial scales, sampling strategies should stratify locations by habitat type and elevation (or life zone), when possible, to account for naturally occurring variation.

Greater distinctness of high-elevation sites in RA and TWINSPAN plant cover and abundance analyses is important for interpreting grazing disturbance both within and across ranges, and has implications for management. First, however, why did high-elevation sites exhibit greater difference among ranges as compared to low-elevation sites? Because differentiation of horse-removed from horse-occupied sites at high elevation using abiotic variables did not occur in 1998, and because differences observed in 1997 were due merely to earlier sampling of horse-occupied sites, differences in plant communities may reflect both the effects of vicariance and isolation as well as effects of weaker environmental gradients across all high-elevation sites. Secondly, because low-elevation sites are more contiguous, dispersal of plants among ranges can occur more easily within lower-elevation than higher-elevation habitats. Finally, many plant species contributing to the significantly greater species richness of high-elevation (vs. low-elevation) sites were small, poorly dispersing forbs (Hickman 1993) observed in only one range. Because of these between-range differences, it is critical to have, within each stratum, treatment replicates from more than one mountain range; otherwise, treatment effects are confounded by mountain-range effects. In terms of management, monitoring of disturbance based on plants at higher elevations needs to account for greater effects of disjunct species distributions than does monitoring performed at low elevations.

Both increasing the *spatial* domain from one to several mountain ranges and increasing the *temporal* domain from one to two years affected the interpretation of the influence of horses. Stronger biogeographic pattern in both RA and TWINSPAN in 1998 than in 1997 analyses of plant abundance and cover may be due, in part, to the greater number of species observed in 1998. Earlier sampling in 1998 (mean = 27 d earlier), leading to less senescence of plants, and 1.2 times greater precipitation across all sites in 1998 than in 1997 probably led to greater species richness. The effect of a larger sample size was especially evident in analyses of ''key'' plant species, because doubling the number of species (1998 vs. 1997 data) both lessened the segregation of treatment types and increased the effects of biogeography across all analyses.

Do grazing-disturbed semiarid ecosystems exhibit systematic differences from ecologically similar undisturbed (i.e., recovering) sites?

In both RA and TWINSPAIN analyses in both years, disturbance-sensitive variables that are relatively independent of geographic differences distinguished horse-occupied and horse-removed sites more clearly than did cover of all plant species, cover of key species, or abiotic variables. In separate analyses of each disturbance variable (Beever 1999), all variables exhibited overlap in values between treatment groups, and only some variables exhibited significant differences between horse-occupied and horse-removed sites. Because disturbance variables distinguished horse-occupied and horse-removed sites better than did data sets of exclusively plant variables, indirect effects of grazing disturbance (e.g., on small mammals or ants) may combine with direct effects (e.g., vegetation removal) to shape the dynamics of mountain ecosystems in the Great Basin (Hobbs 1996, Keesing 1998). Because RA and TWINSPAN analyses give the strongest representations on the first axis (McCune and Mefford 1995), the ability of disturbance variables to distinguish horse-occupied from horse-removed sites, even in the presence of dominating effects of elevation (Beever 1999),

suggests that there are broadly detectable differences in multiple ecosystem components between these types of sites. Furthermore, because diverse ecosystem components may respond differently to grazing disturbance, monitoring only certain components does not necessarily capture the dynamics of other taxa and processes (Simberloff 1998). Consequently, we suggest that a multifaceted set of disturbance variables may be more appropriate for assessing disturbance than the single-component monitoring strategies previously advocated (Majer 1983, Auble et al. 1994, Bradford et al. 1998, Warwick and Clarke 1998).

Although horse-occupied sites at high elevation received greater horse use than did occupied sites at low elevation (mean = 208.5 vs. 96.8 defecations/site), disturbance variables did not always discriminate sites more clearly at high elevations. Although separation of horse-occupied from horse-removed sites was nearly equal at high and low elevations in 1997, sites of different treatments were more distinct at low elevations in 1998 (especially for site S2; see next paragraph). However, a comparison of the response to disturbance of high- and low-elevation sites with different levels of use by horses is confounded by elevation.

Although we explicitly chose sites with minimal cattle use, horse-removed sites with relatively greater cattle presence more frequently dissociated from other horse-removed sites in analyses of disturbance variables. The only horse-removed site that associated with horse-occupied sites in TWINSPAN disturbance analyses of both years exhibited higher cattle use than any other horse-removed area, based on standardized scat counts averaged across years. Furthermore, in 1997, this site's count of cattle defecations was twice as high as that of any other horse-removed site at high or low elevation. Similarly, the site with the second highest average cattle scat count was one of only two other misclassified horse-removed sites. Thus, although we were largely interested in investigating feral horse disturbance and there was little variability in amount of cattle grazing among sites, our suite of variables may also have utility in detecting disturbance imposed by other grazers.

Comparing characterizations of sites using key plant species and other data sets

Although ecologists increasingly realize the importance of including several ecosystem components in research, management, and monitoring (Archer and Smeins 1991, Franklin 1993, Christensen et al. 1996), management and research of feral horses in the western United States have often assessed disturbance using only vegetative data. In TWINSPAN analyses, cover data of only ''key'' plant species correctly classified 4–6 fewer sites than did our data set of diverse disturbance variables. Furthermore, in 1998, the year in which we encountered the most plant species, key species data performed the most poorly of all five data sets in discriminating horse-occupied and horse-removed sites. Selecting only key plant species to characterize sites also appeared to reduce biogeographic affinity compared to other data sets; TWINSPAN analyses of cover of key species grouped the fewest sites by mountain range of any data set in both 1997 and 1998. Because variables such as ant mounds, number of deer mice, and (at high elevations) shrub cover were indicator variables in first divisions in TWINSPAN analyses of disturbance-sensitive variables, they may contribute to differences between horse-occupied and horse-removed sites. Thus, the current practice of monitoring grasses and low-elevation shrubs may not capture important interactions that affect the composition and function of mountain ecosystems, at least for the range of vegetative values typically encountered. Another potential problem of monitoring only vegetation is that the utility of vegetation for monitoring response to herbivory is likely to vary across ranges and years with changes in precipitation (Detling 1998, Fahnestock 1998).

A wide range of alternative strategies has been proposed for monitoring programs to detect grazing disturbance. Counts of hoofprints or dung patches provide an easily implemented means to index disturbance. Unfortunately, fecal counts can be sensitive to relative digestibility of forage, and in feral horses, concentration of defecations into ''studpiles'' complicates quantification. Similarly, hoofprints are not well preserved and thus cannot be indexed in many soil types of the Great Basin and other semiarid regions. More importantly, neither index includes variables that relate directly to ecosystem function or processes, which are crucial for future site potential and response to management activities. Although collection of remotely sensed data allows assessment over broad spatial scales, to date, unfortunately, it has not achieved fine-scale detection of disturbance, especially in semiarid ecosystems. For example, only one or two of our 10 disturbance variables (shrub cover, cheatgrass abundance) could be reliably censused remotely, underscoring the continued importance of empirical field monitoring. It should be noted that it is possible (although difficult to test) that only our *measurements* of these disturbance indicators are more sensitive in detecting disturbance than are plant-related variables, rather than the ecosystem components themselves being more sensitive to disturbance.

Because current management budgets may not be able to implement monitoring across numerous sites for all of the disturbance-sensitive variables that we censused, we reanalyzed reduced versions of this data set in RA and TWINSPAN analyses, without the plant-related, mammal-related, soil-related, or ant variables. We used this as a crude cost–benefit analysis, in that we sought to see how much extra discriminatory sensitivity (''bang'') one could get from given amounts of monitoring effort ''bucks'' expended by adding more

indicators to the pool of variables. Removal of the ant variable suggested that among our sites this variable contributed least to discriminating sites, as RA analyses without ants separated horse-occupied from horse-removed sites about as well as the full disturbance data set. TWINSPAN analyses of both years were equal to the full data set at the second level of division and, in fact, were *better* than the full data set at the third level. Removal of penetration resistance of soils from the disturbance data set reduced the ability to discriminate sites only marginally in RA analyses compared to the full data set, and TWINSPAN analyses of this reduced data set classified 15 sites according to experimental design criteria in both years.

In contrast, removal of either the five plant-related variables or the three small-mammal variables from the disturbance data set noticeably blurred the distinction between horse-occupied and horse-removed sites. For the data set without mammal variables, in both years, high-elevation horse-occupied and horse-removed sites remained well discriminated in RA analyses; however, lower elevation sites of the two treatment groups appeared more similar than in analyses of the complete disturbance data set. In TWINSPAN analyses of 1997 data, the nonmammal disturbance data set classified 14 sites according to design criteria, whereas nonplant disturbance variables classified only 11 sites this way. In 1998 analyses, nonplant disturbance variables classified 14 sites according to experimental design criteria, whereas nonmammal variables discriminated only 13 sites according to design criteria. Thus, the data set without either mammal or plant variables classified from one to four fewer sites according to design criteria than did the full disturbance data set. We cannot exclude the possibility that relative importance of the five plant-related variables occurred simply because they occupied half of all disturbance-sensitive variables in the data set. Such an argument may also apply, to a lesser degree, to the importance of small-mammal variables. Given that inclusion of small-mammal trapping increased by 20–35% the time necessary to sample a pair of sites, researchers and managers must balance budgetary constraints with how sensitive and clear they desire their sampling strategy to be in order to detect disturbance. Extensiveness of the list of components monitored will vary with the number of sites to be sampled, available monitoring resources, and costs of Type II errors.

Conclusions

Perspectives on disturbance and monitoring of systems depend critically upon the scale at which the disturbance is measured (Brown and Allen 1989). For example, disturbed areas of small spatial extent are generally able to recover more quickly than larger areas. Moreover, results of monitoring to detect disturbance will depend upon which types of ecosystem components are investigated. In our landscape-scale research in the western Great Basin, USA, strikingly different relationships between sites were obtained using data only from key species, using all plant species, and using a suite of disturbance-sensitive variables. In both RA and TWINSPAN analyses, abiotic factors, plant cover, and key plant species cover characterized sites more strongly by mountain range than by presence of horses. Abiotic factors can strongly influence the results of monitoring, and need to be accounted for in any monitoring schemes performed over broad areas. Consequently, if monitoring involves measuring percent cover of only a few or all plant species, sites within mountain ranges will appear most similar to each other, due, in part, to the occurrence of narrowly distributed plant species. In contrast to the other data sets, disturbance-related variables separated all but one or two sites according to the presence of horses in analyses of both 1997 and 1998 data. Of the other four data sets, those of percent cover of all plant species were best able to distinguish horse-occupied from horse-removed sites in both years. Table 2 lists variables potentially useful for monitoring grazing disturbance within the Great Basin, and should be considered an example of a comparatively easy research program to implement, with the exception of mammal trapping.

Acknowledgments

We thank N. Wendel, D. Watterson, and especially J. Landmesser for field assistance, and Craig Allen, Steve Jenkins, John Kie, Bill Longland, and two anonymous reviewers for critical reviews of earlier manuscript drafts. We thank horse managers J. Axtell, J. Gianola, and T. Seley of the Bureau of Land Management for help with site selection, after algorithms in GIS proved ineffective for selecting logistically feasible sites without cattle. Logistic and financial support at the University of Nevada were provided by the Biological Resources Research Center, the Department of Biology, and the Program in Ecology, Evolution, and Conservation Biology. At the University of Nevada, the Nevada Agricultural Experiment Station, Center for Environmental Arts and Humanities, College of Agriculture, Nevada Biodiversity Research and Conservation Initiative, and Graduate Student Association all provided financial assistance to E. A. Beever, as did the Kosciusczko Foundation and the American Museum of Natural History.

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APPENDIX A

A list of plant species of management interest is available in ESA's Electronic Data Archive: *Ecological Archives* A013-003-A1.

APPENDIX B

Means and standard errors for response variables of different data sets (plant abundance, plant cover, abiotic variables, and disturbance-sensitive variables) are available in ESA's Electronic Data Archive: *Ecological Archives* A013-003-A2.

Plant Ecol
DOI 10.1007/s11258-007-9342-5

Multi-scale responses of vegetation to removal of horse grazing from Great Basin (USA) mountain ranges

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Received: 4 January 2007 / Accepted: 23 July 2007
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Abstract Although free-roaming equids occur on all of the world's continents except Antarctica, very few studies (and none in the Great Basin, USA) have either investigated their grazing effects on vegetation at more than one spatial scale or compared characteristics of areas from which grazing has been removed to those of currently grazed areas. We compared characteristics of vegetation at 19 sites in nine mountain ranges of the western Great Basin; sites were either grazed by feral horses (*Equus caballus*) or had had horses removed for the last 10–14 years. We selected horse-occupied and horse-removed sites with similar aspect, slope, fire history, grazing pressure by cattle (minimal to none), and dominant vegetation (*Artemisia tridentata*). During 1997 and 1998, line-intercept transects randomly located within sites revealed that horse-removed sites exhibited 1.1–1.9 times greater shrub cover, 1.2–1.5 times greater total plant cover, 2–12 species greater plant species richness, and 1.9–2.9 times greater cover and 1.1–2.4 times greater frequency of native grasses than did horse-occupied sites. In contrast, sites with horses tended to have more grazing-resistant forbs and exotic plants. Direction and magnitude of landscape-scale results were corroborated by smaller-scale comparisons within horse-occupied sites of horse-trail transects and (randomly located) transects that characterized overall site conditions. Information-theoretic analyses that incorporated various subsets of abiotic variables suggested that presence of horses was generally a strong determinant of those vegetation-related variables that differed significantly between treatments, especially frequency and cover of grasses, but also species richness and shrub cover and frequency. In contrast, abiotic variables such as precipitation, site elevation, and soil erodibility best predicted characteristics such as forb cover, shrub frequency, and continuity of the shrub canopy. We found species richness of plants monotonically decreased across sites as grazing disturbance increased, suggesting that either the bell-shaped diversity-disturbance curve of the intermediate-disturbance hypothesis does not apply in this system or that most sites are already all on the

Electronic Supplementary Material The online version of this article (doi:10.1007/s11258-007-9342-5) contains supplementary material, which is available to authorized users.

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greater-disturbance slope of the curve. In our study, numerous vegetation properties of less-grazed areas and sites differed notably from horse-grazed sites at local and landscape scales during a wetter and an average-precipitation year.

Keywords Community ecology · *Equus caballus* · Feral horses · Intermediate-disturbance hypothesis · Nevada · Sagebrush communities

Introduction

After horses had been absent from North America for some 13,000 calendar years (Grayson 2006), domestic horses *Equus caballus* L. were brought to the southwestern United States by Spanish conquistadors near the end of the 16th century (Wagner 1983). Since their introduction, horses have played a controversial role in ecosystems of western North America (Beever 2003). Free-roaming horses of the Great Basin, USA represent a unique opportunity to investigate plant-herbivore dynamics in a unique management scenario. Whereas the legislation governing their management prevents their capture, branding, harassment, or harvest (unlike species of native ungulates, which are all hunted), it also declares horses "an integral part of the natural system of public lands" and requires a minimal-management mandate (unlike domestic animals, which are fenced and intensively managed).

This research opportunity is especially compelling in Great Basin shrublands, which have less coevolutionary history of abundant grazers than do savannahs, grasslands, or steppes (Grayson 2006). This leads one to predict that vegetation in the Basin may typically respond less favorably to herbivory than will vegetation in grasslands (Mack and Thompson 1982; Milchunas et al. 1988). A review by Milchunas et al. (1998) found that vegetation was one of the ecosystem components least affected by grazing in North American shortgrass steppe. A global analysis by Milchunas and Lauenroth (1993) of grazing-effects studies found that although years of protection from grazing was not important for vegetation in either grasslands or grasslands-plus-shrublands models, the factor was important in the shrublands model. However, although the vast majority of North America's free-roaming equids occur in shrublands (Anonymous 1997), studies of horse-vegetation relationships have occurred largely in grasslands (Detling 1998; Fahnestock and Detling 1999; Peterson 1999) and highly mesic areas (Turner 1987; Rogers 1991; Levin et al. 2002).

Free-roaming horses do not use landscapes homogeneously but instead move both seasonally (e.g., to higher sites in summer) and daily (e.g., to and from water), organized in bands (comprised usually of a stud and one to several mares with their offspring) and groups of one to several bachelor males. Due to differences in habitat use, mode of digestion, diet, evolutionary history, and morphology, it is inappropriate to assume that effects of grazing by feral horses are similar in nature or in magnitude to effects of grazing observed for other introduced or native species (Beever 2003). Furthermore, although numerous studies on grazing ecology of domestic horses have been published (Hafez et al. 1969; Reiner and Urness 1982), extrapolating these results to free-roaming (feral) populations may be problematic, particularly with respect to behavior (see Beever 2003, p. 892, for fuller discussion of this topic). Thus, there are relatively few studies investigating interactions of free-roaming horses and vegetation in semiarid systems of western North America that can be used to address horses' role in these systems, and fewer studies still that were conducted at broad spatial scales.

In the western United States, the domestic cow *Bos taurus* is the most widely distributed nonnative mammalian herbivore (Wagner 1983; Fleischner 1994), and has correspondingly received the greatest amount of synecological research attention. Despite the extensive research that has examined effects of livestock on vegetation and other taxa, research on how feral horses influence their surroundings is just beginning to emerge (e.g., Kissell 1996; Crane et al. 1997; Fahnestock 1998; Fahnestock and Detling 1999; Peterson 1999). Horses are also a common herbivore on the Great Basin landscape—horse management areas occupy fully 29% of Nevada's area (Anonymous 1997) and portions of 10 US states—though horses' potential role in vegetation alteration at landscape scales has rarely been investigated. Because *E. caballus* has occupied the western United States for almost four centuries (Wagner 1983), it is not clear whether plants of the upper and

lower sagebrush zones have evolved mechanisms to respond to horse grazing under field conditions.

Most of the above studies sought greater experimental control by limiting investigation to fewer sites within a relatively small geographic area. In contrast, our comparison of treatments across broad spatial scales encompassed large amounts of environmental variability; therefore, we used a set of response variables that are less influenced by local conditions, and that are applicable across all sites (Beever et al. 2003). For example, instead of comparing percent cover of individual species across sites, variables investigated herein instead included frequency and percent cover of each life-form, overall plant species richness, and cover of *Bromus tectorum* L. and *Artemisia tridentata* Nutt., two of the few species present at all sites.

Beever et al. (2003) sought to determine relationships among all sites (both horse-occupied and horse-removed) in multivariate ordination space, using data sets of plant frequency and cover (all species), cover of only those plant species monitored by managers (i.e., key forage species for horses), abiotic site attributes, and a diverse suite of disturbance-sensitive variables. The two types of sites appeared very similar in TWINSPAN and correspondence (reciprocal-averaging) analyses of data sets of abiotic site properties, cover of monitored plant species, and (to some degree) frequency of all plant species. However, sites were much more clearly discriminated using these multivariate analyses on disturbance-sensitive aspects of soils, ant mounds, plants, small mammals, and reptiles. Results from sampling of these other ecosystem components are detailed elsewhere (Beever and Brussard 2004; Beever and Herrick 2006) and are discussed here only to assist in the interpretation of vegetation findings.

In contrast, we had three objectives in the research reported here. First, we compared across a broad spatial domain (landscape scale) the cover, diversity, and structure of vegetation at sites grazed by feral horses to sites from which horses had been removed for 10–14 years, investigating each aspect of vegetation separately, as opposed to the whole-community multivariate analyses in Beever et al. (2003). For the cover analyses, we were particularly interested in cover of each plant life-form (grasses, forbs, shrubs), and of cheatgrass (the most ubiquitous non-native plant in the Great Basin) and sagebrush (upon which many species in the ecoregion obligately depend). Second, we compared those broad-scale results with plant responses to different grazing intensities within horse-grazed sites (local scale). Finally, using information-theoretic analyses we sought to ascertain which observed vegetation-related differences were explained by the presence of horses when the contributions of other abiotic factors that may have confounded comparisons were accounted for.

Methods

Study AREA

Located between the Sierra Nevada and the Wasatch Mountains of the western USA, the Great Basin has been used as a model system to test predictions of ecological theory because of its unique combination of physiography and climate (e.g., Johnson 1975; Wilcox et al. 1986). Because the Great Basin currently has the highest percentage of its area as public land of any ecoregion in the contiguous United States, it represents an important reservoir for biological diversity (Newmark 1995). However, the sagebrush-steppe, shrublands, and grasslands that dominate the Intermountain western United States are considered by some to be critically endangered ecosystems (Noss et al. 1995). By these authors' assessment, the sagebrush-steppe ecosystem of the Great Basin has been degraded across 98% of its original extent since European settlement, due primarily to livestock grazing.

Selection of study sites

Seven criteria were used to try to achieve ecological similarity between horse-occupied sites and sites from which both resident and immigrant horses had been removed for 10–14 years. Sites were only selected that were: (1) on east-facing (90 ± 45°) aspects; (2) of low (<40%) slope; (3) at elevations loosely corresponding to high-elevation (2,000–2,300 m) and low-elevation (1,350–1,700 m) sagebrush zones in the western Great Basin (Nevada); (4) dominated by sagebrush (*A. tridentata*); (5) within 1 km of a dirt road; (6) relatively unused by cattle in the past two decades, as observed by local land managers (U.S. Bureau of Land Management;

hereafter, BLM) and confirmed with fecal counts (see below); and (7) without evidence of recent (<15 year) fire within or adjacent to the site. These seven criteria were chosen because they are some of the strongest influences on levels of and variability within the response variables (Bonham 1989; Archer and Smeins 1991).

With these criteria, 10 horse-removed and nine horse-occupied sites were selected; each group was stratified nearly evenly into high- and low-elevation sagebrush sites (Table 1; see map in Beever and Brussard 2004). For the horse-occupied sites, we chose (with assistance from that agency's horse specialists) areas where horses had been found at least once during BLM aerial censuses of the past 3–8 years. Consequently, we investigated the ecosystem consequences of horse use of montane sagebrush habitats (relative to areas of horse removal), rather than comparing the average condition of all areas within horse-occupied and horse-removed management areas. Although our horse-occupied sites had all received some use, our adherence to our seven site-selection criteria listed above dictated that these sites did not receive anomalously high use by horses; in every HMA, we found one to several sites that were more heavily grazed. All sites were many kilometers from the nearest paved road and were located on secondary dirt roads infrequently traveled; consequently, ubiquitous presence of horse hoofprints and dungpiles on dirt roads suggested that criterion 5) above did not influence intensity of horse use at our sites. Sites were distributed across a vast area (3.03 million ha) of the western Great Basin.

At the finest spatial scale (e.g., within a basin, canyon, toeslope, or hillside), we located sites within homogeneous areas of vegetation distant from streams, because use by horses and other ungulates can be anomalously high near water sources in semiarid ecosystems (Crane et al. 1997; Beever and Brussard 2000). In practice, the most difficult criterion to satisfy was absence of cattle grazing. In addition to using BLM allotment data, we assessed density of ungulate defecations in the vicinity of each site, to find areas that appeared to have received significantly less use by cattle than by horses, following the approach described in Beever and Brussard (2004). Prior to the initiation of the study (i.e., during 1992–1995), horse densities for the management areas in which our sites were located ranged from 0.005 to 0.015 horses/ha (Anonymous 1997).

Field sampling

Although sampling of other ecosystem components occurred during late May through early September each year, we sought to minimize any potential confounding effect of phenology on our vegetation response variables by concentrating vegetation sampling into much narrower temporal windows–7 July through 13 September in 1997 and 19 June through 29 August 1998. A 10×10 sampling-station grid with 15 m spacing provided the 135 m × 135 m dimensions of the 1.82 ha area within which all sampling occurred. This area constituted the entire site for all metrics except site species richness (see below). The area was situated within the larger homogeneous block of vegetation in a manner that ensured that the seven aforementioned site-selection criteria were met, including minimizing the inclusion of areas heavily used by cattle.

In order to characterize structure, cover, diversity, and composition of vegetation, we used four 50 m line-intercept transects (Bonham 1989) per site. The starting point for each of four transects was placed at a randomly selected sampling station within each quadrant of the grid at each site, and the transect was placed along sampling-station rows. Its direction along the row was chosen to maximize the length that occurred within the quadrant and ensure that no more than 5 m of the transect went outside the grid (these 'overshoot' portions constituted only 0.56% of the total length of transects). In 1998, we allowed no overlap (re-sampling) of the previous year's lines (restricted random sampling; Goodall 1952). We recorded the species and length of intercept of each plant (including perennials and annuals) under the 50 m line. Species-accumulation curves suggested that four dispersed transects were sufficient to characterize the spatial heterogeneity and species diversity consistently at montane sagebrush sites.

Sampling for landscape-scale analyses

For measures of percent cover, dead annual forbs and grasses were not included. Given that phenology of many Great Basin grass and forb species could change

Table 1 Physiographic and habitat characteristics of 19 study sites in the Great Basin of western North America, sampled 1997–1998. Data for horse densities from Anonymous (1997)

	Mountain range	Horse density in HMA (horses/ha)	Site name	Elevation (m)	Site latitude (°N)	Site longitude (°W)	Average slope (%)[a]	Position on slope	Exposure[b]	Mean soil hardness (kg/cm^2)
High-elevation, horse-excluded	Pah Rah Range	~0	Virginia Peak	2134	39.76	119.45	25	Upper	0	0.072
	Sonoma Range	~0	Lake valley hillside	2164	40.82	117.58	40	Middle	1	0.750
	Sonoma Range	~0	Cabin	2118	40.79	117.56	25	Lower	0	0.920
	Humboldt Range	~0	Pflum Creek Mine	2000	40.53	117.15	20	Middle	0	0.193
High-elevation, horse-occupied	Dogskin Mountain	0.00605	Dry Valley Creek saddle	2060	39.92	119.83	20	Upper	1	0.453
	Dogskin Mountain	0.00605	Dry Valley Creek peak	2200	39.91	119.82	30	Upper	1	1.414
	Seven Troughs Range	0.00197	Side road with junipers	2225	40.56	118.78	20	Upper	1	1.999
	Seven Troughs Range	0.00197	High saddle	2286	40.55	118.78	25	Middle	1	1.767
Low-elevation, horse-excluded	Pah Rah Range	~0	Bigmouth Canyon	1500	39.78	119.42	15	Lower	0	0.132
	Truckee Range	~0	Jeep trail	1540	39.98	119.16	5	Lower	1	0.138
	Truckee Range	~0	Sage Hen Creek	1500	39.96	119.11	10	Lower	0	0.173
	Humboldt Range	~0	Low side valley	1433	40.55	118.11	25	Middle	0	N/A[c]
	Virginia Range	~0	Fernley view	1400	39.55	119.27	5	Lower	1	0.062
	Virginia Range	~0	Homogeneous valley	1500	39.53	119.29	5	Middle	0	0.019
Low-elevation, horse-occupied	Dogskin Mountain	0.00605	Winnemucca Valley spur	1646	39.93	119.79	25	Middle	0	0.930
	Clan Alpine Mountains	0.00315	Dixie Valley vista	1340	39.83	117.71	10	Middle	0	2.913
	Clan Alpine Mountains	0.00315	Shoshone Pass	1700	39.74	117.63	15	Middle	1	1.667
	Virginia Mountains	0.00492	Juniper saddle	1646	40.13	119.79	20	Middle	1	2.462
	Virginia Mountains	0.00492	Juniper Basin	1554	40.14	119.80	25	Middle	0	1.173

[a] Obtained using a handheld clinometer, averaged across the entire sampling area

[b] Subjective classification of exposure, after Wentworth (1976). 0 = site somewhat protected by adjacent slopes, 1 = site on open slope, unsheltered by adjacent slopes

[c] This site could not be sampled for soil-surface hardness using our standardized criteria

during our sampling periods, we performed an unpaired *t*-test on the Julian date of vegetation sampling across all sites to compare the timing of sampling at horse-occupied versus -removed sites. Julian date of sampling did not differ significantly between treatments in either year, although horse-occupied sites were sampled slightly earlier than horse-removed sites in 1997 (mean = day 213 vs. 232). Earlier sampling at horse-occupied sites in 1997 should have translated into finding relatively more grass and forb cover at occupied (vs. removed) sites, given that senescence of plants was advancing at our sites during sampling periods. We generally visited sites in 1998 in reverse order of the sampling order used in 1997.

We recorded the number of individuals from each vegetation class (grass, forb, and shrub) intersected on each 50 m transect as an estimate of frequency, and averaged counts across the four transects within each site. The exotic grass *B. tectorum* (cheatgrass) was always senescent when we sampled vegetation (and thus not included in live grass cover); therefore, cheatgrass counts represent the number of stems (tillers) with heads that intersected the transect. To investigate richness at a broader scale than transects, cumulative lists of plants at each site ("site species richness") were created by adding all species from transects and other plants encountered in and immediately adjacent to (within 10 m of) the sampling-station grid (see Beever 1999 for plant species lists). We combined data from 1997 and 1998 to get an 'interannual' measure of species richness. Species were identified using Cronquist et al. (1972), and we used taxonomic affiliation and life forms of Hickman (1993) for our analyses.

Digging of four soil pits per site and subsequent textural analysis via the hydrometer method (BYU Soil Analysis Lab, Provo, UT) revealed that horse-occupied and -removed sites were similar in their texture (coarse-fragment, clay, silt, and sand fractions), soil color, degree of calcic soils, and depth to bedrock. Complete details on field methods used to sample soils and other indices appear in Beever et al. (2003). Because soil properties exhibited significant variability within the 1.82 ha area at each site, we estimated values of several other soil variables at sites using an average weighted to reflect the percentage of area of the soil-map unit that each soil series occupied, as indicated by NRCS soil surveys. These analyses showed that sites also did not differ systematically in their permeability, consistence, structure, or plasticity (Beever et al. 2003). Furthermore, horse-occupied and -removed sites were indistinguishable in multivariate ordinations of all uncorrelated abiotic variables in both 1997 and 1998 (Beever et al. 2003). PRISM-estimated precipitation at our sites was 1.04 times higher than the 30 years (1961–1990) average in 1997, and 1.20 times higher in 1998.

Horse-trail transects (local scale)

To provide smaller-scale, more-controlled comparisons within horse-occupied sites, we created one to two 50 m transects along the most-evident horse trails within the 135 m × 135 m area by placing a tape 25–30 cm away from and parallel to the center of the trail. Measuring vegetation along the center of the trail would be tautological, because the existence of a linear path of (largely) bare earth in these semiarid ecosystems is the most reliable way to identify animal trails. Instead, we measured vegetation out of the path of direct trampling, yet within the lateral domain in which the herbivory and rubbing of horses might still occur. We measured the same variables in these 'horse-trail' transects as we did in regular transects to examine effects of heterogeneity of horse grazing within small areas. Because we desired to maintain similarity between horse-trail and randomly selected transects, we limited investigations to trails within and immediately adjacent to (i.e., within 10 m of) the grid. For horse-trail transects, a coin flip determined if the transect was placed on the uphill or downhill side of the trail. We completed two horse-trail transects in 1997: one at a high-elevation site and one at a low-elevation site. During 1998, we sampled either two trails or two distant (≥35 m apart) sections of the same trail within the sampling grid at each of five sites. Within each site, we compared these horse-trail transects to the transects that were designed to characterize vegetation across the entire horse-occupied site; hereafter, we refer to this latter type simply as "randomly located transects."

Fecal counts

Standardized counts of fecal piles from cattle, horses, and other ungulates revealed that horses were the

dominant non-native grazer at our sites in recent years, as the ratio of horse defecations/cattle defecations, averaged across years, at all horse-occupied sites exhibited a geometric mean of 10.4:1 (Beever et al. 2003). Furthermore, fecal counts suggested that intensity of herbivory by cattle or by other ungulates (primarily mule deer, *Odocoileus hemionus*, and pronghorn antelope, *Antilocapra americana*) did not differ between horse-grazed and horse-removed sites (Beever et al. 2003).

Analytical methods

To characterize plant composition at each site from our line-intercept transects, we calculated Simpson's and log-series diversity indices with frequency values, following Magurran (1988). To characterize vegetation structure at each site, we defined shrub-continuity (i.e., the opposite of canopy-dissectedness) indices as the average of the four largest intercept lengths of shrubs from the pool of line-intercept transects ($n = 4$) at the site. We used two such indices (for all species combined and for sagebrush only) to test whether, within elevational strata (high- or low-elevation sites), the trampling, herbivory, or rubbing (physical damage) associated with grazing would cause horse-occupied sites to have smaller maximum sizes of shrubs.

Tests of the intermediate-disturbance hypothesis (landscape scale)

The intermediate-disturbance hypothesis (Connell 1978) predicts that species richness should exhibit a bell-shaped curve over a gradient of disturbance frequency, balancing the inhibition by dominant competitors (in the absence of disturbance) with physiological and energetic costs of very frequent disturbance. To test whether sites exhibited a unimodal relationship between plant diversity and disturbance frequency/intensity (as predicted by Connell 1978), we compared the fit (using adjusted r^2 values) of linear and quadratic regressions of site species richness (using 1997, 1998, and cumulative lists) against number of either horse or horse + cattle defecations.

Comparing horse-occupied and horse-removed areas (landscape scale): analytical techniques

Because we performed tests on numerous permutations of diversity indices, we evaluated significance of these tests using sequential Bonferroni corrections (Sokal and Rohlf 1995). For comparisons of each response variable of vegetation, we performed a two-way analysis of variance (ANOVA) using horse presence and elevation as binary categorical variables, reflective of our 2×2 factorial research design. Probabilities in Table 2 refer to main effects of horses across all sites when stratified by elevation. For probabilities of effects of elevation on plant response variables, see Beever (1999). If the horse presence × elevation interaction was significant, we tested for a main effect of horses within each elevational stratum. We used Bartlett's test of homogeneity of variances to identify significant heteroscedasticity or severely non-normal distributions (Sokal and Rohlf 1995).

When needed, arcsine (for all percentage variables) or logarithmic transformations (for some diversity indices, and for cheatgrass frequency in 1998) were used to achieve homoscedasticity, normality, and additivity of treatment effects (Sokal and Rohlf 1995). For logarithmic transformations with 0 values, we added 1 to the value of all sites before transforming the data for count variables, and 0.1 to all sites for variables with lower values (i.e., diversity indices) (Sokal and Rohlf 1995). In the absence of significant interaction and non-significant effect of horse presence when stratified by elevation, we used post hoc Bonferroni–Dunn comparisons to identify cases in which horse presence exerted a significant main effect ($N = 2$; Table 2). Unless otherwise noted, we used $\alpha = 0.05$ to determine significance for all statistical tests. Statistical comparisons and correlations were performed using StatView v4.02 and v5.0 (SAS 1998), and evaluation of numerous alternative mixed-effects models in an information-theoretic framework were performed in WinBUGS (for species richness only; Spiegelhalter et al. 2003) or S + (Pinheiro and Bates 2000).

Horse-trail transects (local scale)

Variation in shrub cover was statistically analyzed with a paired-sample *t*-test (i.e., horse-trail vs.

Table 2 Means ± 1 SE for each plant response variable at sites in the western Great Basin, USA, during 1997 and 1998 for each treatment-elevation category

	1997						1998					
Elevation	High		Low				High		Low			
Horse presence	Removed	Occupied	Removed	Occupied	*F*	Probability[a]	Removed	Occupied	Removed	Occupied	*F*	Probability[a]
Percent cover grasses (%)	5.8 ± 1.2	2.0 ± 0.3	3.2 ± 1.3	1.7 ± 0.9	5.65	0.034[d]	12.6 ± 1.7	4.5 ± 1.2	6.7 ± 2.2	3.6 ± 1.2	8.41	0.011[d]
Abundance of grasses (*/transect)	28.3 ± 2.9	13.7 ± 3.4	11.3 ± 4.3	5.6 ± 2.5	9.60	0.009[d]	52.3 ± 6.0	21.8 ± 5.4	15.1 ± 4.6	13.3 ± 4.2	10.1	0.006[c, d]
Percent cover forbs (%)	4.1 ± 1.7	12.9 ± 3.2	2.2 ± 1.1	1.5 ± 0.3	5.07	0.042[c, d]	14.3 ± 2.7	22.7 ± 4.4	2.6 ± 1.5	1.4 ± 0.3	1.26	0.28[d]
Abundance of forbs (*/transect)	19.4 ± 4.2	35.9 ± 8.5	7.2 ± 3.5	9.9 ± 2.6	3.73	0.075[d]	90.0 ± 13.7	73.8 ± 11.0	11.5 ± 5.0	16.8 ± 3.6	0.44	0.52[d]
Percent cover shrubs (%)	51.1 ± 0.9	32.7 ± 5.4	26.3 ± 3.8	24.9 ± 3.7	6.23	0.027[d]	53.1 ± 4.0	27.8 ± 2.9	28.9 ± 2.8	23.3 ± 2.3	24.0	0.0002[c, d]
Abundance of shrubs (*/transect)	47.9 ± 5.0	44.8 ± 3.3	24.6 ± 3.9	26.5 ± 2.7	0.03	0.87[d]	48.4 ± 6.1	42.6 ± 2.7	28.0 ± 2.5	27.2 ± 2.6	0.27	0.61[d]
Total percent cover (Grasses + Forbs + Shrubs) (%)	61.1 ± 2.2	47.5 ± 4.6	31.7 ± 4.4	28.1 ± 4.3	4.17	0.062[d]*	80.0 ± 5.1	55.0 ± 6.3	38.2 ± 4.9	28.2 ± 2.8	12.8	0.003[d]
Total percent cover (G + F + S + Trees) (%)	61.1 ± 2.2	47.5 ± 4.6	32.9 ± 5.0	28.1 ± 4.3	4.67	0.051[d]*	82.5 ± 5.1	55.0 ± 6.3	38.4 ± 4.8	28.2 ± 2.8	15.0	0.001[d]
Cheatgrass abundance (stems / 50-m transect)	34.1 ± 22.8	54.9 ± 27.2	289.3 ± 76.5	197.4 ± 61.1	0.43	0.52	39.3 ± 14.2	103.4 ± 55.8	266.9 ± 46.0	419.5 ± 126.8	1.06	0.32 [b]
Transect species richness	12.1 ± 0.9	10.9 ± 0.9	7.3 ± 0.6	7.0 ± 0.4	1.22	0.29[d]	22.8 ± 2.1	18.5 ± 0.8	10.5 ± 1.0	10.5 ± 0.4	3.62	0.077[d]
Site species richness	20.8 ± 1.3	18.0 ± 1.2	14.8 ± 0.8	12.4 ± 1.0	5.50	0.036[d]	39.0 ± 4.1	27.0 ± 1.7	22.3 ± 2.0	18.6 ± 1.7	10.3	0.006[d]
Interannual site species richness (both years)							43.0 ± 5.1	31.0 ± 2.9	25.8 ± 1.7	22.4 ± 1.9	6.13	0.028[d]

Table 2 continued

	1997						1998					
Elevation	High		Low				High		Low			
Horse presence	Removed	Occupied	Removed	Occupied	*F*	Probability[a]	Removed	Occupied	Removed	Occupied	*F*	Probability[a]
Simpson's index (cheatgrass excluded)	6.3 ± 0.1	7.5 ± 0.9	5.4 ± 1.6	4.7 ± 0.6	NT	NT	14.9 ± 2.2	27.2 ± 13.8	272.1 ± 92.1	134.7 ± 44.6	0.25	0.63[b]
Simpson's index (cheagrass included)	6.0 ± 0.9	6.3 ± 1.4	1.4 ± 0.1	2.4 ± 0.6	1.03	0.33 [b]	9.8 ± 0.8	6.2 ± 1.9	1.5 ± 0.1	1.7 ± 0.3	NT	NT
Log-series index (cheatgrass included)	3.9 ± 0.3	4.0 ± 0.4	3.0 ± 0.9	2.3 ± 0.3	0.25	0.63	4.8 ± 1.1	2.2 ± 1.6	3.4 ± 1.5	0.4 ± 0.1	11.4	0.004[b]
Log-series index (cheatgrass excluded)	3.9 ± 0.4	3.9 ± 0.5	2.3 ± 0.3	2.0 ± 0.2	0.14	0.71	8.2 ± 1.1	5.7 ± 0.5	4.4 ± 0.6	3.5 ± 0.4	6.53	0.022[d]
% cover sagebrush shrubs (%)	34.4 ± 4.2	16.6 ± 4.6	23.4 ± 6.0	19.9 ± 3.5	1.69	0.22[d]	32.0 ± 3.8	14.8 ± 2.7	20.3 ± 4.3	18.5 ± 2.7	5.11	0.039[d]
Sagebrush abundance (stems / 50-m transect)	25.9 ± 1.6	17.1 ± 2.6	19.8 ± 4.0	19.0 ± 3.0	2.83	0.12[d]	25.1 ± 2.5	16.9 ± 2.7	17.4 ± 2.9	20.7 ± 3.3	0.67	0.43[d]
Average of 4 longest shrub tape lengths (m)	1.7 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.1 ± 0.1	13.20	0.003[d]	1.5 ± 0.0	1.0 ± 0.1	1.2 ± 0.1	1.0 ± 0.1	28.0	<0.0001[dc]

[a] Probability refers to *P*-value of the test of the effect of presence of horses on each response variable at 19 sites, as measured by two-way ANOVAs with elevation as a binary cofactor. In the few instances in which the (horse presence × elevation) interaction was significant, horse effects were assessed within each elevational stratum

[b] Log 10-transformed data

[c] Significant interaction; presence of horses only significant among high-elevation sites

[d] (Absolute) difference between horse-occupied and horse-excluded values for variable was greatest at high-elevation sites

*Bonferroni-Dunn post hoc tests showed effect of horse presence was significant ($P < 0.050$) as a main effect

randomly located transects). For the other comparisons, we investigated direction and magnitude of differences in vegetation between the two types of transects as a second scale of investigation of horse influences.

Interannual variability (landscape scale)

To determine interannual variability in our response variables (and ultimately, the sensitivity of our results to climatic and other interannual fluctuations), we compared values of selected variables at each site between 1997 and 1998 using paired *t*-tests. In addition, we used correlation coefficients to determine relationships between values of different years and employed Fisher's *R*-to-*z* transformation to test whether the correlation differed significantly from 0. Furthermore, we included 'year' as a fixed and a random effect in information-theoretic analyses.

Testing for confounding of apparent (landscape-scale) horse effects by abiotic factors

To assess whether our results were confounded either by a site's position on a slope (upper, middle, or lower) or level of exposure (exposed or sheltered; both variables follow descriptions of Wentworth 1976), we performed two-way ANOVAs of each response variable against position and exposure. Results of these ANOVAs suggested that these factors were not significant determinants of any response variable that differed significantly ($P < 0.05$; Table 2) between horse-occupied and removed sites. Beever and Brussard (2004) provide further commentary on the topic.

To ensure that spatial interspersion of horse-occupied and horse-removed sites was effective in achieving ecological equivalency between the two groups, we tested for the occurrence of pre-existing differences (independent of horses) by comparing abiotic properties of horse-occupied and -removed sites (Table 5). We used two-way ANOVAs and unpaired *t*-tests to test for differences at either high or low elevations in the following conditions at sites: exact (±15 m) elevation; mean slope gradient (%); precipitation during 1997, 1998, and the average during 1961–1990, each estimated (Hungerford et al. 1989) using information from the nearest weather station and a correction factor from PRISM model data (Daly et al. 1994); and mean annual temperature, frost-free days, soil productivity, available water capacity, and erosion factors K and T (from published and unpublished soil surveys). PRISM data have become a data source of choice in the Intermountain West for estimating by interpolation the conditions at sites not near weather stations, in the absence of long-term climatic data at the remote field site. Erosion factor K is an index of susceptibility of soils to erosion by rainfall, and erosion factor T estimates the maximum rate of soil erosion tolerated to permit sustained crop productivity. Because we had no a priori predictions about directionality of differences and because the question was essentially the same across abiotic variables, we employed sequential Bonferroni corrections for multiple tests to maintain experimentwise α values at 0.05 (Sokal and Rohlf 1995).

Finally, we used mixed-effects models in an information-theoretic framework to determine whether presence of horses significantly predicted vegetative response in the face of dominant abiotic variables (Tables 3 and 4). Because we were particularly interested in the residual effect that the addition of horse presence would have on analyses of response variables, we paired our candidate models into different collections of environmental covariates; in each pair, one model included horse presence, and the other model did not include the factor. Mixed-effects models are comprised of fixed effects, which are parameters associated with an entire population, and random effects, which are individual experimental units drawn at random from a population. The generic form of a mixed-effect model is:

$y_{ij} = \beta + \beta_1 X_j + b_i + \varepsilon_{ij}$, where β is the grand intercept, β_j is the slope for the jth covariate (X_j), the random effects (i.e., site or year) are expressed as b_i and are assumed independent for different i, and ε_{ij} are the within-group independent errors.

This mix of fixed and random effects allowed us to control for sampling variability resulting from the grouping of data by site and year and thus, in turn, provide unbiased parameter estimates for the environmental characteristics we were interested in (Pinheiro and Bates 2000). By associating random effects to observations sharing the same level of a

Table 3 Variable weights of explanatory variables used in information-theoretic analyses, for each of ten response variables

Response variables	Explanatory variables											
	Fixed effects										Random effects	
	Presence of horses	Precipitation[a] (cm)	Elevation (m)	Julian date of sampling	Frost-free days/year	Available water cap.	Exposure[b]	Erosion Factor K	Site	Year[c]	Site	Year[c]
Percent cover grasses (%)	0.783	0.022	0.008	~0	0.109	~0			~0	1.000	1.000	~0
Frequency of grasses (#/transect)	1.000	0.560	~0	~0	1.000	~0			~0	~0	~0	1.000
Percent cover forbs (%)	0.162	0.954	0.014	~0	~0	~0			~0	0.381	1.000	~0
Frequency of forbs (#/transect)	0.284	0.800	1.000	~0	0.102	0.021			0.471	1.000	~0	~0
Percent cover shrubs (%)	0.461	~0	~0		0.298	0.013			~0	0.015	1.000	~0
Frequency of shrubs (#/transect)	1.000	0.120	1.000		~0	~0			1.000	~0	1.000	~0
Total percent cover (all life-forms) (%)	0.555	0.033	0.554	~0	0.257	0.008			0.138	0.978	1.000	~0
% cover sagebrush shrubs (%)	0.436	~0	~0		0.007	0.004			~0	~0	0.989	0.011
Frequency of sagebrush	0.860	~0	~0		0.234	0.424			~0	~0	1.000	~0
Average of 4 longest shrub tape lengths (m)	0.157	~0	~0		0.011		0.477	0.740	~0	0.388	1.000	~0
Site species richness	0.964	0.988	0.949[d]	0.693	0.330	0.633			~0	~0	1.000	1.000

If a given explanatory variable was not used in analyses for a particular response variable, that cell is blank; in contrast, if the variable was used but simply did not appear in any of the highest-ranking models, we denote that variable weight as "~0"

[a] Precipitation received at site in previous 12 mos, estimated using PRISM data as described in text

[b] A site on an open, unsheltered slope was coded as 1; a site somewhat protected was coded as 2

[c] 1997 was coded as 0, 1998 as 1

[d] In addition to this linear effect of elevation, species richness also was well modeled by a quadratic term of elevation (variable weight = 0.949)

Table 4 Model-averaged estimates of coefficients for effects of various predictor variables on each of 10 response variables

		Explanatory variables														
		Fixed effects										Random effects		Top-ranked model		
Response variable	Link	Presence of horses	Precipitation[a] (cm)	Elevation (m)	Julian date of sampling	Frost-free days/year	Available water cap.	Exposure	Erosion Factor K	Site	Year[b]	SD (Site)	SD (Year)[b]	r^2	ω	residual σ
Percent cover grasses (%)	Log	–0.650	0.021	0.001	~0	–0.020	~0			~0	0.972	0.869	~0	0.64	0.66	0.56
Frequency of grasses (#/transect)	normal	–5.628	0.530	~0	~0	–0.532	~0			~0	~0	~0	6.495	0.65	0.56	9.42
Percent cover forbs (%)	Log	0.073	0.083	0.00005	~0	~0	~0			~0	0.098	0.979	~0	0.92	0.61	0.001
Frequency of forbs (#/transect)	normal	24.571	0.269	3.676	~0	–1.367	0.0022			0.198	23.351	~0	~0	0.66	0.32	19.45
Percent cover shrubs (%)	normal	–0.139	~0	~0		–0.004	0.0004			~0	–0.0005	0.308	~0	0.95	0.34	0.12
Frequency of shrubs (#/transect)	normal	–8.589	–0.008	0.035		~0	~0			0.476	~0	5.908	~0	0.96	0.84	3.17
Total percent cover (all life-forms) (%)	normal	–0.196	0.0004	0.0006	~0	–0.004	0.000001			–0.006	0.150	0.248	~0	0.96	0.48	0.19
Percent cover sagebrush shrubs (%)	Log	–0.043	~0	~0		–0.00002	–0.000005			~0	~0	0.081	0.0009	0.94	0.54	0.09
Frequency of sagebrush	normal	–3.162	~0	~0		–0.03400	–0.209000			~0	~0	5.456	~0	0.96	0.43	3.17
Average of 4 longest shrub tape lengths (m)	normal	–0.138	~0	~0		–0.0003		0.542	1.548	~0	–0.129	0.339	~0	0.93	0.25	0.57
Site species richness	Log	–0.301	0.004	0.242[d]	–0.056	–0.004	–0.034			~0	~0	0.075	5.617	0.90	0.27	0.06

If a given explanatory variable was not used in analyses for a particular response variable, that cell is blank; in contrast, if the variable was used but simply did not appear in any of the highest-ranking models, we denote that coefficient as "~0". Three digits after the decimal are given, except for coefficients of very small magnitude. The rightmost three columns pertain only to the top-ranked model for each response variable

[a] Estimated precipitation received at site in previous 12 mos, estimated using PRISM data as described in text

[b] A site on an open, unsheltered slope was coded as 1; a site somewhat protected was coded as 2

[c] 1997 was coded as 0, 1998 as 1

[d] In addition to this linear effect of elevation, species richness also was well modeled by a quadratic term of elevation (model-averaged coefficient = –0.120)

classification factor (i.e., site or year), the mixed-effects models accommodated the covariance structure caused by the grouping of data. For a number of models we evaluated whether intra-class correlation structures might more credibly describe the variance structure than the assumption that they were independent.

A priori-identified abiotic fixed effects used in competing models included elevation, elevation^2, precipitation received at the site during the previous 12 months (see Beever et al. 2003 for detail on how this was estimated), number of frost-free days per year, Erosion Factor K, available water capacity, and Julian date of sampling. In addition to evaluating the effect of site and year as random effects, for a number of models we evaluated them as fixed effects as well. We evaluated the effect of elevation as a binary variable (low- vs. high-elevation sites, following our experimental design) compared to as a continuous variable. Because all models in which elevation was treated as a continuous variable performed better than the corresponding model with elevation treated as binary, we restricted our inferences and presentation of model results to those using the continuous form of the variable. Including the quadratic term for elevation allowed us to evaluate potential nonlinearities (specifically, a peaked distribution, as has often been found for species richness and other vegetative characteristics) in the effect of elevation on vegetative response. However, because the quadratic contributed little to explained variance but had the effect of adding parameters, excluding it always led to models with lowered Akaike's information criterion (AIC_c); the factor was removed from the final suite of models except for species richness.

To accommodate the distributional assumptions of the response data, we employed three approaches: linear (identity link on a normal distribution), log-linear (log link on a normal distribution), and Poisson (log link on a Poisson distribution) regression (Table 4). For all models, we fit null models without random effects, models with random effects but no fixed-effect covariates, models with fixed-effect covariates but no random effects, and the global model with all fixed and random effects. In cases in which the fit of both site and year as random effects was not possible, we proceeded to fit models of fixed effects for the random effect that resulted in a lower information criterion.

We fit and predicted models of site species richness with WinBUGS 1.4.1 (Spiegelhalter et al. 2003), a statistical package for conducting Bayesian inference with Markov chain Monte Carlo analyses. Parameters were assigned diffuse or non-informative priors and hyperpriors. For each model, we ran the Markov chain until convergence occurred (500 iterations) and for an additional 14,000 iterations past convergence. We used the Gelman–Rubin diagnostic to evaluate model fit between three replicate chains (Spiegelhalter et al. 2003), comparing within-chain and between-chain variability. We guarded against multicollinearity in the environmental variables by inspecting the multi-chain iteration histories and the Gelman–Rubin diagnostic plots of the slope parameters. Fixed effects for these models were standardized by subtracting the mean and dividing by the standard deviation to aid model convergence.

We fit all other models with S + (Pinheiro and Bates 2000, including the CorrelatedData library). To avoid underestimation of the variance parameters, restricted maximum likelihood was used. Because the average of four longest shrub tape lengths and average of four longest sagebrush tape lengths were highly correlated ($r = 0.89$), we modeled only the relationship between environmental characteristics and the average of four longest shrub tape lengths.

We employed an information-theoretic perspective to our modeling by comparing the deviance information criterion (DIC) (for site species richness) and Akaike's information criterion for small sample sizes (AIC_c; for all other variables) among models. DIC is an information criterion analogous to AIC that evaluates models in a Bayesian framework (Spiegelhalter et al. 2002); for each information metric, the most parsimonious model possesses the smallest information criterion value. We calculated model weights, variable weights, averaged parameter estimates, and model-evidence ratios according to Burnham and Anderson (2002).

Results

Tests of the intermediate-disturbance hypothesis (landscape scale)

In all six tests of the relationship between plant-species richness (three alternative measures) and

disturbance (two measures), the linear regression achieved better fit of the data (i.e., higher adjusted-r^2 values) than did the quadratic, and the regression coefficient was negative in each case. In other words, variability in species richness was best described by a monotonically decreasing trend as disturbance intensity increased.

Landscape-scale comparisons of horse-occupied versus horse-removed sites

All plant response variables (except for frequency of shrubs and forbs, cover of forbs, and cheatgrass-related variables; see Table 2 for list) had higher values at horse-removed sites than at horse-occupied sites in both elevational strata (see coefficients in 'presence of horses' column in Table 4), and the magnitude of difference was greatest among high-elevation sites (Table 2). Our explanatory variables were successful in accounting for most (64–96%; average = 85.1%; Table 4) of the variability in all response variables modeled in information-theoretic analyses except cheatgrass frequency.

During 1997 and 1998, horse-removed sites averaged 2.94 and 2.81 times greater grass cover than horse-occupied sites at high elevations, and 1.89 times greater cover at low elevations ($P \leq 0.03$; Table 2). Similarly, in both years we encountered a lower frequency of grass intercepts per transect at horse-occupied sites, ranging from 14.6 to 30.4 fewer plants/transect at high elevations and 1.8–5.7 fewer plants/transect at low-elevation sites ($P \leq 0.006$; Table 2). Information-theoretic analyses indicated that frequency and cover of grasses were two of the variables most strongly affected by the presence of horses (variable weight = 1.000 and 0.783, respectively), in spite of marked interannual variability in both response variables (Table 3).

Horse-removed sites also averaged 1.56 and 1.91 times greater total shrub cover than horse-occupied sites at high elevations in 1997 and 1998, and 1.06 and 1.24 times greater shrub cover at low elevations ($P < 0.03$; Table 2). Accordingly, no explanatory variable other than a random effect of site had a higher variable weight than did presence of horses, in information-theoretic analyses (Table 3). Although frequency (i.e., stem density) of shrubs did not differ meaningfully between horse-occupied and horse-removed sites in either year, information-theoretic analyses suggested that when influences of other variables were accounted for, shrub density varied with presence of horses and elevation, as well as among sites (Table 3).

Not surprisingly in light of the above differences in grass and shrub cover, total plant cover was significantly higher at horse-removed sites in both years, and averaged 1.29–1.50 times greater cover among high-elevation sites and 1.17–1.36 times higher among low-elevation sites ($P \leq 0.05$; Table 2). As was true for grass cover and shrub cover, total plant cover had only one fixed-effect variable that appeared more influential than presence of horses—in this case, the effect of interannual variability (i.e., 'year'; Table 3).

When all shrub species were pooled within sites, maximum lengths of shrub intercepts at horse-removed sites averaged 0.17–0.24 m longer than lengths at horse-occupied sites at low-elevation and 0.56–0.57 m longer at high elevations ($P \leq 0.003$; Table 2). Similarly, mean length of the four longest sagebrush intercepts averaged 0.07–0.10 m longer at low elevations and 0.54–0.63 m longer at high elevations ($P \leq 0.03$; Beever 1999). Although variable weight of the presence of horses was lower than for 'year' and two abiotic characteristics of sites, the 95% confidence interval on the parameter estimate of the horse-presence model-averaged coefficient (–0.272, –0.072) did not overlap zero, suggesting that the effect of horse presence was consistently negative on maximum shrub lengths, across all models. This non-overlap of zero by the parameter estimate for presence of horses contrasted with all three variables with greater variable weight than horse presence (erosion factor K, exposure, year).

Horse-removed sites had significantly higher richness of plant species than did horse-occupied sites in both years and cumulatively, averaging 3—12 more species per site at high elevations, and 2—4 more species at low elevations ($P < 0.04$; Table 2). As was the case for maximum length of shrub interceptions, the 95% confidence interval on the horse-presence coefficient (–0.482, –0.117) did not overlap zero; elevation was the only other fixed effect for which this was true for species richness.

Although there was no difference in the frequency (i.e., stem count) of sagebrush shrubs in either year, percent cover of sagebrush was significantly (1.1–

2.2 times) higher at horse-removed than at horse-occupied sites during 1998 but not during 1997 (1.1–2.1 times higher, but more variable among sites within treatments; Table 2). Information-theoretic analyses confirmed that presence of horses (variable weight = 0.436) was a strong determinant of sagebrush cover when influences of abiotic variables were included in competing models; a random effect of site was the only other explanatory variable with a weight >0.011 (Table 3).

In addition, although the trend was not significant in 1998, sites with horses had 1.44–3.13 times greater forb cover than did horse-removed sites in 1997, due largely to greater abundance of unpalatable *Lupinus* and grazing-tolerant *Wyethia* forbs at high elevations ($P = 0.04$; Table 2). Abundance of forbs did not differ meaningfully between treatments in either year (Table 2). Information-theoretic analyses indicated that cover and frequency of forbs were the only response variables of those analyzed for which the coefficient of the presence of horses was positive (Table 4); that is, presence of horses appeared to increase, rather than decrease, them, after the influence of abiotic covariates were accounted for. Nonetheless, among the ten response variables in Table 3, variable weights for presence of horses suggested that the partial effect of horse presence was more marginal on forb cover and frequency, compared to other response variables.

Frequency of the non-native annual cheatgrass (*B. tectorum*) was usually higher at horse-occupied sites. These sites possessed an average of 1.61–2.63 times more intersecting cheatgrass stems at high elevations across years than did horse-removed sites, and 1.57 times more intersecting stems at low elevations in 1998 (Table 2). Cheatgrass stem intercepts were 1.47 times more frequent at low-elevation sites without horses in 1997 (Table 2), due in part to an exceedingly high value of cheatgrass stem counts at the most recently (but ≥15 years ago) burned site, which was a horse-removed site (12th site, Table 1). Information-theoretic analyses, which used a log-linear mixed-effects model fitted by restricted maximum likelihood, suggested that two models (each with $r^2 \approx 0.88$) were relatively superior to others. In the first (which had $\omega = 0.65$), inference suggested that the frequency of *B. tectorum* stems varied by site and year but little at all relative to the other environmental covariates. The competing model ($\omega = 0.35$) suggested that stem frequency varied only by site and patterns in annual precipitation. However, residuals from both models were heteroscedastic, indicative of a problem with model fit. Therefore, inference from these models should be used with caution. Although trends of greater cheatgrass cover at horse-occupied sites were not significant at $\alpha = 0.05$ because of relatively high coefficients of variability for horse-occupied sites (especially at lower elevations), this is the first investigation of this relationship, the outcome of which has important implications for management of Great Basin resources.

Simpson's and log-series diversity indices did not differ meaningfully between treatments in either year (Table 2). For a number of conceptual and analytical reasons, these indices were not modeled with information-theoretic analyses.

Horse-trail transects (local scale)

Comparisons within sites between the randomly located vegetation transects (which sought to characterize vegetation within the entire site) and transects located adjacent to horse trails, although naturally limited in sample size, largely showed the same trends (with respect to direction and magnitude of effect) observed in comparisons between horse-occupied and horse-removed sites, especially at high-elevation sites. In 1998, randomly located transects had from 21 to 218% greater percent cover of grasses than horse-trail transects at three of the five sites. At the other two (lowest-elevation) sites, one had equivalent cover between the two types of transects, and one had lower grass cover in the randomly located transects. Percent cover of forbs along horse trails was either equivalent to or greater than forb cover in randomly located transects at all five sites in 1998. Percent cover of shrubs differed strongly between transect types, and was 9–146% (mean = 61%) greater in randomly located transects at all five sites (paired $t = 3.0$, d.f. = 4, $P = 0.04$). Species richness of shrubs was greater in randomly located transects at three of the five sampled sites, equal at another site, and slightly lower at the fifth site. However, mean difference between the transect types ranged from only 0.25 to 0.75 species per transect. At four of the five sites, total species richness was higher

in the randomly located transects, ranging from 6 to 29% greater species richness, and was 9% lower at the fifth site.

Results of horse-trail sampling in 1997, the year in which we sampled trails less extensively, mirrored the direction and magnitude of results from 1998 sampling. Percent cover of grasses was notably higher in randomly located transects than in horse-trail transects—2.3 times higher at high elevation, and 9.5 times higher at low elevation. Forb cover along a horse trail was 37% higher than for randomly located transects at high elevation, but was marginally lower than the average for randomly located transects at low elevation. Species richness of shrubs was 56% higher in randomly located transects than along a horse trail at high elevation, and twice as high at low elevation. As compared to the horse-trail transect, total species richness was 23% higher in randomly selected transects at high elevation, but about equal (6.5 vs. 7 species) at low elevation.

Interannual variability (landscape scale)

Five of eight plant variables exhibited significant differences in means between years ($P < 0.05$), yet all variables except cheatgrass frequency ($r = 0.68$, $P = 0.002$) were very highly correlated between years ($r > 0.75$, $P \leq 0.0004$; 6 variables had $r \geq 0.825$). Whereas cover of grasses and forbs were, respectively 9.7% and 8.2% higher in (the wetter) 1998 than in 1997, shrub cover averaged <1% less in 1998 ($P > 0.55$; all percentages are absolute differences) and the sagebrush continuity index also differed little between years ($P > 0.15$). In information-theoretic analyses, modeling year as a fixed effect suggested strong interannual contribution to variability in forb frequency, grass cover and total plant cover, and to a lesser degree, forb cover and connectedness of the shrub canopy. Counts for all fecal types generally exhibited strong correlation between years ($P < 0.03$), and were generally not statistically different between years. Finally, mean sampling date of sites occurred approximately 28 days earlier in 1998 ($t_{16} = -3.12$, $P = 0.007$). However, contrary to our predictions, sampling date had a non-zero variable weight in information-theoretic analyses for only two of 10 response variables, neither one of which was herbaceous—species richness (the variable that had greatest likelihood of being overfitted) and shrub cover (variable weight = 0.100).

Confounding effects of abiotic variables (landscape scale)

When we corrected alpha levels using sequential Bonferroni corrections, none of the ten abiotic variables differed significantly between horse-removed and horse-occupied sites, either across all sites or among high- or low-elevation sites only (Table 5). Among high-elevation sites only, horse-occupied sites averaged an estimated 27 more frost-free days per year than did horse-removed sites, even though they occurred at slightly higher (89 m) elevations (Table 5). Horse-occupied sites tended to receive slightly more precipitation than did horse-removed sites using NRCS estimations, 1997 PRISM estimates, 1998 PRISM estimates, and especially on average during 1961–1990, but no comparison was significantly different (Table 5). Furthermore, even if these two trends were *biologically* important although not statistically significant, they are counterintuitive to our finding of lower plant cover and diversity at horse-occupied sites (Table 2); greater precipitation or longer growing seasons (at high-elevation sites) would have been expected to dampen (rather than magnify) the magnitude of horse-grazing effects.

Discussion

Feral grazers may alter vegetation in semi-arid ecosystems via (1) soil compaction (and subsequent increased runoff), (2) selective plant consumption, (3) trampling and rubbing, (4) removal of terminal meristems, and (5) redistribution of nitrogen and other nutrients (Kauffman and Krueger 1984; Archer and Smeins 1991; Butler 1995; Belsky and Blumenthal 1997). Of these five mechanisms, strong negative correlations between plant cover and *both* fecal counts and penetration resistance of soils (e.g., $r < -0.7$ for both relationships, among low-elevation sites in 1998) suggest that all of the first three mechanisms are acting to some degree. Penetration resistance was the variable most strongly different between horse-removed and horse-occupied sites

Table 5 Comparison of 10 abiotic variables between horse-occupied and horse-removed sites in the Great Basin of western North America. Data sources are listed in the text

Abiotic site attribute	*F*-value	*P*-value*	Mean difference with respect to horses [(removed)–(occupied)]
Mean slope gradient (%)	0.43	0.52	–3.61
Arcsin (% cover bedrock)[a]	0.20	0.66	–1.56
Available water capacity (in/in)	2.21	0.16	1.11
Erosion factor K	0.07	0.80	0.006
Erosion factor T	0.01	0.92	–0.18
Non-horse disturbance[b]	0.80	0.39	0.40
Frost-free days/year, high-elevation sites[c]	$Z = -2.31$	0.02	–27.5
Frost-free days/year, low-elevation sites[d]	$t = 0.08$	0.93	0.67
Frost-free days/year, all sites combined[e]			–10.2
Production (lb/ac), high-elevation sites	1.37	0.29	201.0
Production (lb/ac), low-elevation sites	2.83	0.13	–178.0
Production (lb/ac), all sites combined[e]			–11.69
Precipitation (cm/year), 1997 PRISM	0.91	0.36	–3.50
Precipitation (cm/year), 1998 PRISM	0.58	0.46	–5.60
Precipitation (cm/year), 1961–1990 PRISM	6.56	0.02	–7.45
Precipitation (cm/year): NRCS estimates	0.32	0.58	0.00
Elevation, all sites combined	4.40	0.06	–121.9

[a] Values taken from 1998 sampling at 19 sites, $N = 4$ transects per site

[b] Subjective classification of disturbance by humans and livestock during 1997–1998, after Wentworth (1976). 1, apparently undisturbed; 2, slight disturbance; 3, moderate; 4, heavy; 5, severe. Due to small *N* within categories, data were analyzed as if continuous

[c] Mann-Whitney test

[d] Unpaired *t*-test

[e] Significant (horse presence × elevation) interaction. Presence of horses not tested as a main effect

*Except for cases of significant treatment–elevation interaction, two-way ANOVAs of horse presence and elevation were used to analyze variables. Due to the large number of variables analyzed, critical levels of alpha were adjusted using sequential Bonferroni corrections

(Beever and Herrick 2006), and the fact that other authors have attributed catastrophic shifts in vegetation of grazed systems to altered soil properties (e.g., Van de Koppel et al. 1997) may have relevance here. Previous research has shown that the degree to which grazing affects soil compaction (measured as bulk density or a surrogate, infiltration rates) depends upon soil texture (with finer soils more vulnerable to compaction; Van Haveren 1983), grazing system (Wood and Blackburn 1984), and stocking rate (Van Haveren 1983). Fewer studies have addressed, however, how long such compaction will persist under various freeze-thaw cycles.

In addition to soil changes, observed losses to the granivorous rodent guild and mound-building ants (both of which can assist in seed dispersal and germination) may be other potential drivers of vegetation alteration (Andersen 1991; Beever and Brussard 2004; Beever and Herrick 2006). In contrast to our results in support of the first three mechanisms, our finding of largest shrub lengths at horse-removed sites suggests that a wider, more bushy growth form due to meristematic removal is either not occurring in shrub species at our sites, or its effect is overshadowed by the first three mechanisms.

Numerous exclosure studies have suggested that vegetation retrogression in arid and semi-arid systems of North America may be protracted and unpredictable (McLean and Tisdale 1972; Rice and Westoby 1978; West et al. 1984), in part because successional trends do not necessarily follow previously conventional paradigms of linear return to some equilibrium

climax state (Laycock 1991). Our results, however, demonstrated many significant differences in vegetation between sites from which horses have been removed for 10–14 years and sites currently occupied by horses (Table 2). As a result of our numerous site-selection criteria (e.g., low slope gradient, east-facing aspect, no recent fires), horse-occupied sites in this study do not represent extreme cases of horse use (see Beever and Brussard 2000, 2004), a commonly used experimental approach criticized by Brown and McDonald (1995). If transition thresholds (Laycock 1991) are not crossed, current grazing can influence foliar cover without directly affecting species frequency, whereas changes in density often reflect longer-term impacts on the plant community. We chose to record and analyze foliar rather than basal plant cover because in the Great Basin and surrounding ecoregions (e.g., Mojave Desert communities), a 50-m line with no width intercepts herbaceous plant bases so infrequently that basal cover is often a highly variable and inconsistent indicator of grazing intensity (E.A. Beever and D.A. Pyke, unpublished data; E.A. Beever, unpublished data).

Tests of the intermediate-disturbance hypothesis (landscape scale)

Our finding of monotonically decreasing species richness across sites as grazing disturbance (indexed by fecal counts) increased suggests that either the bell-shaped curve of the intermediate-disturbance hypothesis does not apply in this system or that contemporary influences or the long-term past grazing history of these sites has resulted in generally all of them being located on the more disturbed side of the bell-shaped curve.

Landscape-scale influences of horses on vegetation

Because horses primarily consume graminoids (Hanley and Hanley 1982; McInnis and Vavra 1987), our findings of lower frequency and percent cover of grasses at horse-occupied sites (Table 2) as well as strong variable weight for presence of horses in information-theoretic analyses of these two response variables (Table 3) is not surprising. Our finding of greater species richness (2–4 species/site at low-elevation sites, and 3–12 species/site at high-elevation sites) at horse-removed compared to horse-occupied sites agrees with previous work that found decreased richness of plants under greater livestock grazing (Rusch and Oesterheld 1997; Ludwig et al. 1999). In contrast, grazing can lead to increased species richness when grazers suppress the ability of competitive dominants to exclude other species or when grazing creates gaps that allow density increases in existing species or colonizations by other species (Milchunas et al. 1988; Archer and Smeins 1991). Especially at high-elevation sites, we observed (as did Ruthven 2007) slightly greater forb cover at horse—occupied sites—not surprising, given that two of the most abundant forb species at the horse-occupied sites are unpalatable or toxic to large herbivores (Hickman 1993). Decreases in grass cover may also have contributed to greater forb cover at horse-occupied sites, via competitive release.

While care must be taken to ensure that other factors such as soil type, precipitation, and others are accounted for when making comparisons of maximum shrub length, we believe that shrub-continuity variables are of value in assessing the degree to which a landscape has been structurally modified by a large herbivore. Although horse diets have been shown to contain minor amounts of shrubs (e.g., McInnis and Vavra 1987), our finding of greater shrub dissectedness and 1.1–1.9 times lower shrub cover in the presence of horses may be instead due to trampling and rubbing. Loss of connectivity in the shrub canopy may increase rates of insolation, evapotranspiration, and soil loss at small spatial scales and may lessen habitat value of a site for animal species that obligately use shrubs for shade, food, or escape cover (Hoffmeister 1986; Butler 1995; Belsky and Blumenthal 1997).

Our finding of decreased shrub cover agrees with results of Brady et al. (1989), who observed increased shrub species richness and cover 16 years after removal of livestock, as well as with the majority of studies in western North America reviewed by Jones (2000). In contrast, however, other authors have documented increases in sagebrush and other shrubs in the presence of herbivory (Dobkin et al. 1998; many authors cited in Archer and Smeins 1991). The relative dominance of shrubs in grazed landscapes will depend upon the

comparative strength of the processes of shrub trampling by horses and release of shrubs from competition with sympatric grazed plant species, as well as on the longer-term history of livestock use.

The fact that plant-related variables at horse-occupied sites were most different from horse-removed sites at high elevations may be due to a number of factors. First, most of the vegetation-class variables responded significantly to elevation, with high-elevation sites exhibiting higher absolute levels. In other words, high-elevation sites had more vegetation to alter, as compared to low-elevation sites. Furthermore, a global analysis revealed that effects of grazing by large herbivores increased with increasing primary productivity of the site (Milchunas and Lauenroth 1993). Finally, feral horses generally graze at higher elevations during late spring, summer, and early fall, the periods when most plant growth occurs.

As a result of the influences mentioned above that large mammalian herbivores exert on landscapes, these animals can modify ecosystems by altering spatial heterogeneity, modulating successional processes, influencing size/density relationships within species, and controlling the switching of ecosystems between alternative states (Hobbs 1996). As with other large herbivores (Milchunas et al. 1988), the effects that horses impose upon a given ecosystem depend upon many factors, including the plant-animal coevolutionary history, soil development, climate, recent weather, frequency and seasonality of the grazing, effects of other sympatric species, animal density, and longer-term grazing history of the site. Particularly in semiarid ecosystems, degradation of vegetation occurs most commonly under excessive livestock grazing pressure, spring grazing, or long-term continuous grazing, although some authors have found grazing to have no significant effect on these ecosystems (see Milchunas et al. 1988).

Ecosystem components in semiarid regions such as the Great Basin are predicted to respond less favorably to herbivory than are components in systems (such as grasslands) having a long, continuous coevolutionary history of grazing pressure (Mack and Thompson 1982; Milchunas and Lauenroth 1993). *E. caballus* has inhabited North America for only the past ~400 years, after an absence of all equids from the Great Basin for some 13,000 calendar years (Grayson 2006). Thus, horses may be considered ecologically as part of a novel disturbance regime in the Great Basin rather than as a native species.

Perhaps because vegetation is sampled easily and is influenced directly by horses, research to this point on grazing ecology of feral horses (Turner 1987; Rogers 1991; Detling 1998; Fahnestock 1998; Fahnestock and Detling 1999) or domestic horses in seminatural conditions (Reiner and Urness 1982) has focused almost exclusively on interactions of horses with vegetation. In contrast, research on interactions of free-roaming horses with other ecosystem components in arid or semiarid regions is just beginning to emerge (Peterson 1999; Beever and Brussard 2004; Beever and Herrick 2006). As a result of the non-uniform patterns of habitat use by horses (as for other ungulates; see Hobbs 1996), the magnitude of grazing impacts will vary widely across the landscape, from areas minimally affected to areas used heavily.

Horse-trail transects (local scale)

Stronger statistical inference could be gained in future studies by sampling more transects along horse trails. However, the 1998 sampling represented the upper bound for sample size for 1.82 ha sites, as it was difficult to find more sampling locations (trails) in a small 135 m × 135 m grid without placing horse-trail transects immediately adjacent to each other. Differences between horse-trail and randomly located transects at each horse-occupied site (e.g., grass, shrub, and forb cover, species richness) occurred in the same direction and magnitude as differences between horse-occupied and horse-removed sites. Thus, we were able to document differences in vegetation apparently caused by horses at both local and landscape scales. We advocate that future research into characterization of animal-trail effects seek to elucidate how far impacts extend (i.e., how rapidly effects subside as one moves) laterally from the trail center.

Although natural animal trails have been noted anecdotally numerous times in ecological literature, they have rarely received quantitative treatment (Butler 1995). Antelope in arid grassy dunes that spent much time under shade trees were found to trample soil locally but also enrich it with their fecal pellets (Dean and Milton 1991). Even though animal-

generated trails have been noted for bison (*Bos bison* L.) in the Great Plains grasslands, mountain goats (*Oreamnos americanus* de Blainville) in the Rocky Mountains, caribou (*Rangifer tarandus* L.) in arctic tundra, and elephants (*Loxodonta africana* Blumenbach) in tropical grasslands (e.g., Eaton 1917; Clayton 1975; Butler 1995), this work is the first to our knowledge to quantitatively compare transects along trails to randomly-chosen transects within the same site yet more distant from trails. In the absence of available manipulative experiments, horse-trail transects allow investigation of heterogeneity of use within horse-grazed areas and provide another level of evidence to suggest that horses (rather than other factors) are altering communities at our sites.

Interannual variability (landscape scale)

Much of the interannual variation we observed in herbaceous-plant variables may be attributed to earlier sampling in 1998 (mean = 28 days earlier). The robustness of our results across years in spite of significant interannual variation suggests that climatic variations did not eclipse effects imposed by horses on semiarid ecosystems, contrary to findings from research on feral horses in two grassland national parks (Detling 1998).

Conclusions and management implications

Investigating response of various aspects of vegetation to a large-bodied herbivore across regional scales requires separation of clinal and abiotic influences on vegetation from herbivore-induced alterations to the plant community. Although this broader spatial scale does not allow for the same degree of experimental control as is found in smaller-scale studies, managers benefit from the knowledge that the domain of inference for such larger studies represents a significant fraction of land under their jurisdiction, rather than merely several to a few hundred ha in one valley or range, for example. Furthermore, because horses in the US are currently managed to be 'free-roaming' under a minimal-management mandate, experimental manipulation of horse density is often exceedingly difficult to implement. In the absence of a true experiment, we instead employed several methods such as interspersion of sites from different treatments, comparison of abiotic site attributes between treatments, and multi-scale investigations of effects of herbivory through use of horse-trail transects, and evaluation of numerous competing models that asserted importance of different subsets of abiotic factors to address alternative hypotheses about causes of vegetation differences. Collectively, our results suggest that effects of free-roaming horses constitute a non-trivial contribution to landscape condition, at least in semiarid regions such as the Great Basin at the local and landscape scales we investigated.

As this study illustrates, much remains to be learned about small- and broad-scale response of Great Basin vegetation to varying densities of or removal of free-roaming horses; how fire, invasions of cheatgrass and other non-native plants, and other sympatric grazers alter horse-vegetation relationships; and how horse effects are quantitatively distributed across the landscape. Given the ever-increasing importance of cheatgrass in landscape dynamics of the Great Basin, our finding of higher frequency of cheatgrass at horse-occupied sites (as Whinam et al. 1994 and Weaver and Adams 1996 have found in Australia for other non-native plants, due to horses' transport of seeds via their excreta or externally via their coat) arguably demands highest future research priority for broad-scale investigations. With a better understanding of horses' ecology and the response of components of semiarid ecosystems to this non-native yet charismatic herbivore, future management can be adapted to prescribe grazing intensities and mosaics that accommodate many species occupying western public lands.

Acknowledgments We thank horse specialists J. Axtell, J. Gianola, and T. Seley of the Bureau of Land Management for help with site selection, J. Fisher of the Natural Resources Conservation Service for assistance with soil data and interpretation, and J. Tiehm of the Northern Nevada Native Plant Society for identifying numerous rare-plant specimens. We thank N. Wendel, D. Watterson, and especially J. Landmesser for field assistance. D. Clausnitzer, K. Crane, S. Jenkins, J. Jenks, and two anonymous reviewers all provided critical reviews of earlier manuscript drafts. Logistic and financial support at the University of Nevada was provided by the Biological Resources Research Center, the Department of Biology, and the Program in Ecology, Evolution, and Conservation Biology. At the University of Nevada, the Nevada Agricultural Experiment Station, Center for Environmental Arts and Humanities, College of Agriculture, Department of Biology, Nevada Biodiversity Research and

Conservation Initiative, and Graduate Student Association all provided financial assistance, as did the Kosciusczko Foundation and the American Museum of Natural History. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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BIOLOGICAL SOIL CRUSTS:
ECOLOGY AND MANAGEMENT



Technical Reference 1730-2
2001

U.S. Department of the Interior

Bureau of Land Management

U.S. DEPARTMENT OF THE INTERIOR
BUREAU OF LAND MANAGEMENT

U.S. Geological Survey

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This publication was jointly funded by the USDI, BLM, and USGS Forest and Rangeland Ecosystem Science Center. Though this document was produced through an interagency effort, the following BLM numbers have been assigned for tracking and administrative purposes:

Technical Reference 1730-2

BLM/ID/ST-01/001+1730

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Produced By

United States Department of the Interior
Bureau of Land Management
Printed Materials Distribution Center
BC-650-B
P.O. Box 25047
Denver, Colorado 80225-0047

Technical Reference 1730-2
2001

ACKNOWLEDGMENTS

We gratefully acknowledge the following individuals for their contributions to the publication of this text:

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CHAPTER 1

INTRODUCTION TO BIOLOGICAL SOIL CRUSTS

In arid and semi-arid lands throughout the world, vegetation cover is often sparse or absent. Nevertheless, in open spaces between the higher plants, the soil surface is generally not bare of autotrophic life, but covered by a community of highly specialized organisms (Fig. 1.1). These communities are referred to as biological soil crusts, or cryptogamic, cryptobiotic, microbiotic, or microphytic soil crusts (Harper and Marble 1988; West 1990). Biological soil crusts are a complex mosaic of cyanobacteria, green algae, lichens, mosses, microfungi, and other bacteria. Cyanobacterial and microfungal filaments weave through the top few millimeters of soil, gluing loose particles together and forming a matrix that stabilizes and protects soil surfaces from erosive forces (Cameron 1966; Friedmann and Galun 1974; Friedmann and Ocampo-Paus 1976; Belnap and Gardner 1993). These crusts occur in all hot, cool, and cold arid and semi-arid regions. They may constitute up to 70% of the living cover in some plant communities (Belnap 1994). However, biological soil crusts have only recently been recognized as having a major influence on terrestrial ecosystems.

Globally, this consortium of soil biota has many similarities in function, structure, and composition, in spite of their unconnected

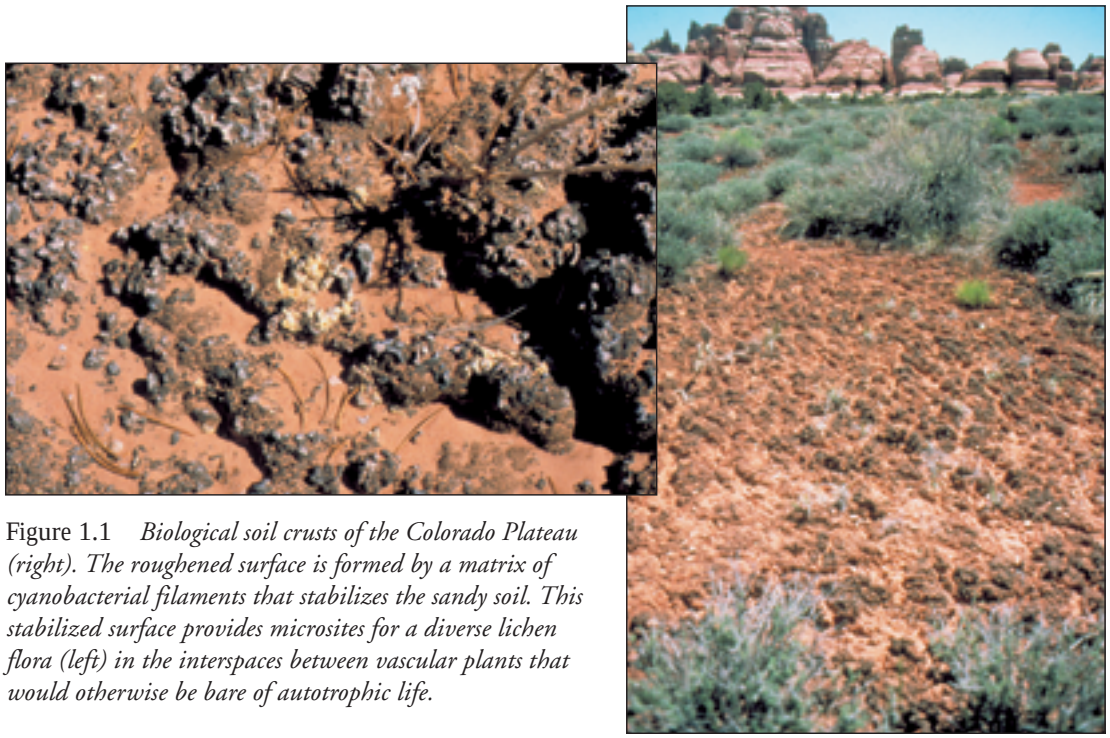


Figure 1.1 *Biological soil crusts of the Colorado Plateau (right). The roughened surface is formed by a matrix of cyanobacterial filaments that stabilizes the sandy soil. This stabilized surface provides microsites for a diverse lichen flora (left) in the interspaces between vascular plants that would otherwise be bare of autotrophic life.*

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and seemingly dissimilar environments. Crusts are found in an astonishing variety of habitats throughout the world: in desert and semi-desert plant communities, ranging from shrub and succulent deserts to open woodlands; in steppe formations in both the northern and southern hemispheres; in the gaps between evergreen shrubs and in forests in the Mediterranean-type climate; and on open ground or between alpine or tundra vegetation. On a small scale, biological soil crust communities are found in open types of vegetation in temperate climatic regions; for example, they are frequently present in (and often restricted to) areas of a few square meters in xerothermic local steppe formations in central Europe and in the pine barrens of the eastern United States.

In rangelands, biological soil crusts can be viewed from functional, structural, and compositional perspectives. They function as living mulch by retaining soil moisture and discouraging annual weed growth. They reduce wind and water erosion, fix atmospheric nitrogen, and contribute to soil organic matter (Eldridge and Greene 1994). Structurally, biological crusts are a rough, uneven carpet or skin of low stature (1 to10 cm in height). Below ground, lichen and moss rhizines, fungal hyphae, and cyanobacterial filaments form a matrix that binds soil particles together (Belnap 1995). Horizontally, soil crusts occupy the nutrient-poor zones between vegetation clumps in many types of arid-land vegetation. Compositionally, biological soil crusts are diverse. In many arid and semi-arid communities there are often many more species associated with the biological soil crust at a given site than there are vascular plants (Rosentreter 1986; Ponzetti et al. 1998).

Rangeland managers in North America have historically used key indicator plants for determining the ecological trend and health of vegetation (USDA 1937; Stoddart et al. 1943). Biological soil crusts can also be used as indicators of ecological health. In addition, they act as indicators of abiotic factors, such as the presence of calcareous soils. Crustal organisms read environmental factors differently from and on separate time scales than do vascular plants (McCune and Antos 1982). Most crustal organisms are biologically active during the cool seasons when the soil surface is moist (Rosentreter 1986). In contrast, vascular plants are active in spring and summer when air temperatures are above freezing.

Unlike vascular plants, crustal organisms, particularly lichens, are not greatly influenced by short-term climatic conditions. This makes them ideal indicators of long-term environmental factors. Therefore, each community component can provide information that may complement, explain, or indicate something about a site's characteristics and disturbance history for rangeland management and evaluation. Just as plants increase or decrease with livestock grazing, many biological soil crust components are good indicators of physical

disturbance, such as by livestock, human foot traffic, or motorized vehicles (Belnap 1995).

Land managers have been slow to use biological soil crusts in rangeland evaluations. Descriptions of vegetation or "habitat types" used by public land management agencies sometimes include biological soil crusts (e.g., Daubenmire 1970; Hironaka et al. 1983) but rarely present them as a dominant factor even when they are prevalent. This is partly because of perceived difficulties with identification (see Chapter 6). The problem of identification is exacerbated by the small size of these organisms, which often lack reproductive structures due to the harsh environments where they grow. However, identification problems can be substantially reduced by grouping organisms by function or general morphological characteristics (see sections 1.3 and 6.1.2).

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1.1 Biological Soil Crust Components

Biological soil crusts are usually composed of multiple, unrelated organisms that occur together on the soil surface. The various types of organisms that comprise the crust share some interesting physiological traits. They are all capable of drying out and temporarily suspending respiration without negative effects, unlike vascular plants that either die or must regrow new tissue. These types of organisms are referred to as "poikilohydric." Most of them equilibrate their water content with the atmospheric humidity or soil surface moisture content. Poikilohydric organisms generally become photosynthetically active very quickly, producing carbohydrates or sugars minutes after wetting. However, most species still require high levels of hydration for optimal physiological functioning. The moisture content threshold for activity is species specific and helps determine the distribution of the various taxa that make up the biological crust. Many of these organisms perform under a variety of light intensities and prefer to dry out rapidly. Because they lack a waxy epidermis, crustal organisms also tend to leak nutrients into the surrounding soil upon wetting and drying.

Biological soil crusts have both macro- and microscopic components. Components that comprise these crusts are common in desert soils throughout the world. They will be discussed throughout this document in the context of their roles when they combine with other organisms as part of a biological soil crust. The term "total soil crust" will be used to refer to the combination of organisms. When visible cover (i.e., moss and/or lichen cover) alone is being discussed (thus excluding cyanobacteria), this will be specifically stated.

Bacteria are a diverse group of primitive, single-celled organisms. Bacteria can be either autotrophic (i.e., they synthesize

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carbon compounds from inorganic sources) or heterotrophic (i.e., they utilize carbon-containing substrates, such as organic matter in soil, for food). Some bacteria contribute to soil fertility by fixing nitrogen. Others are important in decomposition.

Microfungi occur either as free-living organisms or in mycorrhizal associations with plant roots. Free-living microfungi function as decomposers. They also contribute substantially to the living biomass in soils. Fungal filaments (hyphae) bind soil particles together, increasing soil water-holding capacity.

Cyanobacteria ("blue-green algae") are primitive filamentous or single-celled bacteria that can photosynthesize and, under anaerobic conditions, fix atmospheric nitrogen into a form that is available to higher plants (NH_4^+). Cyanobacteria can be heterocystic (i.e., they have special cells where nitrogen fixation takes place), or non-heterocystic (i.e., they lack these specialized cells). One of the most common cyanobacteria worldwide is the non-hetero-cystic, filamentous species *Microcoleus vaginatus. Microcoleus* can be seen with a 10x hand lens on the edge of a broken clump of soil. Under higher magnification, *Microcoleus* occurs as a cluster of filaments surrounded by a gelatinous sheath (Fig. 1.2). Single-celled cyanobacteria appear as small, blackish cells mixed with surface soil. When soils contain high amounts of cyanobacteria, they often have a slightly to highly roughened surface due to the organisms' binding of soil particles, coupled with processes like frost-heaving and erosion. For nitrogen fixation to occur in non-heterocystic cyanobacteria, the organisms need to be in an anaerobic environment, created by layering of cyanobacterial filaments just beneath the soil surface.

Green algae are light green to black, single-celled, photosynthetic organisms. Algae that occur on or just below the soil surface dry out in a vegetative condition and become physiologically functional when moistened. They do not rely on resting spores to regrow after dry periods, as do aquatic algae that inhabit ephemeral ponds or lakes. Therefore, they are well adapted to living and reproducing in dry desert environments. Algae are difficult to observe without a microscope (100x to 400x), but sometimes give the soil surface a green tint. Their growth period is often linked to cool, moist weather, and they may be difficult to detect when dry.

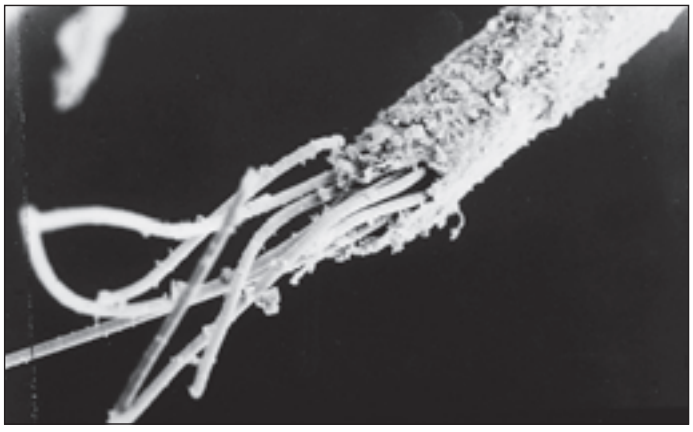


Figure 1.2 Microcoleus vaginatus*, one of the predominant cyanobacteria comprising biological soil crusts.* Microcoleus *exists as a cluster of filaments, surrounded by a gelatinous sheath (seen here with soil particles attached). The living filaments can migrate through the soil, leaving abandoned sheath material and a stabilized soil matrix behind. (2000x magnification)*

Bryophytes are tiny non-vascular plants. This group includes both mosses and liverworts. Having greenish leaves when moist, mosses are generally easy to identify. They reproduce by spore capsules that rise above the leaves. The spore capsules greatly simplify the identification of genera and species. However, in arid environments, mosses often lack reproductive structures and will reproduce asexually by simple or specialized fragmentation. Therefore, arid-land mosses are often difficult to identify in the field. Liverworts come in two general forms: thalloid or leafy. The thalloid form has a greenish-black thallus or flat, narrow ribbon of dichotomously branching material. Thalloid liverworts are adnate to the soil surface, and some can fold in half, almost disappearing from view (they look like thin black lines on the soil surface when dry). Leafy liverworts are rare in arid environments. They look like mosses but are smaller, and when dry the leaves are very black . Both types of liverworts reproduce by spores and by specialized asexual structures called "gemmae." The spores are often produced in a structure within the upper surface of the liverwort and look like a black or smutty spot on a green background. The asexual gemmae are variable in size (1 to 3 mm), but are usually green, circular structures that easily break off the parent plant when mature.

Lichens are fungi that capture and cultivate algae or cyanobacteria, resulting in a new morphological entity. Lichens are typically used in ecology courses to illustrate the concept of symbiosis, as the algae or cyanobacteria provide the fungus with energy in the form of carbohydrates produced by photosynthesis, while the fungus provides protection from desiccation. Lichens come in a wide variety of shapes, sizes, and colors. They generally have an outer fungal layer, which, if cut in cross section, reveals a layer of algal cells. Lichens can cover the soil surface like a layer of skin or they can be three dimensional and leaf-like in appearance. Lichens occur in a variety of colors, including green, red, brown, white, and black. Sexual reproduction is limited to the fungal partner. Reproductive structures are generally round, dark-colored sessile disks on the lichen surface. Lichens can also reproduce asexually (as the combined organism) and have several types of specialized fragmentation structures to facilitate this type of dispersal. Lichens that reproduce asexually can colonize disturbed sites much more rapidly than those species that lack this ability.

1.2 Microstructure

The dominant components of biological soil crusts are photosynthetic and therefore require sunlight. When soils are dry, the bulk of the cyanobacterial biomass is 0.2 to 0.5 mm below the soil surface,

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where sufficient light for net carbon gain is available but UV exposure is reduced. *Microcoleus vaginatus*, which lacks UV-screening pigments, migrates to the surface for short time periods when soils are moistened and returns to subsurface zones as they dry (Fig. 1.2). Populations of *Scytonema* and *Nostoc*, cyanobacteria containing UV-screening pigments, are more commonly found directly on the soil surface.

1.3 Morphological Groups

Morphological groups consist of organisms that are similar in shape and general appearance. The crust morphology largely determines its ecological function relative to water infiltration, erosion, water retention, and resistance and resiliency to disturbance (Eldridge and Rosentreter 1999). Morphological groups also convey an image of a particular organism. Table 1.1 outlines the major morphological groups for biological crusts. Ecological function and management implications relative to morphological groups will be discussed in detail in later chapters.

1.4 Differentiating Types of Biological Soil Crusts in the Field

Biological soil crusts are usually composed of various organisms and morphological groups, unless the crust is in an early-successional stage. However, one or two morphological groups will normally dominate the crust. The following are examples of morphological groupings:

- *Cyanobacterial crusts* are dark colored or black. When moist, the organisms may be visible as black filaments on and near the soil surface.
- *Green algal crusts* are not always visible, but might appear as a green cast on the soil surface when it is moist.
- *Moss crusts* are easily observed as a furry carpet with patches of green, gold, brown, and/or black.
- *Liverworts* are difficult to detect and usually occur in a mosaic with other dominant organisms. Close examination with a hand lens will reveal tiny black ribbons that become more obvious with moistening.
- *Lichen crusts* can be identified by their diversity of shapes and colors. The lichen morphological groups form an anatomical gradient from a low, simple morphology to taller and three-dimensional growth forms.
    - *Crustose lichens* are flat and fused to the substrate.
    - *Gelatinous lichens* are usually black and may appear flat or three-dimensional. They become jelly-like in texture when

moistened and will swell to several times their size when wet. This is an important group to identify from a functional perspective because they have cyanobacteria as their phytobiont and therefore fix atmospheric nitrogen.

- *Squamulose lichens* occur as small individual flakes or scales that often grow in colonies or clusters.
- *Foliose lichens* are leaf-like and loosely appressed to the substrate. In dry habitats, foliose lichens inhabit the relatively moist microsites under plant canopies and on north aspects.
- *Fruticose lichens* are three dimensional and are often upright, branched, or thread-like.

1.5 What Biological Soil Crusts are Not: Physical Soil Crusts

Non-biotic soil surface crusts are a major structural feature in many arid regions. Their properties and manner of formation have been studied for many years, primarily because of their detrimental effects on agricultural crops. These crusts are transient soil-surface layers (ranging in thickness from less than 1 mm to a few cm) that are structurally different from the material immediately beneath them. Physical crusts reduce water infiltration and can prevent the emergence of vascular plant seedlings (Fig. 1.3).

The most important process in the formation of non-biotic crusts is generally raindrop impact, which breaks up soil aggregates on unprotected surfaces. Smaller particles wash into spaces between larger particles, clogging soil pores and reducing infiltration rates by as much as 90%. This can occur within the first few minutes of a rainstorm. As drying takes place, surface tension pulls soil components together, forming a dense, strong layer. Thackett and Pearson (1965) showed that physical crusts formed under simulated rainfall had a dense surface layer 1 to 3 mm thick, coated with a thin layer of well-oriented clay. The crust was underlain by a more porous structure, and the water permeability of the underlying material was about five times that of the surface 0 to 5 mm. Rain-formed crusts are thicker when the raindrops are larger because these larger drops have more energy and "blast" deeper holes, destroying the original structure to a greater depth. In general, rain-formed crusts are less than 5 mm thick. This layer is often harder than the rest of the soil because compounds such as salts, lime, and silica are deposited at the surface as water evaporates. Because large pores are absent, the crust usually has low saturated hydraulic conductivity and limits infiltration. This increases water runoff and soil erosion.

Soil aggregate structure is also destroyed by machinery or the hooves of grazing animals. Trampling moist soils destroys existing soil

Table 1.1 *Morphological groups for biological soil crust components with examples of common taxa or groups.*

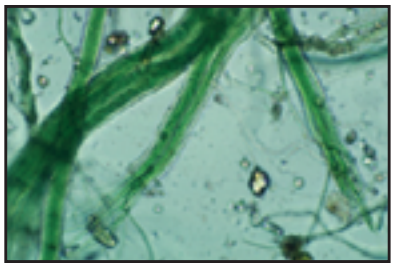
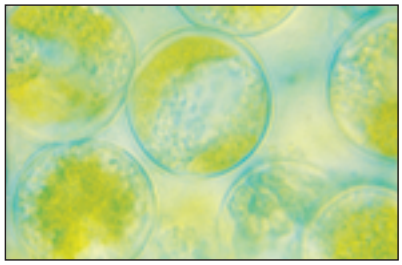
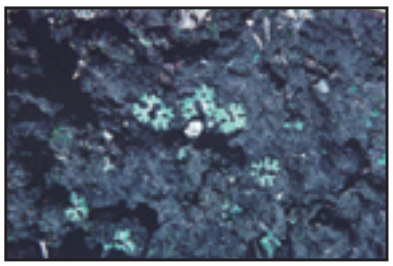
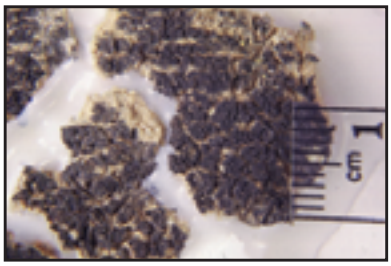
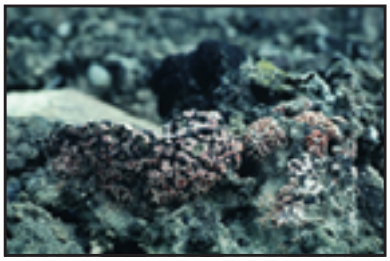
Morphological Group		Description and Representative Taxa
cyanobacteria		colonies are black to blue-green and visible primarily when moist *(Microcoleus vaginatus)*
algae		primarily occur as single-celled organisms; difficult to detect (coccoids)
BRYOPHYTES: short moss		mosses <10mm in height *(Bryum* spp.*, Ceratodon purpureus)*
tall moss		mosses >10mm in height *(Tortula ruralis)*
liverwort		flat, narrow ribbon or green-black dichotomously branching material on the soil surface *(Riccia)*

Table 1.1 (continued)

Morphological Group		Description and Representative Taxa
LICHENS:		
crustose lichen		crust-like growth tightly attached to the substrate *(Lecanora muralis)*
gelatinous lichen		blackish, jelly-like when moistened *(Collema coccophorum)*
squamulose lichen		discrete flakes that are round or ear-shaped, convex or concave, and often have lobed margins *(Psora decipiens)*
foliose lichen		"leafy," tending to be flattened with definite upper and lower surfaces *(Peltigera occidentalis)*
fruticose lichen		three-dimensional, ropey or branching, without definite upper and lower surfaces *(Aspicilia hispida)*

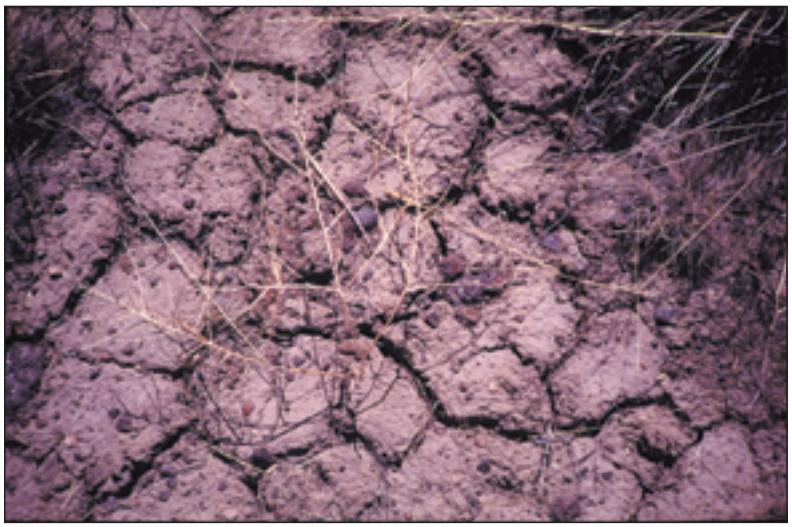


Figure 1.3 *Physical soil crusts. Vascular plant establishment is limited to cracks between polygons on physically crusted areas due to an impenetrable surface layer.*

aggregates by compacting them into a comparatively impermeable surface layer. These compacted surfaces have reduced infiltration rates and increased surface runoff. In this sense, they function hydrologically in a manner similar to raindrop-induced crusts.

Physical crusts may form on soil of almost any texture except coarse sandy soils containing very low silt and clay (Lemos and Lutz 1957). Soils especially susceptible to crusting are those with low organic matter and high silt, sodium, or calcium carbonate content. These characteristics are all related to soils with low structural and aggregate stability. Organic matter increases aggregate stability (through gluing of particles and moderation of forces that reduce aggregate stability), and places where plant residues are incorporated generally become planes of weakness, decreasing crust strength. Silts form strong bonds on drying, thus forming a hard crust. Silts also have low swelling and shrinking properties, so that the crust does not crack or disintegrate by itself.

Intensive grazing is often used to break up physical crusts. However, this result is short-lived, as the soil surface is resealed after the first minutes of an intense rainstorm. To effectively address a physical soil crusting problem, livestock grazing systems must promote greater soil aggregate stability (Thurow 1991). Therefore, management systems that promote soil surface protection (through plant and biological soil crust cover) and increase soil organic matter are the only lasting solution to physical soil crust reduction (Blackburn 1983).

CHAPTER 2

DISTRIBUTION AND FACTORS INFLUENCING SPECIES COMPOSITION

2.1 Distribution

Biological soil crusts in North America are diverse and are most evident in arid and semi-arid ecoregions (Fig. 2.1, 2.2). They are also found on shallow lithic sites and in alpine habitats throughout the continent and in many early-successional vegetation types in moister ecoregions. Some crustal organisms are good indicators of a specific vegetation type or ecoregion. Others, including *Microcoleus*, *Nostoc*, *Collema*, *Psora decipiens*, *Cladonia* spp., and *Bryum* spp. are common to many different geographic, climatic, and vegetation types. For instance, the same soil lichens (*Collema*, *Placidium*, *Psora*) dominate crusts of both the Sonoran and Great Basin deserts, as well as areas of South Africa and Australia, although vascular plant species and climate vary greatly between these regions. While most algae, lichens, and bryophytes are cosmopolitan, a few are endemic and may be common on a local or regional level (Table 2.1). For example, several of the squamulose lichens, such as *Placidium squamulosum*, *Psora decipiens*, *Psora cerebriformis*, and *Psora tuckermanii*, have very broad geographic ranges. Others, including *Catepyrenium congestum* and *Psora montana*, are endemic to North America or have narrow geographic ranges within the continent. Squamulose lichens have more endemic species worldwide than any other lichen morphological group.

Similarities in species composition may occur due to similar environmental conditions during the active growth period for crustal organisms. For example, alpine biological crusts actively grow in summer under moisture and temperature conditions that are similar to winter environmental conditions in the Sonoran Desert. Most crust growth occurs during wet, cool periods. In most North American deserts, this is generally late fall to early spring.

The appearance of biological crusts is variable. Physical structure of biological crusts is very similar in the hot deserts of the world, such as the Atacama, Sonoran, Chihuahuan, and Australian deserts, while very different from the physical structure in cool and cold deserts, such as the Colorado Plateau, Great Basin, and the Arctic (Fig. 2.3). Pinnacled crusts are found in areas where crusts are dominated by cyanobacteria, freezing temperatures are common, and vascular plant roots are lacking. Winter freezing heaves the soil upward, forming pinnacle-type microtopography. Subsequent



Figure 2.1 *Arid and semi-arid ecoregions of western North America. Areas shaded in black are cool deserts, while grey-shaded areas are hot deserts.*



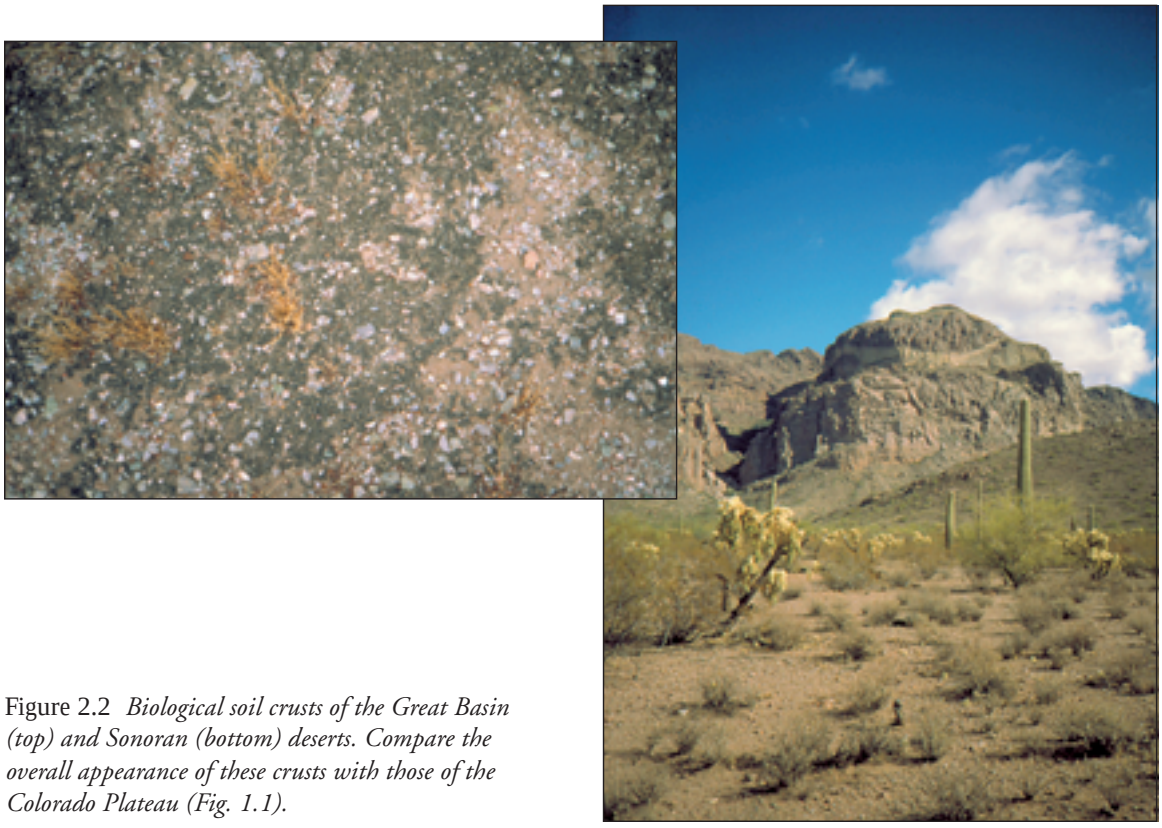


Figure 2.2 *Biological soil crusts of the Great Basin (top) and Sonoran (bottom) deserts. Compare the overall appearance of these crusts with those of the Colorado Plateau (Fig. 1.1).*

Table 2.1 *Soil crust lichens endemic to North America with both wide and limited distributions. Note that there are very few endemic species.*

Species	Distribution	Reference
Aspicilia californica	California Chaparral	Rosentreter 1998
Aspicilia filiformis	western North America	Rosentreter 1998
Aspicilia reptans	North America	Looman 1964
Catapyrenium congestum	Great Basin	Bruess and McCune 1994
Psora montana	western North America	Timdal 1986
Psora tuckermanii	Great Basin	Timdal 1986
Texosporium sancti-jacobi	western North America	McCune & Rosentreter 1992

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differential growth and erosion results in highly dissected pinnacles to 10 cm high (e.g., Colorado Plateau). Where freezing is common but soils are held in place with a heavy cover of lichens, mosses, and vascular plant roots, soil surfaces have a rolling rather than pinnacled topography (e.g., northern Great Basin). Where freezing is rare, crusts are flat when only cyanobacteria are present or rugose where lichens and/or mosses occur (e.g., the Sonoran Desert; Fig. 2.2, 2.3). In non-freezing regions, a layer of pebbles often covers cyanobacterial portions of the crust.

On the broad scale of western North America there are several different vegetation zones or ecoregions that contain biological soil crusts as major components (Fig. 2.1, Table 2.2, 2.3). The ecoregions used here are similar to those used by Bailey (1998). The most prevalent arid soils in North America are silt-loams and are more susceptible to physical disturbance than are clay-loams common to many other arid regions in the world, such as the red clay-loams of Australia.

2.2 Factors Influencing Distribution

2.2.1 Elevation

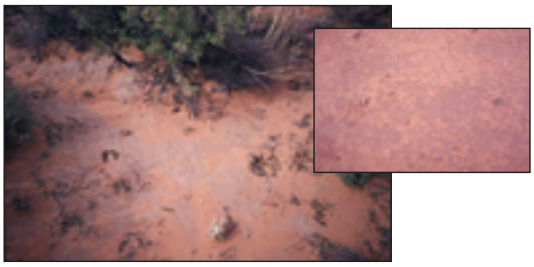
Total crust cover is inversely related to vascular plant cover, as less plant cover results in more surface available for colonization and growth of crustal organisms (Fig. 2.4-A). Thus, when all crust types are combined (cyanobacterial, moss, lichen), cover is greatest at lower elevation inland sites (less than 1,000 m) compared to mid-elevation sites (1,000 to 2,500 m; Hansen et al. 1999; Fig. 2.4-B). However, relative lichen and moss cover increases with elevation and effective precipitation until vascular plant cover precludes their growth (Fig. 2.4-C). Crust organisms have reduced water and nutrient

Figure 2.3 *Biological soil crust forms based on temperature characteristics of the environment.*

HOT DESERTS

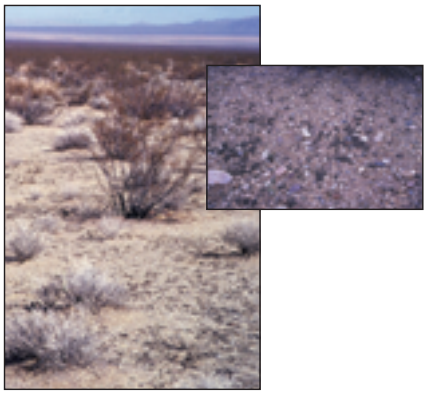
flat





rugose

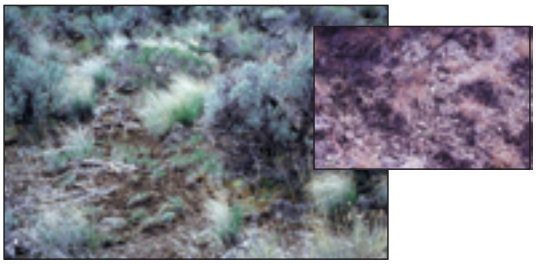




COOL DESERTS

rolling





pinnacled



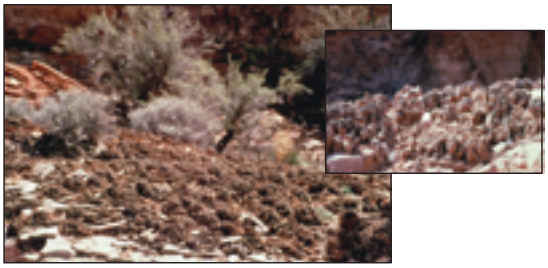


Table 2.2 *Soil, climatic, and vegetative characteristics for low and mid elevations in temperate North American arid and semi-arid ecoregions. Adapted from Bailey (*1995).

Ecoregion (Bailey's Ecoregion Province)	Dominant Soil Order	Soil Moisture/ Temperature	Average Annual Precipitation (mm)	Moisture Season/Form	Mean Annual Temperature Range (°C)	Predominant Evolutionary Disturbance	Vegetation Type
COOL DESERTS							
Columbia Basin (temperate semidesert)	mollisol	xeric/mesic	230-635	winter/rain spring/rain	4-14	drought	perennial grassland
Great Basin (temperate semidesert and desert)	aridisol	aridic/mesic to cryic	180-380	winter/snow spring/rain	4-13	drought	sagebrush steppe
Colorado Plateau (temperate semidesert and desert)	alfisol	xeric/thermic	205-510	winter/snow spring/rain summer/rain	4-13	drought	shrubland woodland
Great Plains (temperate steppe and dry steppe)	mollisol	ustic/mesic	485-735	winter/snow spring/rain summer/rain	8-15	fire, grazing	prairie
HOT DESERTS							
Mojave Desert (tropical/subtropical desert on sand)	aridisol	aridic/hyperthermic	100-150	winter/rain	13-29	drought	shrubland
Chihuahuan Desert (tropical/subtropical semidesert and desert on sand)	aridisol	aridic/thermic	205-325	summer/rain	10-18	drought	shrubland
Sonoran Desert (tropical/subtropical desert on sand)	aridisol	aridic/thermic	75-255	summer/rain fall/rain	10-24	drought	mixed thorn scrub
COASTAL CHAPARRAL							
California Chaparral (Mediterranean dry steppe)	mollisol	xeric/thermic	255-635	winter/rain	16-18	fire	chaparral

Table 2.3 *Dominant biological soil crust components and forms in North American arid and semi-arid ecoregions.*

Ecoregion	Dominant Biological Crust Components	Crust Morphology
Columbia Basin	tall mosses, green algae	rolling
Great Basin	moss, lichen	rolling
Colorado Plateau	non-heterocystic cyanobacteria *(Microcoleus)*, nitrogen-fixing lichens *(Collema)*	pinnacled
Great Plains	vagrant and foliose lichens	flat to rugose or rolling
Mojave Desert	non-heterocystic cyanobacteria *(Microcoleus)*, nitrogen-fixing lichens *(Collema)*, squamulose lichens, short mosses	flat to pinnacled
Chihuahuan Desert	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, short moss	flat
Sonoran Desert	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, gelatinous (nitroen-fixing) lichens (e.g., *Collema*), squamulose lichens, short mosses	flat
California Chaparral	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, lichens, liverworts	flat

needs compared to vascular plants and can withstand the harsh growing conditions found in plant interspaces (Anderson et al. 1982a).

The positive relationship between biological crust cover and available soil surfaces has been amply demonstrated (Rogers 1972; Harper and Marble 1988; West 1990; Eldridge 1993b; Johansen 1993). As harsh environmental conditions limit vascular plant cover, greater cover of crusts in lower elevation sites probably occurs in spite of, not because of, these conditions.

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2.2.2 Soils and Topography

Stable or embedded rocks near or at the soil surface can increase the percent crust cover by perching water and armoring the surface from physical disturbances (Fig. 2.4-D). Shallow soils often support a wide variety of cyanobacteria, lichens, and mosses, regardless of soil texture (Fig. 2.4-E).

Soil texture heavily influences the species composition of biological crust communities. The more stable, fine-textured soils (such as gypsum and silty loams) support greater cover and more varied populations of cyanobacteria, lichens, and mosses (Fig. 2.4-F)

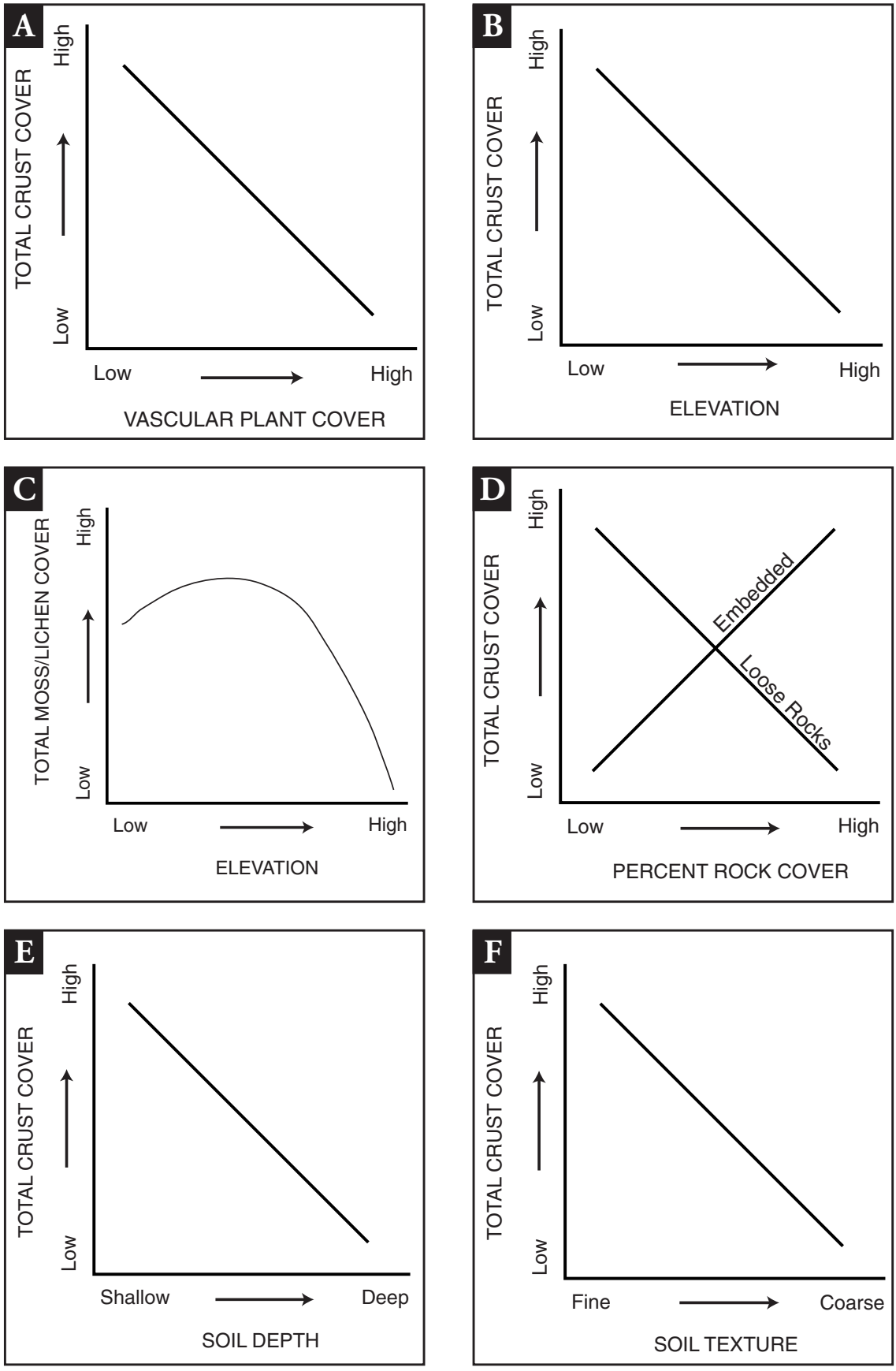


Figure 2.4 *General ecological relationships for biological soil crusts.*

than less stable, coarse-textured soils (Kleiner and Harper 1977b; Hansen et al. 1999). Coarse-textured soils may have only large filamentous cyanobacteria that are highly mobile (such as *Microcoleus*). However, once coarse-textured soils are sufficiently stabilized by larger cyanobacteria, other crustal organisms can then colonize, including smaller green algal and cyanobacterial taxa (such as *Scytonema* and *Nostoc*). Regardless of soil type, the first lichen to colonize is generally *Collema*, followed by *Placidium* (and *Caloplaca* in the northern Great Basin). In more unstable soils, lichens and mosses may be found only under vascular plants, where some protection from sediment burial is provided, or on north slopes, where greater moisture availability favors growth. Soil surface stability is influenced by texture (percent of sand, clay, silt), depth, and moisture content (wet, moist, dry). Sand and silt are more susceptible to surface disturbance when dry, while clay is highly stable (Fig. 2.5).

In later successional stages on stable surfaces, common lichen species include *Fulgensia bracteata*, *F. desertorum*, *Squamarina lentigera*, *Diploschistes muscorum*, and *Psora* spp. Common moss genera include *Tortula*, *Bryum*, and *Grimmia*. As soil stability increases, rich communities of cyanobacteria, lichens, and mosses become more widespread, covering all surfaces not occupied by vascular plants or rock.

Soil chemistry can also influence crust cover and composition. Calcareous and gypsiferous soils generally support high coverage of species-rich crust with some taxa being excellent indicators of soil chemistry (Table 2.4). Often physical crusts form stable surfaces that perch soil moisture, and given long periods without physical disturbance, will support both biological soil crusts and lichens or mosses normally found on rocks. Other abiotic factors that influence relative cover of microbiotic crusts are slope and aspect. Crustal organisms are only active when moist, and most active when warm. Therefore, north and east slopes generally favor crustal development in lower elevation desert regions. Slope angle does not generally affect crust cover or species richness, except where the slope or soils are unstable (Rosentreter 1986; Kaltenecker et al. 1997; Belnap and Bowker, unpublished data).

2.2.3 Disturbance

Intensity and type of soil surface disturbance, along with time since disturbance, influence the composition of biological crusts (see Chapter 4). The presence, absence, and abundance of early- or late-successional taxa can provide information regarding a site's disturbance history. This information, combined with data on vascular plant community composition, can assist the land manager in understanding a site's history, potential productivity, and ecological integrity.

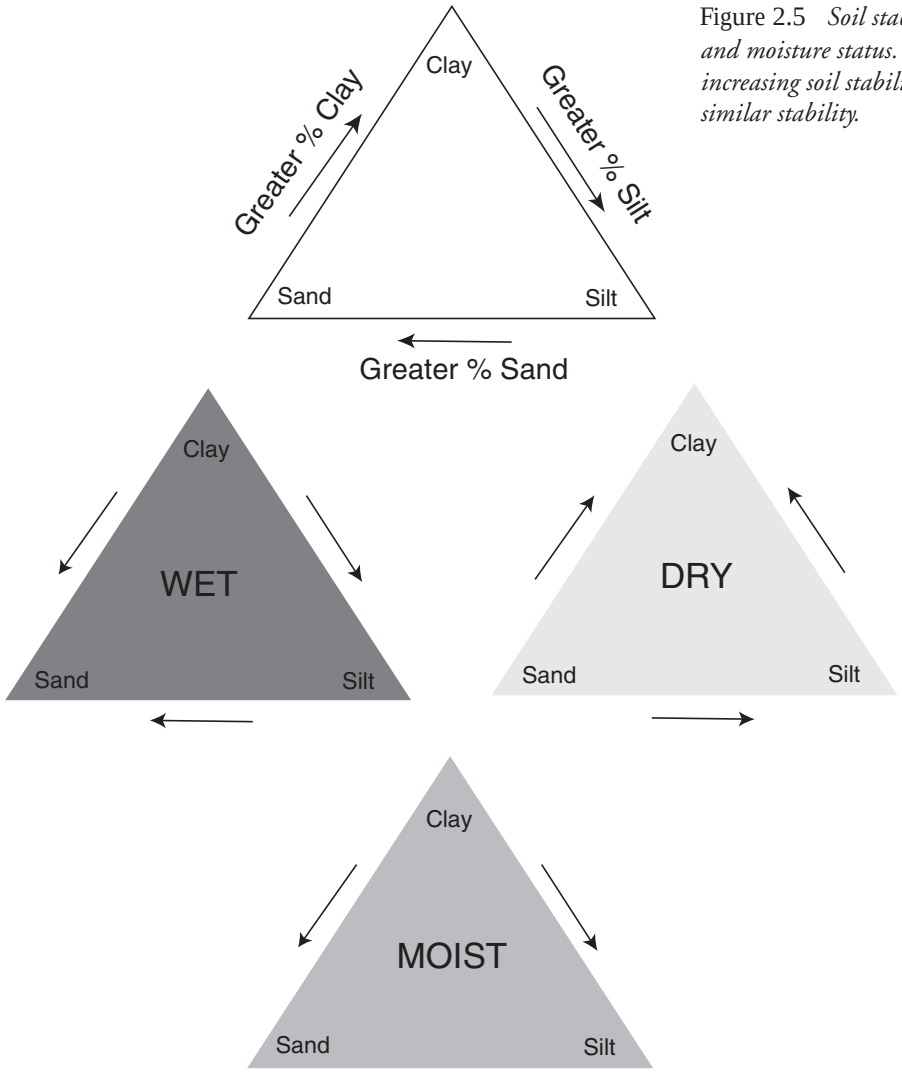


Figure 2.5 *Soil stability relative to texture and moisture status. Arrows indicate increasing soil stability. No arrow indicates similar stability.*

		Soil Texture		
		Sand	Clay	Silt
Soil Moisture Content	Frozen	High	High	High
	Wet	Medium-High	Low	Medium
	Moist	Medium	Low	Medium
	Dry	Low	High	Medium-Low

Table 2.4 *Soil crust lichens that are calcium carbonate indicators. Adapted from McCune and Rosentreter 1995.*

Low calcium carbonate	High calcium carbonate
Acarospora schleicheri	*Aspicilia fruticulosa*
Arthonia glebosa	*Aspicilia hispida*
Aspicilia reptans	*Buellia elegans*
Aspicilia filiforma	*Caloplaca tominii*
Cladonia borealis	*Collema tenax*
Diploschistes muscorum	*Fulgensia* spp.
Leptochidium albociliatum	*Heppia lutosa*
Megaspora verrucosa	*Phaeorrhiza nimbosa*
Ochrolechia upsaliensis	*Psora cerebriformis*
Placynthiella spp.	*Psora decipiens*
Psora nipponica	*Psora tuckermanii*
Xanthoparmelia wyomingica	*Toninia sedifolia*

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Intense disturbance results in bare soil. Severely, newly, or frequently disturbed soils are generally dominated by large filamentous cyanobacteria (Anderson and Rushforth 1976; Johansen et al. 1981, 1984; Johansen and Rushforth 1985; Harper and Marble 1988). When disturbance is less severe, less frequent, or some time has elapsed since the disturbance, crusts are generally in some mid-successional state, with some lichens and mosses present. Most of these species reproduce asexually, a life-history strategy that increases the probability of establishment (Rosentreter 1994). If disturbance continues, crusts will stay in early-successional stages (i.e., cyanobacteria only).

2.2.4 Timing of Precipitation

Dominance of biological crusts is highly influenced by seasonal precipitation patterns. Ecoregions that receive summer monsoons (e.g., the Sonoran Desert) tend to have a greater diversity of heterocystic cyanobacteria (such as *Lyngbya*, *Calothrix*, *Schizothrix*, and *Nostoc*) and lower lichen abundance. Lichens in these areas generally include the gelatinous genus *Collema* and squamulose genera *Placidium* and *Peltula* (Table 2.3). Large thalloid liverworts are more common in warm deserts than in the cool deserts of North America. In cool deserts, crusts are dominated by non-heterocystic cyanobacteria (such as *Microcoleus vaginatus*) and a diverse lichen flora, including *Acarospora schleicheri*, *Aspicilia* spp., *Candelariella*

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spp., *Collema* spp., *Diploschistes muscorum*, *Endocarpon pusillum*, *Placidium* spp., and *Psora* spp. These lichens physiologically prefer cool-season moisture and are adapted to lower light intensities common during winter months. The Columbia Basin, which receives more moisture and has more winter rain than the Great Basin, has a greater abundance of mosses than lichens (Ponzetti et al. 1998).

Biological soil crusts in regions influenced by fog, such as portions of the California Chaparral, support fruticose lichens that intercept moisture from the air (*Dendrographa* and *Schizopelte*). Biological crusts in many regions are best developed in interspaces between shrubs. In contrast, fog deserts show the best crust development under shrubs, due to the moisture intercepted by plant structure or by rock surfaces.

2.2.5 Vascular Plant Community Structure

The vertical and horizontal vascular plant structure of many arid and semi-arid vegetation communities optimizes growth of biological soil crusts. In cooler regions, greater structural diversity of vascular vegetation generally results in greater compositional diversity of biological crusts. Vascular plants create windbreaks and shade, influencing how much moisture and light reach the soil surface. They also trap leaf litter, keeping the interspaces free of substantial or persistent litter cover (Rosentreter and McCune 1992).

Invasive exotic plants generally decrease the structural diversity of native vascular plant communities by creating monocultures of densely spaced plants and by homogenizing litter distribution. They also lead to decreased biological crust cover and species richness in most ecosystems (Rosentreter 1994; Kaltenecker 1997). In addition, if moisture is retained under a litter layer for long periods while temperatures are warm, lichens can become parasitized by ubiquitous molds (Rosentreter 1984).

2.2.6 Ecological Gradients

Some lichens form natural replacement series along the same ecological gradients that influence vascular plants, although some lichen taxa are not good indicators of site conditions due to broad ecological amplitudes. For example, gelatinous lichens are most common in aridic calcareous sites and mesic non-calcareous sites (Fig. 2.6). Sites with frigid soil temperature regimes (mean annual temperature less than 8°C) lack significant cover of gelatinous lichens. The genus *Leptogium* might be present; however, *Peltigera* and *Massalongia* tend to be more common. Some species display a shift in substrate preference in different ecoregions. For example, *Leptochidium albociliatum* occurs on mosses in the Great Basin, while in the Columbia Basin it is more common and occurs on bare mineral soil (Rosentreter 1986; Ponzetti et al. 1998).

2.2.7 Microhabitats

Biological soil crusts can also create their own microstructure, which influences species distribution. Mosses create microsites that are very low in nutrients, low in calcium carbonate, and that retain moisture longer than bare mineral soil. This creates favorable sites for lichens that may benefit from the improved moisture regime and do not require many soil nutrients. Common examples include *Leptogium lichenoides*, *Massalongia carnosa*, and *Peltigera* spp. that grow only on mosses and are found in many sagebrush (*Artemisia*) steppe habitats.

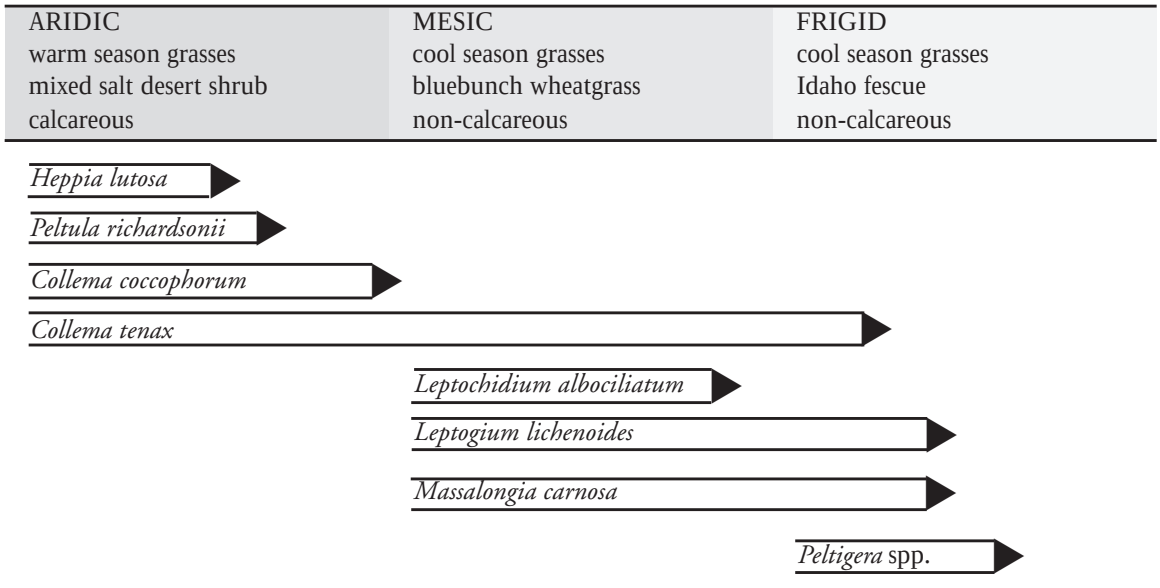
2.3 Unique Crustal Communities in North America

Special geologic features or soils create conditions that promote growth of biological soil crusts. Some of these sites support crusts containing uncommon associations or rare species. These unique crustal communities are not common across the landscape but are at times locally abundant. Some unique crustal communities are discussed below.

2.3.1 Gypsum

Gypsiferous outcrops are comprised of soils that are fine textured and have high concentrations of sulfate and calcium. Vascular plant cover at these sites is generally sparse with limited species diversity. Gypsiferous soils can support well-developed

Figure 2.6 *Gelatinous and other nitrogen-fixing lichens by relative soil temperature and calcareous influence.*



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biological crusts with a high lichen diversity (Anderson and Rushforth 1976; St. Clair et al. 1993), although sites in the hot deserts of the southwestern U.S. lack the species diversity of the cool deserts to the north. Common species include *Diploschistes diacapsis*, *Psora decipiens*, *Collema tenax*, *Placidium squamulosum*, *Buellia elegans*, and *Squamarina lentigera*. Several lichens are restricted to gypsiferous soils, including *Acarospora nodulosa* var. *nodulosa* (St. Clair and Warrick 1987), *Gypsoplaca macrophylla* (Timdal 1990), and *Lecanora gypsicola* (Rajvanshi et al. 1998). Gypsiferous sites are worthy of protection because of their high potential for cover and biological crust diversity. These sites are often threatened by mining activity due to the commercial value of gypsum.

2.3.2 Glades (Lithic and Shallow Soil Sites)

Glades are widespread across North America but are limited both locally and in overall area. Lithic and shallow soil sites are often colonized by biological crusts because these sites are extremely droughty and vascular plant growth is limited. In eastern forests, shallow disturbed or compacted soil (e.g., along roadsides) may be dominated by biological soil crusts, with *Baeomyces rufus* or *B. fungoides* often forming extensive crustal colonies. Pine barrens generally support extensive biological crusts. In western and more northern boreal forest openings, *Cladonia* spp., *Peltigera* spp., and occasionally *Multiclavula* spp. are dominant. These genera are also common on disturbed soil along roadways and cutbanks throughout the non-arid portions of the continent. Some lithic sites in wet climates are leached of soil nutrients and are often dominated by gelatinous lichens such as *Leptogium* or nitrogen-fixing cyanobacteria such as *Nostoc*.

2.3.3 Thermal Springs

Some parts of western North America contain extensive active or dormant thermal (hot) springs. Conditions in these areas are harsh, limiting vascular plant growth. Soil temperatures are often extremely high in summer and warm in winter. Soils containing thermal springs are often infertile, as warm water leaches many minerals, including calcium, magnesium, nitrogen, and phosphate. Toxic heavy metals can be present in the water and thus get deposited on the soil surface. These areas are covered with specialized thermic cyanobacteria when moist. When dry, they support either non-specialized biological crusts or crusts characteristic of gypsum.

2.3.4 Cold Desert Playas

Small ephemeral pools form in parts of the Pacific Northwest where summers are hot and dry and winters are cool and moist (Rosentreter and McCune 1992). These sites are located on poorly drained basalt or other rock types, often barren of vascular vegetation and usually surrounded by some species of sagebrush (*Artemisia*). Drainage may be impaired by rock type or frozen soils, causing water to pond seasonally in flat, exposed areas. In late winter and early spring these sites experience cool, yet above freezing, temperatures for portions of the day. These conditions allow for slow evaporation of standing water. Such sites are sometimes referred to as playettes, as they are similar to but smaller than large seasonal lakes called playas. Playas support either attached or vagrant forms of *Dermatocarpon miniatum* and *Nostoc*. *Nostoc commune* found in these sites includes the common filamentous form, the colonial-eggs form, and occasionally the long, hair-like unattached form (referred to as var. *flagellaris*). Small playettes covered with fine silts can be colonized by *Nostoc* and by crustose lichens more typically occurring on rocks, such as *Lecanora muralis* (Rosentreter 1986).

2.3.5 Alpine Sod

Biological soil crusts are either dominant or common community components in many alpine and subalpine sites in North America. Alpine and subalpine sites contain some species common to the continent's arid regions. In contrast, a few lichens are characteristic of alpine crusts alone and include *Lecidoma demissum*, *Solorina* spp., *Lepraria neglecta*, *Ochrolechia frigida*, and *Thamnolia* spp. (DeBolt and McCune 1993). A genus that occurs on soil or rock in both alpine and arctic sites is *Stereocaulon*, which fixes nitrogen and is common worldwide in montane and alpine habitats (Lamb and Ward 1974). In the subalpine zone, biological crusts are often associated with areas where snowdrifts occur. Lichens characteristic of snow-patch sites are *Solorina crocea* and *Lepraria neglecta* (McCune 1998). Cyanobacterial crusts are also common in these areas and are generally dominated by *Nostoc* species (Reisiegl 1964).

2.3.6 Arctic Tundra

Alpine and tundra soils are often dominated by fruticose lichens (*Cladina* and *Cetraria*) and graminoids. Some areas are dominated by fruticose lichens that start out as crust communities in the early stages of succession. Tundra areas in North America have poor drainage due to frozen ground and are similar to other portions of the northern hemisphere, including Greenland. In some arctic regions there are also large areas of dry steppe-like vegetation, open

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Dryas heaths, and fell-fields with extensive coverage of biological crusts. Cyanobacterial crusts are commonly extensive and often dominated by *Nostoc* species (Hansen 1997).

2.4 Example: Biological Soil Crusts in Sagebrush Communities

Sagebrush species are common in western North America, particularly in the Great Basin and Columbia Plateau vegetation zones. Some of the same characteristics that influence sagebrush taxa distribution also influence biological crust development. Relative cover of biological crusts in various sagebrush vegetation types is presented in Table 2.5. Biological soil crusts tend to be lacking in sagebrush types that occur on seasonally flooded soils (silver, alkali, and fuzzy sagebrush; Winward 1980), as flooded soils create anaerobic conditions that are not well tolerated by lichens. Heavily saline soils also lack lichen cover, although moss is sometimes present if the salt concentration is not too great. Mountain, subalpine, and xeric big sagebrush types often lack significant biological crust cover due to dense vascular vegetation and accumulating plant litter. Other sagebrush types support higher biological crust cover unless soil surfaces are greatly disturbed or the current vegetation is in an early-successional stage.

Some lichens are good indicators of late-successional stages in sagebrush communities. The dual gradient theory proposed by McCune (1993) for lichen species succession in forested habitats applies well to arid and semi-arid regions in that species respond to time (age) and moisture in similar successional trajectories. Therefore, the length of time since the last major site disturbance or an increase in effective soil moisture will both provide suitable ecological conditions to support specific lichen species. This is why biological soil crust communities in different ecoregions recover at different rates (Table 2.2, Chapter 4).

Late-successional indicator species in sagebrush-steppe include *Acarospora schleicheri*, *Massalongia carnosa*, *Pannaria cyanolepra* (type b), *Trapeliopsis wallrothii*, *Trapeliopsis* sp. nov. (McCune, unpublished), and *Texosporium sancti-jacobi*. Some lichens are only present in late-successional communities because they grow upon other lichens or mosses. For example, *Acarospora schleicheri* grows upon *Diploshistes muscorum*, which in turn parasitizes the lichen genus *Cladonia*. Therefore, *Cladonia* can be considered a keystone organism influencing a site's diversity. *Massalongia carnosa* primarily grows on mosses and is not present until mosses become well established within a site. *Texosporium sancti-jacobi* is restricted to old-growth sagebrush communities and occurs only on decaying organic matter (McCune and Rosentreter 1992). Other lichens that commonly occur on decayed organic matter but are not restricted to old-growth sites include *Buellia papillata*, *B. punctata*, *Caloplaca* spp., *Lecanora* spp., *Megaspora verrucosa*, *Ochrolechia upsaliensis*, *Placynthiella* spp., and *Phaeophyscia decolor*.

Table 2.5 *Relative cover of biological soil crusts in sagebrush (Artemisia) vegetation types.*

HIGH biological crust cover	LOW biological crust cover
Tall Sagebrush	
Wyoming big sagebrush *(A. tridentata* ssp. *wyomingensis)*	subalpine big sagebrush *(A. tridentata* ssp. *spiciformis)*
basin big sagebrush *(A. tridentata* ssp. *tridentata)*	xeric big sagebrush *(A. tridentata* ssp. *xericensis)*
mountain big sagebrush** *(A. tridentata* ssp. *vaseyana)*	mountain big sagebrush** *(A. tridentata* ssp. *vaseyana)*
	silver sagebrush *(A. cana)*
	three-tip sagebrush *(A. tripartita)*
Short Sagebrush	
low sagebrush *(A. arbuscula)*	alkali sagebrush *(A. longilobia)*
black sagebrush *(A. nova)*	fuzzy sagebrush *(A. papposa)*
stiff sagebrush *(A. rigida)*	
Bigelow sagebrush *(A. bigelowii)*	
fringed sage *(A. frigida)*	

**Biological crust cover high or low depending on site characteristics.

CHAPTER 3

ECOLOGICAL ROLES

In a given ecoregion, ecological roles of biological soil crusts can vary widely in their importance and will depend on crust composition and biomass, as well as characteristics of the specific ecosystem being considered.

3.1 Species Composition and Biomass

The relative importance of biological crusts and their different ecological roles within an ecosystem is highly dependent on relative cover of various crustal components. For example, carbon inputs are higher when mosses and lichens are present than when the crust is dominated by cyanobacteria. Nitrogen inputs are higher with greater cyanobacterial biomass and greater cyanolichen cover. Water infiltration and soil surface stability are related to cyanobacterial biomass as well as moss and lichen cover.

3.2 Carbon Fixation

Biological soil crusts can be an important source of fixed carbon on sparsely vegetated areas common throughout western North America (Beymer and Klopatek 1991). While vascular plants contribute organic matter to soils directly beneath them, large interspaces between plants receive little plant material input. Where biological soil crusts are present, carbon contributed by these organisms helps keep plant interspaces fertile, providing energy sources for soil microbial populations.

Crustal organisms are physiologically active only when wet, and metabolic functions begin almost immediately. Respiration begins less than 3 minutes after wetting, while photosynthesis reaches full activity after 30 minutes or more. Soil oxygen concentrations, a by-product of photosynthesis, reach steady states within 1 to 2 hours of wetting (Garcia-Pichel and Belnap 1996). Rain during hot months can place lichens in a state of carbon deficiency, as the lichens can dry out before photosynthesis has begun. Jeffries et al. (1993a, b) showed cyanobacterial crusts from the Colorado Plateau had positive carbon balances only during prolonged wet periods, such as winter and spring, and that short-term wet-dry cycles, which often occur in low-elevation inland sites during summer, resulted in net carbon loss for both *Microcoleus*- and *Scytonema*-dominated crusts (this would also be expected for *Collema* and other soil lichens). Consequently, timing

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and duration of precipitation may heavily influence carbon budgets in crustal organisms and thus influence the distribution of individual species.

Winter-rain deserts (e.g., Mojave and Great Basin) have a rich soil lichen flora, with the cyanobacterial flora heavily dominated by *Microcoleus*. In contrast, summer-rain deserts (e.g., Sonoran) have only a small subset of the lichens found in winter-rain deserts, while the cyanobacterial flora is a complex community co-dominated by up to 10 species. Different responses to timing and amount of precipitation and temperature may mean species composition will shift in response to predicted climate changes. Since many areas that are currently winter-rain dominated are predicted to receive increased summer rain, effects of climate change may be reflected in different soil crust composition than that currently found in the summer-rain versus the winter-rain deserts.

Soil lichens have several different strategies to optimize carbon gain (Lange et al. 1992, 1994, 1997). While photosynthesis is activated at low-water content for all species, each varies in response to higher water content. Cyanolichens, such as *Collema tenax*, showed dramatic drops in carbon fixation when water content exceeded 60 to 80%. Conversely, green algae generally showed little, if any, depression at high-water content. Water-holding capacity varies between lichens and will also influence time of carbon fixation for a given species.

Table 3.1 *Common nitrogen-fixing lichens and cyanobacteria in cool and hot deserts of the western U.S.*

Cool Deserts	Hot Deserts
Lichens	
Collema coccophorum	*Collema coccophorum*
Collema tenax	*Collema tenax*
Heppia	*Heppia*
Leptochidium albocilitatum	*Peltula*
Leptogium	
Massalongia carnosa	
Pannaria	
Peltigera	
Polychidium	
Cyanobacteria	
Microcoleus vaginatus (non-heterocystic)	*Schizothrix* (heterocystic)
Nostoc (heterocystic)	*Nostoc* (heterocystic)
Scytonema (heterocystic)	*Scytonema* (heterocystic)

Photosynthetic rates are also dependent on temperature (Rychert et al. 1978; Lange 1980; Nash et al. 1982; Nash and Moser 1982; Lange et al. 1997). Photosynthetic rates increase with increasing temperatures to about 28°C, above which rates decline dramatically. *Collema tenax* is an exception, with no such decline seen up to 36°C.

3.3 Nitrogen Fixation

Nitrogen concentrations are known to be low in desert soils compared to other ecosystems. Total atmospheric input over the past 10,000 years has been conservatively estimated at about 3 kg nitrogen/m^2, with 77% lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990). Extensive surveys in cool deserts have revealed only a few nitrogen-fixing plants (Farnsworth et al. 1976; Wullstein 1989). Since nitrogen can limit net primary productivity in many desert ecosystems (Ettershank et al. 1978; James and Jurinak 1978; Romney et al. 1978; Nobel et al. 1988), maintaining normal nitrogen cycles is critical to soil fertility and prevention of desertification (Dregne 1983).

Cyanobacteria and cyanolichens can be an important source of fixed nitrogen for plants and soils in desert ecosystems (Evans and Ehleringer 1993; Belnap 1995). Many biological soil crusts in western North America are dominated by nitrogen-fixing cyanobacteria and lichens (Table 3.1). These organisms are capable of both light and dark nitrogen fixation (Rychert and Skujins 1974; Pearson et al. 1981; Paerl 1990; Belnap 1994). Nitrogen fixation is highly dependent on past and present water and light regimes, as well as species composition (Rychert et al. 1978; Belnap 1994). Fixation rates are highest after photosynthesis has replenished lichen carbon stores. For most lichen species, nitrogen-fixation rates increase with temperature to 25°C, given sufficient moisture. Since nitrogen-fixation rates depend on the cover of specific crust species, timing, extent, and type of past disturbance are also critical factors (Belnap 1995, 1996). Nitrogen-fixation rates in biological soil crusts have been estimated at 2 to 365 kg/ha annually (Mayland et al. 1966; MacGregor and Johnson 1971; Rychert and Skujins 1974; Eskew and Ting 1978; Jeffries et al. 1992), with recent studies indicating that higher rates are probably more accurate (Belnap, unpublished data). Still, rates are expected to vary greatly, depending on the species present and environmental conditions.

Five to 88% of nitrogen fixed by *Nostoc* has been shown to leak into the surrounding substrate (Magee and Burris 1954; Silvester et al. 1996; Belnap et al. 1997). Nitrogen released from crustal

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Figure 3.1 *Disturbance plots on the Colorado Plateau showing the difference in soil surface color between undisturbed (dark) and disturbed (light) plots. Note that the undisturbed plots have greater surface roughness than the disturbed plots.*

organisms is readily taken up by surrounding vascular plants, fungi, and bacteria (Mayland and MacIntosh 1966; Mayland et al. 1966; Stewart 1967; Jones and Stewart 1969). Vascular plants growing in biologically crusted soils show higher tissue concentrations of nitrogen than plants grown in uncrusted soils (Harper and Pendleton 1993; Belnap 1994, 1995; Belnap and Harper 1995). As with carbon, crusts contribute nitrogen to soils both under plants and in plant interspaces, thereby counteracting the tendency of these nutrients to concentrate around perennial plants.

3.4 Albedo

Soil albedo is a measure of the energy reflected off the soil surface. Dark surfaces absorb more energy, are warmer than light surfaces, and thus have lower albedo. Because soils with well-developed biological crusts are dark, they can be up to 23°F warmer than adjacent crusted surfaces (Fig. 3.1; Belnap 1995; Belnap, unpublished data). Disturbance of biological crusts increases albedo and therefore decreases soil temperatures. This affects many ecosystem processes. Metabolic processes, for example, including photosynthesis and nitrogen fixation, decrease at lower temperatures (see Sections 3.2 and 3.3; Nash 1996). Lower soil temperatures decrease microbial activity, plant nutrient uptake rates, and soil water evaporation rates; delay seed germination time; and decrease seedling growth rates. Timing of these events is often critical in deserts, and modifications can reduce species fitness and seedling establishment, which in turn may eventually affect plant community structure (Bush and Van Auken 1991). Changes in albedo can also affect animal populations. For instance, foraging times are often partitioned among ants, arthropods, and small mammals on the basis of soil surface temperature (Doyen and Tschinkel 1974; Wallwork 1982; Crawford

1991). In addition, many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth 1978). Consequently, altering surface temperatures can affect desert ecosystems at numerous levels.

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3.5 Effects on Vascular Plants

3.5.1 Seed Germination

Biological crusts can affect vascular plant germination. While small cracks and crannies on the soil surface are generally sufficient for small-seeded plants to lodge and germinate, most large-seeded plants need soil or plant litter cover to germinate. In deserts where plant litter is often limited in interspaces, large native seeds generally have self-burial mechanisms (such as hygroscopic awns) or are cached by rodents. Many exotic species, however, lack self-burial mechanisms. Because biological crusts stabilize soils, germination of such seeds can be inhibited in sites with well-developed crusts and low plant litter, as was recently demonstrated for the annual exotic grass, cheatgrass (*Bromus tectorum*), in both the field and laboratory (Larsen 1995; Kaltenecker et al. 1999a; Belnap, unpublished data). Though crusts can reduce germination of some seeds, seedling germination *per se* has not been shown to limit species density in desert plant communities. Rather, studies worldwide show vascular plant cover and structure are most often controlled by water and/or nutrient availability rather than other site factors (Mabbutt and Fanning 1987; Tongway and Ludwig 1990; Dunkerley and Brown 1995).

3.5.2 Plant Establishment and Cover

Biological soil crusts have not been shown to present a barrier to seedling root penetration once seeds germinate (Belnap, unpublished data; Pendleton and Meyer, unpublished data). This is in contrast to physical crusts, which often inhibit root penetration. Areas



Figure 3.2 *Sandberg bluegrass* (Poa secunda) *growing in well-developed biological soil crusts in the northern Great Basin.*

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that have been lightly trampled (to keep crusts from developing) over a 5-year period that included both wet and dry years show no additional plant establishment (Belnap, unpublished data; Fig. 3.1). Many authors have shown that seedling establishment of both forbs and grasses is either not affected or is increased by the presence of biological soil crusts, on both coarse- and fine-textured soils (Fig. 3.2; St. Clair et al. 1984; Harper and St. Clair 1985; Eckert et al. 1986; Harper and Marble 1988; Lesica and Shelley 1992; Belnap 1993).

Numerous authors have reported that biological crusts either do not compete with vascular plants (Kleiner and Harper 1972, 1977a, b; Anderson et al. 1982b; Jeffries and Klopatek 1987; Beymer and Klopatek 1992) or that vascular plant cover is enhanced by the presence of a biological crust (Dadlich et al. 1969; Graetz and Tongway 1986; Rosentreter 1986; Mucher et al. 1988; Carleton 1990; Ladyman and Muldavin 1994; Ladyman et al. 1994). This suggests that the presence of plants can aid the survival of crustal components, perhaps because of microclimate conditions associated with clumped perennial vegetation (such as decreased soil surface temperatures, increased surface moisture due to shading, and decreased wind speed on the soil surface). A few authors have speculated that there is a negative relationship between cover of biological crusts and vascular plants (Savory 1988 reviewed in West 1990). However, this view is not supported by the numerous studies that have directly addressed this issue. Rather, it appears more likely that biological crusts simply cover soils unoccupied by vascular plants.

3.5.3 Nutrient Levels in Vascular Plants

Plants growing in biologically-crusted soil often show higher concentrations and/or greater total accumulation of various essential nutrients than do plants growing in adjacent, uncrusted soils (Belnap and Harper 1995; Harper and Belnap in press). In one study, leaf tissue nitrogen was 9% higher in the perennial shrub *Coleogyne*, 31% higher in the perennial forb *Streptanthella*, and 13% higher in the annual grass *Festuca* (*Vulpia*), for plants growing in biologically-crusted soil compared to plants in adjacent uncrusted soil. Dry weight of *Festuca* plants in the crusted soil was twice that of plants in the uncrusted soil (Belnap 1995; Belnap and Harper 1995). Nitrogen concentrations in leaf tissue of the biennial *Mentzelia multiflora* was higher in plants growing in a biologically-crusted area relative to plants from an adjacent sand dune that lacked a crust. In greenhouse experiments, nitrogen levels in *Sorghum halepense* were higher when the plant was in pots with cyanobacteria than when in pots without cyanobacteria. Dry weight of plants in pots with cyanobacteria were up to four times greater than in pots without cyanobacteria (Harper

and Pendleton 1993). Other authors have obtained similar results with other species (Shields and Durrell 1964; Brotherson and Rushforth 1983; Pendleton and Warren 1995).

Several mechanisms may explain this enhanced effect on vascular plant growth and nutrient status. Material blowing across biological soil crusts can become trapped, either accumulating within low pockets in the microtopography or sticking by exudate to cyanobacterial sheaths. These sheaths are phototropic, and if not buried too deeply, will push through loose soil and organic matter, further trapping or entangling soil in the process (Fryberger et al. 1988; Campbell et al. 1989; Gillette and Dobrowolski 1993). Danin et al. (1989) proposed a positive feedback loop in which crusts trapping fine particles create nutrient-rich microsites, increasing germination and growth of vascular plants, which in turn reduces erosion potential and increases accumulation of washed or wind-blown soil.

In addition, cyanobacterial sheath material is often coated with negatively charged clay particles. These clay particles are more nutrient rich than sand (Black 1968), as they bind positively charged macronutrients and prevent them from leaching through the soil profile (Belnap and Gardner 1993). Lange (1974) demonstrated that compounds in the gelatinous sheath material of several cyanobacteria taxa were able to chelate iron, copper, molybdenum, zinc, cobalt, and manganese. Four of the five genera shown to possess this ability (*Anabaena*, *Anacystis*, *Lyngbya*, and *Nostoc*) are commonly represented in biological crusts of western North American deserts (Shields and Durrell 1964). It is also possible that the nutrient differences result from thermal effects, as crusted soils are darker and warmer than uncrusted soils; nutrient uptake by vascular plants would occur at a higher rate.

Herbivores and other consumers may benefit directly from the enhanced nutrient status of plants grown in healthy, biologically-crusted soils (Belnap and Harper 1995). Indirect effects include positive correlations between soil mycorrhizae and microarthropod populations with the presence of well-developed biological soil crusts (Harper and Pendleton 1993; Belnap, unpublished data).

3.6 Water Relations

The effect of biological soil crusts on soil-water relations is highly site dependent. Level of crustal development (e.g., cover and relative composition of cyanobacteria, lichen, moss), climatic regimes, the amount of surface roughness, time since destructive disturbance, soil texture, and soil structure can all heavily influence hydrologic cycles at a given site. Soil texture is especially important and can

override any effect of biological soil crusts. For instance, soils high in shrink-swell clays have relatively low infiltration rates, regardless of biological crust presence or absence.

Research conducted under a variety of soil and climate conditions around the world shows variable and interactive effects of biological crusts and soil properties. Biological crusts influence soil hydrology because they alter soil surfaces. Aggregate stability, soil structure, organic matter, and rough microtopography are all attributes associated with superior hydrologic properties, and biological soil crusts enhance these attributes in soil (Booth 1941; Fletcher and Martin 1948; Shields and Durrell 1964) on both micro- and macro-scales (Belnap and Gardner 1993; Belnap 1994).

Infiltration rates are controlled by the interaction of water-residence time on a soil surface and the permeability of that surface.

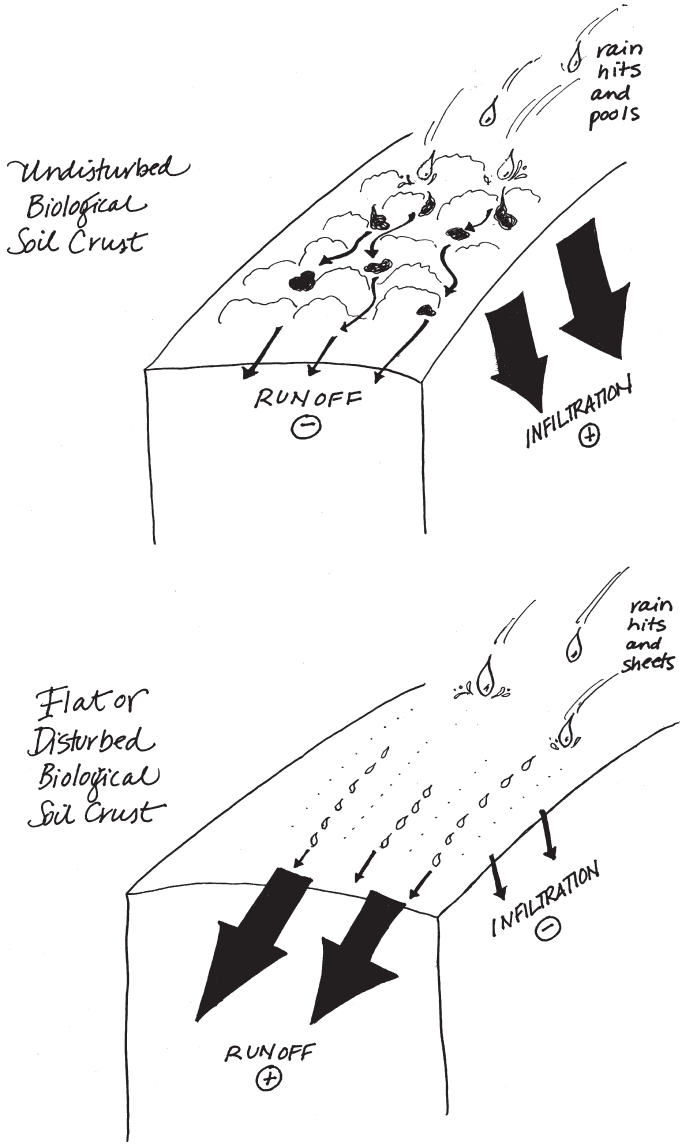


Figure 3.3 *Soil-water relationships with biological soil crusts. In the cool deserts (Colorado Plateau, Great Basin), roughened soil surfaces created by biological crusts act to impede overland water flow, resulting in increased infiltration. When biological soil crusts are removed, or with flat crusts in the hot deserts (Sonoran, Mojave, Chihuahuan), water runs over the soil surface unimpeded and infiltration is reduced.*

Biological crusts can produce a rough surface microtopography (less than 100 mm vertically) that acts as detention structures for water (Danin and Barbour 1982). This is especially pronounced in cool deserts (e.g., the Colorado Plateau), where frost-heaving is common and crusts are highly pedicelled. In these regions, biological crusts generally increase water infiltration (Fig. 3.3; Loope and Gifford 1972). In warm deserts, where frost-heaving is not present and biological soil crusts are flat, infiltration rates depend more on soil type and climatic regimes.

While greater surface roughness can increase water pooling and residence time, the presence of mucilaginous cyanobacteria in soil crusts can also decrease soil permeability. These cyanobacterial components of biological soil crusts rapidly swell up to 13 times their dry volume (Shields and Durrell 1964; Campbell 1977), potentially closing flow pathways through the soil surface. Scanning electron microscopy shows sufficient openings in sandy loam soils for water flow (Belnap and Gardner 1993), but concentration of silt and clay particles in the crust, in combination with swelling, may restrict infiltration even in sandy soils when they are wet (Verrecchia et al. 1995). Some authors speculate that the hydrophobic nature of some crustal components contributes to soil surface sealing (Bond 1964; Dulieu et al. 1977; Walker 1979; Rutin 1983; Jungerius and van de Meulen 1988); however, others have shown crustal organisms at some sites are highly hydrophilic (Kidron et al. 1999).

Overall, infiltration rates appear to be increased in regions where crusts are pinnacled and decreased in regions where crusts are flat. This has been reported for sandy soils in Arizona (Brotherson and Rushforth 1983), Australia (Bond 1964; Rogers 1977; Stanley 1983; Graetz and Tongway 1986; Eldridge 1993a, b), and Israel (Yair 1990). In New South Wales, Australia, infiltration rates increased on a transect through a sandy-loam soil as grazing decreased and biological soil crust cover increased. However, compared with adjacent ungrazed soils with a continuous cover of lichens and mosses, the lightly grazed areas showed greater infiltration (Eldridge 1993b). Infiltration studies conducted on sandy soils in Oklahoma and Kansas (Booth 1941) and silt-loams and clayey silt loams in Arizona (Faust 1970, 1971) failed to find any influence of biological soil crusts on infiltration rates.

The influence of biological soil crusts on effective hydraulic conductivity (the rate at which water moves through the soil profile under field conditions) is also variable. Lichen-dominated crusts in Utah showed decreased hydraulic conductivity (Loope and Gifford 1972). Lichen and algal crusts in Australia were associated with high conductivity (Greene et al. 1990). Three-year-old algal crusts in Utah and non-disturbed crusts in Nevada showed no discernible influence on conductivity (Williams 1993; Dobrowolski 1994).

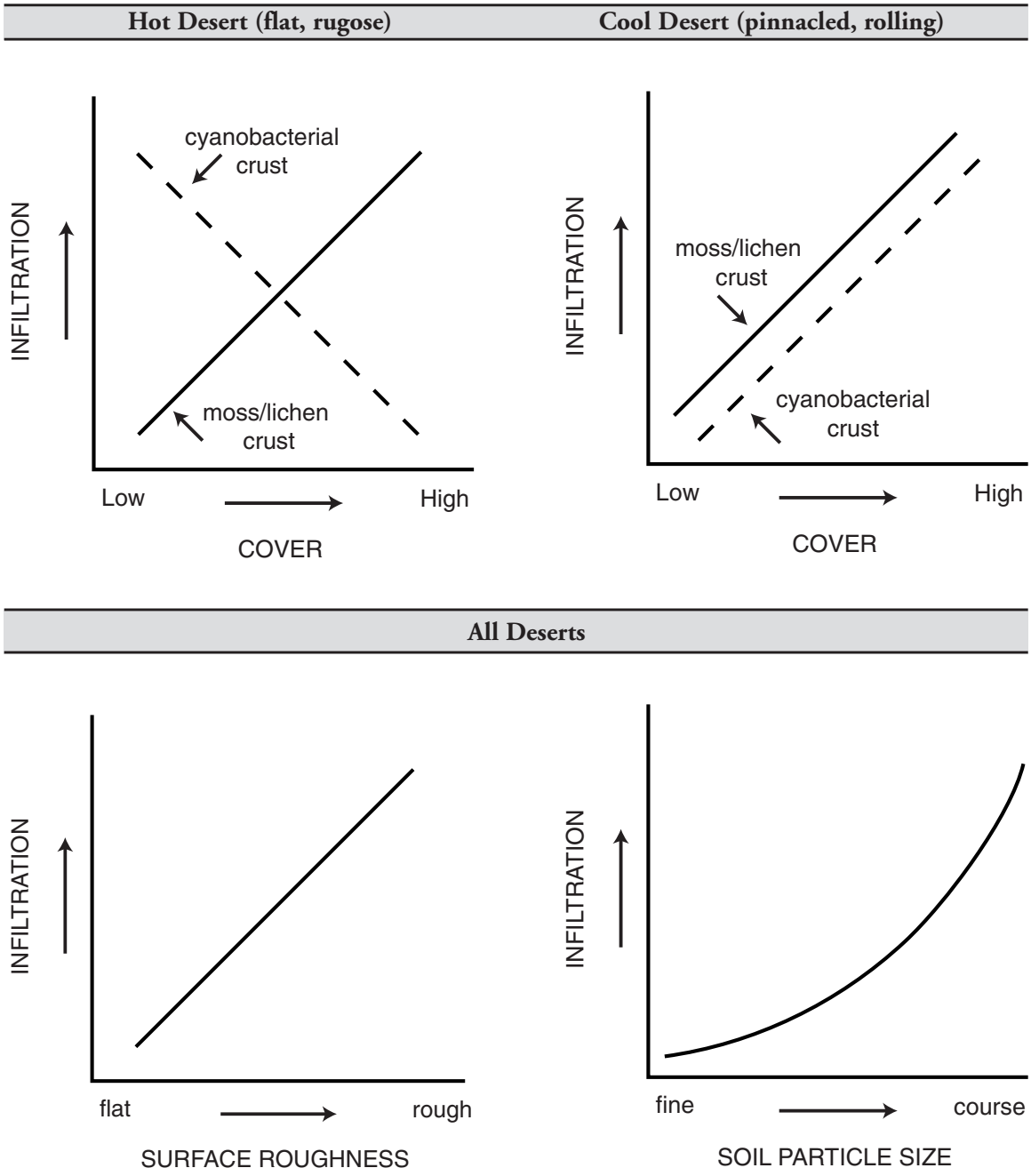
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Biological soil crusts have varied effects on soil moisture at any given time. However, research results have been variable and again appear to depend on soil type and crust composition. The crust's ability to seal the soil surface and reduce evaporation because of its associated high clay and silt concentrations has been repeatedly proposed (Danin 1978; Brotherson and Rushforth 1983; Williams et al. 1995a). While some studies show soil moisture is greater under well-developed crusts (Harper and Marble 1988; Meyer and Garcia-Moya 1989; Verrecchia et al. 1995; Belnap et al. 1996), other studies have found decreased soil moisture under crusted surfaces (Harper and Marble 1988).

Though overall infiltration of precipitation is critical for plant growth, the location of water entering the soil can also be critical in maintaining plant community structure. Recent work has shown that the pattern of water infiltration and runoff is important in maintaining vegetative community structure, especially in hyper-arid zones where rainfall is too low to support homogenous distribution of vegetation. Instead of being distributed across the landscape, plants are concentrated in bands that occur perpendicular to the water flow. These bands or vegetation clumps capture water, nutrients, and fine soil particles. The bigger the bands, the more effective they are in resource capture; however, their overall size is limited by rainfall and nutrients. Biological soil crusts often cover interband soils. When these interband areas are disrupted, water infiltration can increase between vegetated areas; thus, less water is available for the vegetation, often deep-rooted, woody perennials (Eldridge et al. 2000). This decrease in water availability may lead to changes in plant community structure by enabling establishment of shallow-rooted species in the interband areas or by die-off of the perennial shrubs. Over time, changes in hydrology and plant community structure result in modification of site potential and ecological function. A similar situation applies to exotic plant invasions and their effects on site function. In the Great Basin, invasive exotic annual grasses modify the native community's patchy structure to a more homogenous structure (Kaltenecker 1997). The resultant increases in plant and litter density in interspaces previously occupied by biological crusts affect moisture infiltration, which may further facilitate changes in community structure because less moisture becomes available for deeply-rooted perennial plants.

As can be seen above, the impact of biological soil crusts on hydrologic cycles can be highly variable and can result from a combination of site, soil, and crust factors (Fig. 3.4). However, lack of standardized data collection methods and descriptions of soil, biological crust, and climatic characteristics at study sites makes comparison of research results difficult. These shortcomings have

Figure 3.4 *Biological soil crust and soil characteristics that influence infiltration.*



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undoubtedly contributed to much of the seemingly contradictory published information.

3.7 Soil Stabilization

Biological soil crusts are unambiguously effective in reducing wind and water erosion of soil surfaces (Belnap and Gillette 1997, 1998; McKenna-Neumann et al.1996). Wind can be a major erosive force in deserts, as sparse vegetation leaves large patches of soil unprotected by plant litter or vegetative cover (Goudie 1978). Interspace soils are most often stabilized by rocks or biological soil crusts. Biological crusts play an important role both in preventing soil loss and facilitating soil accretion. The degree to which different types of crusts protect the soil surface from both wind and water erosion is hierarchical in the following manner: bare soil < cyanobacterial/algal crust < lichen crust < moss crust (Tchoupopnou 1989; Kinnell et al. 1990; Eldridge and Greene 1994; Belnap and Gillette 1998). Polysaccharides exuded by cyanobacteria and green algae, in combination with lichen and moss rhizines, entrap and bind soil particles together, increasing the size of soil aggregates (Fig. 3.5). As soil aggregates enlarge, they become heavier, have a greater surface area, and are more difficult for wind or water to move. Biological soil crusts keep otherwise loose sandy soils in place on steep slopes; they also stabilize pockets of very shallow soil (Bond and Harris 1964; Marathe 1972; Gayel and Shtina 1974; Danin and Yaalon 1980; Schulten 1985; Graetz and Tongway 1986; Campbell et al. 1989; Danin et al. 1989; Belnap and Gardner 1993). Rough microtopography creates a still-air boundary layer that protects the soil surface from wind erosion. Detention dams pool and slow overland water flow, giving sediment time to settle out, reducing sediment loss (Fig. 3.3; Brotherson and Rushforth 1983; Alexander and Calvo 1990).



Fig. 3.5 *The sheath of* Microcoleus vaginatus *contains sticky polysaccharides that entrap soil particles and bind them together.*

CHAPTER 4

NOTES

RESPONSE TO NATURAL IMPACTS AND HUMAN ACTIONS

4.1 Evolutionary History of Natural Impacts

Euro-American settlement of western North America in the 19th and 20th centuries changed the type, timing, and intensity of natural disturbance. The following is a discussion of the nature of two processes—grazing and fire—in presettlement ecosystems.

4.1.1 Grazing Characteristics

Soil and plant characteristics of low- and mid-elevation arid and semi-arid ecosystems in North America west of the Rocky Mountains indicate that these ecosytems evolved with low levels of soil surface disturbance. This is suggested by these ecosystems' dependence on nitrogen provided by the biological soil crusts (Evans and Ehleringer 1993; Evans and Belnap 1999) and by dominant bunchgrasses' lack of adaptation (such as tillering, secondary compounds, or high tissue silica content) to grazing (Mack and Thompson 1982; Martin 1975; Stebbins 1981). Large mammal numbers would have been low due to limited surface water and sparse vegetation. Limited water availability would have restricted use of lower elevations to winter seasons, as is seen today (West 1988; Parmenter and Van Devender 1995). Dung beetles, present globally in other systems with large mammal herds, are also lacking in western North America (Fig. 4.1; Mack and Thompson 1982). Shallow soils can also limit distributions of burrowing vertebrates and invertebrates, further reducing soil surface disturbance. Current natural

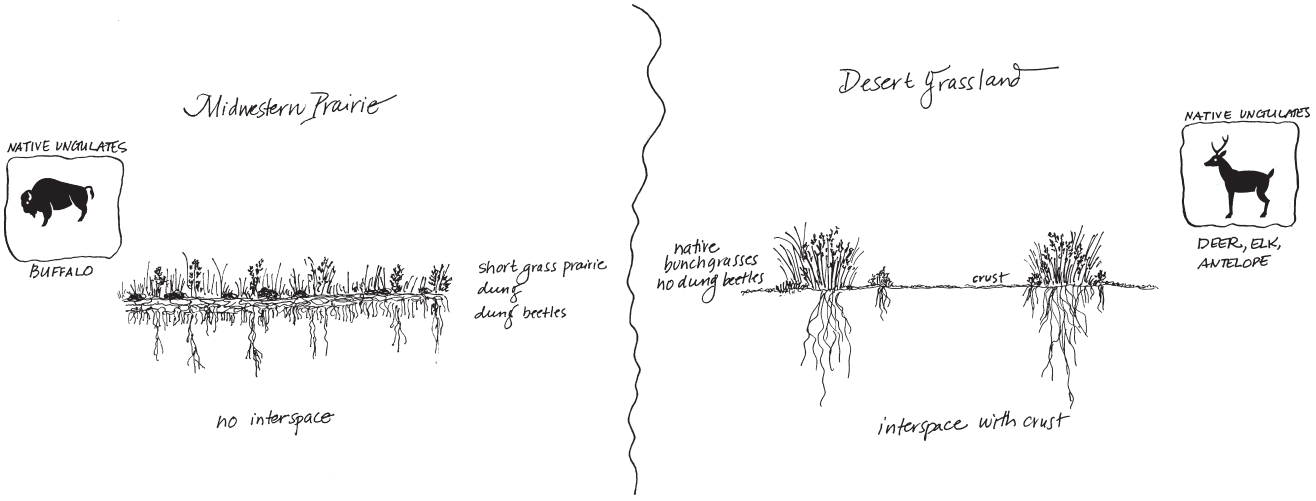


Figure 4.1 *Comparison of community structure in ecosystems that evolved with (midwestern prairie) and without (desert grassland) large herds of grazing mammals.*

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disturbance by large mammals and burrowing fauna in western North American deserts is greatest in the Sonoran and Chihuahuan Deserts, moderate in the Mojave Desert and Great Basin, and low in the Colorado Plateau. Because of their evolutionary history, these regions appear to be more negatively affected by soil surface disturbances than regions like the Great Plains that evolved with higher levels of surface disturbance (see section 4.2).

4.1.2 Fire

In arid and semi-arid native communities, plants have patchy distributions that result in discontinuous fuel and mosaics of various fire intensities (Whisenant 1990). Biological soil crusts provide little fuel to carry a fire through interspaces, thereby acting as "refugia" to slow the spread of fire and decrease its intensity (Rosentreter 1986). Unburned islands of vascular vegetation and biological soil crust provide propagules for reestablishment in burned areas (Fig. 4.2). Johansen et al. (1993) observed that the crust's structural matrix was left intact following low-intensity fire, indicating that a lightly burned crust still functions to maintain stability against erosive forces for both vascular plants and biological soil crusts during the recovery period.

Fire is a natural determinant of the sagebrush-steppe potential vegetation types. Historical fire patterns helped create mosaics of successional stages in both vascular plant and biological soil crust communities. More productive sites generally have fire-return intervals of less than 30 years (Burkhardt and Tisdale 1976; Arno and Gruell 1983; Fisher et al. 1987). Although this time period might constrain biological soil crust recovery, higher precipitation enhances regrowth (see section 4.3.3; McCune 1993). Fifty to 100 years has often been cited as the average return interval in shrub-steppe regions (Wright et al. 1979; Peters and Bunting 1994) and is adequate to restore biological soil crust components. However, there is no direct evidence for fire being a cyclic disturbance in lower elevation shrub-steppe. Here, shrub die-off from insect, disease, and winter kill is common and is probably responsible for most shrub turnover (McArthur et al. 1990). Historic fires were probably small, low intensity, patchy, and uncommon because of sparse and discontinous vegetation. Fire was not historically a common disturbance in most salt-desert shrub types (West 1994), except for the more productive types supporting Great Basin wildrye (*Elymus cinereus*). Likewise, sparsity of vegetation in the southwestern deserts resulted in long fire-return intervals and low-intensity fires (Allen 1998).

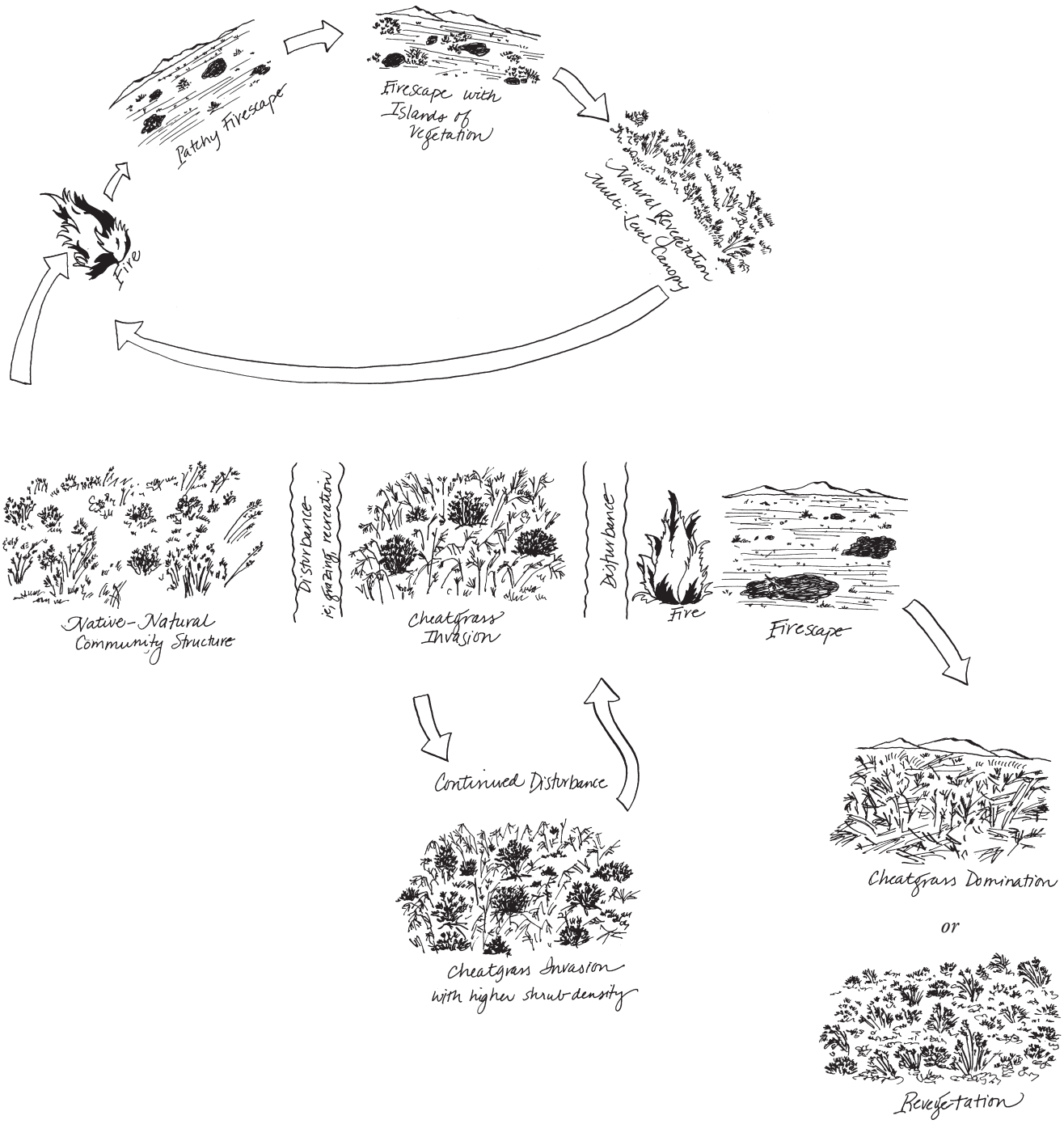


Figure 4.2 *Natural and altered fire cycles in sagebrush communities of the Great Basin. Fire at natural frequencies (50-100 year intervals or longer) occurred in a mosaic of intensities over the landscape due to discontinuity of fuel. This allowed natural regeneration of both the vascular plant and biological soil crust communities. Invasion of exotic species such as cheatgrass into these communities resulted in continuous fine fuels and larger, more intensive fires. Cheatgrass will often dominate the community following fire. Revegetation with perennial species can help reestablish a more natural community structure.*

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4.2 Disturbance Effects

Disturbance can directly and indirectly affect many aspects of the structure and function of biological crust communities, including cover, species composition, and carbon and nitrogen fixation. The impact of a given disturbance depends on its severity, frequency, timing, and type, as well as the climatic conditions during and after it.

Methods of assessing impacts of, and recovery from, disturbance have been highly variable. Generally, measurements have been limited to visual estimates of crust cover. However, Belnap (1993) showed visual assessment can only accurately assess moss and lichen cover, and cannot be used to measure the degree of recovery of cyanobacterial biomass, soil stability, and/or physiological functioning of crustal organisms. In addition, some studies have only considered total crust cover but have not delimited the relative cover of cyanobacteria, mosses, and lichens. The relationship between total crust cover and disturbance impacts can be weak, as cyanobacterial cover generally increases, while moss and lichen cover decreases, after disturbance. This often makes total crust cover a poor measure of the dynamics of soil crust recovery. Differentiating between crustal components is also important because alteration of species composition can heavily influence the crust's ecological functioning (Eldridge 1998). Comparing recovery rates from different studies can be problematic, as factors known to control recovery rates (such as site stability and precipitation following disturbance) are often not reported. More importantly, disturbance severity is seldom quantified. Studies generally report disturbance levels as "light," "moderate," or "heavy" without any definition of these categories; thus, what is "moderate" in one study may be considered "heavy" in another. As studies cover a large range of climatic zones, soil types, and levels of disturbance, and as there has been no standard for measuring crust recovery, it is not surprising that in the literature recovery rates have ranged widely (2 to more than 3,800 years), and either appear to show no pattern or often appear contradictory (Anderson et al.1982a; Callison et al. 1985; Jeffries and Klopatek 1987; Cole 1990; Belnap 1995, 1996; Belnap and Warren 1998).

4.2.1 Disturbance Severity, Size, Frequency, and Timing

The impact of a disturbance is affected by its severity, size, frequency, and timing. While most compressional disturbances (such as from vehicles and trampling by people or animals) result in similar types of impacts, severity can vary widely depending on disturbance source. For instance, vehicles and trampling exert compressional and shear forces; however, these forces are much greater for vehicles than trampling. In addition, vehicles often turn soils over and bury crustal

organisms, while trampling tends to only compress the surface. Vehicle tracks often channel water off-site and thus slow or prevent recovery (Webb and Wilshire 1983). Intensifying physical impacts (such as high-intensity, short-duration grazing) is deleterious to biological soil crust cover and its species richness (Johansen 1993). Disturbance that removes or kills crustal organisms results in greater impact and slower recovery than disturbance that leaves crushed crust material in place. As lichens and mosses are less tolerant of disturbance than cyanobacteria, frequent disturbance can maintain the biological soil crust at a low-successional stage (e.g., dominated by cyanobacteria; Fig. 4.3, Harper and Marble 1988).

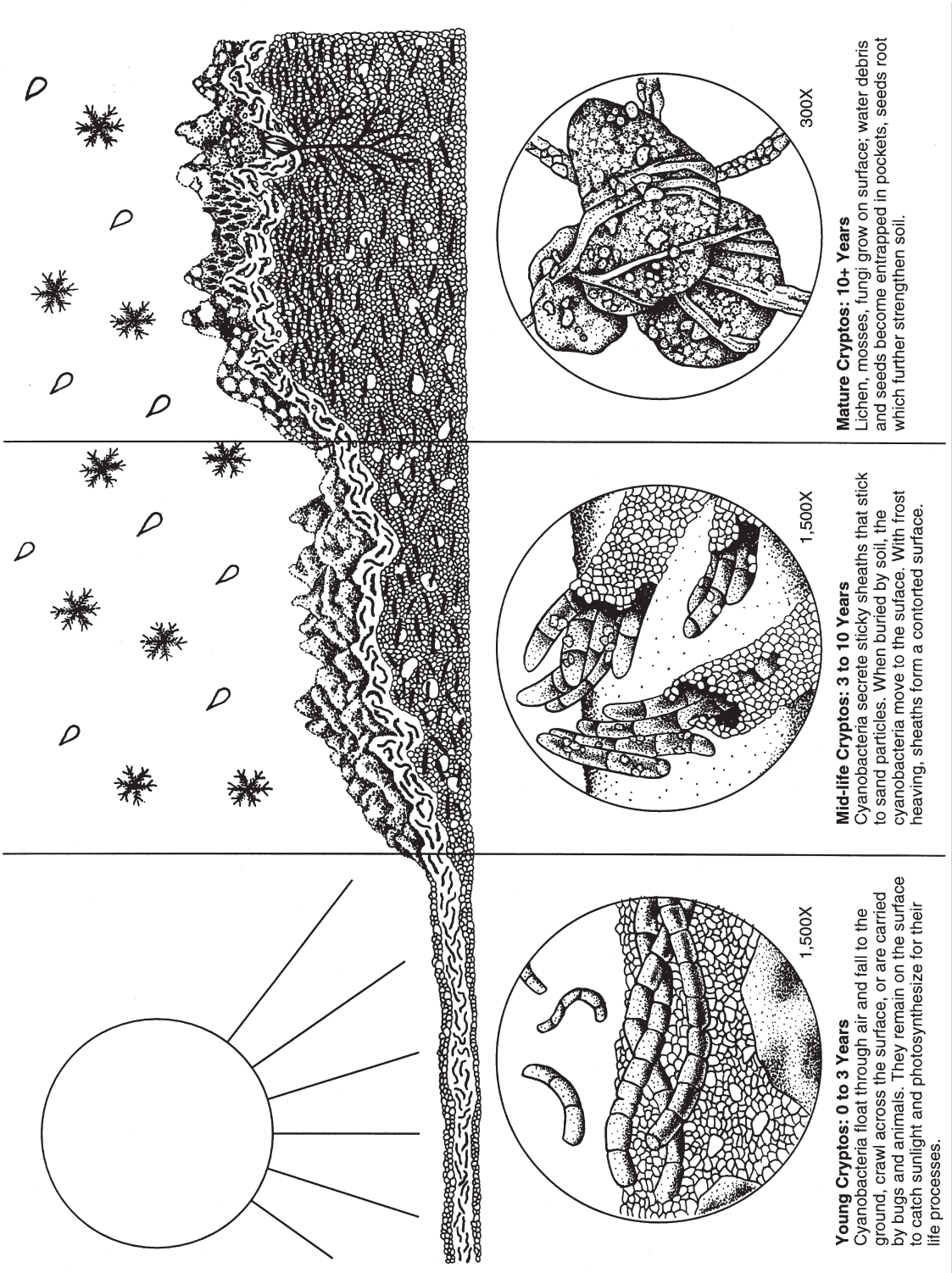
Disturbance timing can affect the degree to which the cover and species richness of a biological crust is reduced. Soils have different intrinsic soil strengths that vary with moisture content (see Fig. 2.5). Soils with little tendency to form aggregates, such as sands, are more susceptible to compressional stresses when dry. Fine-textured soils or those with inorganic crusts are more vulnerable to compressional disturbance when wet (Webb and Wilshire 1983). Crust components are brittle when dry, and the connections they make between soil particles are easily crushed. Thus, compressional disturbances can severely affect the crust's ability to stabilize soils, especially in dry sandy and silty soils. On silty soils of the Great Basin, early wet season (winter) use by livestock has been shown to have less impact on crust cover and species composition than late winter or spring use. As crustal species are only metabolically active when wet and are brittle when dry, disturbance in dry seasons is generally more destructive, and organisms are less able to recover, than when disturbed in wet seasons (Harper and Marble 1988; Marble and Harper 1989). Crusts on clay soils can be an exception, as they are often more vulnerable when wet (Fig. 2.5).

4.2.2 Disturbance Effects on Species Composition

Disturbance generally results in loss of species diversity, biomass, and surface cover of biological crust components. The more severe the disturbance, the greater the loss. Thus, after severe disturbance, the resulting crust community is generally greatly simplified from multiple species of cyanobacteria, lichens, and mosses to a community often dominated by one or a few species of cyanobacteria.

4.2.2.1 Air Pollution: A few studies have addressed the impact of air pollutants on soil lichens in desert environments. No differences have been found in species composition near pollution sources when compared to control sites. It is reasoned that lichens with thalli closely appressed to the soil surface, a condition common

Figure 4.3 *Successional sequence for biological soil crusts. This example is for* Microcoleus vaginatus*-dominated crusts on the Colorado Plateau. Sequences in other ecoregions are similar but may involve different taxa. (Illustration by Gloria Brown)*



to most desert soil crust lichens, are less susceptible to damage by air pollutants than lichens whose tissues are more exposed to air. In addition, most desert soils are very alkaline, and thus thought to buffer acidity from pollutants (Sheridan 1979; Nash and Sommerfeld 1981).

4.2.2.2 Oil Spills, Insecticides, and Herbicides: No known studies have directly addressed the effects of oil, oil dispersants, or insecticides on species composition of intact soil crusts. However, there has been a great deal of work on individual cyanobacteria, green algae, and mosses isolated from soil crusts. These experiments have shown that crustal species are differentially affected, depending on the compound and the species tested. Thus, exposure to these agents could potentially alter species composition of crusts (Metting 1981).

One study addressed herbicide effects on intact biological soil crusts. Direct application of two glyphosate herbicides (Roundup® and Accord®) on moss-dominated biological soil crusts had no short-term negative impact on bryophyte cover (Youtie et al. 1999). In fact, bryophyte cover decreased significantly in control plots due to litter buildup from exotic annual grasses that had invaded the site (see 4.2.2.3 below), while cover stayed the same or increased slightly in treated plots. However, repeated treatments are often required to effectively control weedy species. There is little information on the effects of repeated application or long-term effects of glyphosate and other herbicides. Therefore, caution should be used when applying these chemicals to remnant native areas supporting biological soil crusts (Youtie et al. 1989).

4.2.2.3 Annual Plant Invasion: Invasion of exotic annual plants into perennial plant communities can pose a long-term threat to biological soil crusts, as the crust-dominated interspace between perennial plants is often heavily invaded. Surveys in invaded communities show rich perennial moss/lichen communities are quickly replaced with only a few species of annual mosses and cyanobacteria (Kaltenecker 1997; Belnap and Phillips in press). The mechanism by which this shift occurs is not known, but probably results from a decrease in available soil surfaces (via increased cover of live plants and litter; Fig. 4.2, 4.4), higher cover of plant material shading the soil surface, and/or increased fire frequency (Kaltenecker 1997; Kaltenecker et al. 1999a; Youtie et al. 1999).

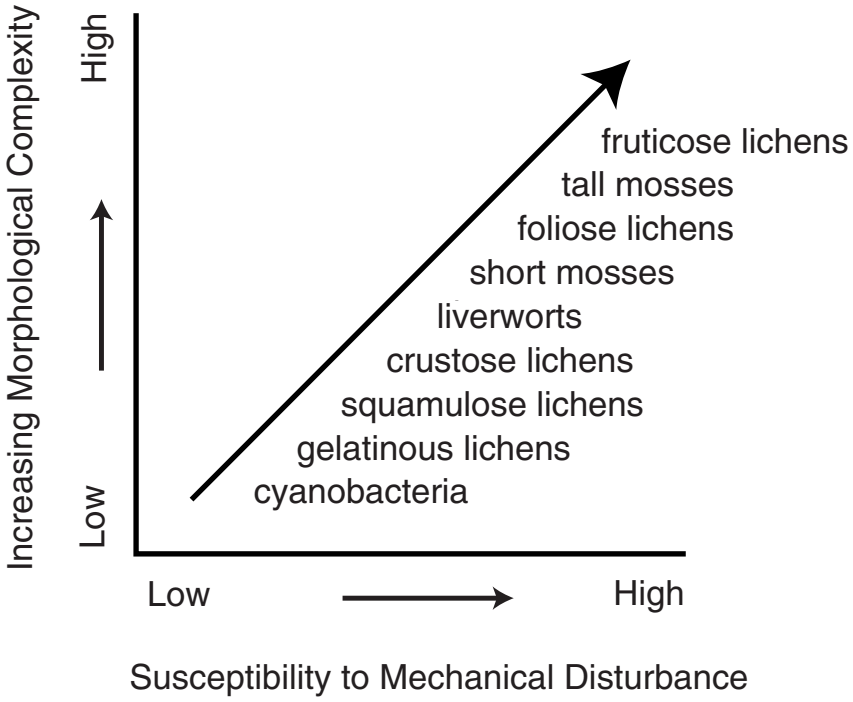
4.2.2.4 Fire: Biological crusts are generally killed by hot ground fires, resulting in loss of biomass and visible cover (Johansen et al. 1993). Frequent fires prevent recovery of lichens and

Figure 4.4 *Changes in the vascular plant community structure due to cheatgrass invasion.*



mosses, leaving only a few species of cyanobacteria (Whisenant 1990; Eldridge and Bradstock 1994). Damage to, and recovery of, biological crusts depend on the pre-fire composition and structure of the vascular plant community and on fuel distribution, fire intensity, and fire frequency. Historic fire regimes in semi-arid and arid landscapes generally left small-scale patches of unburned areas between perennial plants, and/or larger-scale patches of unburned shrubs across the landscape (Fig. 4.2). This resulted in a mosaic of successional stages of plants and biological crusts, with propagules readily available to replenish burned sites. Historic fires were also relatively infrequent, leaving time for later-successional crustal organisms to recolonize (Whisenant 1990; Peters and Bunting 1994). Many semi-arid areas are now invaded by annual weeds, and unnaturally frequent, large fires that preclude crustal species' recolonization or succession are common.

Figure 4.5 *Susceptibility of biological crusts to mechanical disturbance based on dominant morphological group.*



4.2.2.5 Mechanical Disturbance: Mechanical disturbance results from activities such as vehicle traffic (military and recreational), trampling by livestock and people, and land-clearing (such as mining). Such uses are increasing exponentially in arid and semi-arid areas of the world. Effects of mechanical disturbance are especially noticeable at sites with highly erodible soils and large topographic relief (Harper and Marble 1988).

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Over 30 studies on four continents document that livestock grazing, vehicle use (both recreational and military), and human trampling dramatically reduce lichen/moss cover and species richness of crusts. Resistance to disturbance generally decreases as the organisms become more morphologically complex (Fig. 4.5; Harper and Marble 1988; West 1990; Johansen 1993; Eldridge and Greene 1994; Ladyman and Muldavin 1996). Cyanobacteria, the most resistant to disturbance, are highly mobile and can recolonize disturbed surfaces rapidly. Lichens use a combination of adaptive thallus structures and pigments (Blum 1973; Galun et al.1982), water storage capacities, tolerance of frequent and/or prolonged inundation, and/or an ability to fix atmospheric nitrogen to increase resistance to disturbance. For example, Rogers and Lange (1971) showed that lichens *Collema coccophorum* and *Heppia lutosa* (*H. despreauxii*) were the least affected by sheep trampling around a watering point compared to other taxa. These lichens are able to fix atmospheric nitrogen and to store greater amounts of water than stratified green lichens (Galun et al. 1982). In a comparison of species inside and outside a grazing exclosure, vagrant foliose lichens *Chondropsis semiviridis* and *Xanthoparmelia convoluta*, crustose lichens *Diploschistes scruposus* and *Caloplaca* spp., and the squamulose lichens *Peltula imbricata* were associated with ungrazed sites (Table 4.1; Crisp 1975; Eldridge and Koen 1998). The gelatinous lichen *Collema coccophorum* was the most tolerant of livestock trampling (Rogers and Lange 1971; Eldridge 1996).

Most soil surface disturbance compacts soils. Compaction influences soil water and nutrient-holding capacity, which can lead to changes in soil crust community species composition. These subtle compositional changes often occur before cover changes are apparent (Eldridge 1996).

4.2.2.6 Burial: Crust disruption often destabilizes underlying soils, leaving adjacent crusts vulnerable to burial by wind- and water-moved sediments. When soils are moist, the large filamentous cyanobacteria can respond to burial by moving up to 5 mm every 24 hours. When dry, these organisms are not able to move. Burial kills non-mobile photosynthetic components of the crust, including mosses, lichens, green algae, and smaller cyano-bacteria (Campbell 1979). Therefore, burial generally results in a greatly simplified crustal community.

4.2.3 Disturbance Effects on Nutrient Inputs and Retention

4.2.3.1 Carbon Fixation: Cyanobacterial crusts near coal-fired power plants have greater chlorophyll *a* per unit soil surface area

Table 4.1 *Percent frequency of biological soil crust organisms on loamy and sandy soils inside and outside the exclosure at Koonamore Vegetation Reserve, South Australia, in May 1972. Adapted from Crisp (1975).*

		LOAMY SOIL		SANDY SOIL		
Species	Morphological Group	Exclosed	Grazed	Exclosed	Grazed	*p*
Lichens						
Acarospora smaragdula	crustose	2.4	0.5	7.6	2.2	n.s.
Aspicilia calcarea	crustose	39.4	20.6	26	26.2	*
Aspicilia calcarea	fruticose	13.6	1.1	18.2	2.4	*
Chondropsis semiviridis	foliose	0.08	0	0.1	0	n.s.
Collema coccophorum	gelatinous	81.4	63.6	21	0	*
Diploschistes scruposus	crustose	0.6	0	2.4	35.6	n.s.
Fulgensia subbracteata	crustose	20	5	25.2	14.2	*
Psora decipiens	squamulose	38.7	15.1	33.8	24.6	*
Psora crystallifera	squamulose	11.4	0.7	13.8	2	*
Toninia sedifolia	squamulose	13.1	3.8	13.8	7.6	*
Xanthoparmelia convulata	foliose	0.04	0	0.1	0	n.s.
Liverworts						
Riccia lamellosa	liverwort	4.2	0.4	8.2	1.2	*

** Indicates significant effect of exclosure at p<0.10; n.s. = effect of excosure was not significant.*

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than crusts away from the plant, implying higher levels of carbon fixation. This is partially a result of fertilization by nitrogen and sulfur compounds from effluents (Sheridan 1979; Belnap 1991). Photosynthesis-inhibiting herbicides show significant impact on *Nostoc* growth and nitrogen fixation (Gadkari 1988). In general, herbicides inhibit growth and reproduction in culture (Metting 1981). However, effects appear to be more pronounced in the laboratory than the field, and may be transitory (Prasad et al. 1984).

Alteration in crust species composition will affect total carbon fixation, as lichens and mosses fix more carbon per unit soil surface area than cyanobacteria (Phillips and Belnap 1998). Because much of the carbon fixed by crustal organisms is released into the surrounding soils (Lewin 1956), crust cover reduction is expected to reduce soil carbon available for microbial populations that are often carbon limited. This, in turn, may affect decomposition rates of plant litter, and thus, levels of nutrients available to vascular plants (Paul and Clark 1996).

Table 4.2 *Reduction of nitrogenase activity for new and older disturbances on silty soils of the Dugway Proving Ground, Utah. All disturbance types resulted in material left on site except "Scalp," which removed the top 1 cm of crust.*

Age of Disturbance	Type of Disturbance	Percent Reduction in Nitrogenase Activity
New	Vehicle	68
New	Bike	79
New	Foot	62
6 months	Vehicle	100
9 months	Tank	83
9 months	Scalp	95
9 months	Rake	81

4.2.3.2 Nitrogen Inputs: Power plant effluents have been shown to decrease nitrogen fixation in *Collema* and *Microcoleus/Nostoc/Scytonema*-dominated crusts (Sheridan 1979; Belnap 1991). Atmospheric nitrogen deposition may offset reduced nitrogen inputs from crusts; alternatively, anthropogenic nitrogen deposition may aggravate nitrogen loss through increased ammonia volatilization and denitrification. In addition, biological soil crusts release ammonia in the soils, while anthropogenic nitrogen deposition contains large amounts of nitrate (Garcia-Pichel, unpublished data). Microbial and vascular plant species differentially use ammonia and nitrate; thus, deposition of additional nitrates may alter the dynamics of both soil and plant communities (Binkley et al. 1997).

Free-living or lichenized *Nostoc* show stimulation of nitrogen fixation at low concentrations of, or short exposure to, arsenic, nickel, lead, palladium, and zinc. However, longer-term exposure to cadmium, lead, and zinc inhibits fixation (Henriksson and DaSilva 1978). Exposure to crude oil and oil dispersants decreases nitrogen fixation in *Nostoc* (Marowitch et al. 1988). Nitrogen fixation is significantly inhibited in *Nostoc* by many insecticides, herbicides, and phenolic compounds tested (Bhunia et al. 1991; Megharaj et al. 1988).

Mechanical disturbance can result in large decreases in soil nitrogen through a combination of reduced input and elevated losses (Peterjohn and Schlesinger 1990; Evans and Belnap 1999). In all soils tested, disturbance by vehicles, human foot traffic, mountain bikes, and raking immediately reduces nitrogen input from crusts (25 to 40% on silty soils; 76 to 89% on sandy soils). Over time, nitrogenase activity can drop by 80 to 100% relative to controls, due to subsequent death of buried material (Table 4.2; Belnap et al. 1994; Belnap 1995,1996).

Species composition changes also affect nitrogen inputs, as cyanolichens (such as *Collema*) fix an order of magnitude more nitrogen than the equivalent soil surface area of cyanobacteria. Thus, the shift from a lichen crust to a cyanobacterial crust can result in less nitrogen entering the ecosystem, as has been shown in multiple studies. Jeffries et al. (1992) showed that heavy grazing reduced nitrogen fixation in sandy soils by 95%. In silty loam soil, Terry and Burns (1987) showed a 64% reduction of nitrogen fixation in burned areas, 85 to 94% reduction in grazed areas, and 99% reduction in a tilled area. *Collema* cover was reduced 50 to 80% in grazed areas relative to adjacent ungrazed areas (Brotherson et al. 1983; Johansen and St. Clair 1986). Expected nitrogen inputs would be reduced accordingly. Evans and Belnap (1999) showed nitrogen fixation in an area released from grazing 25 years was still 2.5 times less than an adjacent, never-grazed area due to reduction in *Collema* cover.

Decreased nitrogen inputs from crusts can have long-term impacts on soil nitrogen levels. Jeffries (1989) found 50% less nitrogen in grazed soils compared to adjacent ungrazed soils. Evans and Belnap (1999) found a 42% decrease in soil nitrogen and 34% decrease in plant tissue nitrogen when comparing a previously grazed (released 30 years previous to the study) site to an adjacent ungrazed area. In the same area, stable nitrogen isotopes showed that both soil and plants in the grazed area contained less newly fixed nitrogen than the ungrazed area, and nitrogen mineralization potential decreased almost 80% (Rimer and Evans 1997). This has large implications for ecosystems that are dependent on biological crusts for nitrogen inputs, such as those on the Colorado Plateau (Evans and Ehleringer 1993).

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4.2.4 Disturbance and Vascular Plants

Crusts can affect vascular plant germination, survival, and nutrition. Lichen-moss crusts in areas with frost heaving (as in cool deserts) increase perennial vascular plant seed entrapment, germination, establishment, survival, biomass, and nutritional status (Belnap and Harper 1995). In these deserts, disturbance that flattens frost-heaved surfaces and/or eliminates mosses and lichens can have a negative effect on some or all of these characteristics. However, germination and survival of some exotic annual grasses can be enhanced with biological crust disturbance.

In hot deserts, seed entrapment, biomass, and fecundity of annual plants is generally increased when smooth cyanobacterial crusts are disturbed (Prasse 1999), although there are some exceptions (Gutterman 1994). Disturbance of smooth cyanobacterial crusts enhances germination of some annual species, while decreasing germination of others (Zaady et al. 1997). Rugose crusts in hot deserts have received little study, and no work has addressed the effects of disturbance on seed entrapment. Effects on germination in rugose crusts appear to be species dependent. In contrast to smooth crusts, disturbance to hot desert rugose crusts lessens survival and biomass of perennial plants (McIlvanie 1942; Crisp 1975).

Biological soil crusts have been shown to influence availability of many plant-essential nutrients. Crust loss can result in less plant-available magnesium, potassium, iron, calcium, phosphorus, manganese, and sulfur (Harper and Belnap in press). The spatial distribution of nutrients is also affected by disturbance, as disturbance will alter the relative distribution of biological crust components (i.e., lichens, mosses, cyanobacteria) across the landscape (Klopatek 1992).

4.2.5 Disturbance and Surface Albedo

Trampling of dark-crusted surfaces exposes underlying, lighter soils, thus increasing albedo (reflectance) by up to 50% at most wavelengths measured (Fig. 3.1). This increased albedo represents an energy loss from the soil surface of approximately 40 watts/m^2 and can reduce soil temperatures by up to 14°C (Belnap 1995). Such changes in reflectance are especially apparent using satellite imagery, as can be seen in the Negev Desert, along the U.S.-Mexico border, and in Australia. Much of this difference is attributed to loss of biological soil crusts (Graetz and Tongway 1986). Large-scale changes in surface albedo may contribute to changes in regional climate patterns (Sagan et al. 1979).

4.2.6 Disturbance and Soil Hydrology

The effect of biological soil crust disturbance on soil hydrology is very site specific. Water infiltration, runoff, and resultant soil moisture are influenced by soil surface roughness, soil texture, microtopography, surface albedo and temperature, vegetative cover (both vascular and non-vascular), and climatic conditions. All these factors can be altered when biological crusts are disturbed. In general, disturbance flattens pinnacled and rolling crusts, thus decreasing water infiltration and increasing runoff (Fig. 3.3). In hot deserts, disturbance to smooth and rugose lichen- or cyanobacterial-crusted surfaces can increase overall infiltration rates (Greene et al. 1990; Eldridge et al. 2000). However, this increase in infiltration may negatively affect nearby vascular plants that depend on interspace runoff for survival (see Section 3.6). Soil structure alteration as a result of soil compaction can also reduce infiltration rates. Available soil moisture results from a complex interaction of many soil and plant characteristics, including infiltration, soil moisture-holding capacity, albedo, plant root density, etc. Only two studies have addressed the combined effects of crusts on available soil moisture, with disparate results. One study found increased soil moisture under intact crusts, while the other found soil moisture increased under disturbed crusts (reviewed in Harper and Marble 1988).

4.2.7 Disturbance Relative to Water and Wind Erosion

Compressional disturbance damages soil-stabilizing cyanobacterial sheath material both at and below the soil surface. The damage below the surface is irreparable, as living cyanobacteria are not present to regenerate sheath material. As greater than 75% of photosynthetic biomass and productivity is from organisms living in the top 3 mm of soils, disturbance that results in even small soil losses can dramatically reduce site fertility and further reduce soil surface stability (Garcia-Pichel and Belnap 1996).

4.2.7.1 Water Erosion: Globally, all studies show crust cover loss significantly increases water erosion of both coarse- and fine-textured soils. Continuous tracks have a greater impact than non-connected disturbances (such as hoof prints) because of increased water flow volume and velocity along the tracks (Webb and Wilshire 1983). Crushing of cyanobacterial connections between particles results in smaller, isolated soil aggregates that are then more easily moved by water. In addition, surfaces flattened by compressional disturbances are less able to reduce water velocity, thereby allowing

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movement of larger soil particles and reducing opportunities for sediment to settle out.

4.2.7.2 Wind Erosion: All studies of wind erosion indicate that disturbed soils are more susceptible to wind erosion than undisturbed soils when dry (Fig. 4.6). When crusts are crushed or absent, soil particle movement is initiated at lower wind speeds, as resistance to wind erosion increases with better soil crust development. Well-developed crusts (with lichens and mosses) on both silt and sandy soils have 2 to 130 times greater resistance to soil erosion than less well-developed crusts or bare soil (Fig. 4.7; Williams et al. 1995b; McKenna-Neuman 1996; Belnap and Gillette 1997, 1998; Leys and Eldridge 1998). Vehicle tires result in greater damage than hooves on a given soil type (Belnap and Gillette 1998).

Decreased resistance of soils to wind erosion is directly associated with increased sediment movement. All experimental disturbances applied to crusts show increased sediment production—up to 35 times that of adjacent undisturbed crusts (Leys and Eldridge 1998; Williams et al. 1995b). Nearby soil crusts are often buried by blowing sediment, resulting in death of photosynthetic organisms.

4.3 Factors Influencing Natural Recovery Rates

Recovery rates are dependent on many factors, including disturbance type, severity, and extent; vascular plant community structure; adjoining substrate condition; inoculation material availability; and climate during and after disturbance. Comparing recovery rates reported in the literature is highly problematic, as studies range over a wide array of climatic zones, soil types, and levels of disturbance, and these factors are seldom quantified. Thus, most studies can only be used to define the general range of recovery rates. Some studies do report climate, soil, and/or disturbance data such that comparisons are possible (Anderson et al. 1982a; Jeffries and Klopatek 1987; Callison et al. 1985; Cole 1990; Belnap 1995, 1996; Eldridge 1996; Belnap and Warren 1998).

Examination of these studies indicates that general recovery times can be predicted for soil crusts in different environments. Most recovery time calculations for crust cover assume a linear recovery rate. On the Colorado Plateau, scalped plots were reassessed 2 to 5 and 10 to 14 years after disturbance. After 2 to 5 years, cyanobacterial cover was predicted to recover in 45 to 110 years, whereas it recovered within 14 to 34 years. Thus, linear assumptions greatly overestimated recovery time. Lack of moss recovery prevented useful estimates at two of the three sites at the earlier sampling time. At one site, early estimates were 400 years to recovery, while later estimates were 42

Figure 4.6 *Resistance of sandy loam soils to wind erosion following disturbance to a well-developed biological soil crust in four time classes. Threshold friction velocity is the force required to detach soil particles from the surface. Time classes indicate the length of time since disturbance to the control. Following determination of threshold friction velocities for controls, treatments were applied as follows: Foot = one pass wearing lug-soled boots; Tire, 1 Pass = one pass of a four-wheel drive vehicle with knobbed tires; Tire, 2 Pass = two passes of a four-wheel drive vehicle with knobbed tires. Within each time sequence, controls were significantly more resistant to wind erosion than treated surfaces. Adapted from Belnap and Gillette (1997).*

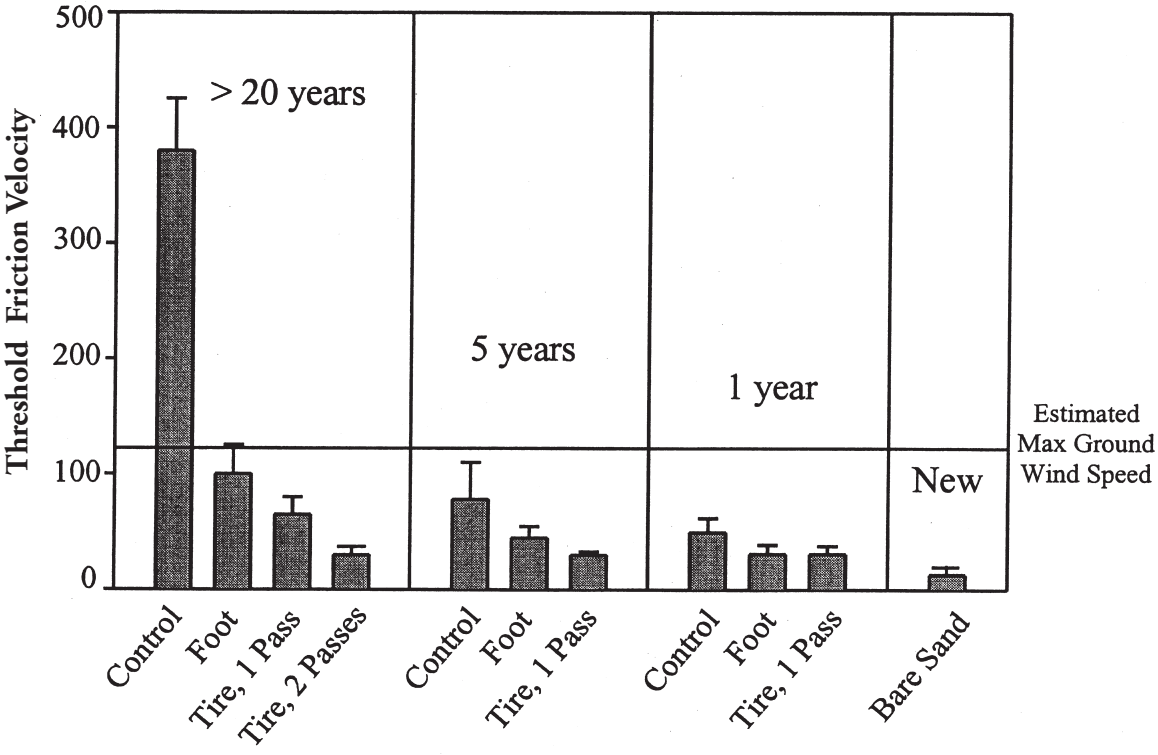
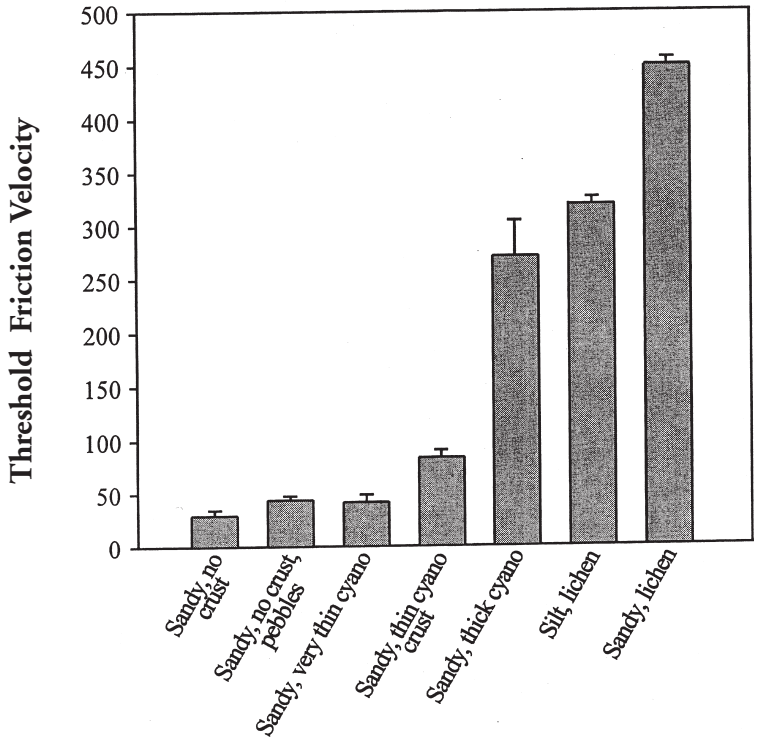


Figure 4.7 *Resistance of soil surfaces to wind erosion. Resistance increases with surface protection and development of the biological soil crust. The greatest amount of resistance is demonstrated by soils with well-developed biological crusts characterized by a diverse lichen flora. Adapted from Belnap and Gillette (1998).*



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years. As with cyanobacteria, linear extrapolations overestimated recovery time. In contrast, *Collema* recovery after 3 years was estimated at 85 years; after 14 years, the estimate for full recovery was 50 years, a fairly close match. *Collema* recovery at a second site was highly variable: after 2 years, recovery time was estimated at 487 years; after 11 years, estimates were site dependent, ranging from 40 to 766 years. Original estimates were therefore both under and over estimated, depending on individual site characteristics. Sites with more shade and less sandy soils were quicker to recover than original estimates predicted, while more exposed sites with sandier soils were less able to recover than originally estimated (Belnap, unpublished data).

4.3.1 Sequence of Species Appearance

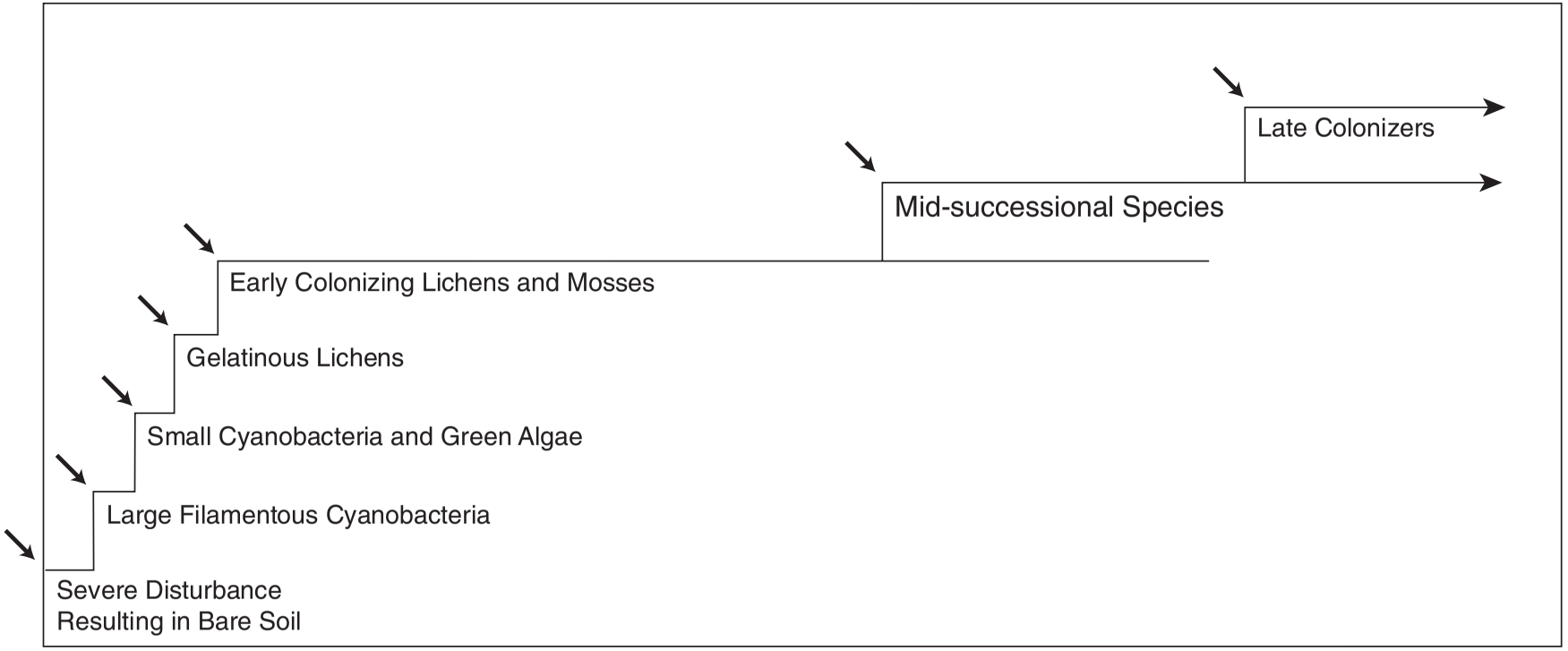
Cyanobacteria and green algae are generally the first photosynthetic species to appear on disturbed soils, probably because of their mobility across soil surfaces and their ability to colonize from the air (Schlichting 1969). Large filamentous cyanobacteria such as *Microcoleus* generally appear first (Fig. 4.3, 4.8), especially on unstable sandy soils (Ashley and Rushforth 1984; Belnap 1995). This species is then followed by smaller cyanobacteria and green algae. Occasionally, desert soils are slightly acidic, and here green algae can be the first to appear (Johansen 1993).

Lichens and mosses require stable soil surfaces for growth. This can be provided by a physical crust or by large, filamentous cyanobacteria. Once soils are stabilized, gelatinous nitrogen-fixing lichens (e.g., *Collema* spp.) are generally the first lichens to appear in disturbed areas, followed by other early-successional lichens and mosses (Table 4.3; Johansen et al. 1984; Belnap 1993). Early-colonizing lichens often disperse phytobiont-containing tissue (e.g., isidia, soredia, or algal-covered spores), as opposed to bare spores, thus precluding the need to find phytobionts on-site.

4.3.2 Soil Texture

Soil texture influences crust recovery rates. Recovery of all crust components is faster in fine-textured soils than in coarse-textured soils, as fine-textured soils are often stabilized by chemical and rain crusts and retain soil surface moisture longer (Fig. 4.9; as reviewed in Harper and Marble 1988; Johansen 1993; Ladyman and Muldavin 1996). Recovery of the site's wind resistance is also more rapid in fine-textured soils, probably due to crust formation after rainfall. While silty and sandy soils show a similar reduction in wind resistance to vehicle disturbance (83% and 74%, respectively), silty soils show a 50% recovery of wind resistance after a single large rain

Figure 4.8 *Generalized recovery sequence for biological soil crusts. Successional stages are illustrated as steps on the diagram. Disturbance input (indicated by arrows) will cause the crust to revert to an earlier successional state, with severe disturbance resulting in complete destruction of the crust. Recovery time is dependent on environmental conditions, including effective precipitation (see Chapter 2). Note that recovery times, for mid- and late- successional species in areas with lower effective precipitation are unknown, as recovery times are so long no estimates are possible.*



Geographic Region (elevation, average annual precipitation)	**Estimated Years to Recovery**			
	Gelatinous Lichens	Early Colonizers	Mid Successional	Late Successional
Lower Mojave (<1500 m, 100 mm)	1,200 →	3,800	unknown	unknown
High Mojave (1500 m, 200 mm)	200 →	800	unknown	unknown
Colorado Plateau (1500 m, 200 mm)	50 →	500	unknown	unknown
Northern Great Basin (1000 m, 350 mm)	20 →	25 →	60 →	125

Figure 4.9 *Biological soil crust vulnerability and recoverability based on site stability, effective precipitation, and disturbance regime. Vulnerability decreases and recovery rates increase with increased site stability and effective precipitation, and infrequent disturbance.*

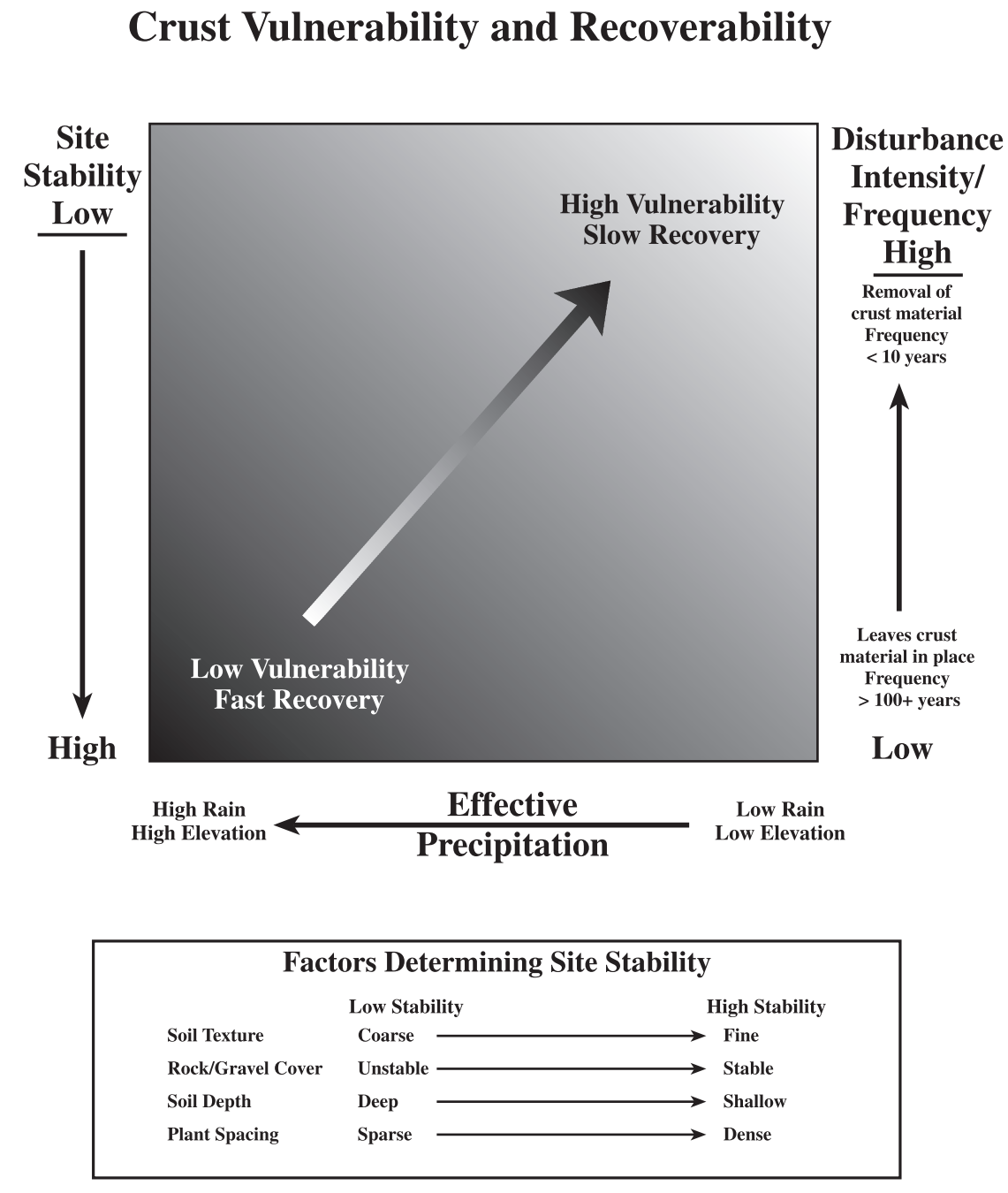


Table 4.3 *Characteristics of early-colonizing lichens.*

Species	Phytobiont	Reproductive Units
Caloplaca tominii	green algae	soredia
Cetraria islandica	green algae	isidia-like cilia
Cladonia chlorophea group	green algae	soredia
Collema spp.	cyanobacteria	isidia
Cornicularia normoerica	cyanobacteria	finger-like lobes
Endocarpon pusillum	cyanobacteria	algal-covered spores
Leprocaulon microscopum	green algae	soredia
Leptogium corniculatum	cyanobacteria	isidia
Peltigera didactyla	cyanobacteria / green algae	isidia
Peltigera rufescens	cyanobacteria	spores, unspecialized thallus fragmentation
Placidium squamulosum	green algae / cyanobacteria	algal-covered spores

event, while very sandy soils can take up to 10 years for similar recovery (Belnap and Gillette 1997; Belnap and Herrick, unpublished data).

4.3.3 Climate Regimes

Crustal organisms are metabolically active only when wet; thus, recovery is faster in regions and microsites with greater effective precipitation (Fig. 4.8, 4.9; Johansen et al. 1993; Harper and Marble 1988). Crusts on north and east slopes, as well as at higher elevations, will recover more quickly than crusts on south and west slopes and at lower elevations. However, as discussed in Sections 2.2.1, 2.2.5, and 2.2.6, there are thresholds along ecological gradients where adequate precipitation results in development of a more diverse and dense vascular flora in lieu of the biological crust.

4.3.4 Disturbance Type, Frequency, Severity, and Size

No work has addressed recovery rates of lichens or cyanobacteria from air pollution. In general, crusts are highly susceptible to hot fires; thus, recovery will depend on the size and intensity of fires. As noted previously in "Disturbance Effects" (Section 4.2), most compressional disturbances have similar types of impacts. However, severity of mechanical disturbance can vary widely with disturbance type. Thus, on similar soils, vehicle tracks generally have longer recovery times than disturbances that do not churn the soil or make continuous tracks (Wilshire 1983; Belnap 1996).

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Repeated disturbance will generally keep crusts at an early-successional stage (e.g., cyanobacteria-dominated) by preventing lichen or moss colonization (Fig. 4.8; Belnap 1996).

Disturbance severity often controls recovery rates. In western North America, site recovery within a given soil and climate type is faster where disturbances are not severe enough to remove crustal material than it is at sites where crusts were removed. When crusts are completely removed, recovery can be excessively slow, especially in areas with low effective precipitation and/or sandy soils (Fig. 4.9; Eldridge 1996). In contrast, crusts crushed in place with vehicles, foot traffic, and horses recover much faster, especially on fine-textured soils.

Because recolonization of disturbed areas occurs mostly from adjacent, less-disturbed areas, the size and shape of disturbance can affect recovery rates. This is especially true for lichens. Desert soil lichens colonize only infrequently through spores; thus, recovery of lichen cover is mostly dependent on material washing or blowing in from adjoining areas (Eldridge and Ferris 1999). The rate of lichen recovery is much slower in areas with higher internal surface areas relative to perimeter area (Belnap, unpublished data).

4.3.5 Condition of Adjoining Substrate

In general, crust recovery is slower if soils adjacent to disturbed areas are destabilized. Detached sediment can both bury adjacent crusts, killing many crustal organisms, and/or provide material for sandblasting nearby surfaces, thus increasing wind erosion (Belnap 1995; McKenna-Neumann et al. 1996; Leys and Eldridge 1998).

4.3.6 Vascular Plant Community Structure

Crusts recover more quickly under shrub canopies than in adjacent plant interspaces. This is probably due to greater soil moisture and fertility under shrub canopies. In the Mojave Desert lichen recovery (after complete removal 50 years previously) was 36% under shrub canopies, compared with 4% in the shrub interspaces (Belnap and Warren 1998). A similar pattern was seen in plots established on the Colorado Plateau, where lichen recovery was 2 to 3 times faster under shrubs than adjacent interspaces (Belnap, unpublished data).

The growth of biological soil crusts and vascular plants can be an interactive process (Danin et al. 1989). Eldridge and Greene (1994) present a conceptual model in which crust development at sites is strongly linked to restoration of vital soil processes. As primary colonizers of recovering sites, biological soil crusts enhance microsite fertility and provide safe sites for seeds. In turn, established vascular

plants help stabilize soils, provide shade, and reduce wind speeds at the soil surface, providing conditions conducive to further development and diversification of the biological soil crusts (Wood et al.1982; Danin et al. 1989).

4.3.7 Nitrogen and Carbon Fixation

Overall, nitrogen and carbon fixation rates in biological soil crusts are dependent on its species composition, biomass, and physical structure. Thus, recovery is dependent on recovery rates of specific crustal components. Recovery of nitrogen fixation is dependent on recovery rates of cyanobacteria and cyanolichens. Nitrogen fixation in crusts can require anaerobic microzones in the soils, which may be dependent on buildup of cyanobacterial biomass (Belnap 1996). Carbon fixation increases when lichens and mosses colonize (Phillips and Belnap 1998). As recovery is faster with higher available moisture, both nitrogen and carbon fixation rates are expected to recover faster in cool deserts than in hot deserts, other factors being equal.

Lichen cover may not fully recover after disturbance. On the Colorado Plateau, soils previously occupied by cyanolichens were often occupied by mosses after release from grazing (Belnap, unpublished data). As long as cyanolichen recovery does not occur, reduced nitrogen inputs are expected, and soil and plant nitrogen levels may remain lower (Evans and Belnap 1999).

4.3.8 Surface Albedo

Restoration of normal surface albedos and temperatures will depend on the restoration of pre-disturbance cover of cyanobacteria, lichens, and mosses. While cyanobacteria do form a darkish matrix in which other components are embedded, mosses and lichens are much darker and can contribute 40% or more of the cover in an undisturbed crust (Belnap 1993). Consequently, surface albedo recovery will be controlled by factors that control lichen and moss recovery.

CHAPTER 5

MANAGEMENT TECHNIQUES TO MAINTAIN OR IMPROVE EXISTING BIOLOGICAL SOIL CRUSTS

While total protection from disturbance is often the easiest way to maintain or improve biological soil crusts, this is not often possible or desirable. There are many factors to consider in the management of soil communities, including disturbance type, intensity, timing, frequency, duration, or extent. Research is needed to determine realistic biological soil crust objectives by soil type in most potential vegetation types, but initial estimates can be determined by using "healthy" reference areas as described by the National Research Council (1994). Protection of relic sites as rangeland reference areas is important, as these sites provide baseline comparisons for ecological potential and future scientific research.

5.1 Fire

Proactive management is needed to prevent unnaturally large and/or frequent fires in areas where fuel build-up or annual grass invasions have occurred. Such management actions may include altering grazing regimes to prevent annual plant invasions, prescribing fire to prevent fuel build-up, and/or restricting off-road vehicle use.

5.1.1 Prescribed Fire

Used cautiously, prescribed fire can be a useful tool in some situations for renewing community vigor. However, the site's ecology and evolutionary history need to be understood, as burning can result in conversion of some sites to exotic vegetation. Thus, even though a community evolved with fire, fire may no longer be desirable because of exotic plant invasions. Prescribed fire is not recommended for such sites unless post-fire restoration treatments are planned. Prescribed fire may be useful on more productive sites with low potential for exotic plant invasion to reduce high woody vegetation densities resulting from overgrazing. Other impacts (such as recreational or domestic livestock use) should be limited following treatment to allow full site recovery.

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5.1.2 Post-fire Management

Once a site has burned, evaluation is needed to determine whether recovery will occur naturally or if revegetation is needed. Many burned sites, particularly those in the Great Basin and Intermountain regions, require revegetation to stop exotic plant invasion, and most techniques require some soil surface disturbance (Fig. 5.1). This may not appear consistent with recovery of biological crusts. However, failure to treat sites can result in irreversible dominance by annual species (such as cheatgrass), which prevents the return of well-developed biological soil crusts (Fig. 4.2, 4.5, 5.2; Kaltenecker 1997, Kaltenecker et al. 1999a). Once revegetated, protection from grazing and recreational use is often necessary for recovery of the biological soil crust and the vascular plant community. Recovery in these areas can be further facilitated by use of minimal-till or no-till drills or other seeding methods that minimize soil surface and compressional impacts. Emphasis should be placed on restoring the native plant community using local ecotypes, if available.

In the western U.S., revegetation of salt-desert shrub and lower-precipitation Wyoming big sagebrush communities presents some unique problems. West (1994) presents evidence that cheatgrass will remain and potentially increase in these types, as revegetation is difficult because of arid conditions and unpredictability of wet years. He suggests that without livestock consumption of cheatgrass, susceptibility to fire could increase. However, the effective use of livestock in long-term control of cheatgrass has not been demonstrated. In addition, such grazing would occur well into the growing season and thus to the potential detriment of biological crusts and native vascular plants.



Figure 5.1 *Soil surface disturbance associated with post-fire revegetation projects. This site was drill-seeded with a rangeland drill.*



Figure 5.2 *Biological crust development in a successful seeding in the northern Great Basin (above) and lack of development in an exotic annual grass community (below). Note the difference in plant density and the accumulation of litter on the soil surface that limits biological crust development in the exotic community.*

5.2 Livestock Grazing

Managing for healthy biological soil crusts requires that grazing occur when crusts are less vulnerable to shear and compressional forces. Timing for this is highly dependent on soil type and climatic regimes (see Chapter 4). Crusts on all soil types are least vulnerable to disturbance when soils are frozen or snow covered. Biological crusts on sandy soils are less susceptible to disturbance when moist or wet; on clay soils, when crusts are dry (Fig. 2.5; Marble and Harper 1989; Memmott et al. 1998). In general, light to moderate stocking in early- to mid-wet season is recommended. On low- to mid-elevation sites, winter use is advantageous to most vascular plants, including riparian communities, and substantially reduces supplemental feed costs associated with livestock production. Winter grazing also most closely replicates the grazing strategy of native herbivores, who use more productive, higher-elevation sites during summer and lower-elevation sites in winter (Fig. 5.3; Miller et al. 1994; Burkhardt 1996). It is important to remove livestock well

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before wet season's end to allow regrowth of crustal organisms before extended drought. Use when soil surfaces are very wet and muddy should also be avoided to prevent burying the crust (Kaltenecker and Wicklow-Howard 1994; Kaltenecker et al. 1999b). Implementation of rest-rotation strategies that minimize frequency of surface disturbance during dry seasons and maximize periods between disturbances will reduce impacts to biological soil crusts.

Dispersal of livestock throughout useable portions of pastures should also be emphasized. Disturbance of sensitive sites should be avoided or minimized when they are a small proportion of the overall pasture or landscape. Ways to disperse livestock include the following:

- Locating water and salt (or other supplements) on sites with low potential for biological soil crust development and in areas that discourage livestock from loitering. In many areas, sites with high rock cover are good options. Livestock trailing preferences need to be considered when evaluating locations.

- Using brush barriers or fence segments to divert trailing. Sites with high potential for biological soil crust development are often not preferred by livestock for forage; however, these same sites may be open and easy to walk across. Because of lack of forage, minimal barriers are usually sufficient to discourage access.



Figure 5.3 *Native grazers in the western U.S., such as pronghorn antelope and muledeer, tend to use higher, more productive sites during summer and move to lower elevation sites for winter forage. They may also move through areas, rather than staying in one area. This type of seasonality and intensity minimizes impacts to biological crusts by concentrating use when crusts are frozen or moist.*

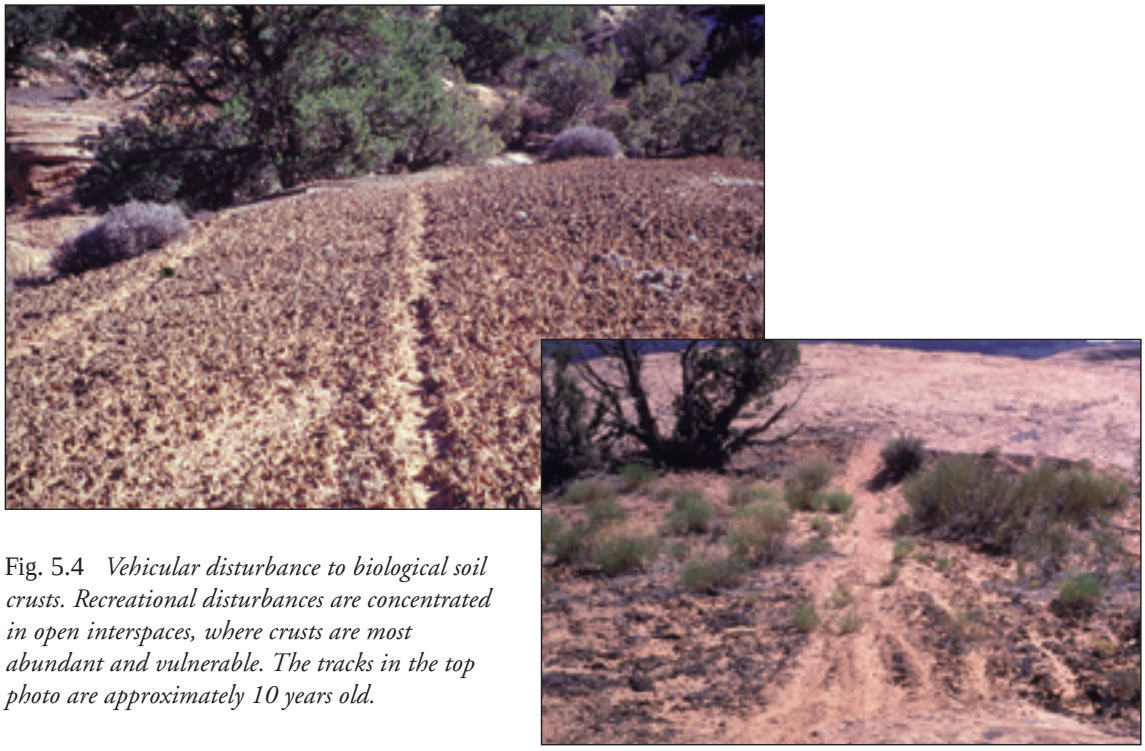


Fig. 5.4 *Vehicular disturbance to biological soil crusts. Recreational disturbances are concentrated in open interspaces, where crusts are most abundant and vulnerable. The tracks in the top photo are approximately 10 years old.*

Stocking levels and season of use should be ascertained on an annual basis, jointly by managers and users, with optimal coverage of both vascular plants and biological soil crusts as the management goal (Kaltenecker and Wicklow-Howard 1994; Kaltenecker et al. 1999b). Optimal coverage should be based on site capability and rangeland health indicators of site stability and nutrient cycling. Livestock exclusion from reference areas and sites with highly erodible soils or low vascular plant cover is appropriate to protect biological crusts and site stability.

5.3 Recreational Use Management

Many recreational activities have impacts similar to those of livestock use. Therefore, principles relating to management of livestock disturbance intensity, timing, frequency, duration, or extent apply to recreational impacts as well. However, there are also major differences. People are often harder to control than livestock. People can carry food and water; thus, access to these essentials does not limit their activities. People tend to go where they want, even in the presence of barriers such as fences. People also have a greater affinity for open vegetation, as it is easier to walk or drive through; however, these same open sites are generally dependent on biological soil crusts for stability (Fig. 5.4). Education, legal restriction and/or use stipulations, and compliance activities may require proportionately

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higher management priorities and time requirements than for the control of livestock.

Concentration of recreational use is generally desirable. Designated campsite use reduces the impact of haphazard placement of sites by individuals. Trails minimize the amount of biological soil crust that is disrupted by trampling. Education can be used to teach people how to camp in areas without designated campsites (e.g., on hardened surfaces, such as rocks, or in areas with minimal crust potential) and how to travel cross-country in areas that lack trails (e.g., in washes, on rock, on fallen logs).

Recommended management practices include the following:

- Restrict road locations to less sensitive areas. Road drainage (culverts, water bars) should be designed so that erosion or sediment fill of adjacent off-site areas is minimized.

- Promote extensive, low-density uses, such as hiking and backpacking, during late fall and winter periods. Restrict access during dry seasons.

- Permit high-density, high-impact uses, such as Christmas tree and firewood cutting areas, for short durations during late fall and winter, preferably when soils are frozen. Areas should be rotated based on a total allowable disturbance threshold with long recovery periods (greater than 10 years minimum on moderate- to high-resiliency sites, such as in sagebrush communities [greater than 230 mm average annual rainfall] in the northern Great Basin) before redesignation for use. Exclude low-resiliency sites.

- Provide designated trails, and restrict use to trails in high-density recreational areas.

- Provide interpretive sites and literature on recognition and value of protecting biological soil crusts at major access points in areas of extensive or unique crust formation.

- Require an analysis of impacts to biological soil crusts and appropriate stipulations on all use applications, such as rights-of-way, oil and gas and other exploration permits, permits to drill, etc.

CHAPTER 6

MONITORING BIOLOGICAL SOIL CRUSTS

Monitoring is the collection and analysis of repeated observations so that trends can be assessed. Typically, monitoring is used to evaluate landscape condition changes over time, often in relation to defined management goals. A monitoring program's objectives will determine the position in the landscape at which measurements will be made and the period over which data will be collected and assessed. Monitoring is often designed so that measurements can be made by more than one observer, and the level of acceptable change is usually determined before monitoring commences.

Monitoring studies often differ from traditional research studies in that they are not designed to infer the cause of any observed changes. Monitoring studies usually lack replication and often have no controls. Plot sizes and measurement protocols may be similar in both monitoring and research studies, but the management objectives are often widely different. The following is a discussion of field-based monitoring strategies and procedures for biological crusts. Key attributes for each strategy are summarized in Table 6.1.

6.1 Monitoring Methods

During the past century, rangeland managers have grappled with methods to assess the health and trend of landscapes (Tueller 1988). Techniques have concentrated primarily on vascular plant attributes, such as cover, frequency, presence/absence, abundance, and biomass of various species, particularly perennial plants (Stoddart et al. 1975; Friedel and Bastin 1988; Friedel et al. 1988; Holechek et al. 1989; Milton et al. 1998). Recently, there has been more emphasis on soil surfaces, and monitoring techniques to assess soil surface condition have been developed (Tongway 1994; Pellant 1996; Whisenant and Tongway 1996; de Soyza et. al. 1997).

While many scientists acknowledge the close links between biological soil crusts and rangeland condition (Klopatek 1992), crusts and their component organisms have rarely been recorded during field-based assessment (West 1990). Early efforts to classify soil surfaces and include biological soil crusts were developed in the semi-arid woodlands of eastern Australia (Tongway and Smith 1989). This assessment showed differences in the stability, erosion, and nutrient status of soil surfaces, and provided a reliable estimate of potential productivity of the surface independent of vascular

Table 6.1 *Attributes of biological crust monitoring strategies. See the text for detailed discussion of each method.*

Recording Method: Individual Taxa vs. Morphological Groups	
Individual taxa	• Allows documentation of biodiversity. • More sensitive to change over time.
Morphological groups	• Quicker, easier identification. • Good evaluation of ecological function. • Less variability. • Less sampling time and intensity to get reliable estimates.
Sampling Methods	
Quadrats (using point or cover class estimates)	• Useful if clumps are <2 cm diameter or groups/taxa are highly interspersed. • Use if information on spatial relationships is not desired. • Provides cover estimate.
Line-point Intercept	• Useful if clumps are <2 cm diameter or groups/taxa are highly interspersed. • Provides information on spatial relationships. • Provides cover estimate.
Line Intercept	• Best if clumps are >2 cm diameter and groups/taxa are not highly interspersed. • Provides information on spatial relationships. • Provides actual measure of cover.

vegetation. The method used four classes for soil surfaces: Class 1 = stable, productive surfaces with high biological crust cover and species diversity; Class 2 = slightly unstable, moderately productive surfaces with broken biological crust cover and moderate species diversity; Class 3 = moderately unstable and unproductive surfaces with low biological crust cover and species diversity; and Class 4 = very unstable and unproductive surfaces where biological crusts are absent (Mucher et al. 1988).

This system was later refined and extended to other landscape types (Tongway and Hindley 1995) and other soil characteristics, such as the degree of cracking, surface coherence, microtopography, and biological crust cover. U.S. workers (Pellant 1996; USDI 1997) have also included biological crust cover as a component of federal land monitoring programs. In eastern Australia, the Department of Land and Water Conservation has been collecting data (including biological crust cover) on the condition and trend of rangelands since the mid-1980s (Green 1992). Monitoring staff in Canyonlands

National Park in southeastern Utah have been collecting cover estimates for biological crusts since 1987 (Belnap, unpublished data).

6.1.1 Sampling Design and Procedures

Biological crusts are typically measured using standard or slightly modified rangeland assessment techniques. These are generally based on measurement of plant and soil attributes within permanent sampling units (quadrats), stratified within relevant vegetation or soil zones (Ludwig and Tongway 1992). Stratification may be necessary where the landscape is composed of a number of homogeneous land units. On degraded sites, nearby reference areas should be measured in order to determine the site's potential for biological crust development. Biological crusts are likely to be most pronounced in areas protected from trampling, such as under shrubs or adjacent to obstacles such as fallen trees and rocks. Shallow, rocky soils often provide "refugia" for crustal organisms that have been destroyed by livestock on more productive soils. However, reference areas should be as identical as possible to their paired disturbed sites with regards to soil characteristics (texture, chemistry, depth), placement on the landscape, and vegetation production potential.

6.1.2 Using Morphological Groups for Monitoring

Biological crust organisms are rarely recorded during routine rangeland monitoring despite increased acceptance over the past decade of their importance in ecosystem processes (Harper and Marble 1988; West 1990; Eldridge and Greene 1994; Ladyman and Muldavin 1996). West (1990) contends that this is due to difficulties in identifying the organisms *in situ*, lack of a standardized sampling procedure with often undue emphasis on laboratory culturing, lack of conspicuousness of some organisms (particularly when the soils are dry), and their patchiness in time and space. As identification is problematic, monitoring can be a daunting task to all but the most experienced (Eldridge and Rosentreter 1999).

However, strong relationships exist between form (morphology) of biological crust organisms and their ecological functioning in relation to landscape processes and disturbance (Eldridge and Rosentreter 1999). Morphology determines how crust organisms function ecologically (relative to erosion and water retention) and their tolerance to, and recovery from, physical disturbance. Morphological groups have been proposed as surrogates for species in biological crust monitoring (see Table 1.1; Kaltenecker 1997; Ponzetti et al. 1998; Eldridge and Rosentreter 1999).

Morphological groups are biologically and ecologically efficient and convey to non-specialists a better image of the

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organismal form and its likely impact on soils and landscapes. These relationships hold true in different regions and continents and eliminate the need for complex, often confusing changes in nomenclature. Other advantages of morphological groups for rangeland monitoring include ease of identification, which is independent of sexual reproductive structures, and the ability to monitor sites more quickly with less specialized staff (Eldridge and Rosentreter 1999). Cover and abundance measures of morphological groups can be obtained more rapidly than measuring each individual species. This allows use of the same size plot for varied sites and assessment of more sites per unit time.

Although morphological groups are appropriate for broad-scale or regional monitoring, their use may not allow the detection of individual species, particularly rare or uncommon taxa. Specific goals of individual studies (i.e., determination of total diversity vs. functional diversity vs. site stability) need to be determined prior to initiation of monitoring. This will determine whether morphological groups can be used or whether monitoring needs to occur at the generic/species level. In all cases, crustal organisms are best detected or identified when moist. When sampling during dry weather, the soil surface to be measured can be moistened with water mist prior to reading to make the organisms more visible.

6.1.3 Quadrat Methods

In communities where biological crusts are patchy, lichen and moss cover is sparse, and/or large areas are being assessed, crust monitoring is often done using quadrats. These can be located either randomly or along a line transect. Quadrats can be used to estimate both biological crust and vascular plant cover (Anderson et al.1982a, b; Brotherson et al. 1983), using either point-intercept or cover classes (Fig. 6.1, 6.2). While cover of the various strata within the community (i.e., biological crusts, herbaceous plants, and shrubs) can be determined, horizontal spatial relationships between groups of organisms cannot be defined using quadrat methods. Where biological crust cover is relatively dense or where personnel turnover is high, microplot sampling effectively estimates cover (McCune and Lesica 1992). Reduced quadrat size is also useful if a goal of the study is to observe greater detail in biological crust composition in relation to environmental variation within the site. For example, Rogers and Lange (1971) used 15 x 20-cm quadrats to examine changes in crust floristics related to stock watering points in semi-arid and subtropical Australia. Other Australian studies have employed 0.5 m^2 subplots within larger plots to assess cover and frequency of crustal organisms (Eldridge and Bradstock 1994; Eldridge 1996; Eldridge and Tozer

1996; Eldridge 1999). U.S. workers have adapted a 20 x 50-cm quadrat and cover classes traditionally used for vascular vegetation monitoring (see Daubenmire 1959) for estimating biological crust cover (Rosentreter 1986; Ponzetti et al. 1998).

Destructive sampling might be necessary if detailed documentation of biological crust species composition is desired. Eldridge and Semple (unpublished data) removed small cores (4 cm^2) from an area of high biological crust cover and diversity and used a dissecting microscope to record cover and abundance of crustal organisms. Use of a short-focus telescope is a similar, non-destructive method (Pickard and Seppelt 1984), but is less accurate.

Within a quadrat, cover and frequency are relatively quick to assess, can be recorded by taxa or morphological groups, and are often good indicators of the ecological and hydrological status of the landscape (Eldridge and Koen 1998). Frequency is determined as the number of times that an organism or group is recorded within a given number of sampling units (expressed as a percentage). This measure describes the abundance and distribution of species and is useful to detect changes in community composition over time. It is one of the easiest and fastest methods available for monitoring changes in vegetation (USDI 1996). Frequency methods are used extensively by federal land management agencies for monitoring changes in landscape condition or trend in relation to vascular plants, and can easily incorporate biological soil crusts.

6.1.4 Line-intercept Methods

Line-intercept has been used in the northern Great Basin in studies that characterized both the crust and vascular plant



Figure 6.1 *Quadrat frame used for point-cover estimation. This frame is 25 x 25 cm in size. Hits are determined by dropping a pin vertically from each intercept within the frame.*

Figure 6.2 *Data form for point-intercept using a quadrat method (left) and example of data collection (right).*

Date:			**Personnel:**						**total = 20/stake**	
Plot	**Stake**	**Cyano**	**Collema**	**Moss**	**Litter**	**Bare**	**Placidium**	**Psora**		

Date: 5-4-01 **Personnel:** JHK, RR **total = 20/stake**

Plot	Stake	Cyano	Collema	Moss	Litter	Bare	Placidium	Psora		
1	1	III	~~IIII~~	I	II	~~IIII~~	II	II		
1	2	~~IIII~~ I	III	II	~~IIII~~	IIII				

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communities (Kaltenecker 1997; Kaltenecker et al. 1999a, b; Kaltenecker, unpublished data). Using line-intercept (see Canfield 1944 for a description of the original methodology developed for vascular plant communities), taxa or morphological groups (Eldridge and Rosentreter 1999) are recorded every centimeter along a number of 10-m or 20-m line transects (Fig. 6.3, 6.4), with cover and floristics of the biological crust and vascular plant communities calculated as a percentage of the total line transect length (Rogers 1994). Each line forms a single, independent sampling unit.

Line-intercept is a rapid and efficient method of sampling when the vegetation community is strongly patterned and is therefore useful in many arid and semi-arid ecosystems. Line-intercept is easiest



Figure 6.3 *Use of line-intercept for measuring biological crust cover along with other community attributes (vascular plant cover, litter, bare mineral soil, rock). Note the placement of the transect line close to the soil surface. Cover of each entity is measured along the top edge of the tape. A misting of water makes crustal organisms more visible and therefore easier to measure.*

when organisms have a definitive boundary, and can be difficult to apply in sites with dense or intermingling vegetation. An advantage of line-intercept over quadrat methods is the ability to derive linear spatial relationships between organisms from the data.

Lines should be long enough to include most of the variability in both the vascular vegetation and biological crust. Optimum line length should be determined from pilot sampling. It is imperative that the line is placed in exactly the same location each time to prevent sampling error associated with repeated measure. Permanent markers, such as steel stakes or nails, may be located along the line to ensure correct placement. If vascular vegetation is measured at the same time, a longer transect might be required with intensive sampling of the biological crust along a shorter portion of the line (USDI 1997).

Figure 6.4 *Line intercept data form (this page) and example of data collection (next page).*

Site Name:				**Date:**			
Treatment:		**Transect #:**		**Reader:**		**Recorder:**	
Cover Type	**From (cm mark)**	**To (cm mark)**	**Under (Cover Type)**	**Cover Type**	**From (cm mark)**	**To (cm mark)**	**Under (Cover Type)**

Site Name: Kuna Butte				Date: 4-18-01			
Treatment: unburned		Transect #: 1		Reader: JHK		Recorder: EM	
Cover Type	From (cm mark)	To (cm mark)	Under (Cover Type)	Cover Type	From (cm mark)	To (cm mark)	Under (Cover Type)
Artrw	0	40					
tall moss	0	36	Artrw				
short moss	36	40	Artrw				
short moss	40	52					
crustose	52	55					
squamulose	55	62					
short moss	62	70					
Agsp	70	85					
short moss	70	74	Agsp				
short moss	83	85	Agsp				

6.1.5 Line-point Intercept Methods

The line-point intercept method is similar to line-intercept, but uses random or predefined points along a line rather than intercepts, and records only the entity or entities (if recording over- and understory) associated precisely with that point. Cover and floristics of the biological crust and vascular plant communities are then calculated as a percentage of the total number of points. Line-point intercept is useful for estimating cover in communities where the crust and vascular vegetation are not strongly patterned. As with line-intercept, linear spatial relationships can be assessed using this method.

6.1.6 The Issues of Scale

Size and shape of the sampling unit depends upon the vegetation type and spatial distribution. Ultimately, the size and number of quadrats will depend on a compromise between statistical considerations (see Section 6.1.8) and what is logistically possible. Generally, in sparsely vegetated landscapes, larger linear quadrats are useful in decreasing variability because of cover heterogeneity. Circular quadrats are often preferred to square because they reduce edge effects. The nature of the impact being investigated will also influence the monitoring method(s) used. For example, studies focusing on species composition will require microplot sampling, while compressional impacts (off-road vehicles, grazing) on biological soil crusts may be best examined by using repeated photo-points, remote sensing, or aerial photography interpretation on large plots of up to several hectares in area.

6.1.7 Voucher Specimens

Representative specimens of each crustal organism should be collected as vouchers for each site. Voucher specimens should include all the variation within a morphological group. A site's biodiversity can later be assessed by identification of voucher specimens by an expert and application of diversity indices.

Voucher specimens require specialized preparation to preserve them for long-term storage (Rosentreter et al. 1988). This often includes removal of excess soil, stabilization of the underlying substrate, and fixation of the specimen onto a stiff card to protect it from breakage. A collection of local or regionally occurring crustal organisms stored in a herbarium is useful for future identification of taxa and for describing a study area's floristics. This enables other researchers and land managers to evaluate differences in biological crust composition between regions.

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6.1.8 Statistical Considerations

Statistical considerations are important when designing any sampling procedure. It is important that the size and number of sampling units, their placement in relation to landscape heterogeneity, and their replication (if significance testing is required) do not compromise any future data analyses. The most efficient design is usually the one that yields the highest statistical precision (smallest standard error and narrowest confidence interval around the mean) for a given amount of effort or money. It is therefore crucial that a biometrician or a statistician with an ecological background be consulted prior to establishment of a monitoring program.

While the value of statistical analysis regarding changes in biological soil crust cover or floristics cannot be undervalued, rigorous statistical examination might not always be necessary or even desirable for a monitoring program (Eldridge and Rosentreter 1999). The danger, however, is that subsequent personnel may wish to look for statistically significant results using a monitoring protocol that was not established to allow rigorous examination. Monitoring sites are frequently unreplicated or pseudo-replicated, and analyses may therefore result in erroneous conclusions (Hurlbert 1984).

A pilot study may be necessary to determine optimal quadrat size, the shape or number to be used, or the transect length that will enable the operator to reduce Type I error (erroneously rejecting a true null hypothesis). For any site-by-time combination, a species-area curve (McCune 1992) can be calculated to give the optimal sampling intensity needed to estimate parameters for a given proportion of the population. For example, in semi-arid eastern Australia, Eldridge and Tozer (1995) found that between six and eight 0.5-m^2 quadrats were needed to adequately describe the biological crust in a woodland community, while only three quadrats were required to describe the crust in a grassland.

Species-area curves are likely to vary in relation to landscape heterogeneity, and the observers must ensure that all site measurements are made from a homogeneous sample. For example, in the patterned semi-arid woodlands in eastern Australia, where groves of trees located on the contour are separated by treeless inter-groves, the biological crust cover varies markedly between the two zones (Eldridge 1999; Tozer and Eldridge, unpublished data). Monitoring should occur within, rather than across, geomorphic zones; otherwise, species-area curves are meaningless and will fail to reveal the optimal number of units necessary to detect differences.

Despite the importance of statistical considerations, the sampling intensity may depend entirely on sampling efficiency. This is particularly important in studies where cores or samples are

collected for laboratory identification and analysis. As a broad generality, one day of collecting and recording crustal organisms in the field can generate up to 10 days of processing and identification in the laboratory. Sampling intensity, therefore, is often a compromise between what is statistically necessary and what is logistically feasible.

6.2 Other Monitoring Methods

As discussed in Chapter 4, changes in biological crust biomass and function often cannot be assessed by visible cover change (Belnap 1993). Obviously, monitoring of cover changes is the easiest and most practical method. However, if resources are available, additional methods should be used to more accurately track biological crust responses to disturbance or management change. The methods described below are examples of monitoring that provides information about biological crusts from a functional perspective.

Determination of cholorophyll *a* using spectrophotometric or high pressure liquid chromatography (HPLC) analysis is an efficient and reliable measure for monitoring changes in photosynthetic biomass, even when visible cover is difficult to detect (Belnap 1993). In areas dominated by cyanobacteria and cyanolichens, monitoring nitrogenase activity is an effective way to determine functional changes in the biological crust (Belnap et al. 1994; Belnap 1996). Both methods require destructive sampling, but can provide valuable information regarding stages in biological crust development.

The slake test is a simple method of determining soil surface stability under wet conditions. Small soil surface fragments (6 to 8 mm diameter) are immersed in rain-quality water, observed over a period of several minutes, and rated according to cohesion of fragments after soaking (Table 6.2). Biological crusts will maintain cohesion when soaked, while physical or chemical crusts will tend to slake or disperse (see Tongway and Hindley 1995 for detailed methods regarding this test). More complicated methods of determining stability include the use of wind tunnels and simulated rainfall.

6.3 Impacts of Monitoring

Care should be taken to establish rigorous protocols when sampling within quadrats and along lines. Because crustal organisms are susceptible to damage by humans, inadvertent trampling within the sampling units may create biased results. Studies on biological soil crusts require that voucher specimens be collected to provide a

Table 6.2 *Classification of results from the slake test. Adapted from Tongway (1995).*

Class	Stability Rating	Observed Behavior of Soil Fragment
1	Very unstable	Fragment collapses completely in <5 seconds into a shapeless mass. A myriad of air bubbles is often present.
2	Unstable	Fragment substantially collapses over about 5-10 seconds with only a thin surface crust remaining; >50% of the sub-crust material slumps to an amorphous mass.
3	Moderately stable	Surface crust remains intact; slumping of sub-crust material is <50%.
4	Stable	Entire fragment remains intact after 5 minutes. This level of stability can remain for many hours.

permanent record of the species found in an area. Removal of voucher specimens or destructive sampling modifies the community and should occur away from permanent plots.

CHAPTER 7

INTERNET RESOURCES FOR BIOLOGICAL SOIL CRUSTS

The Internet has a number of valuable resources for information on biological soil crusts or the organisms that comprise crusts (lichens, algae, etc.). Below we have listed several of the most useful web pages currently available.

Web Address	Author or Organization	Description
www.soilcrust.org	U.S. Geological Survey (Jayne Belnap) Bureau of Land Management National Park Service	Biological soil crust information, based in Canyonlands National Park. This web page contains a near exhaustive bibliography for all things crust-like and a recent version of this reference.
www.id.blm.gov/iso/soils/index.html	Bureau of Land Management, Idaho State Office	This site contains an introduction to soil biological communities, including soil crusts and subsurface micro-and macro-organisms.
www.ucmp.berkeley.edu/fungi/lichens/lichens.html	University of California, Berkeley, Museum of Paleontology	Introduction to lichens.
www.unomaha.edu/~abls/resources.html	American Bryological and Lichenological Society (ABLS)	Checklists and floras; links to institutions and individuals that are resources for information on nonvascular plants and lichens.
mgd.nasce.org/hyperSQL/lichenland	Department of Botany and Plant Pathology, Oregon State Univ.	One of the best introductions to lichens, complete with great color photos.
ucs.orst.edu/~mccuneb/	Bruce McCune Oregon State University	Bruce McCune is a leading ecologist in North America and specializes in lichen and moss ecology and taxonomy.

Web Address	Author or Organization	Description
www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklst7.htm		
	Theadore Esslinger Department of Botany North Dakota State University	*Cumulative Checklist for the Lichen-forming, Lichenicolous and Allied Fungi of the Continental United States and Canada.*
www.fs.fed.us/land/ecosysmgmt/ecoreg1_home.html		
	USDA Forest Service Robert G. Bailey	Descriptions of Bailey's ecoregions of the U.S., including maps.
www.accessexcellence.org/BF/bf05/johansen/web.html		
	California Academy of Sciences Jeffrey Johansen	Text of a talk presented to high school teachers for the California Academy of Sciences. A layman's introduction to biological crust, focusing on algal and cyanobacterial components and research on inoculation to speed recovery following disturbance.
www.biblio.bio.purdue.edu/www-cyanosite		
	Department of Biology, Purdue University; Foundation for Microbiology	Web server for cyanobacterial research; includes a link to CyBib, a bibliographic database containing references on cyanobacteria.

GLOSSARY

adnate: Pressed closely against a surface.

aggregate stability: The degree to which a group of soil particles cohere so as to behave mechanically as one unit.

albedo: A measure of the energy reflected off a surface. Dark surfaces have a lower albedo than light surfaces; therefore, light surfaces absorb less energy than dark surfaces.

ammonia volatilization: The vaporization of ammonia into the atmosphere.

anaerobic: The absence of oxygen. Also refers to organisms able to live or grow in the absence of free oxygen.

appressed: Pressed closely against a surface.

autotroph: An organism whose growth and reproduction are independent of external sources of organic compounds. Carbon compounds are created by autotrophic organisms via the reduction of carbon dioxide (CO_2), with light energy driving the process.

bacteria: Members of a group of diverse and ubiquitous prokaryotic, single-celled organisms.

bryophytes: Tiny plants lacking vascular tissues. This group includes mosses and liverworts.

calcareous: Substrates rich in calcium carbonate, such as limestone or dolomite. Also refers to soils derived from or containing these substances.

cosmopolitan: Found worldwide.

crustose lichens: Lichens that form a crust-like growth form that is closely applied to the substrate.

cyanobacteria: "Blue-green" algae; prokaryotic, photosynthetic organisms that generally have a blue-green tint and lack chloroplasts.

cyanolichen: Lichen that contains a cyanobacterium as its phytobiont.

denitrification: The formation of gaseous nitrogen or gaseous nitrogen oxides from nitrate or nitrite by microorganisms.

desertification: Land degradation in arid, semi-arid, and dry subhumid regions of the world resulting from climatic and other natural stresses coupled with human activities. Processes that lead to desertification include soil loss through wind and water erosion; changes in soil quality due to salinization, waterlogging, and nutrient depletion; loss of vegetative biomass and cover; and compositional and structural changes in plant communities due to exotic plant invasion (Mouat et al. 1995).

foliose lichens: Lichens that are leaf-like in growth form, flattened with definite upper and lower surfaces, and usually loosely attached to the substrate.

fruticose lichens: Lichens with three-dimensional growth forms that are ropey or branching and do not have definite upper and lower surfaces.

gelatinous lichens: Lichens that are non-stratified (algal and fungal layers are not distinct) and that have a jelly-like appearance when moistened. All gelatinous lichens have cyanobacteria as their phytobiont.

gemmae: Structures produced by liverworts that function in vegetative reproduction.

green algae: Photosynthetic unicellular and multicellular organisms that lack true tissue differentiation.

heterocysts: Specialized cells occurring in some filamentous cyanobacteria that are the sites of nitrogen fixation.

heterotrophs: Organisms that require organic compounds for growth and reproduction.

***hydraulic conductivity (K_s)*:** The rate at which water moves through the soil profile under field conditions.

***hyphae*:** Fungal filaments.

***infiltration*:** The downward entry of water into the soil.

***interspace*:** The spaces in a plant community between shrubs or trees.

***lichen*:** A symbiotic relationship between a fungus and an algae or cyanobacterium.

***lithic*:** Pertaining to rock; rocky.

***liverwort*:** A small, non-vascular plant.

***microfungi*:** Fungi that occur free-living in the soil or in association with roots of vascular plants (mycorrhizae).

***mucilaginous*:** Having a sheath composed of sticky polysaccharides surrounding cyanobacterial, algal, or fungal filaments.

***mycorrhizae*:** A stable, symbiotic association between a fungus and the root of a plant.

***nitrification*:** The process in which ammonia is oxidized to nitrite and nitrite to nitrate.

***nitrogen fixation*:** The conversion of elemental nitrogen (N_2) to organic combinations or to forms readily usable in biological processes.

***nitrogenase*:** The enzyme that catalyzes biological nitrogen fixation.

***permeability*:** The ease with which gases, liquids, or plant roots penetrate or pass through the soil.

***photosynthesis*:** The process in which light energy is absorbed by specialized pigments of a cell and converted to chemical energy. The ultimate result of photosynthesis is the fixation of CO_2 and the production of carbon compounds (sugars).

***phytobiont*:** The photosynthetic partner in the lichen symbiosis, i.e., the algal or cyanobacterial component of a lichen.

***poikilohydric*:** Organisms that are capable of becoming physiologically dormant under dry conditions.

***prokaryotic*:** Cells that lack a nucleus.

***propagules*:** Material that results from either sexual or asexual reproduction by crustal organisms and disperses into areas where the biological soil crust has been removed by disturbance. This material "germinates" and grows to establish a new crust.

***resilience*:** The ability to recover following disturbance.

***resistance*:** The ability to withstand disturbance.

***respiration*:** The biological process whereby organisms oxidize carbon compounds to CO_2 and water as a source of energy.

***rhizines*:** Root-like structures of lichens and mosses that function to attach the organism to the substrate.

***saline soil*:** A soil containing sufficient soluble salts to impair its productivity.

***sessile*:** Attached to a surface without a stalk but not imbedded in the surface.

***squamulose lichens*:** Lichens that occur as discrete flakes or scales that are often round or ear-shaped. Squamulose lichens may be convex or concave and often have lobed margins.

***symbiosis*:** An obligatory, interactive association between two organisms, producing a stable condition in which they live together in close physical proximity to their mutual advantage.

***thallus*:** The vegetative body of a lichen or liverwort.

***xerothermic*:** Dry, hot conditions.

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REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

Pubic reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden to Washington Headquarters Services, Directorate for inform ation Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Managem ent and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503.

1. AGENCY USE ONLY (Leave Blank)	1. REPORT DATE	1. REPORT TYPE AND DATES COVERED
	January 2001	Final

1. TITLE AND SUBTITLE	1. FUNDING NUMBERS
TR-1730-2 – Biological Soil Crusts: Ecology and Management	

1. AUTHOR(S)	
Jayne Belnap, Julie Hilty Kaltenecker, Roger Rosentreter, John Williams, Steve Leonard, David Eldridge	

2. PERFORMING ORGANIZATION NAMES(S) AND ADDRESS(ES)	1. PERFORMING ORGANIZATION REPORT NUMBER
U.S. Department of the Interior Bureau of Land Management National Science and Technology Center P.O. Box 25047 Denver, CO 80225-0047	BLM/ID/ST-01/001+1730

1. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)	1. SPONSORING/MONITORING AGENCY REPORT NUMBER

1. SUPPLEMENTARY NOTES

12a. DISTRIBUTION/AVAILABILITY STATEMENT	12b. DISTRIBUTION CODE

13. ABSTRACT (Maximum 200 words)

This technical reference presents a review of current scientific knowledge on the ecology of biological soil crusts, then integrates this information into a discussion on monitoring and management of arid and semiarid lands in the western United States. The document begins with a discussion on the composition, structure, and distribution of biological crusts relative to environmental factors such as climate and soil characteristics. This information is then synthesized into guidelines on development of monitoring strategies as well as site-specific management prescriptions regarding livestock, recreation, and other multiple-use activities. The material is presented from a practical and applied management perspective and is summerized in numerous tables and figures.

14. SUBJECT TERMS	14. NUMBER OF PAGES
Biological Soil Crusts, Soils, Stability, Hydrology, Nutrient Cycling, Disturbance, Management, Monitoring, Ecology	119 + covers
	15. PRICE CODE

14. SECURITY CLASSIFICATION OF REPORT	14. SECURITY CLASSIFICATION OF THIS PAGE	14. SECURITY CLASSIFICATION OF ABSTRACT	14. LIMITATION OF ABSTRACT
Unclassified	Unclassified	Unclassified	UL

(Text of rebuttal by Bleich et al., in response to Lundgren et al. 2021 paper claiming that equids are ecosystem engineers. This "eLetter" in the journal Science was not peer-reviewed, but was published on the Science journal web site, accessed on 9 August 2021: https://science.sciencemag.org/content/372/6541/491/tab-e-letters)

Citation:
Bleich, V.C., J.S. Sedinger, C.M. Aiello, C. Gallinger, D.A. Jessup, and E.M. Rominger. 2021. RE: Ecological "benefits" of feral equids command disclosure of environmental impacts. Science eLetters. 19 July 2021. https://science.sciencemag.org/content/372/6541/491/tab-e-letters accessed 9 August 2021. Response to Lundgren et al., 2021, "Equids engineer desert water availability," *in* Science 372: 491–495.

RE: Ecological "benefits" of feral equids command disclosure of environmental impacts

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(19 July 2021)

Feral equids recently were ascribed the moniker "ecosystem engineers" (1), but their propensity to seek shallow, subsurface water in sandy washes had been described many decades earlier (2). "Digging" may temporarily increase surface water available to native wildlife or create conditions that "… serve as flood-mimicking [plant] nurseries"; how these perceived benefits fit in the context of landscape-level impacts, however, was not discussed (1). Sympatry between North American feral equids and dozens of native species, among which are four desert-adapted ruminants (3), is widespread and federal law mandates feral equids be managed "… to protect the natural ecological balance of all wildlife species…" (4, 5). Seeking subsurface water may mimic the behavior of long-extinct North American equids, but the surrounding context has changed dramatically.

Today's hotter and drier ecosystems lack the once diverse suite of Pleistocene predators (6), and unchecked populations of feral equids compete with extant wildlife for forage and water (7–11), preclude access to resources or alter behavior of numerous species (11–15), impact soils (16, 17), reduce vegetative cover or forage biomass (11, 17, 18), or increase abundance of non-native

plants (17, 18). Feral equids also contaminate natural water sources (5), thereby enhancing habitat for arthropods (19) that may vector pathogens to native ruminants and birds (20). In addition, fouled water also encourages Clostridium botulinum, which has devastated bighorn sheep (Ovis canadensis) and other species (21–23). Feral equids further provide alternative prey for mountain lions (Puma concolor) and likely increase apparent competition and its impacts on small populations of native herbivores (24–26). Moreover, overabundance of feral horses has altered behavior of, and decreased habitat quality for, Greater Sage-grouse (Centrocercus urophasianus), and is directly associated with population declines in those specialized Galliformes (11, 27, 28). Finally, feral burros have had devastating effects on archaeological and historical resources (29, 30) that are protected by federal law (31–33).

Wildlife occupying arid environments are attracted to surface water, no matter its origin, and conservation agencies for many decades have developed water sources to enhance wildlife habitat (34). Negative effects of anthropogenic developments are unconfirmed (35–39), but feral equids often are prevented access to those developments because of the aforementioned impacts to native species (40, 41).

Organizations advocating expansion of feral equid populations have seized upon (1) to support their positions (42–44). That impacts of feral equids were not mentioned (1) is unfortunate, and confounds compliance with federal law and agency mandates. Effects of feral equids, "… may be a function of many factors…" (45), but must be considered in the context of legislation (5) and contemporary conservation (46) and not exclusively that of long-extinct congeners. Degree of environmental impact is the metric best used to assess effects of non-native species (47).

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Competing Interests: VCB is a member of the National Wild Horse and Burro Advisory Board, on which he represents wildlife management issues and concerns in the context of feral equid management. JSS is an active member of the Coalition for Healthy Nevada Lands, Wildlife and Free-roaming Horses, which works to educate the public about the detrimental effects that overpopulations of free-roaming horses and burros are having on the land.

THE ABOVE IS A RESPONSE TO A REPORT IN THE JOURNAL "SCIENCE"

Lundgren, E.J., D. Ramp, J.C. Stromberg, J. Wu, N.C. Nieto, M. Sluk, K.T. Moeller, and A.D. Wallach. 2021. Equids engineer desert water availability. *Science* 30 Apr 2021: Vol. 372, Issue 6541, pp. 491-495. DOI: 10.1126/science.abd6775

The Journal of Wildlife Management 1–13; 2021; DOI: 10.1002/jwmg.21995

Review

Ecological Interactions Involving Feral Horses and Predators: Review with Implications for Biodiversity Conservation

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ABSTRACT For many ecosystems, feral horses are increasingly becoming an important if not dominant component of ungulate biomass and hence influence on community dynamics. Yet we still know little of how horses contribute to key ecological interactions including predator-prey and indirect competitive relationships at a community level. Notably, feral species like horses can exhibit life-history traits that differ from that of native (mainly artiodactyl) herbivore competitors. Artificial selection for traits like increased, early, or extended reproduction that have yet to be reversed by natural selection, coupled with naturally selected differences in anatomy and behavior, in addition to unique management objectives for horses compared to other species, means that the dynamics of feral horse populations are not likely to align with what might be expected of other large herbivores. Unexpected population dynamics and inherent biological asymmetries between native ungulates and feral horses may therefore influence the former via direct competition for shared resources and through enemy-mediated interactions like apparent competition. In several localities feral horses now co-exist with multiple native prey species, some of which are in decline or are species at risk. Compounding risks to native species from direct or indirect competitive exclusion by horses is the unique nature and socio-political context of feral horse management, which tends towards allowing horse populations to be limited largely by natural, density-dependent factors. We summarize the inherent asymmetries between feral horse biology and that of other ungulate prey species with consequences for conservation, focusing on predator-prey and emerging indirect interactions in multi-prey systems, and highlight future directions to address key knowledge gaps in our understanding of how feral horses may now be contributing to the (re)structuring of food webs. Observations of patterns of rapid growth and decline, and associated skews in sex ratios of feral horse populations, indicate a heightened potential for indirect interactions among large ungulate prey species, where there is a prevalence of feral horses as preferred prey, particularly where native prey are declining. In places like western North America, we expect predator-prey interactions involving feral horses to become an increasingly important factor in the conservation of wildlife. This applies not only to economically or culturally important game species but also at-risk species, both predators (e.g., wolves [*Canis lupus*], grizzly bears [*Ursus arctos*]) and prey (e.g., woodland caribou [*Rangifer tarandus caribou*]), necessitating an ecological understanding of the role of horses in natural environments that goes beyond that of population control. © 2021 The Wildlife Society.

KEY WORDS apparent competition, artificial selection, community ecology, conservation, feral horse (*Equus ferus caballus*), life history, predator-prey dynamics.

Understanding the strength and direction of species interactions is important to biodiversity conservation (McDonald-Madden et al. 2016). We now have greater appreciation for the importance of apex predators (Hebblewhite et al. 2005, Ripple and Bestcha 2012), trophic cascades (Hairston et al. 1960, Estes and Duggins 1995), trophic downgrading (Estes et al. 2011), and the role of direct and indirect species interactions in governing animal behavior (Fortin et al. 2005) and population dynamics (Wittmer et al. 2005, Burgar et al. 2019). Our understanding of how introduced, non-native species might destabilize community structure, however, is still limited (Ruscoe et al. 2011). We particularly lag in understanding how feral species now fit within the context of predator-prey interactions and food-web ecology (National Research Council 2013). This is important because unlike native equivalents, in some environments feral species are likely to have superior competitive abilities due to artificially selected traits that have yet to be reversed by natural selection. Feral horses are one such species.

Feral horses have expanded in range and population size throughout the world (Fig. 1) and are increasingly becoming important components of ungulate biomass in

Received: 20 May 2020; Accepted: 16 November 2020

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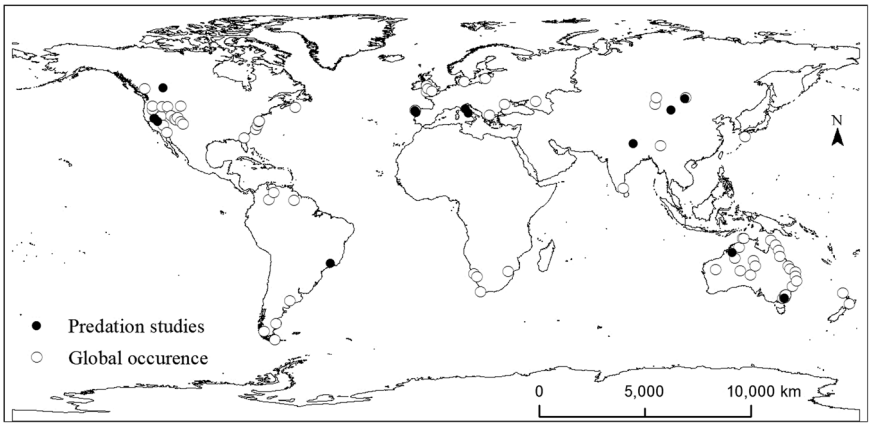


Figure 1. Global distribution of the occurrence of feral horse populations with locations of studies assessing predation on feral horses. Occurrence data are from the thinned dataset ($n = 76$) as published in Naundrup and Svenning (2015). Continent data from Esri (Esri, Redlands, CA, USA).

ecological systems (Andreasen 2014, Nuñez et al. 2016). Artificial selection during domestication for traits such as reproductive output (Clutton-Brock 1981) may influence population growth rates in feral horses (Grange et al. 2009), which can grow at a natural (intrinsic) rate of increase that is unexpectedly high. For example, Eberhardt et al. (1982), modeling the dynamics of feral horses in Oregon, USA, reported how the combination of high adult survival and shifts in age at first reproduction from 4 to 3 years of age is possible to produce observed growth rates of 20% per year—even when foal survival is 60% of adults.

High reproductive capacity in combination with high adult survival can have important consequences for interactions between feral and native species. For example, reproduction in feral pigs can override the effect of high predation levels, increasing predator abundance and subsequently affecting native species (Corbett 1995, Roemer et al. 2002). In feral horses, artificial selection for increased reproduction may also mean that females continue to invest in reproduction even at a cost to their own survival, resulting in marked population fluctuations as has been observed in feral sheep (Mysterud et al. 2002, Grange et al. 2009). Researchers using natural and artificial experiments have reported that rapid changes in prey availability can affect rare, native prey species (Serrouya et al. 2015). The altered biology and subsequent population dynamics of feral horses may mirror these occurrences seen in nature by rapidly adding then removing prey biomass as populations fluctuate. Such dynamics differ from most other wild, large prey populations, which typically have stable adult survival over a range of environments and where females first trade-off reproduction to preserve their own survival as density increases (Gaillard et al. 2000, Gaillard and Yoccoz 2003), and thus contrast with established models describing life-history trade-offs during periods of limitation (Eberhardt 1977).

Feral horses also possess behavioral and biological traits unrelated to domestication that differ from most native prey animals. For example, long-term, female-defense polygyny and a complex social structure (Linklater 2000), an ability to use relatively high volumes of low-quality forage in addition to high-quality foods (Janis 1976), and large relative body size (Knopff 2010) may enhance interspecific competitive ability and reduce the relative vulnerability of horses to predation. Although much is known about the varied environments, which horses can exploit and thrive in, and how horses can displace native herbivores in direct competitive interactions (Hall et al. 2018), much less is known of how horses might interact with competitors indirectly (e.g., by sharing predators through apparent competition; Holt 1977).

In multi-prey systems, the presence or absence of a shared predator plays an important role in shaping community structure (Payne 1966); however, the introduction of new prey can also be significant. Numerous examples highlight how asymmetries in prey vulnerability, resource use, and indirect interactions can alter effects of predation among species and destabilize community structure. For example, Roemer et al. (2002) reported how introduced feral pigs, by providing abundant food, enabled golden eagles (*Aquila chrysaetos*) to colonize the California Channel Islands, USA, and subsequently prey heavily on the endangered island fox (*Urocyon littoralis*), which released populations of the competitively inferior island spotted skunk (*Spilogale gracilis amphiala*). Similarly, invading white-tailed deer (*Odocoileus virginianus*) in the boreal forests of western Canada appeared to almost double wolf (*Canis lupus*) densities, increasing predation risk to alternate prey like threatened boreal caribou (*Rangifer tarandus caribou*; Latham et al. 2011). Under these scenarios, negatively affected species can experience additional risk from shared predators if the more abundant prey population crashes or is suddenly eliminated because predators can rapidly switch to remaining prey to survive (e.g., effects of mountain lions [*Puma concolor*] on caribou after moose [*Alces alces*] populations were culled; Serrouya et al. 2015). Vital to conserving vulnerable prey species is an understanding of the mechanistic pathways in which introduced species might contribute to ecosystem shifts, for example by indirectly causing predation on native species by supporting predators (Holt and Lawton 1994, Roemer et al. 2002). Effective management of native prey species therefore also requires careful evaluation of the potential unintended consequences of controlling introduced species (Ruscoe et al. 2011).

Feral horses have expanded into multiple ecosystems where large predators and native prey exist (Ransom et al. 2016), but predator-prey interactions involving feral horses are not well known despite their relative abundance as prey biomass and the regularity with which horses are reported as components of predator diets. Predator preferences to prey on horses, particularly where they are abundant (Vos 2000, Gray et al. 2008, Knopff 2010, Andreasen 2014, Palmeira et al. 2015), has clear implications for conservation of native prey because of apparent competition. Yet unique biological characteristics coupled with management challenges of feral horses means much of our understanding of predator-prey dynamics and management methods derived from natural or native systems may not translate to feral horse-predator-native prey systems.

In most areas where feral horse populations have established, contention over environmental effects and competition for resources between native species and livestock is common, and public opposition limits many typical population management strategies (Linklater et al. 2002, Nimmo and Miller 2007, Kincaid 2015, Scasta et al. 2018). Fundamental interactions between native prey, predators, and horses and the latter's relevance to conservation may be overlooked in the effort to quantify expected ecological effects and to develop management strategies (Sundararaj et al. 2012). At the same time, biological differences in horses and peculiarities of their population ecology continue to engender largely unknown effects on the long-term viability of competing prey species. As horses expand in range, and with rewilding proposals to actively introduce horses into ecosystems alongside large predators and rare native species (Cromsigt et al. 2018), knowledge gaps stand to exacerbate management challenges.

We review important aspects of feral horse ecology and evolution as they apply to management and the conservation of native biodiversity, with emphasis on the often overlooked, indirect interaction of apparent competition. We discuss the negative conservation outcomes that might emerge because of knowledge gaps regarding the now *de facto* place of horses within terrestrial food webs against the backdrop of management practices for horses relative to that of other wild ungulates. We conclude by proposing several key questions aimed at filling these current knowledge gaps, particularly around interactions between feral horses and predators, and the relevance of these interactions to wildlife management.

METHODS

Our review was based on a comprehensive literature search of the ecology and management of feral horses using the academic search engine Google Scholar (Google, Mountain View, CA, USA), ISI Web of Knowledge (Clarivate Analytics, London, United Kingdom), and the University of Saskatchewan library database for dissertations and theses. We included in our search numerous key words including feral, free-ranging, wild, semi-feral, equid, horse, predator, predation, and depredation. To compile data on the prevalence of predation-prey interactions regarding feral horses (Table 1), we screened publications and unpublished reports for their inclusion of feral horses in predator-diet analysis or inclusion of kill rates. We then selected studies that quantified predation rates of feral horses or reported dietary composition that included feral horses, and excluded those that did not provide any quantification of predation. We included studies that explicitly measured and stated values with dietary analyses or predation rates (e.g., frequency of occurrence; livestock kill rates) and excluded studies that noted only anecdotal or unquantified predation on horses. We also excluded studies where feral horses were not free-roaming in a predator-prey system for at least part of the year (e.g., within fences or enclosures year-round).

ARTIFICIAL SELECTION AND POPULATION DYNAMICS OF FERAL HORSES

Although much of the evolution of the modern caballine horse (*Equus ferus* spp.) took place in North America, horses went extinct in the wild in North America during the late Pleistocene and more recently in Eurasia, excepting reintroductions of the Przewalski sub-species (*E. f. przewalskii*; Haynes 2009, Barrón-Ortiz et al. 2017). Modern descendants of wild horses (*E. f. caballus*; first domesticated around 5500 B.C.E.; Outram et al. 2009) appear relatively unchanged from their wild ancestors in both morphology and behavior (Clutton-Brock 1981, Linklater 2000, Barrón-Ortiz et al. 2017). Artificial selection for reproductive traits in horses, however, may have increased fecundity resulting in life-history trade-offs that depart from typical expectations of large herbivores. Grange et al. (2009) reported that prime-aged Camargue mares continued to invest in reproduction at a cost to their own survival under density-dependent food stress, which was unexpected for a large mammal. Stability in reproductive output at the expense of survival departs from Eberhardt's (1977) empirically supported model describing self-regulation in large-mammal populations, and counters typical investment strategies of survival over reproduction in *K*-selected species (Sinclair 2003).

Theory suggests that selection for high reproduction at the expense of survival should increase instability in feral populations (Barraquand et al. 2015), and this may be responsible for the steep decline and rapid growth observed in some feral horse populations (Grange et al. 2009). Similar population dynamics have recently been observed for feral horses on Sable Island, Nova Scotia, Canada. Over its >250-year existence, the Sable Island population has shown wide fluctuations since records have been kept, declining by approximately 50% in cases over brief (1–2 yr) periods, followed by rapid growth before plateauing and subsequent population decline (Fig. 2). The mechanisms causing these historical cycles had not been studied, but during the most recent population increase from approximately 130 individuals in 2003 to a peak at 579 individuals in 2019, foal survival declined (Laforge et al. 2016) and sex ratios shifted towards a strong male bias in the adult (≥4 yr old)

Table 1. Locations of studies reporting predation on feral horses (FH). We obtained numbers of horses sampled in the study (*n*) and horse density (horses/km^2) directly from study descriptions. Percent of feral horses (%FH) represented in predator diets relates to particular analysis method stated (FO = frequency of occurrence; NS = not stated).

Location	*n*/horses/km^2	Predator(s)	% FH in diet[a]	Alternative prey	Analysis	References
Europe						
Spain						
Eume River Valley	448/1.48	Wolf[b]	37.13	Domestic and commercial livestock	FO	Lagos and Bárcena (2018)
Dorsal Galega	215/0.83		33.93			
Italy						
Northern Appennines	400/0.80	Wolf[b]	1.3	Fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), red deer, mouflon (*Ovis orientalis*), wild boar (*Sus scrofa*), livestock	% scat volume	Meriggi and Lovari (1996), Patalano and Lovari (1993)
Abruzzo National Park[c]	200/11.7		7[c]			
Portugal						
Peneda-Gerês National Park	895/3.7	Wolf[b]	41.3	Livestock	FO	Vos (2000)
North America						
Nevada, USA						
Virginia Range	1,500/1.03	Cougar[b]	77	Mule deer[d], bighorn sheep[d], feral goats (*Capra aegagrus*), pronghorn (*Antilocapra americana*)[d], livestock	% kill site prey species	Andreasen (2014), Gray et al. (2008)
North area	1,185/0.18		45			
California, USA	162/0.27	Cougar	48	Mule deer	% foals killed	Turner et al. (1992)
Canada						
Alberta[e]	749/0.05	Cougar[b]	10–13	Elk[d], deer, moose	frequency relative biomass	Knopff (2010), Webb (2009)
		Wolf[b]	12			
South America						
Brazil						
Serra da Mantiqueira[c]	279/NS	Puma[b]	51	Livestock, native small mammals	% livestock predation[f]	Palmeira et al. (2015)
Asia						
Mongolia[c]						
Hustai National Park	NS	Wolf	32	Przewalski horses[d], red deer, livestock	relative biomass	van Duyne et al. (2009)
South Gobi	120/0.07	Snow leopard	12	Ibex (*Capra ibex*), argali (*Ovis ammon*), livestock	% kill site prey species	Johansson et al. (2015)
Nepal						
Himalayas	NS/1.24	Snow leopard	11.46	Bharal (*Pseudois nayaur*), Himalayan thar (*Hemitragus jemlahicus*), Tibetan argali (*Ovis ammon hogdsoni*), Tibetan gazelle (*Procapra picticaudata*), kiang, livestock	relative biomass	Chetri et al. (2017)
		Himalayan wolf (*Canis lupus chanco*)	9.03			
Oceania						
Australia[g]						
Kosciuszko National Park	NS	Dingo	3.1	Feral and domestic ungulates, native small mammals	FO	Newsome et al. (1983)
Kimberley	NS		5.0			Brook (2013), Forsyth et al. (2019)

[a] Where a range of values are reported, for instance when diet composition of predators is separated by sex, age, and season, we report maximum rates. All other values are averages or as reported in publications.
[b] Indicates where preference or selection for horses was inferred.
[c] Free-roaming domestic horses or grouped with livestock.
[d] Declining, rare, or of conservation concern.
[e] Horse density values used from Webb (2009).
[f] Values from survey data.
[g] A range of values from Australian data are reported for multiple locations across Australia in Forsyth et al. (2019). Locations of highest values identified in Brook (2013), and Newsome et al. (1983).

population. For example, by 2017 there were 1.7 males for every female on the island, which coincided with decreased adult female survival and female reproduction (Regan et al. 2020). Male-biased adult sex ratios have obvious implications for most populations, though dynamics in feral horses may be exaggerated, with effects such as female harassment under female-defense polygyny further negatively affecting female survival (Linklater et al. 1999, Rubenstein and Nunez 2009). Such dynamics in predator-free Camargue and Sable Island horse populations have

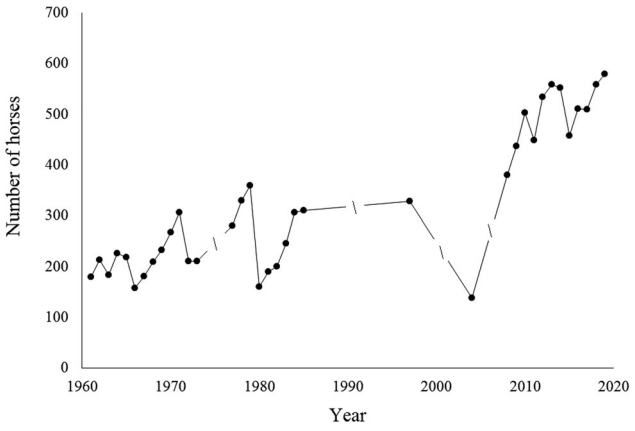


Figure 2. Direct population counts of feral horses on Sable Island, Nova Scotia, Canada, 1961–2019. The authors collected the data since 2008. We obtained data prior to 2008 from air photo interpretation in 2004 (Parks Canada Agency, unpublished data) and as published in Frasier et al. (2016).

been explained as an unexpected life-history trade off arising from a hold-over of artificial selection (Grange et al. 2009) that has yet to be reversed by natural selection. Even if maladaptive over the long term, the consequences of release into the wild of artificially selected feral animals is not likely to be trivial to interacting competitors and predators on ecological time scales.

The high, intrinsic rate of increase of feral horse populations (Eberhardt et al. 1982) and unique sex-structuring that can result at high density (Grange et al. 2009) may have important consequences for predator-prey dynamics in other settings, especially if differential mortality between sexes in feral horses at high density is exacerbated by predation (Berger and Gompper 1999, Grange et al. 2009). For example, where predation is higher on females compared to males as is seen in some native (Kruuk 1976, Berger 1983*b*) and feral equids (Knopff 2010), we can expect accelerated population declines if environmental conditions are disproportionately affecting reproductive females (Grange et al. 2015). In multi-prey systems, accelerated declines of 1 prey species can generate conditions for apparent competition that can be strongly detrimental to vulnerable native prey (other ungulates), if the former has been supporting predators (Wittmer et al. 2013). Differing rates of decline in deer (*Odocoileus* spp.) and moose resulted in differing rates of mountain caribou predation whereby rapid reductions of deer as primary prey for mountain lions increased caribou mortality. In contrast, gradual declines in moose populations were matched in numerical responses of wolves, and sympatric caribou populations remained stable (Serrouya et al. 2015). Regular cycles of rapid growth and steep decline in feral horses, which are likely characteristic as an introduced species (Abrams and Matsuda 1996) and given historical artificial selection, are expected to have important consequences for predators and prey overlapping with feral horse populations.

Predator-prey interactions are system specific (Messier 1995); hence, what constitutes rapid and gradual declines within a given system will be dependent on system characteristics (Holt 1977). Population oscillations in unmanaged populations of feral horses, however, suggest potential for apparent competition to occur in multi-prey systems where feral horses are present. Moreover, if feral horse reproduction (and its subsequent effect on survival) is more influenced by environmental conditions as predicted for species exhibiting these life-history traits (Barraquand et al. 2015), conditions sufficient to affect body condition may arise within relatively narrow environmental ranges for feral horses (Berger 1983*a*, Grange et al. 2009). Significant mortality (e.g., >50%) in native and feral equid populations can occur during periods of heavy snow or rainfall, or drought (Ransom et al. 2016), with female-biased mortality occurring in some cases (Garrott and Taylor 1990, Dobbie and Braysher 1993, Scorolli et al. 2006). In feral horses, poor-condition mothers and their offspring may therefore be more accessible to predators during severe environmental or high-density conditions (Barraquand et al. 2015, Grange et al. 2015), effectively increasing prey biomass over otherwise limiting conditions, where other ungulates are less affected (Novaro et al. 2000, Scorolli et al. 2006). Such supplementation of predator populations during conditions that would typically reduce reproduction and associated survival costs in native prey species (Festa-Bianchet and Jorgenson 1998) may be an overlooked but important factor influencing apparent competition in systems containing feral horses.

RESOURCE USE AND ENVIRONMENTAL VULNERABILITY

Habitat modification can favor introduced species and create asymmetries with native prey that influence apparent competition (Sinclair et al. 1998, Festa-Bianchet et al. 2011). For example, exotic ungulate species in Patagonia, Argentina, exploited modified habitats that negatively affected native species, elevating predator populations and increasing guanaco (*Lama guanicoe*) mortality (Novaro and Walker 2005); habitat change in Alberta, Canada, facilitated invasions of white-tailed deer, which increased wolf numbers in regions supporting threatened caribou populations (Latham et al. 2011). The ability of horses to exploit high-volume, low-quality forage (Grange et al. 2004, Schoenecker et al. 2016) means habitat modifications that otherwise reduce the abundance of quality forage or fragment habitat for native species may do less to affect relative resource availability to horses (Beever and Brussard 2000*b*, De Villalobos and Zalba 2010, Girard et al. 2013). Indeed, where habitat alteration increases the carrying capacity for feral horses, prey biomass and predator abundance may increase in response to growing horse populations despite declines in native prey species (McShea 2005).

Landscape complexity in fragmented environments can also impede animal movement and hence have strong but variable effects on different species and their relative vulnerability to predators (Wittmer et al. 2007). Flight from predators, for example, can be hindered in landscapes with hard edges, rugged terrain, or extensive tree fall

(Bergman et al. 2006). In Yellowstone National Park in the United States, larger and more aggressive bison (*Bison bison*) were less vulnerable to these habitat differences than were elk (*Cervus canadensis*), and only suffered predation when elk numbers dropped substantially relative to bison (Garrott et al. 2008). In predator-prey systems where horses are now present, horses are one of the largest (kg), if not the largest, and hence potentially least vulnerable prey species (Gula 2008, Webb 2009, Knopff 2010, Forsyth et al. 2019). Horses may also not rely on flight to defend against natural predators, rather adopting assertive anti-predator behaviors (i.e., behaviors that increase exposure to a predator or decrease the distance between an animal and a predator on encounter; Dorn 2009) that are weapon-based (striking, biting and kicking; Feh et al. 1994) in concert with social-group defence. Habitat alteration may therefore exacerbate inherent advantages of horses compared to alternate prey species through 2 mechanisms: the provision of additional resources, and hence reduced vulnerability to predation at a population scale (Holt and Bonsall 2017), and lower relative vulnerability for individual animals through anti-predator behaviors as a result of inherent morphology.

Where human modification of habitat facilitates feral horse population growth (e.g., forest conversion to grassland, or where rangelands are actively managed for large grazers including cattle), grazing pressure may induce plant-community feedbacks (Forsyth and Caley 2006). Increased abundance of horses reduces plant biodiversity but increases overall productivity (Beever et al. 2008, De Villalobos and Zalba 2010), which supports higher grazer abundance (McShea 2005) and in turn maintains altered successional trajectories and vegetation states (Sinclair 2003). Vegetation shifts are likely to reduce (relative) resource limitation for feral horses with unknown but likely negative consequences for browsing native prey like deer, moose, and at times elk, all of which feed on woody browse especially in winter. Both elk (Christianson and Creel 2009) and feral horses will, however, use graminoids in greater proportion to availablity (King and Schoenecker 2019), and so the effects of landscape conversion in favor of graminoid abundance may reduce (winter) habitat suitability for deer and moose but also lead to direct competition between elk and feral horses and other grazers including bison and cattle.

The role of humans in modifying resource limitation in favor of horses versus other ungulate prey is not restricted to actions of landscape or rangeland management, however. In contrast to most native prey populations, feral horses may also benefit from competitive subsidies of forage and water intended for domestic species. In some cases, direct supplementation of horses may be a legislative requirement (Scasta et al. 2018) to reduce mortality in populations experiencing resource limitation (Nuñez et al. 2016). Artificial supplementation undoubtedly benefits horses relative to native prey species, particularly where inherent equid biology would otherwise disadvantage the species (e.g., water dependency; Dobbie and Braysher 1993). Management requirements for some feral horse populations may facilitate apparent competition with native species, particularly in arid environments (e.g., as observed in African multi-prey systems containing native equids). Roan antelope (*Hippotragus equinus*) declined sharply following artificial water supplementation in Kruger National Park in South Africa where water-dependent zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) populations increased markedly, in-turn increasing predator numbers and predation on antelope (Harrington et al. 1999). Similar dynamics could be predicted for systems that include feral horse populations where resource limitation would otherwise limit abundance (Scasta et al. 2016). As habitat alteration, climate change, and management approaches continue to shift vulnerability of environmental limitation in favor of horses, negative effects of direct and apparent competition on native prey species are likely to be non-trivial.

HORSES AS PREY

Most feral horse populations are not subject to significant predation simply because of a lack of large predators (Ransom et al. 2016). But continued range expansion of feral horses and direct introduction of feral horses in trophic rewilding projects (Donlan et al. 2006, Cromsigt et al. 2018), coupled with the reintroduction of and growth in populations of large predators including wolves (Ray et al. 2005, Wolf and Ripple 2018), means that predation is likely to increase in importance as an ecological interaction where feral horses occur. Despite widespread extirpation of large carnivores, generalist predators capable of attacking and killing adult horses and foals now do so in several ecosystems (Table 1).

In the Sierra Nevada Mountains of the United States, mountain lions have taken up to 48% of foals born, potentially limiting growth in small feral horse populations (Turner et al. 1992); several individual lions specialize in hunting adults and young in areas where horses are abundant, and native prey such as mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) are declining (Gray et al. 2008, Andreasen 2014). In the Canadian Rockies, feral horses live with mountain lions, wolves, and grizzly (brown) bears; comprise significant proportions of the available prey biomass; and are the sole prey hunted by some individual (lion) predators (Knopff 2010). Free-roaming domestic horses in Mongolia live alongside recently reintroduced Przewalski horses, where wolves regularly hunt and kill horses in both populations (van Duyne et al. 2009); snow leopards (*Panthera uncia*) in Nepal show a preference for free-roaming horses among a suite of wild and domestic prey including the rare native equid, kiang (*Equus kiang*; Chetri et al. 2017). In several European regions, feral and free-roaming (domestic) horses are present in predator diets including brown bears and wolves (Cozza et al. 1996), with preferences for horses observed in multiple wolf packs (Vos 2000). As in well-studied native systems (Owen-Smith and Mills 2008*b*), relative abundance, predator preference, and changing vulnerability play significant roles in determining predation rates on horses (Cozza et al. 1996, Schiess-Meier et al. 2007) and the potential negative interactions of shared predation among alternate

prey. Parameterization of even simplistic equations regarding predator-prey interactions (e.g., exclusion criteria; Holt and Lawton 1994) from the perspective of horses as prey is notably lacking, compared to the abundance of information regarding competition among native prey and horses—processes that are intimately linked (Chase et al. 2002).

Much of the literature regarding predation on feral horses is limited to predator dietary analyses, making inference about the effect of predator-prey interactions difficult (Ransom et al. 2016). Key differences in feral-horse biology compared to that of native ungulate prey species means predator-prey interactions involving horses are likely to differ from those of sympatric prey. For example, availability of foals to predators may occur over extended periods throughout the year compared to distinct and synchronous pulses of fawns, kids, and calves in native ungulates because gestation is long in horses (~11 months) and produces a single offspring (Berger 1986, Grange et al. 2004). Differences in birthing intervals between horses and other ungulate prey can be significant, with foaling periods extending over 6 months in the Canadian West (Salter and Hudson 1982), whereas intervals in sympatric ungulates such as elk and moose may only range over 2 months (Poole et al. 2007, Hebblewhite and Merrill 2011). Such extended birth periods mean new foals arrive before juveniles reach sizes sufficient to defend against predators (Gray et al. 2008), and such a prey base may be consistent during environmental conditions that would otherwise reduce availability of native juveniles. The provision of predator populations with a feral horse prey-base, even where horses and native prey are spatially or temporally separated, could mean predators are effectively bridged throughout the year, where there would usually be distinct gaps in native prey availability (e.g., seasonally or over extended periods of severe environmental conditions; Holt and Lawton 1994).

Similarly, behavioral responses and anti-predator strategies are poorly understood in feral horses compared to those for native prey species, with much inference being drawn from African equids (Brubaker and Coss 2015). Intra- and interspecies variations in predator hunting tactics differentially affect sexes and age groups of prey species including native equids. Predators can reduce resource use (Kruuk 1976, Thaker et al. 2011) and increase grouping behavior in predator-dense areas (Feh et al. 1994, Hebblewhite and Pletscher 2002); aggressive anti-predator responses can reduce predation risk (Garrott et al. 2008, Forsyth et al. 2019). Effective anti-predator behaviors by equids vary in response to seasonal resource availability, relative prey composition and abundance, and dynamic predator responses (Bowen 1981; Grange and Duncan 2006; Owen-Smith and Mills 2008*a*, *b*). Although African equids provide broad inference for feral horses, predator-prey interactions (Diedrich 2010, Brubaker and Coss 2015), predator and prey guilds, and ecosystem types in the Americas, Australia, and Europe differ greatly. Bears (*Ursus* spp.), wolves, and mountain lions dominate predator guilds in North America and Europe, for example, and feral horse habitat varies from high-elevation forested landscapes (Salter 1978) to arid canyons (Gray et al. 2008). In montane forests, landscape factors such as elevation, snow depth, and tree cover may prove important in minimizing predation risk from some predators such as bears and wolves (Poole et al. 2007, Kittle et al. 2008), and this relative risk will fluctuate seasonally with the migratory movements of sympatric prey species such as elk (Hebblewhite and Merrill 2011). Although volumes have been written on native ungulate prey and predator population ecology, we know little about how feral horses are affected by predation despite their presence in many of the same ecosystems as native prey, or how human modification of habitat can influence predator efficiency or functional responses.

Habitat fragmentation is common where feral horses occur, and this may further increase variation in species vulnerabilities to predation risk (Novaro and Walker 2005). Typical anti-predator strategies of ungulates such as flight (Brubaker and Coss 2015) can be precluded in mosaics of clear-cuts and linear features where deadfall and hard land cover edges are prevalent (e.g., western Canada; Garrott et al. 2008, Latham et al. 2011), meaning anti-predator behaviors used by horses (Feh et al. 1994, Dorn 2009) may become relatively more important for survival. Spatial refugia through proximity to human activity can also reduce predation risk (Hebblewhite et al. 2005), and feral horses are often habituated to humans and human activities because of intense interest from observers and the near absence of hunting of horses by humans (Linnell et al. 2016). Although large predators may avoid proximity to people, feral horses existing in a complex mix of predators and people can still be successfully hunted by predators (Vos 2000, van Duyne et al. 2009, Knopff et al. 2010), but the relative vulnerabilities of native large herbivores compared to horses are not well known.

Despite many unknown aspects of predator-horse interactions, it remains an assumption that adult feral horses are relatively invulnerable to predators because of their size (Knopff 2010, Andreasen 2014, Forsyth et al. 2019). But relative predator and prey size does not necessarily govern prey selection in multi-prey systems (Owen-Smith and Mills 2008*a*) and, as expected, when feral horses comprise the dominant portion of prey biomass, predator diets can be composed solely of horses (Vos 2000, Andreasen 2014). Selection or preference for horses has been inferred in multiple studies where relative feral horse biomass has increased (Table 1). The data suggest that presumptions in the literature around unprofitability and risk to predators in hunting horses appear to be unfounded, and have underestimated the ability of generalist predators to adapt to novel prey (Holt and Lawton 1994, Weitz and Levin 2006). Increases in pack size in canids has been inferred as a potential mechanism to better handle large prey including feral horses (Bowen 1981, Gula 2008, Forsyth et al. 2019).

Where apparent competition limits native prey populations, population modeling and predator-prey theory suggest that populations of predators or non-native prey may need to be eradicated or severely reduced in size (Courchamp et al. 2003). The social and political realities of

feral horse management (and their predators), however, clearly indicate that removal of entire horse populations is very likely impossible (Scasta et al. 2018), demonstrating a need for more detailed understandings of predator-prey interactions involving feral horses. Top predators are capable of hunting and killing male and female feral horses both adult and young, and there is little evidence to suggest that predation will not increase in populations where predation is minor or incidental, particularly in the context of declining populations of native ungulate prey (Owen-Smith and Mills 2008*a*). Apparent competition (or positive indirect effects, discussed below) with feral horses should therefore be expected (Garrott et al. 2008, Gower et al. 2008, Dunkley et al. 2012); however, increasing our understanding of feral horse predator-prey ecology remains an outside priority for most government mandates.

CONSERVATION CONSEQUENCES

Although expansion and growth in feral horse populations may be controlled, once established horses have proven to be resilient and permanent components of food webs. The distinct nature of feral horse biology and ecology, and our approaches to managing horses relative to other wildlife precludes many of the typical strategies directed at minimizing negative ecological interactions, including those used in native large-mammal systems like culling or harvest management (Symanski 1996, Beever and Brussard 2000*a*). In addition, discounting of the importance of feral-horse biomass to community ecology because of how horses are categorized (e.g., as escaped or free-ranging domestic livestock) circumvents questions over their relevance in wider predator-prey systems. Increasingly, however, free-roaming horses can comprise significant portions of seasonal or year-round prey bases, with predators often showing strong preference for horses, particularly in areas supporting reduced availability of native prey (Patalano and Lovari 1993, Meriggi and Lovari 1996, Mishra 2002, Palmeira et al. 2015, Chetri et al. 2019).

For many native species such as elk or caribou in North America, guanacos in South America, or the reintroduced Przewalski horse in Mongolia, potential apparent competition with feral or free-roaming horses presents real conservation risks. Declining populations of elk in the eastern Rocky Mountains of Canada (Berg et al. 2016) contrasts strongly with a rapidly increasing sympatric feral horse population. Indeed, horses in the region are now adding as much as 188 kg/km^2 of live-weight biomass to prey bases in the system (weights from Andreasen [2014]; abundance estimates from Alberta Environment and Parks [2019]). Ungulate biomass is widely accepted (and predictively modeled) to be positively related to wolf density at a macroecological scale (Kuzyk and Hatter 2014). At 188 kg/km^2 (roughly 2 relative ungulate biomass values per km^2), a wolf population as high as 10 wolves/1,000 km^2 may be supported by feral horses alone (quadratic model of Kuzyk and Hatter [2014]). Although predator subsidization by horses to the detriment of native elk, moose, and deer populations may increasingly become important in places like Alberta, habitat loss and apparent competition with native prey is already affecting threatened woodland caribou populations in closely adjacent ecosystems (Wittmer et al. 2007, Hervieux et al. 2013). Apparent competition with feral horses has already been suggested as a contributor to population declines for caribou in central British Columbia (White et al. 2020), and there is little to suggest that feral horses will not also eventually colonize other woodland caribou ranges in western Alberta and eastern British Columbia, imparting further stresses on the at-risk species.

Multiple asymmetries in predator vulnerability and resource use between horses and native species favor horses in areas of sympatry (Garrott et al. 2008), satisfying conditions for apparent competition (Holt and Lawton 1994); this is in addition to issues regarding resource competition, which receives more attention. But high relative abundance, variable vulnerability as a result of artificial selection, and predator preference in systems where feral horses are present may not necessarily translate into negative effects for sympatric, native ungulate competitors. Predators may be drawn away from quality native prey habitat into areas where horses are abundant as seen with livestock and rare prey (Sundararaj et al. 2012). Similarly, predation on horses may facilitate persistence of native prey through sheer division of total predation (Abrams and Matsuda 1996), or preference for the species less invested in survival (i.e., horses) when environmental conditions are severe (Barraquand et al. 2015). Maladaptive trade-offs for survival recognized in feral horse populations (Grange et al. 2009) and discussed above as a potential negative outcome of predator-prey interactions, may in fact benefit alternate prey species and support coexistence, particularly where numerical responses of predators to horse abundance are low (Holt and Bonsall 2017). Potential positive effects of horses (e.g., as diversionary prey), however, are unknown and largely speculative.

Developing an understanding of feral horse predator-prey dynamics will have further value as the reintroduction and natural range expansion of large predators into areas in Europe and North America continues (Wolf and Ripple 2018). In some cases, feral horses are also being used directly in rewilding efforts, as surrogates for extinct native grazers to re-establish large-grazer trophic interactions (Donlan et al. 2006, Rubenstein et al. 2006, Corlett 2016). Longer-term objectives that aim to establish grazing communities using horses inclusive of apex predators will certainly depend on understanding predator-prey dynamics of feral horses. Even scenarios where herds of domestic horses that range freely are preyed upon, such as those in Mongolia (van Duyne et al. 2009) and Iberia (Vos 2000), provide vital information about profitability and risk because horses in these systems are components of fluctuating native prey bases (Holt and Lawton 1994). As reintroduction or rewilding efforts introduce horses into prey bases, and as free-roaming horse and predator ranges naturally expand, information from established predator-prey studies involving horses may provide novel avenues for population management (Gray et al. 2008) and provide tools for the

conservation of vulnerable native species, both predator and prey (Sundararaj et al. 2012). We encourage this work.

EVOLUTIONARY CONSEQUENCES

Our review has focused on the management and conservation implications of indirect ecological interactions involving feral horses. The evolutionary context of predator-prey interactions in free-roaming horse populations, however, also has both historical and current relevance. Much about feral horse behavior and sociality may not have been altered during domestication to the extent that traits of reproduction have (Clutton-Brock 1981, Linklater 2000). Natural selection among directly and apparently competing horses and prey species may be recognizable among contemporary distribution patterns, species composition, and behavior, concomitant with specific physical traits (Holt and Bonsall 2017). Predators might select a particular coat color in horses, for example, which may be related to primary prey abundance (Turner et al. 1992), thus operating in opposition to artificial selection. Similarly, although anti-predator behaviors in feral horses are likely maintained, or at least quick to re-establish (Sih et al. 2010), deeper investigation into predator-prey dynamics of feral horses provides an avenue to study antagonism between natural and artificial selection for traits such as docility (Sundararaj et al. 2012, Brubaker and Coss 2015, Cabrera et al. 2017). Ultimately, for many feral horse populations, particularly in North America, similar predator guilds, although less diverse and smaller in size, exist as those present among megafaunal communities prior to widespread megafaunal extinctions (Haynes 2009). Little is known about predator-prey interactions in extinct species from Late Pleistocene herbivore communities (Lundgren et al. 2020); however, the close relatedness, behavior, and morphology of feral horses to the extinct Pleistocene equids (Barrón-Ortiz et al. 2017) provide a unique opportunity to answer general questions such as those regarding adaptive foraging, ontogeny, and body size, or social and inter-species organization among feral horses under predation (Holt and Bonsall 2017) and their role in community dynamics.

FUTURE DIRECTIONS

With horses already established as *de facto* permanent components of predator-prey systems in many areas, increasing our knowledge base of predator-prey and indirect interactions involving feral horses will be important to managing expanding feral horse populations and, by extension, native-species conservation. We identify 7 outstanding questions as being the most important for addressing current knowledge gaps on predator-prey and indirect interactions involving feral horses.

1. To what extent and in which environments has artificial selection and inherent equid biology (e.g., foraging and survival strategies) shaped differences in competitive ability between horses and native ungulate prey on shared landscapes from direct and indirect competition? That is, what is the potential for horses to exclude competitors through competition and apparent competition? Few researchers have yet to think about the invasion ecology of horses in the context of Lotka-Volterra-type or agent-based competition modeling (Donalson and Nisbet 1999, Haerter et al. 2016), but it may be possible to predict the exclusionary effects of horses and scenarios of management that help promote coexistence.
2. With expanding distributional range in western North America, what role will the increase in biomass of feral horses play in the conservation and management of at-risk species? For species like woodland caribou, we especially require additional quantitative data and analysis on this topic further to the conjecture or anecdote presented herein or in recent papers (e.g., White et al. 2020). Conservation biologists should approach the subject not only in terms of understanding the potential magnitude of negative influences on alternate prey through apparent competition, but also positive influences for at-risk predators including wolves in the lower 48 states of the United States, and grizzly bears in the Rocky Mountains of the United States and Canada.
3. Are there sex differences in predation vulnerability among adult horses, and how does this vary with age, reproductive status, and environmental conditions? Differential predation among sexes could exacerbate declines in feral horse populations given observed trends in female life-history trade-offs. Quantifying differential predation rates between sexes, and how these change with density dependence requires methods beyond dietary analyses of predators, such as rapid kill-site investigation in predator studies (Knopff 2010) and individual-based monitoring of feral horse populations under predation (Grange et al. 2015).
4. How does vulnerability to predation in horses change across landscapes and by predator species, and are anti-predator behaviors related to these factors? Habitat characteristics and spatial distribution influence prey vulnerability, and relative vulnerability can change with predator type and anti-predator behavior (Schneider 2001, Garrott et al. 2008). Determining relative predation risk in the range of landscapes and across the diversity of multi-prey systems that feral horses now occupy requires behavioral observation of predator-prey interactions and quantification of predator success rates in differing landscapes (Forsyth et al. 2019).
5. What role does asynchronous foaling play in relation to fluctuations in native prey availability (i.e., via apparent competition)? Foals can be born at any time of the year, and this may prove important in the maintenance of predator populations during declining abundance of native prey (Gray et al. 2008).
6. What role might predation play in modulating the population oscillations observed in predator-free (mainly island) feral horse populations? Predators can limit growth of feral horse populations under certain circumstances (Turner et al. 1992, Ransom et al. 2016), and this may prove important in mitigating the effects of

density on population dynamics (Grange et al. 2009). Predators may also exacerbate population fluctuations by capitalizing on poor-quality females and their young, particularly under high density or severe environmental conditions, resulting in higher predation rates on alternate prey species (Barraquand et al. 2015). Quantifying factors such as handling time, search rates, and foraging efficiency of predators regarding feral horses has general utility but may also highlight fluctuating profitability throughout population cycles.

7. Do predators alter resource-use patterns of feral horses, and how might this relate to availability of alternate prey species? Predators can significantly alter prey use of resources and the landscape through indirect effects (Laundre et al. 2001). Resource-use and expansion in feral horses may therefore be determined in part by predation risk, yet this can only be determined through detailed analysis of feral horses (e.g., using radiotelemetry data) in landscapes with predators.

MANAGEMENT IMPLICATIONS

Although little is currently known of the place of the feral horse in the context of community ecology relative to other large (native) ungulates, lack of understanding of fundamental horse ecology in modern landscapes and food webs has important consequences for conserving biodiversity where populations of horses have established or are likely to establish. Feral horses differ in many ways from native ungulate herbivores in morphology, behavior, and ecology but also evolution (including history of artificial selection), with the consequence that horses can be highly competitive in anthropogenically disturbed ecosystems relative to native prey species—particularly where given special protections to do so. Superior competitive ability also arises from indirect interactions including apparent competition, of which very little is known in the context of horses. Increasing horse biomass can have predictable effects on predator numbers with implications for regions undertaking large predator reintroduction programs that may be unknown for native prey because of apparent competition. Where horse biomass comprises an increasing relative share of ungulate biomass on landscapes, understanding the strength and direction of direct and indirect ecological interactions between horses and other prey species should be of concern for community ecologists and managers, especially where native ungulate prey may be rare or declining.

ACKNOWLEDGMENTS

We thank J. Poissant and T. K. Shury for discussions leading to this manuscript. Our work was supported by funding from the Alberta Conservation Association, the Wild Horses of Alberta Society (stipend funding to PNB), the University of Saskatchewan, and the Natural Sciences and Engineering Research Council, Canada.

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Associate Editor: Sarah King.

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Author(s): C.S. Boyd, K.W. Davies, G.H. Collins
Source: Rangeland Ecology & Management, 70(4):411-417.
Published By: Society for Range Management
URL: http://www.bioone.org/doi/full/10.1016/j.rama.2017.02.001

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Rangeland Ecology & Management 70 (2017) 411–417

Contents lists available at ScienceDirect

Rangeland Ecology & Management

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Original Research

Impacts of Feral Horse Use on Herbaceous Riparian Vegetation Within a Sagebrush Steppe Ecosystem

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ARTICLE INFO

Article history:
Received 19 April 2016
Received in revised form 26 January 2017
Accepted 9 February 2017

Key Words:
bare ground
herbivory
springs
wild horses
wildlife habitat

ABSTRACT

Feral horses inhabit rangeland ecosystems around the world, and their impacts on riparian ecosystems are poorly understood. We characterized impacts of a free-ranging horse population on the structure and composition of riparian plant communities in the sagebrush steppe ecosystem in the western United States. We used a randomized block design with single 25 × 50 m exclosures and grazed plots on four study sites within Sheldon National Wildlife Refuge in northwestern Nevada. Exclosures were constructed in 2008. Herbaceous plant utilization was measured from 2009 to 2013 by clipping within excluded and grazed plots. Herbaceous production and vertical structure were measured in 2013, and plant functional group and ground cover components were estimated in 2012–2013. Herbaceous utilization ranged from 27% to 84%, and herbaceous production did not differ by grazing treatment ($P = 0.472$). Grazed plots had seven-fold higher bare ground cover ($P < 0.001$), 60% less litter cover ($P < 0.001$), and the basal cover index was 65% higher. Grazing increased rush density by 50% ($P = 0.041$) but did not affect sedge density ($P = 0.514$). Grazing decreased herbaceous stubble height up to 80% and visual obstruction by about 70% ($P < 0.05$). Deep-rooted hydrophytic plant species did not increase with grazing exclusion, but greater vertical structure in excluded plots could improve hiding and nesting habitat for some riparian-associated wildlife species. Additionally, decreased bare ground with grazing exclusion could reduce erosion potential and susceptibility to invasive plant species.

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Introduction

During the Pleistocene, the range of a variety of species of wild horses (*Equus* sp.) covered much of Europe, Asia, North America, and perhaps North Africa (Kavar and Dove, 2008). Wild horse populations underwent a significant range contraction at the end of the Pleistocene and became extinct in North America by approximately 10,500 years before present (Guthrie, 2003, 2006). Free-ranging domestic horses (*E. caballus)* were introduced to North America by Spanish explorers during the 16th and 17th centuries (Haines, 1938) and by inadvertent and purposeful releases associated with the ranching industry and perhaps the military during the late 19th and early 20th centuries (Young and Sparks, 2002). Similar introductions of domestic horse stock have occurred globally, and current feral horse (horses whose ancestors are of domesticated lineage; Ostermann-Kelm et al., 2009) populations are stable or increasing in both the United States and Australia (Nimmo and Miller, 2007; Garrott and Oli, 2013).

Feral horses are currently a management issue on rangelands throughout much of the world. In the western United States, horses lack effective predators to control populations and periodic gathering of horses on federal lands has been necessary to control horse numbers and their associated impact on plant and soil resources (Garrott and Oli, 2013). Gauging the ecological impact of feral horses can be difficult because grazing by these animals often coincides in space and time with utilization by other large herbivores, particularly domestic livestock. In the western United States, most public lands are grazed by cattle and cattle diets overlap substantially with those of horses (Krysl et al., 1984; Scasta et al., 2016). Unlike domestic livestock, feral horse grazing is difficult to manage on a rotational or deferred basis due to difficulties associated with moving horses, resulting in continuous or near continuous use of rangeland plant communities. Previous work suggests that feral horse grazing can alter upland vegetation and soil resources within rangeland ecosystems at local (Fahnestock and Detling, 1999a; Ostermann-Kelm et al., 2009) and landscape scales (Beever et al., 2008; Zeigenfuss et al., 2014). Horse grazing has also been linked to community scale changes in composition and demographics of insect (Beever and Herrick, 2006), small mammal (Beever and Brussard, 2004), avian (Zalba and Conzzani, 2004), and estuarine fauna populations (Levin et al., 2002), as well as competition for water resources with a variety of native wildlife species (Hall et al., 2016).

Impacts of grazing animals on plant and soil resources can be particularly acute in and around riparian areas that serve as an attractant to herbivores due to forage and water availability (Kauffman and Krueger, 1984; Turner, 2015). Riparian areas are critical for maintaining a broad

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http://dx.doi.org/10.1016/j.rama.2017.02.001
1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management.

suite of plant and animal species, contain biotic and abiotic habitats that differ from the surrounding landscape, and may serve as important travel corridors for a variety of wildlife species (Gregory et al., 1991; Naiman et al., 1993; Chambers and Miller, 2011). In the sagebrush steppe of the US Great Basin these habitats harbor the majority of regional biodiversity (Sada, 2008). Research suggests preference of feral horses for riparian areas during summer months with the potential for reduction in plant species richness, height, and cover and for alteration of plant community composition (Ganskopp and Vavra, 1986; Crane et al., 1997; Beever and Brussard, 2000). In desert environments typical of the US Great Basin, upland vegetation surrounding riparian areas may also be impacted by feral horse grazing; for example, Davies et al. (2014) reported reduced sagebrush density in riparian-adjoining upland areas exposed to feral horse grazing relative to grazing exclosures.

Sheldon National Wildlife Refuge in northern Nevada offers a unique opportunity to examine the impacts of feral horses on riparian plant communities that are not currently grazed by domestic livestock. Our objective was to determine habitat structure and composition of plant communities in riparian areas exposed to and excluded from feral horse grazing. We hypothesized that plant basal cover would increase in response to horse grazing exclusion, and that grazing exclusion would shift plant community composition away from grazing-tolerant rush (*Juncus* sp.) species. We further hypothesized that vertical structure of habitat would increase with grazing exclusion in association with increased shrub density, herbaceous stubble height, and visual obstruction.

Methods

Study Area

Our study took place within the Sheldon National Wildlife Refuge (SNWR) in northwestern Nevada. Since the 1880s cattle, sheep, and horses (>20,000 animals) grazed on the SNWR, but cattle and sheep were removed between 1990 and 1994 (U.S. Fish and Wildlife Service, 2013). SNWR covers an area of 230,000 ha of largely sagebrush steppe rangeland, and our study sites were located within an unfenced and contiguous 80,000-ha management unit. Feral horse density within the management unit varied from 0.5 to 0.8 horses.km^{-2} between 2007 and 2013 (USFWS, unpublished data). Free-ranging burros occurred within SNWR, but not within our study area. Elevations within SNWR average approximately 1900 m, and climate is characterized by warm, dry summers and cold, wet winters with most precipitation occurring during the winter and spring periods. Average water year precipitation (1 October to 30 September) for the study area is approximately 300 mm, and during the study period it was 67%, 88%, 148%, 110%, 70%, and 69% of normal for 2008, 2009, 2010, 2011, 2012, and 2013, respectively. Climate information for the study period was collected from remote weather stations located within 50 km of study sites (RAWS USA Climate Archive).

Dominant plant species across study sites included the sedges *Carex nebrascensis* (Dewey) and *Carex microptera* (Mack.), the grasses *Agrostis* sp. and *Poa sp*., and the rush *Juncus balticus* (Willd. Var.). Common forb species included *Veronica americana* (Schwein.), *Polygonum bistortoides* (Pursh.), and *Achillea millefolium* (L). The only shrub species encountered within the riparian zone of the study plots was *Rosa woodsii* (Lindl.). Non-native plant species were almost nonexistent within study plots.

Experimental Design

We used a randomized block design consisting of four blocks (sites) and two treatments. We established 25 × 100 m sites near the origin of perennial springs in 2008. Study sites were chosen by random selection from the population of approximately 40 springs within the 80,000-ha management unit. The long axis of each site was bisected by the dominant riparian channel. Sites were then divided into two 25 × 50 m plots, and plots were randomly assigned to be either excluded from ("excluded") or exposed to ("grazed") feral horse use. Excluded plots were fenced with 1-m high fencing consisting of evenly spaced metal pipe rails. This fence did not completely restrict access of native large mammals (mule deer and pronghorn), but field observations (i.e., lack of fecal matter and lack of utilization in excluded areas) suggest minimal utilization of excluded and grazed plots by these species. Sites varied in elevation from 1 850 m to 1 900 m and consisted of obligate or facultative wetland vegetation (Lichvar et al., 2014) communities associated with outflow from perennial springs. The end of season (October) wetted width (flowing or standing water) of riparian zones varied across both study sites and years and ranged from 0 m to 3.9 m in a dry year (2013) and from 1.4 m to 6.1 m in a wet year (2011; Table 1). Three sites had a flat aspect, and one was located on a northerly aspect. Extreme distance between sites was < 15 km. Most sites were characterized by multiple channels with a single dominant channel. Although springs were perennial, above-ground channel flow through sites was generally ephemeral and associated with the seasonal period of snow melt. However, water availability was sufficient to allow persistence of hydrophytic vegetation species within a defined riparian zone (Winward, 2000) at all sites.

Data Collection

Within each plot, vegetation measurements occurred along two 30-m long sampling transects placed within the riparian zone on both sides of and running parallel to the dominant channel (i.e., two transects total per plot). In grazed plots, utilization of herbaceous biomass by herbivores was estimated by clipping herbaceous materials to ground level in five randomly located 40 × 50 cm quadrats located within the riparian zone on each sampling transect in October of 2009–2013 and expressing remaining biomass as a percentage of ungrazed biomass. Ungrazed biomass was estimated by clipping three 40 × 50 cm quadrats within a 1-m diameter circular wire cage that was randomly located within each grazed plot and moved annually to a new location. Utilization was subjectively characterized as indicative of grazing that is suitable for providing a relatively high level of herbaceous vegetation structure ("light" grazing, < 30%), will allow for limited vertical structure development ("moderate" grazing, 30–60%), or will not allow for significant vertical structure ("heavy" grazing, > 60%, Table 2). Annual herbaceous production was estimated within exclosures in 2013 by separating dead from live plant material in five randomly located 40 × 50 cm quadrats along each sampling transect and weighing clipped materials. Herbaceous production in grazed areas was estimated by randomly locating a total of five (for each plot) 50 × 50 cm wire exclosures along sampling transects in April of 2013 and clipping and weighing live herbaceous plant material in October of 2013. All clipped material was oven-dried to constant weight before weighing.

Ground cover of bare ground and litter was estimated (ocular) in June or July 2012–2013 within thirty 20 × 50 cm quadrats spaced at 1-m intervals along each sampling transect; obstruction of the ground surface when viewed from above due to canopy vegetation was not considered when making these estimates (i.e., we looked under the

Table 1
Wetted width during an above (2011) and below (2013) average precipitation year for riparian study sites in northern Nevada. Values represent site averages of plots that were excluded from or accessible to horse grazing

	2011		2013	
Site	Mean (cm)	SE (cm)	Mean (cm)	SE (cm)
Tenmile	138.3	26.1	0.0	0.0
Buckaroo	607.2	177.8	389.8	92.0
Corral	167.7	45.6	0.0	0.0
Smith	227.8	31.3	302.0	39.4

Table 2
Percent utilization of aboveground biomass for riparian study plots grazed by feral horses in northern Nevada. Data are site averages from 2009 to 2013

Site	Mean (%)	SE (%)	Grazing level
Tenmile	46.9	17.0	moderate
Buckaroo	72.7	6.0	heavy
Corral	27.0	15.4	light
Smith	83.9	5.9	heavy

vegetation canopy). Percent plant basal cover (i.e., "basal cover index") was estimated for each quadrat by summing percent cover of bare ground and litter and subtracting the total from 100. Density of herbaceous plant species was estimated by direct count of either plants for nonrhizomatous species or stems for rhizomatus species within 10 × 20 cm quadrats nested within those used to estimate ground cover attributes. Shrub density was by direct count within 1 × 30 m belt transects centered on each sampling transect. Maximum height was measured for all shrubs within the belt transects.

Herbaceous stubble height was estimated in October 2012–2013 at 1-m intervals along sampling transects by measuring the maximum height of the nearest sedge, grass, or rush. Visual obstruction was measured in July 2013 by noting the highest (from ground) strata of a 2.5-cm diameter pole visible from a distance of 5 m and an observation height of 1 m. The pole was demarcated into 2.5-cm strata of alternating black and white bands, and readings were taken at 1-m intervals along each vegetation transect (Robel et al., 1970).

Data Analysis

For analysis purposes, plant density data were collated by functional group. Functional groups included sedges, rushes, *Eleocharis* sp., grasses, forbs, and shrubs. All statistics were performed using Statistical Analysis Software (v. 9.2; SAS Institute, Cary, NC). The effects of herbivory on variables that were repeated in time were analyzed using repeated measures analysis of variance (ANOVA) with time as a repeated variable, and nonrepeated factors were analyzed using one-way ANOVA (PROC Mixed). Site and the site × treatment interaction were considered random factors and treatment a fixed factor. Because shrubs were only recorded at one site, we did not analyze treatment effects on the abundance of this functional group. Nonproportional data not meeting ANOVA assumptions were weighted by the inverse of the treatment variance during analysis (Neter et al., 1990; James and Drenovsky, 2007). Proportion data not meeting ANOVA assumptions were transformed using the arcsine-squareroot (Sokal and Rohlf, 1995). Nontransformed means are used for presentation and discussion. Covariance structure was selected as detailed by Littell et al. (1996). Main effects and interactions were considered significant at $\alpha = 0.05$. Data are reported as treatment means with associated standard errors.

Results

Herbaceous production varied by site ($P < 0.001$) but not grazing treatment ($P = 0.472$) and ranged from approximately 85.3 $g \cdot m^{-2}$ (± 13.8) at the Tenmile site to 356.4 $g \cdot m^{-2}$ (± 44.1) at the Smith site (Fig. 1). Utilization across study sites varied from 27.0% (± 15.4) at the Corral site to 83.9% (± 5.9) of standing crop at the Buckaroo site (Table 2; Fig. 2).

Cover of bare ground was approximately seven-fold higher in grazed versus excluded plots ($P < 0.001$, Fig. 3) but did not vary by year ($P = 0.524$). Litter cover was > 60% less in the grazing treatment ($P = 0.010$) and was unaffected by year ($P = 0.093$). The basal cover index varied by both treatment ($P = 0.053$) and year ($P = 0.035$), was about 65% higher in grazed plots (see Fig. 3), and was highest in 2013 (2013 = 38.4% [± 4.0], 2012 = 31.1% [± 5.5], data not shown).

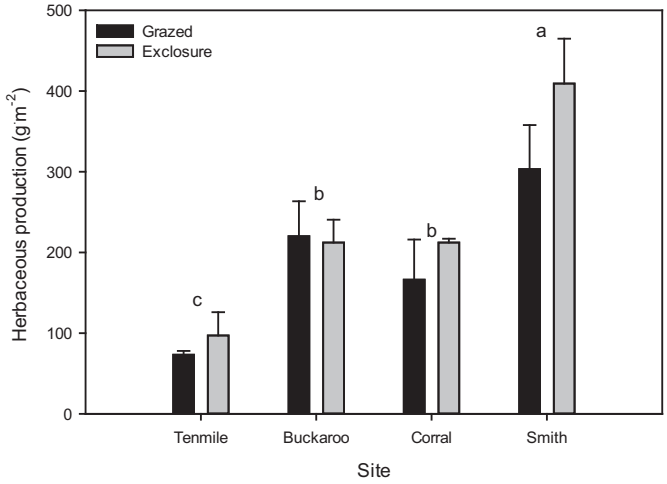


Figure 1. Herbaceous aboveground plant production for riparian study plots in northern Nevada. Data are means for 2013 with associated standard errors. Plots were excluded from horse grazing from 2009 to 2013 or were accessible to grazing during that time period. Sites without a common letter are different at $\alpha = 0.05$.

Sedge stem density was unaffected by treatment ($P = 0.514$) or year ($P = 0.233$) and averaged approximately 30 plants·0.1m^{-2} (Fig. 4). On the basis of density, rushes were the most abundant herbaceous functional group. Stem density of rushes was 50% higher in grazed plots ($P = 0.041$) but was unaffected by year ($P = 0.921$). *Eleocharis* sp. did not vary between years ($P = 0.826$) but was almost 150-fold higher in grazed plots ($P = 0.001$). Grass density in grazed plots was almost double that of excluded ($P = 0.032$) but did not change between years ($P = 0.457$). Density of forbs did not vary by treatment ($P = 0.305$) or year ($P = 0.103$).

Herbaceous stubble height was affected by year ($P = 0.005$) and the year by treatment interaction ($P = 0.016$, Fig. 5). Stubble height values ranged from 8.5 ± 2.5 cm for grazed plots in 2012 to 40.6 ± 3.1 cm for exclosure plots in 2012. Stubble height for grazed plots increased by 72% from 2012 to 2013 ($P < 0.05$). Visual obstruction was about threefold less ($P = 0.038$) in grazed plots (see Fig. 5). This change was associated primarily with reduced presence of sedge vegetation in the upper herbaceous canopy with grazing (see Fig. 2).

Discussion

Our results suggest that the impact of feral horses on riparian plant communities varies depending on the parameter under consideration. We found that exclusion from horse grazing had no impact on sedge density and, consistent with our hypothesis, rush stem density was higher in grazed plots, suggesting that maintenance of key herbaceous plant species is possible under the horse density and grazing patterns encountered in the current study. It should be noted that our study sites were primarily associated with springs, as opposed to perennial riparian drainages with more defined dominant channel systems and higher flows; under higher flow conditions, similar levels of herbivory may impair riparian function if they resulted in compromised bank structure and associated site desiccation followed by loss of deep-rooted plant species (George et al., 2012). This scenario is supported by others who have noted the importance of abiotic factors, specifically water availability, in modulating the impact of herbivory on plant species composition (Fahnestock and Detling, 1999b).

In our study, greater density of *Eleocharis* and *Rush* sp. in grazed areas was associated with greater bare ground. Both of these functional groups have been reported to increase in abundance in response to grazing, perhaps in association with increasing bare ground (Leege et al., 1981; Dobkin et al., 1998; Loucougaray et al., 2004). Changes in functional group abundance can also be associated with preferential

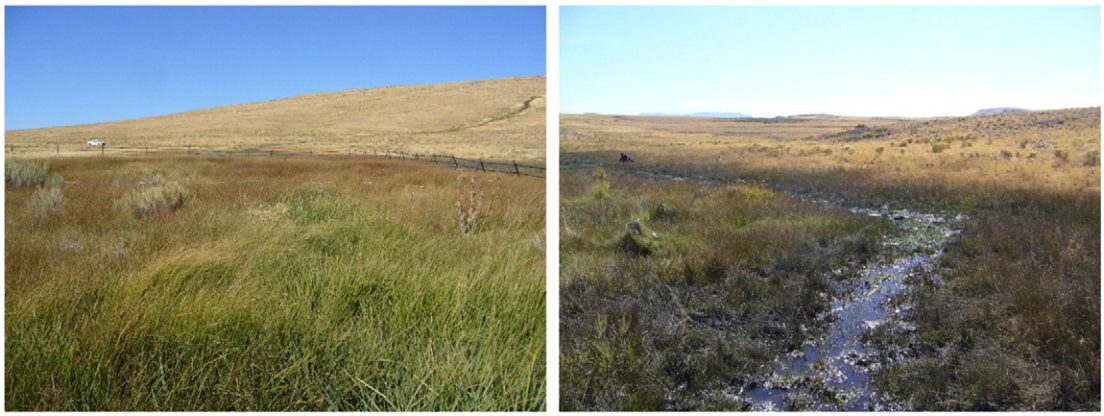


Figure 2. Horse-excluded (left image) and adjacent horse-grazed (right image) plots at Buckaroo Spring, Sheldon National Wildlife Refuge, Nevada, in summer 2012. The exclosure was constructed in summer 2008. A strong reduction in herbaceous plant vertical structure with horse grazing is apparent.

selection by grazing ungulates (Kauffman and Krueger, 1984), however, horses are not highly selective grazers (Hanley and Hanley, 1982). Other work has indicated sedges (*Carex* sp.) and perennial bunchgrasses are key dietary components for free-ranging horses (Crane et al., 1997).

Published studies indicating the impacts of horse grazing on spring-associated riparian plant species are limited. Our work is in agreement with Dobkin et al. (1998), who found that rush abundance increased with horse use of riparian vegetation around springs. However, dissimilar to Dobkin et al. (1998), we did not find decreased grass and sedge density with horse grazing. Our results may differ from Dobkin et al. (1998) because we measured herbaceous plant response based primarily on density as opposed to foliar cover, the latter being more sensitive to plant canopy structural alterations associated with grazing; such alterations in cover may or may not relate to changes in biotic potential of a plant functional group to produce biomass. Beever and Brussard (2000) also recorded reduced herbaceous plant abundance, as well as reduced plant diversity with horse grazing, but levels of utilization and trampling appear to have been much higher in that study compared with average utilization in the present study.

Shrubs were only present at one of our study sites, and only one species of shrub *(R. woodsia)* was encountered. Previous work suggests that this species may be somewhat tolerant to herbivory, and thus its singular presence could represent initial shrub recovery from long-term herbivory (Bailey et al., 1990). The fact that shrubs remained absent throughout our 5-year study on the remaining sites suggests that shrub propagules were not present at these sites. Because shrub distribution was limited across study sites, we are not able to make definitive statements regarding the impacts of horse grazing on shrub abundance. However, limited riparian-associated shrub populations (both *R. woodsia* and *Salix* sp.) were present in the vicinity of our study sites on similar slopes, gradients, and landscape positions (in some cases within the same drainage way). Thus, it is possible that historic livestock and horse grazing or perhaps other management practices may have led to reduced shrub abundance for long enough to limit propagule availability. Strong decreases in shrub populations with unrestricted horse grazing have been previously reported for spring-associated plant communities in Nevada (Beever and Brussard, 2000), and Davies et al. (2014) found decreased sagebrush density in horse-grazed uplands adjacent to riparian areas.

From a plant production standpoint, exclusion from feral horse grazing did not change herbaceous productivity within the time-frame of our study. This does not preclude the possibility that longer-term exposure to horse utilization could impact plant production. Lack of a difference in aboveground production between grazed and excluded areas suggests that grazing is not impairing basic ecological processes of these sites. Alternatively, exclusion for 5 years may not have been

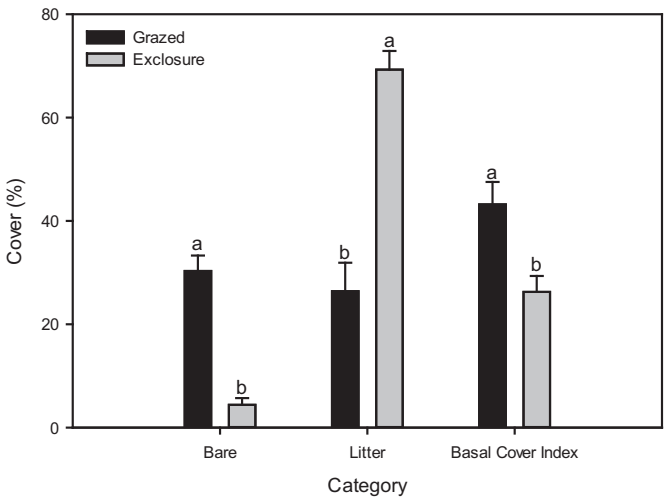


Figure 3. Ground cover for riparian study plots in northern Nevada. Data are means for 2012−2013 with associated standard errors. Plots were excluded from horse grazing from 2009−2013 or were accessible to grazing during that time period. Within a category, bars without a common letter are different at $\alpha = 0.05$.

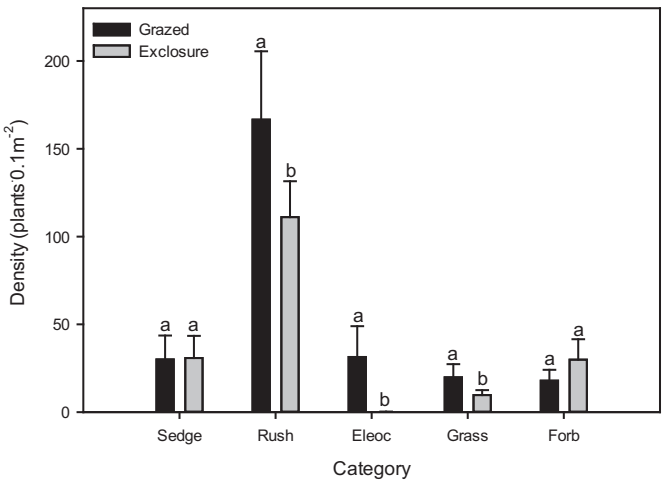


Figure 4. Herbaceous plant density for riparian study plots in northern Nevada. Data are means for 2012−2013 with associated standard errors. Plots were excluded from horse grazing from 2009 to 2013 or were accessible to grazing during that time period. Bars represent treatment means with associated standard errors. Within a category, bars without a common letter are different at $\alpha = 0.05$.

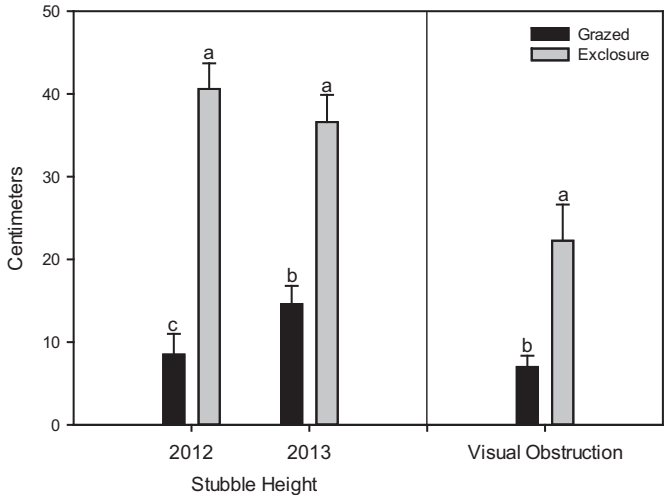


Figure 5. Herbaceous stubble height and visual obstruction for riparian study plots in northern Nevada. Stubble height is the average maximum height of herbaceous plants, and visual obstruction represents the highest (from ground) portion of a 2.5-cm diameter pole visible from a distance of 5 m and an observation height of 1 m. Data are means and associated standard errors for 2012−2013 (stubble height) and 2013 (visual obstruction). Plots were excluded from horse grazing from 2009 to 2013 or were accessible to grazing during that time period. Within a panel, bars without a common letter are different at $\alpha = 0.05.9$

long enough to have elicited vegetation recovery from decades of horse use (and cattle and sheep use prior to the 1980s). We did not measure below ground production and thus cannot speculate on the effects of horse herbivory on primary production of study sites. Our results are consistent with those of others reporting either no effect of grazing or clipping on aboveground (Leege et al., 1981) or total (above and belowground) plant production (Boyd and Svejcar, 2012) or increased aboveground production with grazing (Boyd and Svejcar, 2004). In contrast, Fahnestock and Detling (1999a) reported that aboveground plant production in arid and montane grasslands could be decreased by horse grazing during wet years, but increased with grazing on montane sites during dry years via compensatory production. In this same study, belowground biomass was invariant to horse grazing treatment. Working within the same area of the Great Basin sagebrush steppe as our study and over a longer time period, Zeigenfuss et al. (2014) reported that aboveground plant biomass decreases as horse density increases and that this effect is amplified during dry years.

Contrary to our hypothesis, the plant basal cover index was higher in grazed areas (see Fig. 3), which is somewhat counterintuitive given that percent cover of bare ground was also higher in grazed areas. However, the majority of the ground surface within exclosures was covered by litter (see Fig. 3), which may have acted to limit sites available for plant establishment and growth. This litter was predominantly from previous years' production of sedges, and to a lesser extent rushes and grasses, and we commonly observed litter buildup to 10-cm depth. Litter accumulation of this magnitude could reasonably be expected to limit establishment of new plants (Loucougaray et al., 2004). Additionally, because bare ground was higher in grazed areas, this may have acted to create establishment sites for more grazing-tolerant (*Eleocharis* sp. and *Juncus* sp.) plant species (Krueger-Mangold et al., 2006). Put another way, effective area for establishment of plant propagules may have been higher in grazed versus excluded areas. Whether or not this facilitates or detracts from the long-term sustainability of these plant communities depends on 1) whether available sites are colonized by plant species that promote soil stability (e.g., sedges and rushes; Shafroth et al., 2002) and 2) if increased bare ground results in soil loss due to elevated erosion potential (Pearce et al., 1998). In contrast, in a companion study looking at horse grazing effects on upland vegetation adjacent to riparian areas, Davies et al. (2014) reported decreased plant cover with heavy utilization (> 40%) by horses. However, these sites were dominated by caespitose perennial bunchgrasses growing in a more arid environment with low potential for litter buildup in interspace locations.

As predicted by our hypothesis, vertical structure was strongly influenced by the presence of horse grazing, with both stubble height and visual obstruction increasing with horse exclusion. Proportionally, visual obstruction values were within about 60% of stubble heights (see Fig. 5), reflecting the dense nature of vegetation at study sites (i.e., limited horizontal visibility below the upper herbaceous canopy). The degree of vertical structure in our study plots was influenced almost entirely by herbaceous vegetation. Increases in shrub abundance at some point in the future could significantly increase vertical structure of the riparian plant communities in our study. The maximum herbaceous vertical structure recorded in our study was approximately 60 cm, and *R. woodsii* (the only shrub species encountered in our study) can reach heights of 3 m (Pavek and Skinner, 2013).

Changes in vertical structure and plant functional group composition of wetland plant communities associated with horse grazing could have strong guild-dependent impacts on availability and suitability of habitat for a variety of wildlife species (Knopf et al., 1988; Dobkin et al., 1998; Levin et al., 2002). Avian species in particular are tightly linked to vertical structure in riparian habitats (Ammon and Stacey, 1997), and thus differences in vertical structure noted between horse grazing treatments in the current study, as well as other work (e.g., Beever and Brussard, 2000), could logically be expected to impact avifaunal habitat use. For example, Brewer's blackbird *(Euphagus cyanocephalus)* often nests in dense vegetation bordering wetland habitat (Martin, 2002), and this species was frequently found nesting in sedge-dominated plant communities within our riparian exclosures, even though the exclosures occupied a small area. This species was not observed nesting in horse-grazed areas. In contrast, greater sage-grouse *(Centrocercus urophasianus)*, a resident species of critical conservation status within our study area, has been reported to preferentially forage in moderately grazed riparian areas during brood rearing (Klebenow, 1982). Dobkin et al. (1998) observed avian guild separation between cattle-grazed and ungrazed riparian habitats, noting that upland species increased in grazed areas while wetland and riparian species dominated nongrazed plots.

Our study area was grazed by horses throughout the year with no fencing to restrict access. Therefore, from a conservation standpoint, the relatively limited vertical structure we recorded in association with horse use suggests that horse grazing may be limiting vertical structure of riparian habitats at larger scales and, by extension, negatively impacting diversity of avian habitats. Alternatively, with no horse grazing, structural diversity of habitats could be skewed toward increased vertical structure at larger scales. This is particularly true given the absence of other resident-grazing ungulates with a dietary preference for, or capable of subsisting on, riparian graminoid vegetation. Others have suggested that avian diversity could be maximized with heterogeneous levels of grazing intensity (Loucougaray et al., 2004; Martin and McIntyre, 2007).

Management Implications

Although herbaceous plant production between grazed and excluded treatments did not vary in our study, results indicated that year-round exposure to feral horse grazing can result in changes in plant community structure and composition. The most apparent of those changes are related to plant community structural and ground cover attributes. Bare ground decreased dramatically with horse exclusion in association with a strong increase in ground cover of litter. These changes were likely related in the sense that horse grazing removed herbaceous plant material (see Fig. 2) that would otherwise have accumulated as ground litter; and as ground litter is reduced, bare ground can increase. However, herbaceous plant production did not vary between grazed and excluded treatments. Reduced vertical structure with horse grazing,

associated with altered herbaceous canopy structure, may decrease habitat availability for riparian and wetland-associated avian species. Alternatively, foraging habitat for some avian species could increase with reduced vertical structure (Tewksbury et al., 2002). While 5 years of feral horse exclusion did precipitate changes in herbaceous plant species composition, density of deep-rooted species necessary for maintenance of riparian function (i.e., sedges and rushes) was either unaffected or increased with horse grazing. We were unable to experimentally determine horse impacts on shrub communities because only one shrub species was present at only one of the four study sites. Effects of horse grazing on riparian habitat will be density dependent and associated with landscape features and herd management practices that influence horse distribution across the landscape.

Acknowledgments

The authors greatly appreciate personnel from the Sheldon-Hart Mountain National Wildlife Refuge Complex for their assistance in locating study sites and constructing exclosures. We also appreciate the efforts of Clare Poulsen and Jarod Lemos in field data collection and implementation of the experiment. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the US Fish and Wildlife Service. The US Department of Agriculture (USDA) is an equal opportunity provider and employer. Mention of a proprietary product does not constitute a guarantee or warranty of the product by the USDA or the authors and does not imply its approval to the exclusion of other products that may also be suitable.

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The Journal of Wildlife Management 1–11; 2021; DOI: 10.1002/jwmg.22088

Research Article

Lentic Meadows and Riparian Functions Impaired After Horse and Cattle Grazing

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ABSTRACT Perennially and intermittently available water in lentic, spring-fed herbaceous meadows supports wetland plants that build and maintain absorbent soil organic matter, capture sediment, prevent erosion, and thereby sustain riparian ecosystems. Enhanced forage and available water attract a diversity of wildlife and grazing animals that can degrade riparian vegetation through prolonged overuse. We tested novel monitoring methods and adapted existing methods to obtain quantified vegetation data that have been consistently linked to riparian functionality and compared these data to ungulate species use. We quantified ungulate use with time-lapse cameras at 10 Nevada spring-fed herbaceous meadows where core greater sage-grouse (*Centrocercus urophasianus*) habitat, public land grazing allotments, and free-roaming horse (*Equus caballus*) herd management areas (Bureau of Land Management) or territories (U.S. Department of Agriculture Forest Service) overlapped. Free-roaming horses used most study sites over longer periods and grazed more intensely than cattle or domestic sheep. Native ungulate grazing intensity was comparatively negligible. Free-roaming horses selected spring-fed meadow sites on average 51 (±33 [SE]) times more than the surrounding rangelands, and cattle selected them 30 ± 23 times more. Within the wettest area of a site, study sites with longer duration of use, and higher intensity of use, had more soil alteration and bare ground. Riparian ecosystem degradation occurred where meadows had limited rest or recovery time from grazing during the growing season. At all sites we noted loss of riparian function, especially within the hydric areas with the highest potential to grow abundant cover of stabilizing wetland plant species. Transects for monitoring soil alteration and vegetation cover in this hydric location can provide a leading indicator of riparian recovery or degradation and help in adjusting free-roaming horse population levels or livestock management strategies. © 2021 The Wildlife Society.

KEY WORDS cattle, feral horses, monitoring, Nevada, rangelands, sage-grouse, ungulates, wetlands.

Lentic wetlands and riparian areas, when functioning properly, rely on still or slow-moving surface and subsurface water without the energy to form dominant scour channels associated with typical (lotic) fluvial processes (Gonzalez and Smith 2020). A properly functioning wetland supports enough vegetation, soil and landform features, or woody material to dissipate energies associated with overland flows, thereby reducing erosion and directing physical alteration from human and animal activities; enable ponding, storage, and retention of surface water including floodwater; capture sediment; enable groundwater recharge; and maintain wetland soil attributes (Gonzalez and Smith 2020). Lentic wetlands provide economic and ecological value in arid landscapes (Hershler et al. 2007, Fensham et al. 2011). In the Great Basin region of the United States, riparian and aquatic ecosystems cover about 1% of the landscape but support most of the region's biodiversity (Sada 2008). Sada and Vinyard (2002) reported that >125 animal species endemic to the arid Great Basin region in the United States rely on lentic riparian areas associated with desert springs. Because groundwater-dependent springs subsist on either small, local mountain aquifers or large regional aquifers, they can outnumber perennial streams by orders of magnitude in arid regions (Thomas et al. 1996, Ledbetter et al. 2014). Although springs may be overlooked because of their small size and low output of water, their abundance and ability to provide distributed water and persistently green forage offer important habitat features aiding in arid landscape-scale diversity (Sada 2008). Additionally, available free-standing water can enable distribution of wildlife and livestock (Rautenstrauch and Krausman 1989, Ehrhart and Hansen 1997, Rosenstock et al. 1999, Prichard et al. 2003, Wyman et al. 2006) without the need for costly wells or other infrastructure in arid regions (Gurrieri 2020).

Herbivory can enhance or degrade riparian functionality, and it affects ecosystems differently across elevations and climates (Bardgett and Wardle 2003, Singer and Schoenecker 2003, Beever and Aldridge 2011, Holechek et al. 2011). Land

Received: 2 May 2020; Accepted: 5 May 2021

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managers can help maintain riparian functionality for the benefit of grazers, wildlife, and ecosystem diversity and services by applying appropriate livestock management strategies across a grazing area. Limited grazing duration and timing of use can extend vegetation recovery periods, and appropriate density and distribution of grazers can reduce trampling damage and intensity of forage use (Prichard et al. 2003, Wyman et al. 2006, Swanson et al. 2015). Conversely, Ehrhart and Hansen (1997) reported growing-season-long grazing as a universally ineffective grazing management approach to maintaining healthy riparian ecosystems. Growing-season-long grazing can decrease soil organic carbon stocks (Clary and Kinney 2006, Volesky et al. 2011, Dlamini et al. 2016) and was consistently linked to poor riparian conditions in unfenced rangelands of northern Nevada, USA (Swanson et al. 2015). Grazing that does not allow for adequate recovery can negatively affect plant communities, which can cascade to degraded soil and water resources (Prichard et al. 2003, Boyd et al. 2017). As vegetation abundance declines and bare ground increases, the risk of soil erosion increases (Pierson et al. 2008).

Conservation grazing practices that increase plant health by decreasing selective, repetitive, or intense grazing or by increasing recovery time after grazing can improve rangeland, riparian, and soil conditions (Teague et al. 2013, 2016). Many livestock management practices can help maintain riparian functionality by adjusting the timing, intensity, and duration of use in riparian areas (Wyman et al. 2006, Swanson et al. 2015). Managers can use a variety of tools to mix and match strategies and use cattle management to meet objectives of recovery and resilience (Swanson et al. 2015).

Many established tools for effectively managing cattle herds do not function well for managing feral horses (*Equus caballus*; free-roaming horses), whose use of riparian areas can significantly affect functionality (Kaweck et al. 2018). The Wild and Free-Roaming Horses and Burros Act of 1971 (Public Law 92-195 as amended) provides free-roaming horses special protection. The Act also defines excess animals above an appropriate management level (AML) as "wild free-roaming horses or burros which must be removed from an area in order to preserve and maintain a thriving natural ecological balance and multiple-use relationship in that area" on designated Bureau of Land Management (BLM) herd management areas (HMAs) or United States Forest Service (USFS) horse (and burro) territories (HTs).

The 1971 Wild and Free-Roaming Horses Burros Act limits the actions managers can take to control effects caused by the free-roaming horse population. Populations are primarily managed through fertility control or by orchestrating gathers to physically remove horses from the HMA or HT and place them in holding centers until they are adopted or die. Limited funding for the program, including on-range management and off-range holding, has limited effectiveness, resulting in on-range populations remaining well above AML and approaching exponential growth (BLM 2020*a*). The rise in population further increases long-term costs and decreases effectiveness (BLM 2020*b*). Additionally, rest and deferred rotation grazing strategies that deliberately move domestic grazers across the landscape and vary timing of plant consumption with the intention of giving plant communities the opportunity for recovery (Wyman et al. 2006, Swanson et al. 2015) are not allowed because the Act prevents managers from altering natural free-roaming horse distributions within HMAs and HTs. If free-roaming horses do congregate in riparian areas over the growing season, their persistent grazing might negate efforts to manage riparian areas for ecological function. The noted challenges facing riparian areas come to a head within Nevada, which currently supports a rapidly growing free-roaming horse population with more horses than all other states combined. In 2020, BLM estimated populations in Nevada at 46,974 horses, nearly 4 times AML (BLM 2020*a*).

Explicit consideration of riparian functions for free-roaming horse herd management on public lands was not nationally recognized until 2010 (BLM 2010) after AML had been set for most herds by 2005. Therefore, keeping a free-roaming horse population at AML may not adequately protect riparian resources if the population disproportionately congregates within riparian areas. Thus, there is a need for quantifiable data on free-roaming horse and burro effects on riparian resources. Currently the BLM uses riparian proper functioning condition (PFC) assessment (Gonzalez and Smith 2020) to qualitatively assess lentic ecosystem condition and has not adopted a quantitative monitoring protocol as needed for the 7-step integrated riparian management process described in Gonzalez and Smith (2020). The USFS uses a groundwater-dependent ecosystem inventory protocol (Coles-Ritchie and Gurrieri 2012), but this does not offer quantitative monitoring methods that link site condition to grazing.

Our study objective was to describe and quantify the effects associated with free-roaming horse, domestic cattle, domestic sheep, and native ungulate use of spring meadows. We hypothesized that free-roaming horse and cattle use would correspond with degraded riparian function relative to sheep or wild ungulates. We predicted free-roaming horses and cattle would exhibit selection for riparian areas, intensity and duration of use would be higher for free-roaming horses (and also cattle) than wild ungulates, areas receiving greater use or intensity would have greater proportion bare ground and soil alteration, and monitoring the wettest areas within study sites would provide a clearer signal of site function than monitoring across zones of more variable available water.

STUDY AREA

We selected 10 spring-fed lentic riparian-wetland areas (i.e., spring meadows) dominated by herbaceous facultative and obligate wetland plant species classified from Lichvar et al. (2014). We selected sites in 2015 within the part of the Great Basin, Nevada, not dominated by summer monsoon precipitation (i.e., excluding southeast NV, or major land resource areas 28A or 30). This basin and range landscape has fault-block mountains and alluvium-filled graben valleys. We selected sites randomly where areas of core greater

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sage-grouse (*Centrocercus urophasianus*) habitat (Coates et al. 2014), active USFS or BLM grazing allotments, and designated HMAs or HTs overlapped (Fig. 1). We observed no burros during the study.

Study sites occupied valley floor and mountainous terrain occurring at elevations ranging from 1,524 m to 2,546 m and varied from 0.08 ha to 0.35 ha ($\bar{x} = 0.18$ ha). The riparian areas were of 3 meadow hydrogeomorphic classes (Weixelman et al. 2011): discharge slope peatland, discharge slope, or mound peatland. Study sites varied in area, elevation, hydrogeomorphic class, and plant species (Tables S1 and S2, available online in Supporting Information). Sites experience hot and dry summers (Jun–Sep) typical in this cold desert region where most precipitation falls as snow during winter (Nov–Feb), especially at higher elevations, followed by relatively wet springs (Mar–May). Mean annual precipitation from 2016–2018 across all sites was 35 cm and varied from 20 cm at the lower elevations to 44 cm at the highest elevations. All sites had perennial surface water supplied from local or regional groundwater systems. Within the study sites, obligate wetland species including Nebraska sedge (*Carex nebrascensis*) or spikerush (*Eleocharis* spp.) often occupied the wetter interior of sites, whereas Kentucky blue grass (*Poa pratensis*) and facultative sedge (*Carex* spp.) often occupied the drier portions of sites. Vegetation surrounding meadows varied by elevation, aspect, and especially moisture with salt-desert scrub or sagebrush (*Artemisia* spp.)-dominated plant communities in low elevations where pronghorn (*Antilocapra americana*) were more abundant, and mountain shrub with limited forest or alpine vegetation-dominated mountains where mule deer (*Odocoileus hemionus*) or elk (*Cervus canadensis*) were more abundant. This mostly public rangeland was used for extensive roaded and non-roaded recreation, livestock grazing, mining, and other land uses.

METHODS

Camera Monitoring

No animals were handled or managed by researchers, and animals returned to studied meadows soon after researchers occasionally visited to collect vegetation or other observational data. We followed guidelines for animal care and use provided by the American Society of Mammalogists (Sikes and Gannon 2011).

We used 1 Reconyx PC900 Hyperfire Infra-red Professional camera at each of 10 sites to determine the relative amount time spent in the meadow by ungulate species (Fig. 2). We placed cameras in a discrete location on the periphery of the meadow ≤30 m from areas of active use. Cameras captured 1 picture every 5 minutes within the growing season from about April through September and 1 every 30 minutes outside of the growing season. We collected camera data from 1 April 2016 until 5 November 2018. We did not use trigger mode because most meadows were longer than the detection range and a consistent interval helped standardize observations. The exact dates of interval switches varied by location within 4 weeks depending on when we accessed cameras. Camera data included >1,700,000 photos.

To compile a use by species dataset, we first purged photos that did not contain animals. We stitched photos into a time-lapse video at 15 frames/second using ffmpeg software

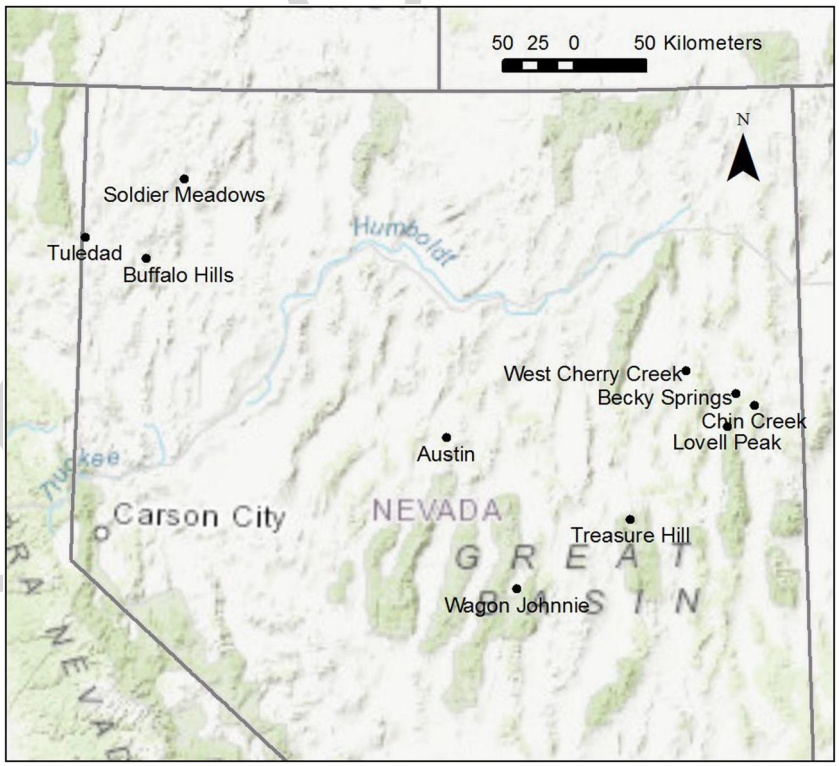


Figure 1. Locations for monitoring wild and domestic ungulate use of lentic riparian study sites across northern Nevada, USA, 2016–2018.

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Figure 2. Sample time-lapse camera photo of horses and cattle at the Treasure Hill allotment lentic riparian study site in Nevada, USA, 2017.

(https://ffmpeg.org/, accessed 5 Nov 2018) to quickly watch through periods of use and non-use and removed photos from the database that occurred during periods of non-use. Purging photos without animals removed 90% of the photo database.

We cataloged animals in the positive frames using an R and Excel tool with a simple and customizable graphic user interface (Christianson 2016). The interface presents photos within a single folder individually and the user inputs the type and number of animals present. We re-cataloged a random week within the growing season for each site without removing any frames using time lapses to validate the accuracy of our cataloguing methods. Our re-catalogue was 97.5% similar to our initial catalogue for the selected dates.

We calculated intensity of use in the riparian meadow as animal units/ha (for time series represented data) or animal unit months/ha (AUM/ha; for data representing cumulative use over a specified time). To tally animal units from each picture, we multiplied each ungulate captured in a frame by an animal unit equivalency: horse = 1.25, cattle = 1, sheep = 0.2, mule deer = 0.23, elk = 0.65, pronghorn = 0.17 (Vallentine 2001). To calculate AUMs, we multiplied the animal-unit-adjusted number by either 5 minutes or 30 minutes (0.00011–0.00068 months) depending on the time interval between photos. To calculate AUMs over an area, we determined the area of the study meadows captured within each frame using ArcGIS (Esri, Redlands, CA, USA) with a known photo point and the camera's 42-degree field of view within the meadow boundaries. We completed meadow boundary surveys with a Trimble Total Station (Trimble, Sunnyvale, CA, USA) and surveyed or recorded photo points with a global positioning system (Garmin GPSMAP 62st, Schaffhausen, Switzerland). For nighttime photos, we reduced the area denominator for the AUMs/ha calculation based on the effective infra-red illumination distance. If researchers changed the camera location during the study period, we re-calculated the area for each camera position. This provided a standardized metric of intensity across meadows and viewing areas of different sizes.

There were extensive periods before the 2017 growing season with missing camera data caused primarily by human error configuring the cameras. The record improved after a new team took over camera operations in spring 2017. Therefore, we restricted most statistical analysis of camera data between 1 June 2017 and 30 September 2018. We adjusted animal use proportionately to account for missing days based on detections during the days when the camera was functional. We determined the percentage of growing season days moderately grazed by dividing the number of days with moderate ungulate use of >1 animal units/ha/day by the number of days within the growing season with camera data.

Transect Layout and Vegetation Monitoring

Spring meadows vary in size with wetland plant species to upland species growing in proximity. This heterogeneity makes monitoring data difficult to interpret across different sites. Meadow hydrology and geomorphology, however, predictably influence species expression. We set up transect layouts according to the direction and concentration of water flow to test a monitoring methodology that might reduce the variability of vegetation potential across transects and sites. We also tested a methodology commonly used for upland strata with less spatial variability.

To set up transects, we identified the top and bottom end of a study meadow by elevation. All meadows were sloped and could be delineated by the presence of wetland-adapted vegetation, surface water, or saturated soils. The top and bottom points of a site, when connected, formed a straight line known as the long axis.

From near the top to the bottom end of the long axis, we placed a tape measure following the primary water flow path (Fig. 3). We referred to this transect as the hydric transect. The hydric transect was curvilinear (Fig. 3) and sat directly on the wettest area of a meadow. In meadows with a well-defined rill or flow channel, transect placement followed all curves of the channel. In meadows without an easily discernable primary flow path, the transect followed the general center of the wettest part of the meadow from top to bottom. All hydric transects had a minimum length of 50 m, which allowed for adequate spacing between sample measurements (see below).

We required the sampled area along the hydric transect to have potential to support wetland perennial vegetation. In a monitored hydric transect, we did not include areas with ephemeral or barely intermittent hydrology that would not support full cover of wetland plant species or open standing water such as deep ponds that could not support wetland perennial species other than aquatic species. Multiple sites contained springs with mounded regions or areas where the wettest region in the meadow did not occur at the lowest point along a cross-section of the site. Often the wettest part of a spring meadow is along the lowest path downslope, but we deviated from a lower drier path to a higher wetter path in those situations.

We used a hydric transect to help make standardized comparisons among sites. We proposed that the most saturated areas of functioning wetlands will consistently have the potential to express abundant obligate wetland vegetation. Researchers can investigate this area for site

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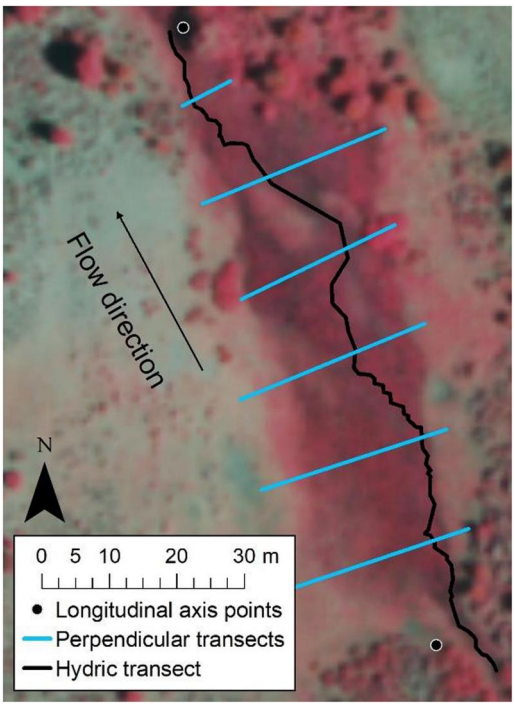


Figure 3. Transect layout at Treasure Hill allotment lentic riparian study site of free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn) in Nevada, USA, 2017. Base map is from 2015 National Agriculture Imagery Program (NAIP) infrared imagery.

condition and replicate their investigations among spring meadows with otherwise variable characteristics like size or geomorphology.

We established transects perpendicular to the long axis to compare the effectiveness of quantifying PFC items with a different sampling geometry. Perpendicular transect lengths and spacing varied to cover a larger spatial extent and included area from the inundated meadow interior to the mesic margins. We placed 5 or 6 perpendicular transects at equal intervals along the long axis. Transects ran perpendicular to the long axis until the point of intersection with obligate upland vegetation. We monitored adjacent upland vegetation with upland transects that extended from the end of the perpendicular transects on both sides by 5 m.

We placed wooden stakes to ensure consistent location of perpendicular and upland transects from year to year. The hydric transect layout was dynamic and varied depending on site conditions at each sampling date. If the meadow contained a well-defined rill or flow channel, the hydric transect would vary little among site visits. If the wettest parts of the meadow were less defined, however, exact placement replication was not possible or necessary if it remained in the wettest part of the meadow where vegetation potential remained similar.

Sampling Methods

We adapted line point intercept (LPI) methods (Herrick et al. 2017) for application to our transect designs. We sampled 200 equally spaced points along each hydric transect and each set of perpendicular and upland transects in 2016, 2017, and 2018. We recorded plant species that hit a dropped pin at each LPI point, and assigned the plants a wetland rating according to the national wetland plant list (Lichvar et al. 2014). We recorded soil alterations by hoof trampling from any ungulate species twice a season along the hydric transect using methods adopted from Burton et al. (2011) to estimate the percentage of the transect altered by hoof action.

We placed 2 circular exclosure cages of 0.75 m diameter at each site in the beginning of the 2018 growing season. We placed 1 cage adjacent to a perpendicular transect and 1 cage adjacent to the hydric transect (Fig. 4). We did not choose random locations for the cages but instead chose an area thought to be representative of overall meadow or hydric transect conditions. Inside the exclosures, we visually estimated percent foliar cover and bare ground using a 50×50-cm quadrat.

We conducted lentic PFC assessments in 2018 following the second edition (Prichard et al. 2003) protocol (similar to the third edition; Gonzalez and Smith 2020) by qualitatively evaluating a standard list of items relating to riparian function with yes or no answers, combined with a written justification. Yes-answered items indicate that the item is not impairing a site's functioning. For example, item 3 in the PFC protocol states "riparian-wetland area is enlarging or has achieved potential extent." A yes answer here, would indicate that wetland extent is not limiting a site's function. A no answer would indicate that riparian function may be impaired by diminished wetland extent. The team considered answers for all items to determine if a wetland was functioning properly (based on the definition and its site-specific potential), functioning at-risk, or non-functional.

Relating Use to Functional Characteristics

We conducted all plots and data analysis using Python 3 and computed 95% confidence intervals using Seaborn's bootstrapping methods (Waskom 2020). We used *t*-tests to test mean differences. For each site we plotted percent bare ground (from 2018 LPI surveys) along the perpendicular and hydric transects against total AUMs/ha (adjusted for missing camera data from 1 Jun 2017–30 Sep 2018). We used the statsmodels (Seabold and Perktold 2010) python



Figure 4. Chin Creek allotment meadow in Nevada, USA, 2018. The highlighted line denotes the hydric monitoring transect. The exclosure cage in the foreground shows plant growth of mostly Nebraska sedge from 1 growing season with no ungulate grazing in late summer.

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module to test for a linear regression between bare ground and total use. We repeated this process to test the relationship between percent bare ground and the percentage of growing season days grazed by any ungulate species. Similarly, we tested the relationship between the percentage of the hydric transect affected by soil alterations measured in 2018 against the use during 2018 up to the date the alteration measurements occurred. We ran a final linear regression to test the relationship of 2018 soil alteration percentages against percent bare ground along the hydric transect measured in 2018.

To estimate if livestock and free-roaming horses used our study meadows disproportionally more than the greater HMA or HT, we compared the use at our study sites in 2017 to a contrived number representing use if the horse or cattle population were to graze the allotment, HMA, or HT evenly. We totaled the site use (AUMs/ha) for 2017 based on the camera monitoring. We calculated free-roaming horse use for the site's entire HMA or HT as if the population of free-roaming horses from the most-recent HMA or HT population survey were to graze the entire HMA or HT evenly over 12 months. To determine the representation of even use by cattle, we used the population prescribed within the grazing permit for each site's allotment. For each site, we divided the AUMs/ha based on camera monitoring by AUMs/ha under the assumption of even grazing to determine the extent ungulates selected study meadows more than the surrounding HMA or HT.

RESULTS

Free-roaming horses and cattle grazed most study sites extensively during the 2016, 2017, and 2018 growing seasons (1 Apr–30 Sep; Fig. 5). Free-roaming horses selected the study meadow on average 51 ± 33 (SE) times more than the surrounding HMA or HT. Cattle selected study meadows 30 ± 23 times more than the surrounding allotment. Use varied among sites and among years from very little grazing to intense, season-long use (Fig. 5). We observed 2.3 times more free-roaming horse than cattle use on average during the growing season ($P = 0.007$; Fig. 6). Domestic sheep use and native ungulate use was <10% of cattle and free-roaming horse use (Fig. 6).

Periods of use and nonuse differed between free-roaming horses and cattle (Fig. 5). Although use for both species overlapped with the growing season and especially with summer, some cattle grazing was apparently prescribed for periods between October and April. Seventeen percent of cattle grazing days observed occurred in winter and 14% of free-roaming horse grazing days occurred in these periods. Seven sites had periods >8 weeks within one or both 2017 and 2018 growing seasons with no cattle present. Only 3 sites (Soldier Meadows, Buffalo Hills, Tuledad) had 8-week periods in one or both 2017 and 2018 growing season with no free-roaming horses present.

We rated all sites using the PFC assessment as functional at risk (Table S3, available online in Supporting Information). Two PFC items (i.e., 6 and 13) always received ratings of no; for item 6 every site had surface flow patterns altered by disturbance and for item 13 none had adequate stabilizing species present to protect soil surface against overland flows. Four other items were marked no for ≥7 of 10 sites: 1 (riparian-wetland area is saturated at or near the surface or inundated in relatively frequent events), 3 (riparian-wetland area is enlarging or has achieved potential extent), 10 (species present indicate maintenance of riparian-wetland soil-moisture characteristics), and 17 (saturation of soils [i.e., ponding, flooding frequency, and duration] is sufficient to compose and maintain hydric soils). These 6 numbered items describe important functional issues leading to or resulting from degradation of these riparian study sites. Where stabilizing species were not present, bare ground, erosion, and flow concentration were often noted (Fig. 7) along with dehydration and shrinkage of riparian meadows.

Plant wetland rating composition varied between transect types across all sites (Fig. 8). The hydric transects contained a higher percentage of obligate or facultative wetland indicator plants ($\bar{x} = 84.0 \pm 5.7\%$, $P \leq 0.001$) than perpendicular transects ($\bar{x} = 53.3 \pm 8.3\%$). Bare ground was higher along the hydric transects compared to the perpendicular transects ($P = 0.003$; Fig. 9). Bare ground also varied most along the hydric transects ranging from 0–78%. Additionally, percent bare ground dropped along the hydric transect ($P = 0.002$) inside the exclosure cages when protected from 1 season of grazing. The bare ground amounts along the perpendicular transects did not change significantly when exclosed from 1 season of grazing.

Bare ground increased with greater intensity of use, but this was not statistically significant at the alpha = 0.05 level (Fig. 10). The percentage of 2017 and 2018 growing season days with moderate ungulate use did correlate with percent bare ground on the hydric transects but not the perpendicular transects (Fig. 11). Soil alterations from hoof prints correlated with intensity of use and with percent bare ground along the hydric transect (Fig. 12).

DISCUSSION

The data collected supported the hypothesis that free-roaming horse and cattle use of our study sites corresponded with degraded riparian function. Our results provide further evidence that current free-roaming horse and livestock management practices do not adequately protect spring meadows in much of the Great Basin. Free-roaming horses and cattle concentrated heavily in these riparian sites compared to native ungulates and domestic sheep. Sites with high amounts of bare ground and soil alterations had intense grazing with little or no opportunity for growing season recovery. Our study predictions were best informed by monitoring the wettest areas consistently across spring meadows of varying size and morphology.

Progressive livestock grazing alone will not improve wetland conditions if free-roaming horse use of the area overrides the balance of use versus recovery needed for wetland function. Free-roaming horse populations have increased

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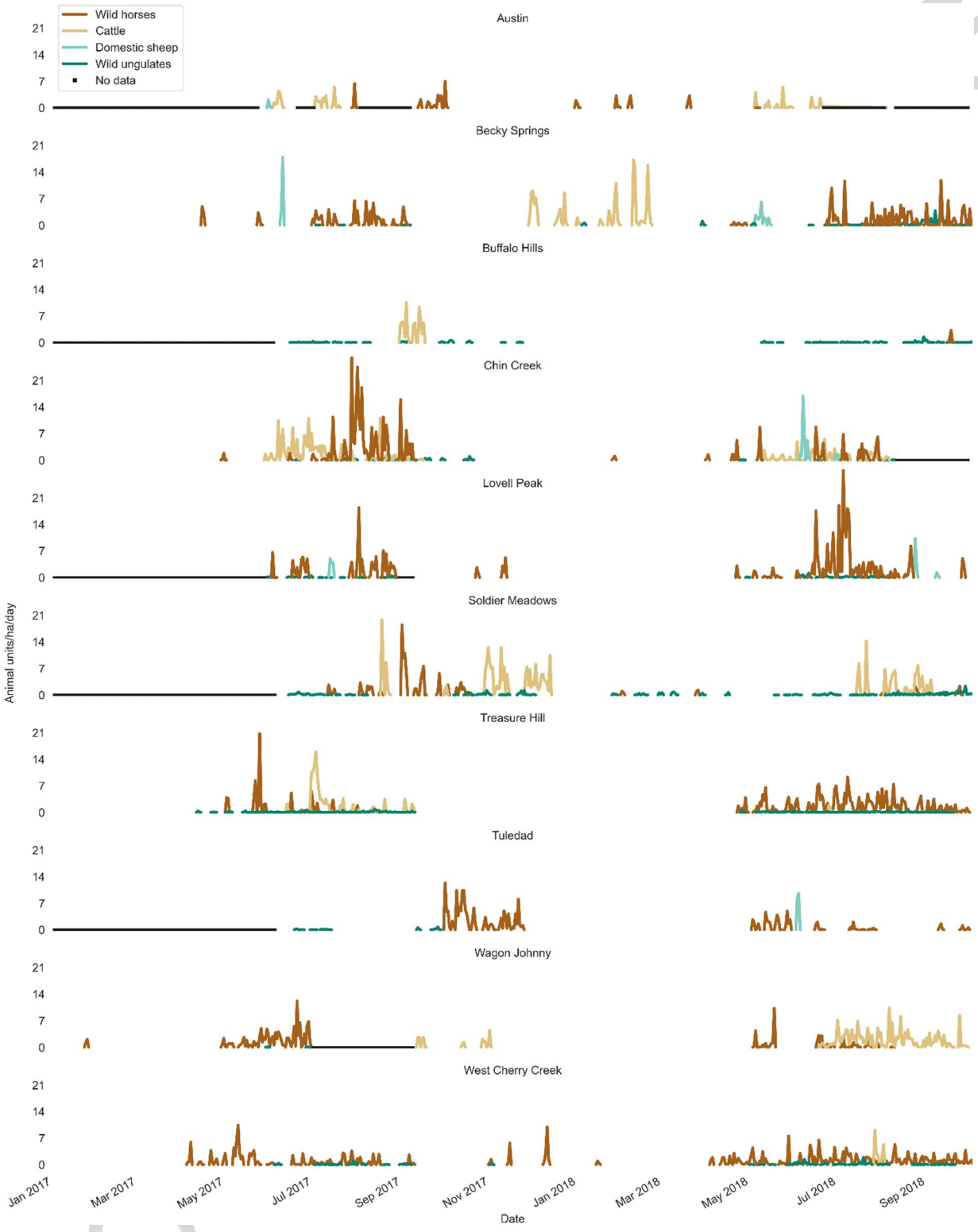


Figure 5. Intensity of use by free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, or pronghorn) at 10 different lentic wetland sites in northern Nevada, USA. Period of record is 2016–2018. The intensity of use is calculated per day (i.e., 10 cattle in 30 5-minute interval frames = 1,500 animal unit minutes or ~1 animal unit for that date).

substantially in many of Nevada's herd management areas (BLM 2019) and they accounted for most of the ungulate use captured in our camera record. As Swanson et al. (2015) indicated, because grazers concentrate in sensitive riparian regions, lowering populations or stocking rate alone often may not provide adequate relief for these sensitive areas without substantial and often uneconomical or otherwise unfeasible reductions of herd numbers. But because legislation and free-roaming horse behavior restrict options for managing free-roaming horse grazing periods, population

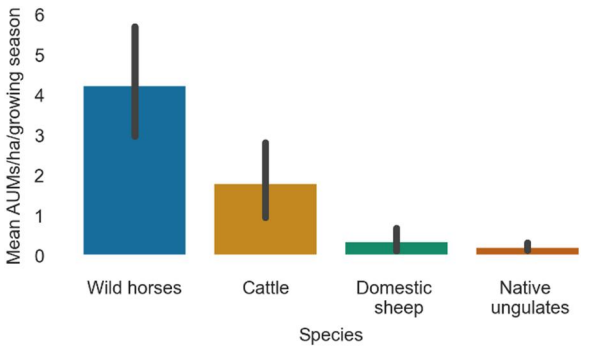


Figure 6. Mean level of use animal unit months (AUM)/ha/growing season in lentic riparian meadows by free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn), Nevada, USA, 2017–2018. Vertical black bars show 95% confidence intervals.

control that brings numbers down to AML or to levels consistent with native ungulate density (AUM/ha) may be the only currently available free-roaming horse management tool to restore riparian functions or keep sensitive areas like spring meadows functioning. Bringing free-roaming horse population densities in line with native ungulates would require reductions in herd size, possibly well below AML for some riparian areas with near continuous growing season use, as we observed with free-roaming horses at 7 of our sites. Additionally, stocking rate reductions for cattle would not likely correct the problems associated with continuous growing season use by cattle observed at 3 sites, unless the stocking rates were reduced significantly. Reductions in livestock numbers may not be needed for those allotments where managers move livestock to provide enough periods of no grazing for riparian plant growth and recovery. Intensity, timing, and duration of grazing by both livestock and free-roaming horses need to provide conditions for healthy vegetation that allows for recovering and sustaining riparian functions.

Healthy vegetation with stabilizing root masses prevents the net loss of soil and organic matter to erosion and organic



Figure 7. Severe soil disturbance relates to soil surface alteration and by grazing and watering free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn), and overland flow at Lovell Peak allotment lentic riparian meadow study site in Nevada, USA, 2018. A hydric transect is highlighted and runs from the right of the photo towards the center of the photo. Perpendicular transect tapes are also visibly spanning the meadow.

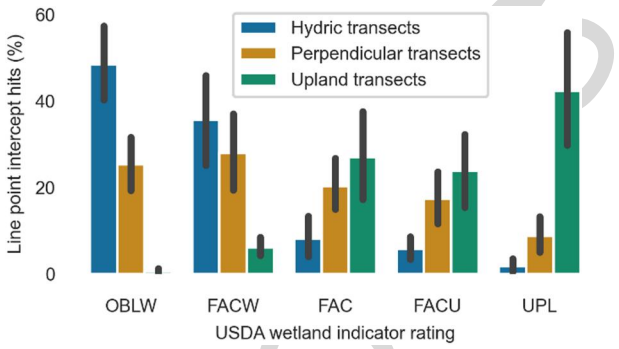


Figure 8. Line point intercepts (LPI) of plant species observed on different vegetation monitoring transect types shown by their United States Department of Agriculture (USDA) plant wetland indicator status: OBLW = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland, and UPL = upland. We took samples at lentic riparian sites across northern Nevada, USA, 2017–2018, to study free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn) effects on core sage-grouse meadows in allotments and Bureau of Land Management herd management areas or Forest Service horse territories. Vertical black bars show 95% confidence intervals.

matter oxidation, which can cause a feedback cycle, altering hydrology, including depth to water table, wetland size, and plant species type and distribution (Pearce et al. 1998, Loheide et al. 2009, Gonzalez and Smith 2020). A highly functioning wetland resists degradation, and can provide succulent forage, water, and habitat for grazing animals and wildlife, including migratory birds, late into the growing season, after most upland plants have senesced in arid regions (Prichard et al. 2003, Weixelman and Cooper 2009, Mitsch and Gosselink 2015, Gonzalez and Smith 2020). Degradation of healthy, stabilizing, plant communities can result in smaller wetland extents with less palatable forage for grazers and wildlife. Most vegetation disturbance at our sites occurred along the hydric transects, which also had higher potential to grow abundant obligate wetland plant

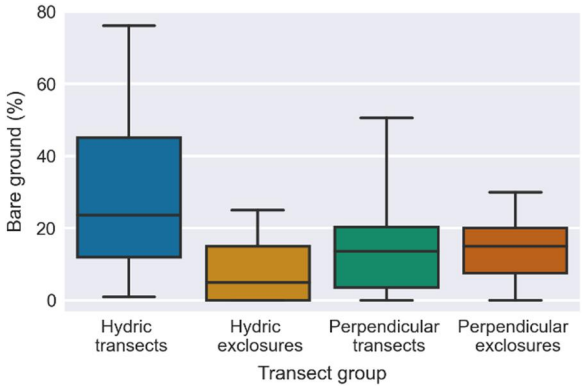


Figure 9. Boxplot chart of percentage of bare ground across different transect types and 1-growing-season grazing exclosures for a study relating grazing by free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn) to vegetation condition in lentic riparian areas in northern Nevada, USA, 2018. The box shows quartiles of the dataset (the line inside the box shows $\tilde{x}$ and the whiskers extend to show the entire range). Hydric transect bare ground was significantly higher ($P < 0.01$) than in near-hydric exclosures or along perpendicular transects.

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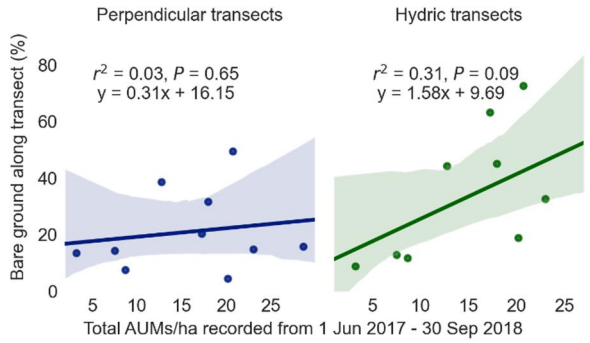


Figure 10. Percent bare ground versus use (animal unit months [AUM]/ha) by free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn) on 2 types of monitoring transect layouts at 10 lentic riparian meadows, northern Nevada, USA, 1 June 2017–20 September 2018. Shaded area represents 95% confidence interval.

species, provide stabilizing plant species, and contain the least amount of bare ground (Figs. 8, 9 and 11). This sensitivity might allow the wettest parts of spring meadows to serve as an easy to interpret leading indicator warning against threats to rangeland and riparian health.

Plant species composition sampling that mimics upland study designs with random or systematically spaced transects, such as our perpendicular transects, are difficult to interpret. In most lentic riparian areas, zones of variable wetness are normal (Gonzalez and Smith 2020) and average metrics for wetland indicator rating, stability rating, or even percent bare ground represent differences in potential and differences in condition. Over a short distance, we noticed perpendicular transects could span a near complete hydrologic gradient that supported obligate upland plants near the edge of a meadow and obligate wetland plants in saturated areas. A site's departure from potential or reference condition was difficult to determine using transects perpendicular to the meadow slope because of large heterogeneity in hydrology and plant community potential. Conversely, the hydric transects consistently supported potential for facultative or obligate wetland-dominated plant communities. Vegetation and soil cover parameters were therefore more easily interpreted and compared among sites using hydric transect data than perpendicular transect data. Thus, hydric transects directly monitor characteristics that support wetland maintenance, expansion, or contraction (Gonzalez and Smith 2020).

The percentage of growing season grazed correlated well with percent bare ground along the hydric transects, better than along the perpendicular transects. We did not find correlation between intensity of use and bare ground along either transect type but especially not along perpendicular transects. Totaling use across time does not account for potential recovery time within the summation period. High intensity grazing may occur during short periods with long recovery periods, or during winter when plants and soil are less sensitive to grazing activity. Rest periods and recovery opportunity for plants during the growing season appear to be vital for spring meadow functional resiliency where stocking rate exceeds the level we observed for native ungulates.

Soil alteration data showed a very strong correlation between hoof action and bare ground along the hydric transect, demonstrating that physical disturbance likely influences vegetation loss and also that high vegetation cover prevents soil disturbance. It was evident from site visits that the soil in these areas was disturbed through hoof action and flow of water, with rilling or concentrated flow channels visible at all sites (Fig. 7). This study did not experimentally test whether ungulate use directly affected bare ground and instead found a strong correlation between the 2, especially within the wettest parts of meadows. Further study could examine how ungulate use affects vegetative cover and how repeat defoliations through grazing and physical alteration of soil through hoof trampling interact to affect plant health and spring meadows.

Another limitation of this study was that it did not investigate recovery of function. The exclosure cage design only allowed for basic observations and provided just 1 season of rest. Dobkin et al. (1998) monitored recovery

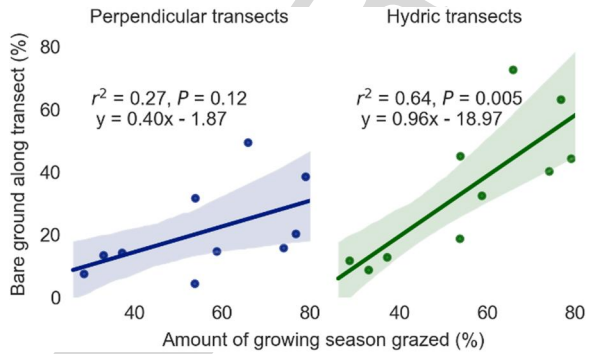


Figure 11. Percent bare ground versus the percentage of growing season days between 1 June 2017 and 30 September 2018 with moderate ungulate use by free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn). The plot compares 2 types of monitoring transects at 10 lentic riparian meadows, northern Nevada, USA. Shaded area represents 95% confidence interval.

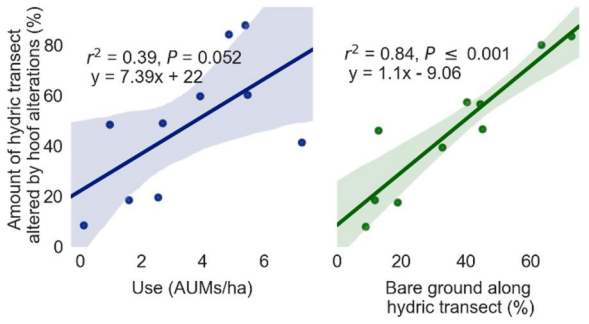


Figure 12. Percentage of hydric transect soil surface altered by ungulate hoof action versus use (animal unit months [AUM]/ha) by free-roaming horses, domestic cattle or sheep, and wild ungulate grazing species (mule deer, elk, pronghorn) and versus percent bare ground along the hydric transect, northern Nevada, USA. Alteration and bare ground measurements occurred in July or August 2018. Use is AUMs/ha from 1 April 2018 to the date of measurement at each site. Shaded area represents 95% confidence interval.

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throughout an entire meadow following total exclosure from grazing. We encourage further investigation of recovery process after varying timing, intensity, and rest at degraded sites. Research could also focus on how different areas of a wetland respond to such changes. With the potential to grow abundant stabilizing species, the wettest parts of a meadow may recover more quickly, influencing soil protection and water storage to benefit livestock, free-roaming horses, and wildlife, including native ungulates and sage-grouse.

MANAGEMENT IMPLICATIONS

Managers should consider cattle, free-roaming horses, and native ungulates when forming a management plan in grazing areas. Managers should pay careful attention to areas of high functional importance, at-risk regions within meadows, and PFC items that most commonly threaten loss of riparian functions by focusing on the wettest part of spring meadows. The wettest part of the meadow provided a clear signal we could relate to animal use and meadow function. If the critical meadow region (i.e., the best watered, most productive part of the meadow) that would otherwise be thickest with vegetation is not, managers should adjust the duration of livestock grazing versus recovery periods, by adjusting AML as needed to ensure that rangelands sustain riparian functions with positive recovery.

ACKNOWLEDGMENTS

We thank all who provided guidance and support while working on this project, especially L. N. Yandell, S. W. Tyler, J. L. Huntington, A. T. Wilbanks, R. D. Strahan, and J. A. Culpepper. Funding and technical support was provided by United States Department of Agriculture National Institute for Agriculture through the Nevada Agricultural Experiment Station, United States Fish and Wildlife Service, United States Environmental Protection Agency, Nevada Department of Wildlife, Nevada Agriculture Foundation, and the BLM.

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Associate Editor: Sarah King.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

UNCORRECTED PROOFS

Summary for Online TOC: Horse and cattle grazing throughout the grazing season impaired functioning of spring-fed herbaceous meadows across Nevada, USA. The wettest portion of the meadow provided a clear signal we could relate to animal use and wetland function.

Feral Asses on Public Lands: An Analysis of Biotic Impact, Legal Considerations and Management Alternatives

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The feral ass, or "wild burro," (*Equus asinus*), a native of northeastern Africa, was introduced into North America in the sixteenth century by Spanish explorers. Their value as "beasts of burden" had been recognized as early as 3400 B.C. in Egypt and Mesopotamia (Peake 1933 and Antonius 1937; fide McKnight 1958) and they are still used as such in many portions of the world. Although the feral ass has been in North America since the sixteenth century, it has been reasoned (McKnight 1958) that the species did not become feral in the southwestern United States until sometime during the nineteenth century. Prior to this, the animal was much too valuable to both Indians and Anglos as a work animal, and possibly food, to be allowed to become feral. It was only after the great impetus of mineral exploration had subsided and the settlement of the region ensued that some animals were released, or escaped, and feralization began. By the end of the nineteenth century, the feral ass had become established in many isolated areas of the Southwest. Since their feralization, they have been credited with a considerable amount of habitat destruction resulting in allegedly depriving native animals of essential food and water. In many areas where the feral ass has become established, it has done so at the expense of the native desert bighorn sheep (*Ovis canadensis*), an animal whose numbers have been severely reduced in the Southwest (Russo 1956; Dixon and Sumner 1939; Ferry 1955; Laycock 1974). Also, in a recent analysis of the problem in New Mexico, Koehler (1974) has found evidence that the feral ass directly competes with the native mule deer on certain ranges.

In a recently completed study on feral ass behavior and ecology in Death Valley, California, an area well known for very high population densities of feral asses, Moehlman (1972) denies noticeable habitat damage by the feral ass by stating . . . "Contrary to a widely held belief, the burros I observed did not strip the land, foul water holes or endanger other animals." She adds . . . "Although heavy browsing occurred within a mile of water, my first appraisal of vegetation data indicates [sic] that plants on which burros feed do not suffer severely." Our photographic evidence from Death Valley and the data presented in this paper from our investigations in other areas show that these conclusions are not valid. Blong and Pollard (1968) found that ewes, lambs, and yearling bighorn were concentrated within .75 miles (.46 km) of water during the summer of 1965. Denniston (1965) working in the River Mountains of southern Nevada found that desert bighorn concentrated within .5 miles (.30 km) of their only water source during the hot, dry months of summer. In a brief review of alleged vegetation destruction by the feral ass, Laycock (1974) writes . . . "The destruction of vegetation may cut sharply into rodent populations, reducing food for birds of prey, while habitat for such small birds as quail vanishes." Moehlman (1974) further attempted to evaluate the impact of feral asses on small rodents by counting the number of supposedly active rodent burrows along transects ranging from high to low ass densities. By using this method, no difference was found in the number of apparently active burrows along these transects. Thus, Moehlman concluded on the basis of this questionable sampling technique that the asses were having little or no effect on the rodent populations.

The objective of our study was to quantitatively and qualitatively evaluate the influence of feral asses on desert and riparian habitats in the Grand Canyon, Arizona. Absolute densities of small mammal populations and vegetative composition and structure were investigated. We selected two similar study plots, separated by the Colorado River, with feral asses present on one plot, but not on the other, thereby providing a "control plot" and an "impact plot."

History of the Feral Ass in Grand Canyon

The history of the feral ass' success in the Grand Canyon may be considered typical of the problem throughout the Southwest. By the early 1920's, many rangers in Grand Canyon National Park were reporting to the superintendent that for the sake of the native wildlife, drastic control measures were needed to restrict the destructive and rapidly expanding feral ass population. Burros were credited with much of the overgrazed range condition within the Inner Canyon. This is illustrated by the following quote found in an unpublished report written by Chief Ranger J. P. Brooks in 1932: "Overgrazed conditions existed on all areas ranged over by burros. In many places herbage growth was cropped to the roots and some species of shrubbery were totally destroyed. Soil erosion was greater in burro infested areas . . . "

From 1924 to 1931, a "burro hunt" was conducted in Grand Canyon National Park. The animals were shot with high powered rifles and left to decompose. During this 7 year period, 1,467 feral asses were killed. It was believed that the burro population in Grand Canyon National Park had been reduced to possibly 50 to 75 head, thus, Park Biologists were confident that no more "burro hunts" would be necessary. Yet, between 1932 and 1956, an additional 370 animals were removed. Between 1956 and 1968, 771 more were destroyed with an additional 252 having been captured and taken out of the park. This represents a total removal of 2,860 feral asses from the park in the 45 year period from 1924 to 1969. No control has been attempted since 1969. One of the main reasons for the lack of control efforts has been the negative public sentiment engendered by the "burro hunts" of the mid and late 1960's. This public sentiment, largely initiated by articles written by assinophiles (burro lovers), was quite effective in pushing through protective legislation for wild horses and burros. An example of the severity of public hysteria with which land managers must deal may be found in the text of an article by Weight and Weight (1953): "From time beyond

memory, the humble, gentle burro has been man's uncomplaining servant and the playmate of his children. There is a legend that because he carried Mary to Bethlehem and Jesus along the desert trails of Palestine, he was given the mark of the Cross—which you can see upon his back and shoulders." An accompanying photo of a dead burro bears the caption, "Sportsmen, satisfied with the thrill of shooting a friendly burro at point-blank range, often do not even carry out the pretense of hunting for meat, but leave the body as it fell. This burro was shot and left in Great Falls Canyon, not far from where the little colts, above, were found."

In the past, little quantitative data have existed to be used by those who suspected or knew of the environmental havoc that would be wrought by these "starlings" of the mammalian world. Logic and other examples of great ecological damage caused by introduced species, such as rabbits in Australia and red deer in New Zealand, fell way to anthropomorphized sentiments for "man's faithful friend." The result was Public Law 92-195 in 1972, which made killing a feral ass on most lands a felony. Killing bighorn illegally is merely a misdemeanor. We wish here to present quantitative and qualitative data on the environmental hazards wrought by wild burros and other information which raise questions concerning the wisdom of this law if not indeed its legality. It may very likely be that Public Law 92-195 is in conflict with the National Environmental Protection Act of 1969 (Public Law 91-190) and the Endangered Species Act of 1973 (Public Law 93-205).

Procedures

The duration of our field studies was from 1 March 1974 through 31 January 1975. Both study plots received identical quantitative and qualitative vegetational and mammalian analyses. Vegetation was sampled by means of the line-intercept technique (Canfield 1941) and the point-quarter technique (Cottam and Curtis 1956; Morisita 1959). Approximately 2,624 feet (800 m) of line-intercept transects and 50 point-quarters stations were censused per study area. Percentage infestation of mistletoe (*Phoradendron californicus*) was measured by absolute counts of parasitized trees and shrubs on each study area. The vegetation data presented herein are a condensation of our field data collected during May, June, and August 1974.

For mammal censusing, each plot was sampled with a 10 by 12, 5.3 acres (2.2 ha.) grid of Sherman live traps placed at 50 feet (ca. 15 m) intervals. These traps were baited with a rolled oat/scratch grain mixture. Traps were set for four consecutive nights at 4:00 p.m. during March, May, June, November, 1974, and January 1975. They were checked once each day at 7:00 a.m. The following data were recorded: species and individual identification, trap number, sex, reproductive condition, weight (0.1 gram), and age class. Females were classed according to obvious signs of pregnancy, lactation, or vulvar condition. Age classes were determined on the basis of adult or immature pelage. All animals were toe clipped for individual identification. The density of each species was estimated separately by a modification of the Lincoln Index (Bailey 1952). The mammal and plant species diversities of each study area were determined by using the diversity index, H′ (MacArthur and MacArthur 1961).

Description of Study Areas

The sites selected for this investigation are located within the lower reaches of the Grand Canyon in the Mohave desert scrub vegetative community (Lowe and Brown 1973). The impact plot, 209 Mile Canyon, is on the west side (right) of the Colorado River and is inhabited by a small herd (8 to 15 individuals) of feral asses. The control plot, Granite Park, is directly opposite 209 Mile Canyon and shows no evidence of occupation by feral asses. Both study plots are 5.3 acres (2.2 ha.) in size and include both desert scrub and riparian habitats on the alluvial fans of the respective drainages.

The riparian zone of the Colorado River in this section of the Grand Canyon is typified by co-linearly arranged belts of mesic to xeric vegetation. In addition, both study plots are fronted by sand and gravel beaches of river deposit origin. Elevations range from approximately 1,503 feet (458 m) at the river's edge to 1,601 feet (488 m) on the upper terraces above the historic high water line (Dolan et al. 1974).

Both plots show more similarities in gross vegetational composition and structure than differences. An east-west orientation, equal proximity to water and the relatively flat topography of the sites, tends to equalize the abiotic factors of irradiation, moisture gradients and protection from local weather for both sites.

Results and Discussion

Vegetation

An analysis of the vegetation on the control plot and impact plot is presented in Table 1. The control plot supported greater vegetative diversity including an understory of sub-shrubs and a dense carpeting of grasses and forbs (especially plantain). The ground cover and sub-shrub components were virtually absent on the impact area. The control plot contained vegetation cover on approximately 80 percent of the total transect area surveyed compared to 20 percent vegetation cover on the impact plot. The number of species found on the control area was 30 percent higher than that on the impact area.

The mean area (m^2) occupied by each individual cat-claw or mesquite on the control plot was 27.9m^2 per plant, while the same species on the opposite side of the river at the impact plot was not as large, occupying only 20.7m^2 per plant. Also, there was a higher infestation of mistletoe (*Phoradendron californicus*) on the impact plot, with 16.5 percent of all cat-claw/ mesquite (*Acacia gregii/Prosopis juliflora*) being infested with this parasite as compared to only 5.4 percent of the same species parasitized on the control plot. Cat-claw and mesquite shrubs on the impact study area had been heavily browsed by asses. The mistletoe infestation may be correlated with over-browsing, but a definite conclusion cannot be drawn without further study.

There was no significant difference in total species diversity from one plot to the next, however, the control plot showed a richer sub-shrub and grass component (H′ = 1.60042 and .821670) than the impact plot (H′ = 1.28478 and .422710).

Small Mammals

The results of the small mammal population censuses are presented in Table 2. The most striking difference between the populations on the two study areas

Table 1. The line-intercept vegetation data summary for the control and impact study areas.

Species		Control				Impact			
		Relative Density	Relative Frequency	Relative Dominance	Importance Value	Relative Density	Relative Frequency	Relative Dominance	Importance Value
Shrubs									
Acacia greggii	[1]a.	01.40	8.24	22.02	31.66	14.98	22.31	23.92	61.21
	[2]b.	15.69	16.28	26.73	58.70	35.22	32.93	26.00	94.15
Baccharis sergilloides	a.	...	...	...	...	00.96	01.65	03.00	05.61
	b.	...	...	...	...	02.27	02.44	03.26	07.97
Brickellia longifolia	a.	...	...	...	...	02.90	04.96	01.68	09.54
	b.	...	...	...	...	06.81	07.32	01.83	15.97
Larrea tridentata	a.	01.40	09.41	13.14	23.95	03.89	03.30	02.47	09.66
	b.	15.69	18.61	15.94	50.24	04.54	04.87	02.68	12.09
Lycium pallidum	a.	...	...	...	...	00.48	00.83	00.24	01.55
	b.	...	...	...	...	01.14	01.22	00.26	02.62
Prosopis juliflora	a.	05.43	32.94	44.15	82.51	21.26	34.70	60.65	116.62
	b.	60.78	61.63	53.59	176.00	50.50	51.22	65.95	167.17
Sueda torreyana	a.	00.70	01.76	03.07	05.53	...	...	...	...
	b.	07.84	03.49	03.73	15.06	...	...	...	...
Sub-Shrubs									
Chaenactis fremontii	a.	00.52	02.35	00.18	03.05	...	...	...	...
	b.	26.09	26.65	08.28	61.02	...	...	...	...
Cryptantha spp.	a.	00.79	02.35	00.18	03.32	...	...	...	...
	b.	39.13	26.50	08.28	74.06	...	...	...	...
Dyssodia pentachaeta	a.	...	...	...	...	00.96	01.65	00.15	02.86
	b.	...	...	...	...	11.76	13.32	03.47	28.55
Encelia farinosa	a.	00.09	00.59	00.25	00.93	03.86	04.96	03.33	12.15
	b.	04.35	06.68	11.59	22.62	47.06	40.03	78.87	165.96
Ephedra spp.	a.	...	...	...	...	00.96	01.65	00.12	02.73
	b.	...	...	...	...	11.76	13.32	02.84	27.92
Lepidium montana	a.	00.44	02.35	00.48	03.27	...	...	...	...
	b.	21.74	26.65	21.85	70.24	...	...	...	...
Opuntia spp.	a.	...	...	...	...	00.48	00.83	00.29	01.60
	b.	...	...	...	...	05.88	06.69	06.94	19.51

[1]Data summary comparing density, frequency and dominance of all species in cat-claw/mesquite area.

[2]Data summary comparing density, frequency and dominance only between species of similar strata, i.e., shrubs, sub-shrubs and graminoids.

Table 1 (cont.)

Species		Control				Impact			
		Relative Density	Relative Frequency	Relative Dominance	Importance Value	Relative Density	Relative Frequency	Relative Dominance	Importance Value
Sub-Shrubs (cont.)									
Porphyllum gracile	a.	00.09	00.59	01.07	01.75	01.93	00.33	03.30	05.56
	b.	04.35	06.68	49.34	60.37	23.53	07.89	26.63	58.05
Sphaeralcea fendleri	a.	00.09	00.59	00.01	00.69	...	...	...	...
	b.	04.35	06.68	00.66	11.69	...	...	...	...
Grasses and Forbs									
Bromus[3] *rubens*	a.	43.13	28.24	07.85	79.22	45.41	20.35	00.85	66.61
	b.	48.22	72.73	52.89	173.84	95.92	85.00	90.14	271.06
Festuca spp.	a.	00.87	00.59	00.09	01.55	01.93	02.48	00.09	04.50
	b.	00.99	01.52	00.58	03.09	04.08	15.00	09.86	28.94
Plantago spp.	a.	20.56	04.71	04.01	29.28	...	...	...	...
	b.	23.18	12.12	22.95	58.25	...	...	...	...
Sporobolus contractus	a.	24.50	05.29	03.50	33.29	...	...	...	...
	b.	27.61	13.63	23.58	64.82	...	...	...	...

[3]Exotic weed species.

is dramatically demonstrated by comparing the average absolute mammal density of both plots for the entire sampling period. The control plot had an average density of 128 mammals/acre (51.8/ha.), whereas the impact plot contained only 32.6 mammals/acre (13.2/ha.). It is also important to note that the species composition was different between the two study areas. The mammalian species diversity indices (H′) on the control plot and the impact plot were .78652 and .69022 respectively. The greater species diversity on the control plot was also complemented by a greater evenness of species distribution (J′) (.56736) than that found on the impact plot (.42886).

The total absolute densities of the small mammal populations on both plots were higher at the onset of this study (March 1974) than they were at its termination (January 1975). The fluctuations found in these densities (a decline of 77.3/acre [31.3/ha] to 10.6/acre [4.3/ha] on the impact plot and 219.7/acre [98.9/ha] to 43.5/acre [17.6/ha] on the control plot) were consistent for both plots and may be reflecting "normal" population fluctuations. Nevertheless, in all trapping periods, the density and diversity of the small mammal populations on the control plot were substantially higher than those across the river at the impact plot.

In addition to the total population densities, another striking difference in the rodent communities of the two study areas is in the relative species composition (Table 2). On the impact area, the density of the cactus mouse (*Peromyscus eremicus*) accounted for an average of 80.8 percent of the entire rodent commu-

Table 2. Small mammal population densities on the two study areas.

Control

Species	Absolute density (per hectare)						Relative density (percent)						
	Mar	May	Jun	Aug	Nov	Jan	Mar	May	Jun	Aug	Nov	Jan	$\bar{x}$
Peromyscus eremicus	53.5	35.3	43.2	27.7	11.4	11.4	60.0	65.0	64.0	45.0	56.0	65.0	59.2
Peromyscus boylii	00.3	00.0	00.3	00.3	00.0	00.0	00.3	00.0	00.3	00.0	00.0	00.0	00.1
Perognathus intermedius	34.3	18.7	23.5	31.3	08.6	06.0	39.0	34.0	35.0	51.0	42.0	34.0	39.2
Neotoma albigula	00.8	00.5	00.8	02.5	00.3	00.2	00.7	01.0	00.7	04.0	02.0	01.0	01.5
Total	88.9	54.5	67.8	61.8	20.3	17.6	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Average total Absolute Density, March 1974 to January 1975 = 51.8 mammals per hectare.

Impact

Species	Absolute density (per hectare)						Relative density (percent)						
	Mar	May	Jun	Aug	Nov	Jan	Mar	May	Jun	Aug	Nov	Jan	$\bar{x}$
Peromyscus eremicus	30.4	09.4	08.2	09.1	07.7	02.9	97.0	94.0	76.0	66.0	85.0	67.0	80.0
Peromyscus crinitus	00.0	00.3	02.3	04.4	01.4	01.4	00.0	03.0	23.0	32.0	15.0	33.0	17.5
Peromyscus boyleii	00.3	00.0	00.0	00.0	00.0	00.0	01.0	00.0	00.0	00.0	00.0	00.0	00.2
Perognathus formosus	00.3	00.3	00.3	00.3	00.0	00.0	01.0	03.0	02.0	02.0	00.0	00.0	01.3
Neotoma lepida	00.3	00.0	00.0	00.0	00.0	00.0	01.0	00.0	00.0	00.0	00.0	00.0	00.2
Total	31.3	10.0	10.8	13.8	09.1	04.3	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Average total Absolute Density, March 1974 to January 1975 = 13.2 mammals per hectare.

nity, whereas on the control plot, this species accounted for an average of 59.2 percent of the population. The only other species which contributed significantly to the impact plot population was the canyon mouse (*Peromyscus crinitus*), averaging 17.5 percent of the total population. The canyon mouse was never encountered on the control plot. Reasons for this are a direct reflection of the habitat requirements of this species and the state of the habitat on each study area. The canyon mouse prefers rocky, near barren areas that are usually devoid of vegetation and may be found commonly throughout the Grand Canyon on upper talus slopes and rocky outcrops. Clearly, the alteration of the impact area by feral asses has permitted a population of canyon mice to become established in an area not normally inhabited by this species.

The distribution and abundance of heteromyid rodents on the two study areas also further demonstrates the detrimental effects of feral asses. On the impact plot, only a few heteromyids, the long-tailed pocket mouse (*Perognathus formosus*), were captured, while the control plot contained a relatively large and stable population of the rock pocket mouse (*Perognathus intermedius*) (Table 2). The rock pocket mouse made up an average of 39.2 percent of the rodent community on the control plot while the long-tailed pocket mouse constituted an average of only 1.3 percent of the population density on the impact plot. In the Grand Canyon, we have found that the long-tailed pocket mouse is exclusively restricted to the north and west banks of the Colorado River and the rock pocket mouse is restricted to the south and east banks. However, where suitable habitat exists, there is no measurable difference in the population densities of these two species. On the two study areas, differences in the population densities of these heteromyid rodents were directly related to their dietary requirements and the availability of food. The primary food of both species of *Perognathus* probably consists of seeds, especially the seeds of forbs (Reichman 1975). As mentioned above (see Table 1) the forb strata of the impacted area has been thoroughly decimated through grazing and trampling by feral asses, thus rendering the habitat of this study area inhospitable to a population of *Perognathus*.

Summary

The results of this investigation demonstrate conclusively that the feral ass has a negative effect on the natural ecosystem of the lower reaches of the Grand Canyon. The principal impact of the feral ass is habitat destruction through grazing and trampling.

On the study area where feral asses occurred the vegetation cover and rodent populations were significantly reduced when compared to the study area where feral asses were absent. On the control plot, 28 species of vascular plants were found compared to 19 on the impact plot. The total vegetation cover on the control plot was 80 percent, compared to 20 percent on the impact plot. The mean area (m^2) occupied by each individual cat-claw or mesquite shrub was 27.9m^2 on the control plot and 20.7m^2 on the impact plot.

The mammal species diversity (H') was higher on the control plot (.78652) than it was on the impact plot (.69022). In addition, the average absolute density of small mammals from March 1974 to January 1975 on the control plot was 128 mammals/acre (51.8/ha.), approximately four times the 32.6/acre (13.2/ha.) found on the impact plot. Thus, differences between the two areas in mamma-

lian species composition and diversity were attributed to the depauperate flora, particularly the forbs and grasses, on the 209 Mile Canyon impact area.

Alternatives and Priorities

We previously questioned not only the wisdom but also the legality of the Wild Horse and Burro Act (Public Law 92-195). News releases during 1975 announced that a three judge federal panel in New Mexico had declared the Wild Horse and Burro Act unconstitutional, stating that, " . . . wild horses and burros do not become property of the United States simply by being physically present on the territory or land of the United States." Even though Public Law 92-195 may eventually be declared unconstitutional throughout the land, the legal ownership of these exotic and destructive animals should not be a central issue. Clearly, the primary consideration should be whether or not wild horses and burros are damaging public lands. Our land managing agencies have been given the responsibility to protect public lands and to control their use in a manner compatible with legislative mandates and sound managerial principles. Although there is certain justification for some measure of protection for small, limited reproducing herds of wild horses and burros, our investigations lead us to the conclusion that Public Law 92-195 is not compatible with proper management concerns on our public lands.

Although the Wild Horse and Burro Act does not specifically apply to National Park Service lands, the public sentiment and political pressures engendered by the issue resulted in a reluctance on the part of National Park Service administrators to initiate or continue feral equine control measures. Recently, with quantitative data on habitat destruction by wild horses and burros becoming available, immediate control measures are being considered on park lands. In Bandelier National Monument a program of direct reduction by shooting for 1975 and 1976 was recently announced by National Park Service officials. The reduction in the Bandelier burro herd seems justified under the congressional mandates for management of park land. The 1975 "Management Policies" for the National Park Service (Washington, D. C.) states, "Control or eradication of noxious or exotic plant and animal species will be undertaken when they are undesirable in terms of public health, recreational use and enjoyment, or when their presence threatens the faithful presentation of the historic scene or the perpetuation of significent scientific features, ecological communities, and native species, or where they are significantly harmful to the interests of adjacent landowners."

There are actually very few control alternatives available to the resource managers on wild horse and burro infested lands. To take no control actions, a course vociferously advocated by some elements of our society, is truly an unacceptable alternative, not only on National Park Service lands, but on all public lands. The wild equines have few, if any, natural predators in North America, and if allowed to go further unchecked, our public lands could suffer irreparable damage, not only to native ecosystems, but also to economically important rangelands. Another alternative, trapping and removal, has met with mixed success. In some areas, with rough terrain and limited access, such as in the Grand Canyon, trapping and removal is virtually impossible. Fencing off some lands to keep wild horses and burros out of sensitive areas has been suggested.

Not only would this measure fail to solve the problem of too many wild equines, but also it would be incredibly expensive and extremely disruptive to the normal dispersal of the large native herbivores. Sterilizing large numbers of wild horses and burros has also been seriously suggested. Although this method might serve to control small herds in certain regions, it too would be an impractical solution to the overall problem now facing land managers. Over most of the isolated ranges currently suffering wild equine impact, the only viable alternative we are left with is direct reduction by shooting. If done properly, this method is the most humane, most effective and least expensive.

Control of the rapidly expanding herds of wild equines is an undeniable necessity on our public lands. Effective management will not be achieved until the resource managers and scientists alike collect adequate data on habitat destruction and relate it in a convincing manner to the general public.

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Discussion

MR. DALE JOHNSON: I do not have a question, but I do have a comment. Yesterday the Supreme Court heard the constitutionality case that was born in New Mexico and I do not know what the Supreme Court is going to do with it; but I would say that Mr. Harris, the attorney in New Mexico, did a tremendous job of arguing the point of unconstitutionality.

FROM THE FLOOR: I was curious about one portion of your paper. Are you starting this experiment with burros on a part of the range that has no current capacity for burros at all in the Grand Canyon?

MR. CAROTHERS: Obviously the range in Grand Canyon has carrying capacity for a large herd of burros. We cannot have both burros and vegetation which is our mandate in the Park Service to maintain.

Bobwhite Quail Population Characteristics and Management Implications in South Texas[1]

William H. Kiel, Jr.
King Ranch and Texas A&M University, Kingsville

Of the three subspecies of bobwhite quail (*Colinus virginianus*) that range in Texas, the Texas bobwhite (*C. v. texanus*) (Aldrich and Duvall 1955) inhabits the region of south Texas often described as the Rio Grande Plain (Carter 1938). This southern tip of Texas comprises some 22 million acres (8.9 million ha) in all or parts of 34 counties south of a line from Del Rio to San Antonio to Victoria. The data on bobwhite production, movements, and mortality were gathered principally during the 1968-74 period on the King Ranch near Kingsville. Information on acreages of rootplowed land and of introduced grasses established in the Rio Grande Plain was provided by the U. S. Soil Conservation Service, Temple, Texas.

Climate, soils, and vegetation of the Rio Grande plain were reviewed in detail by Lehmann (1969). The 16,000-acre study area near Kingsville has a semiarid climate; annual rainfall is about 25 inches (63.5 cm), and the annual evaporation from an open-water surface is more than twice the annual precipitation (Tharp 1952). Some characteristic native grasses on the predominantly sandy to sandy loam soils of the Santa Cruz and Rincon pastures are bluestem (*Andropogon*) *Setania* and *Paspalum*. Goatweed (*Croton*), western ragweed (*Ambrosia psilostachya*), and partridge pea (*Cassia fasciculata*) are among the important quail foods. Dominant woody species are mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), and granjeno (*Celtis pallida*) (Gould 1962). The area is rangeland used for cattle production (Fig. 1).

The purpose of this paper is not to discuss in detail the intricacies of bobwhite population dynamics—for my data cover only a few aspects of bobwhite ecology—but to discuss briefly some population characteristics of bobwhites and attempt to assess the potential impact of regional land uses on bobwhite habitat.

Methods

Trapping and Banding

Bobwhites were trapped and banded during the 1968-74 period on the Santa Gertrudis division of King Ranch in Kleberg and Jim Wells counties, Texas.

Traps were constructed of 1 inch by 2-inch (2.5 by 5.1 cm) mesh welded wire with two funnel entrances. Dimensions were: length - 3 feet (.9 m), width - 2 feet (.61m), and height - 10 inches (.25m). Sorghum (milo) was used as bait. Trapping sites were adjacent to ranch roads and were cleared of vegetation and pre-baited for several days before traps were set. Sites were selected to provide shade for the traps. Generally, birds were trapped only in the early morning to

[1]Technical Article 12466 from the Texas Agricultural Experiment Station.

USDA United States Department of Agriculture

Science Framework for Conservation and Restoration of the Sagebrush Biome: Linking the Department of the Interior's Integrated Rangeland Fire Management Strategy to Long-Term Strategic Conservation Actions

Part 1. Science Basis and Applications

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Forest Service

Rocky Mountain Research Station

General Technical Report RMRS-GTR-360

April 2017

Chambers, J.C.; Beck, J.L.; Bradford, J.B.; Bybee, J.; Campbell, S.; Carlson, J.; Christiansen, T.J.; Clause, K.J.; Collins, G.; Crist, M.R.; Dinkins, J.B.; Doherty, K.E.; Edwards, F.; Espinosa, S.; Griffin, K.A.; Griffin, P.; Haas, J.R.; Hanser, S.E.; Havlina, D.W.; Henke, K.F.; Hennig, J.D.; Joyce, L.A.; Kilkenny, F.M.; Kulpa, S.M.; Kurth, L.L.; Maestas, J.D.; Manning, M.; Mayer, K.E.; Mealor, B.A.; McCarthy, C.; Pellant, M.; Perea, M.A.; Prentice, K.L.; Pyke, D.A.; Wiechman, L.A.; Wuenschel, A. 2017. Science framework for conservation and restoration of the sagebrush biome: Linking the Department of the Interior's Integrated Rangeland Fire Management Strategy to long-term strategic conservation actions. Part 1. Science basis and applications. Gen. Tech. Rep. RMRS-GTR-360. Fort Collins, CO: U.S Department of Agriculture, Forest Service, Rocky Mountain Research Station. 213 p.

Abstract

The Science Framework is intended to link the Department of the Interior's Integrated Rangeland Fire Management Strategy with long-term strategic conservation actions in the sagebrush biome. The Science Framework provides a multiscale approach for prioritizing areas for management and determining effective management strategies within the sagebrush biome. The emphasis is on sagebrush (*Artemisia* spp.) ecosystems and Greater sage-grouse (*Centrocercus urophasianus*). The approach provided in the Science Framework links sagebrush ecosystem resilience to disturbance and resistance to nonnative, invasive plant species to species habitat information based on the distribution and abundance of focal species. A geospatial process is presented that overlays information on ecosystem resilience and resistance, species habitats, and predominant threats and that can be used at the mid-scale to prioritize areas for management. A resilience and resistance habitat matrix is provided that can help decisionmakers evaluate risks and determine appropriate management strategies. Prioritized areas and management strategies can be refined by managers and stakeholders at the local scale based on higher resolution data and local knowledge. Decision tools are discussed for determining appropriate management actions for areas that are prioritized for management. Geospatial data, maps, and models are provided through the U.S. Geological Survey (USGS) ScienceBase and Bureau of Land Management (BLM) Landscape Approach Data Portal. The Science Framework is intended to be adaptive and will be updated as additional data become available on other values and species at risk. It is anticipated that the Science Framework will be widely used to: (1) inform emerging strategies to conserve sagebrush ecosystems, sagebrush dependent species, and human uses of the sagebrush system, and (2) assist managers in prioritizing and planning on-the-ground restoration and mitigation actions across the sagebrush biome.

Keywords: sagebrush habitat, Greater sage-grouse, persistent ecosystem threats, land use and development threats, climate change, management prioritization, resilience, resistance, conservation, protection, restoration

Front cover photo. Spring bloom in sagebrush country in the Bodie Hills overlooking Mono Lake near the Nevada-California State line. Photo by Bob Wick.

Inside cover photos. Natural recovery of native forbs and grasses in the Soda Fire rehabilitation area in southwestern Idaho with native lupine in the upper right (photos by Francis Kilkenny) and a mature mountain big sagebrush and bluebunch wheatgrass community in the upper left (photo by Kirk Davies).

Rear cover photo. Spring bloom in a Wyoming big sagebrush community near Pilot Butte in southwestern Wyoming. Photo by Corey Kallstrom.

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Acknowledgments

We thank the Western Association of Fish and Wildlife Agencies, Great Basin Landscape Conservation Cooperative, and Bureau of Land Management for financial assistance and the numerous other agencies that provided in-kind support of this effort. We received comments from over 50 reviewers from State and Federal Agencies, non-governmental organizations (NGOs), and private individuals during two review periods that helped to improve the manuscript. Technical reviews provided by Michael J. Wisdom, Peter J. Weisberg, Michael J. Haske, Terry A. Messmer, Stanley G. Kitchen, Matt C. Reeves, Peter S. Coates, and David Tart also helped to improve the manuscript.

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consistent in the literature. In particular, some studies have reported grass height as important for GRSG (Aldridge and Brigham 2002; Doherty et al. 2011a, 2014; Gregg et al. 1994; Herman-Brunson et al. 2009; Kaczor et al. 2011; Sveum et al. 1998) and GUSG (Stanley et al. 2015) nesting, whereas others have reported weak (Davis et al. 2014; Dinkins et al. 2016; Holloran et al. 2005) or no effects (Kolada et al. 2009; Lockyer et al. 2015; Popham and Gutierrez 2003). Additionally, other studies concluded no influential effects on GRSG nest survival with any studied grass-related microhabitat variable (Coates and Delehanty 2010; Gibson et al. 2016; Kolada et al. 2009; Lockyer et al. 2015). Recently, Gibson et al. (2016) demonstrated that reported positive effects of grass height may have been an artifact of timing in sampling procedures. Data on grass height were generally collected when nest fate was determined rather than using a predicted hatch date, which can result in a bias towards greater grass heights relative to the true effect. Thus, revisiting management prescriptions based on potential regional variation and potential confounding effects associated with plant phenology within nesting habitat is advised. Nevertheless, repeated heavy grazing of sagebrush bunchgrass communities in MZ II removes bunchgrasses and leads to a sagebrush and rhizomatous grass or bluegrass state, which has reduced resource value for GRSG reproduction (Cagney et al. 2010). Sagebrush cover is inherently lower in the West-Central Semiarid Prairies (MZ I) than in other portions of the species range (Herman-Brunson et al. 2009), suggesting greater reliance by breeding GRSG on herbaceous cover than in other portions of the range.

Infrastructure related to domestic livestock grazing (e.g., water developments) can result in loss of vegetation structure and plant species diversity near these features (Rinehart and Zimmerman 2001). Also, fences to control livestock and manage grazing on western rangelands can contribute to collision related mortality, particularly when located on flat terrain in close proximity to leks (Stevens et al. 2012). Coates et al. (2016d) found that the odds of raven occurrence, a pervasive sage-grouse nest predator, increased by approximately 46 percent in areas where livestock were present. The authors suggested that the increased raven predation may be partially due to the presence of features such as stock ponds and troughs and associated perching structures (e.g. windmills, tanks, and fences) that may increase raven presence.

5.3.8 Wild Horses and Wild Burros

Wild horses (*Equus caballus*) and wild burros (*E. asinus*), like all large-bodied herbivores, can alter sagebrush ecosystem structure and composition and affect habitat quality for sagebrush obligate species (Beever and Aldridge 2011). In the COT Report (FWS 2013) wild horses and wild burros were considered a present and widespread threat in only 1 of 15 populations in the eastern portion of the range (Parachute-Piceance-Roan Basin, MZ VII), but in 10 of 29 populations in the western portion of the range. Wild horses and wild burros were considered a persistent but localized threat in two populations in MZ II (Wyoming Basin and Northwest Colorado), and in one population in MZ IV (Northern Great Basin) (FWS 2013). BLM Herd Management Areas (HMAs) that overlap with GRSG occur in the Northern Basin and Range, Central Basin and Range, and Wyoming Basins (MZs II, III, and IV) (Beever and Aldridge 2011).

Wild horse and burro populations pose long-term challenges to habitat conservation and restoration efforts that differ in several key ways from the challenges posed

by managed livestock grazing (FWS 2013). Wild horse and burro management is primarily limited to managing numbers of animals and their distribution. Wild horses and burros live on the range the entire year and roam freely, and the locations and timing of wild horse and burro grazing are not regulated like livestock grazing.

Wild horse populations have the potential to grow on the order of 15 to 20 percent per year (National Research Council 2013; Ransom et al. 2016), and wild horse population sizes on Federal lands have almost doubled since the COT Report (FWS 2013) was published. It was estimated that 67,027 wild horses and burros occurred on BLM-administered land as of March 1, 2016. Approximately 60 percent of those (39,285 horses) occur within 13 million ac (5.3 million ha) of GRSG habitat. On USFS-administered lands, an estimated 6,000 wild horses and 900 wild burros occupy approximately 2 million ac (8 million ha). An estimated 3,400 of these animals occur within about 446,065 ac (180,516 ha) of GRSG general and priority habitat. In addition, an estimated 650 wild horses occur within bi-State sage-grouse habitat on about 70,000 ac (28,329 ha) administered by the USFS and 82,403 ac (33,347 ha) administered by the BLM.

Wild burros are not nearly as numerous as wild horses in the sagebrush biome. However, the tendency of burros to use low-elevation habitats throughout the year may lead to a high degree of overlap between burros and sage-grouse habitat, where burros and GRSG co-occur (Beever and Aldridge 2011). Also, wild burros can substantially affect riparian habitats (e.g., Tiller 1997) and native wildlife, and have grazing and trampling impacts similar to wild horses (Douglas and Hurst 1993).

The direct effects of wild horses on sagebrush ecosystems have been summarized by FWS (2008) and Beever and Aldridge (2011). Horse presence has broad effects on sagebrush ecosystem functioning. In general, wild horse presence is associated with lower overall plant cover, but greater relative abundance and cover of grazing-tolerant, unpalatable, and invasive plant species (Smith 1986), including cheatgrass. In the Great Basin, areas without wild horses have greater native plant cover, shrub cover, species richness, and overall plant biomass compared to areas with horses (Beever et al. 2008; Davies et al. 2014; Ziegenfuss et al. 2014). Also, there are measurable differences in soil structure, soil penetration resistance, and erosion as well as in invertebrate, small mammal, and reptile communities (Beever and Aldridge 2011; Ostermann-Kelm et al. 2009).

Many studies corroborate the general conclusion that high densities of wild horses can lead to biologically significant changes in sagebrush ecosystems. Although horses are usually considered to be grazers (Hanley and Hanley 1982), sagebrush can represent a large part of their diet in the Great Basin during the summer (Nordquist 2011). Wild horses are potential agents for the spread of nonnative plant species (Couvreur et al. 2004; Loydi and Zalba 2009) and may limit the effectiveness of restoration projects (Jessop and Anderson 2007). Grazing by wild horses can also have severe impacts on aquatic ecosystems and riparian communities (Barnett 2002; Beever and Brussard 2000; Earnst et al. 2012; FWS 2008, 2012). Wild horses can degrade the quality of limited water sources and behaviorally exclude ungulates and other native wildlife (e.g., pronghorn) from these water sources (Gooch et al. 2017; Hall et al. 2016; Ostermann-Kelm et al. 2008; Perry et al. 2015; FWS 2008). Even in areas with long histories of livestock grazing, once domestic livestock are removed, continued wild horse grazing may cause ongoing detrimental ecosystem effects (Davies et al. 2014; FWS 2008). In the sagebrush-steppe ecosystem, plant communities can take several decades to recover from such impacts (e.g., Anderson and Inouye 2001).

The Journal of Wildlife Management 85(6):1132–1149; 2021; DOI: 10.1002/jwmg.22089

Special Section on Management of Feral Equids

Sage-Grouse Population Dynamics are Adversely Affected by Overabundant Feral Horses

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ABSTRACT In recent decades, feral horse (*Equus caballus*; horse) populations increased in sagebrush (*Artimesia* spp.) ecosystems, especially within the Great Basin, to the point of exceeding maximum appropriate management levels (AML_{max}), which were set by land administrators to balance resource use by feral horses, livestock, and wildlife. Concomitantly, greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are sagebrush obligates that have experienced population declines within these same arid environments as a result of steady and continued loss of seasonal habitats. Although a strong body of research indicates that overabundant populations of horses degrade sagebrush ecosystems, empirical evidence linking horse abundance to sage-grouse population dynamics is missing. Within a Bayesian framework, we employed state-space models to estimate population rate of change (λ) using 15 years (2005–2019) of count surveys of male sage-grouse at traditional breeding grounds (i.e., leks) as a function of horse abundance relative to AML_{max} and other environmental covariates (e.g., wildfire, precipitation, % sagebrush cover). Additionally, we employed a *post hoc* impact-control design to validate existing AML_{max} values as related to sage-grouse population responses, and to help control for environmental stochasticity and broad-scale oscillations in sage-grouse abundance. On average, for every 50% increase in horse abundance over AML_{max}, our model predicted an annual decline in sage-grouse abundance by 2.6%. Horse abundance at or below AML_{max} coincided with sage-grouse λ estimates that were consistent with trends at non-horse areas elsewhere in the study region. Thus, AML_{max}, as a whole, appeared to be set adequately in preventing adverse effects to sage-grouse populations. Results indicated 76%, 97%, and >99% probability of sage-grouse population decline relative to controls when horse numbers are 2, 2.5, and ≥3 times over AML_{max}, respectively. As of 2019, horse herds exceeded AML_{max} in Nevada, USA, by >4 times on average across all horse management areas. If feral horse populations continue to grow at current rates unabated, model projections indicate sage-grouse populations will be reduced within horse-occupied areas by >70.0% by 2034 (15-year projection), on average compared to 21.2% estimated for control sites. A monitoring framework that improves on estimating horse abundance and identifying responses of sage-grouse and other key indicator species (plant and animal) would be beneficial to guide management decisions that promote co-occurrence of horses with sensitive wildlife and livestock within landscapes subjected to multiple uses. Published 2021. This article is a U.S. Government work and is in the public domain in the USA. The Journal of Wildlife Management published by Wiley Periodicals LLC on behalf of the Wildlife Society.

KEY WORDS appropriate management level, *Centrocercus urophasianus*, *Equus caballus*, free-roaming, Herd Management Area, Nevada, sage-grouse, state-space model, wild horse.

Preserving the integrity of sagebrush (*Artimesia* spp.) ecosystems within the paradigm of multiple-use on public lands is a common goal of United States resource management agencies. Management of feral horses (*Equus caballus*; horse) within the western United States has been a topic of public debate (National Research Council 2013, Beever et al. 2018, Scasta et al. 2018), wherein litigation favored by animal advocacy groups often contrasts with reported ecological damage to semi-arid environments (Davies et al. 2014, Davies and Boyd 2019). In western landscapes, free-roaming feral horses occupy a

Received: 31 July 2020; Accepted: 18 May 2021

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substantial proportion of public rangeland, and are primarily managed by the Bureau of Land Management (BLM) within Herd Management Areas (HMAs) designated to balance horse populations, cattle, and other livestock grazing with use by native wildlife and Herd Areas (HAs) that encompass the range of feral horses. Currently, the area of HMAs in the United States exceeds 12,500,000 ha (BLM 2020*a*) with the largest areas within the state of Nevada (6,340,696 ha), which consists of the most arid environments across feral horse distributional range (BLM 2020*a*). Additionally, horses occur within 53 Wild Horse and Burro (WHB) Territories managed by the United States Forest Service (USFS 2014). Other smaller areas with feral horses include lands managed by the National Park Service, the United States Fish and Wildlife Service, and the Department of Defense, and state, private, and tribal lands (Beever et al. 2018, Hennig et al. 2018). These animals, however, do not have the same federal protection under the Wild Free-Roaming Horses and Burros Act (1971) as those on lands managed by BLM and USFS. Although numbers of horses within HMAs vary annually, reported estimates have increased approximately 3 times from 2005 (27,369; BLM 2020*a*) to 2020 (79,568; BLM 2020*a*) with populations in Nevada representing the highest estimates (46,974 in 2020, representing ~59.0% of all horses; BLM 2020*a*).

A fundamental goal of the Wild Free-Roaming Horses and Burros Act (1971:649) is to manage herds within a range of population sizes that facilitate and protect "a thriving natural ecological balance." Thus, BLM sets appropriate management levels for each HMA (BLM 2010) based on site-specific environmental analysis under the National Environmental Policy Act (1970). Appropriate management levels (AMLs) are established with the intention of balancing multiple-use mandates, including the protection of ecological processes, with the capacity of HMAs to support livestock and healthy horse and wildlife populations (BLM 2010). Although establishing and adjusting AMLs lacks specificity and consistency across HMAs (National Research Council 2013), maximum (AML_{max}) and lower limits are typically set according to a tiered approach that evaluates 4 habitat components: forage, water, cover, and space (BLM 2010).

Notably, the most influential habitat component is often the availability of forage, which is used to establish use rates and capacity (BLM 2010). The BLM recommends that forage-availability estimates are based on 3–5 years of data on forage use, accompanied by spatial use mapping products, while accounting for animal unit months (AUMs) for free-roaming horses and various domestic livestock (BLM 2010). Use in this context refers to the proportion of forage production consumed by herbivores (i.e., horses, burros, livestock, wildlife) on the range (BLM 2010). The AUM and desired level of use are then typically used to propose lower and maximum AMLs and allocate available forage between free-roaming equids, wildlife, and livestock (BLM 2010). Therefore, population estimates that exceed AML_{max} are taken as a sign that horses may be excessively damaging natural resources because forage use will exceed desired levels. Policies enacted in conjunction with the Wild Free-Roaming Horses and Burros Act (as amended) permit removal of horses from the landscape using various tools, such as helicopter-assisted capture, and tools to manage removed animals, such as private care placements (e.g., adoptions) and permanent holding facilities (Garrott 2018). The BLM and USFS are not permitted to use lethal removal or sell horses to those who would kill otherwise healthy animals (Garrott 2018) as prescribed by annual Department of Interior appropriations acts (BLM 2020*a*). Despite permitted management actions occurring at HMAs range-wide (BLM 2020*a*), estimates have exceeded AML_{max} every year since 2005, which is largely influenced by population growth (Collins and Kasbohm 2017) that exceeds BLM's ability to pay for an adequate number of animal removals or fertility suppression (Garrott 2018). Horse population estimates, as a whole, are currently >1.97 times above AML_{max} across their range for every state except Arizona. The HMAs in Nevada are exceeding AML_{max} by >4 times, averaged across HMAs, and thousands of free-roaming horses occur in Nevada's HAs (BLM 2020*a*). If exceeding allowable use for all ungulates, collectively, defines overgrazing, and free-roaming horse populations exceed AML_{max} based on allowable use, then it is important to know the ecological effects of overgrazing to plant and animal communities that rely on sagebrush ecosystems.

Feral horses can severely affect ecological structure and function of semi-arid rangelands (Davies et al. 2014, Davies and Boyd 2019, Eldridge et al. 2020), particularly sagebrush ecosystems (Beever et al. 2018, Davies and Boyd 2019). For example, areas used by horses exhibit reduced herbaceous cover and biomass (Boyd et al. 2017, Baur et al. 2018, Kaweck et al. 2018), fragmented and reduced shrub cover (Beever and Brussard 2000, Beever et al. 2008, Boyd et al. 2017), and increased soil compaction (Beever and Herrick 2006, Davies et al. 2014) relative to areas where they are absent or excluded. Furthermore, recent evidence suggests that horses may contribute to the spread of harmful invasive grasses such as cheatgrass (*Bromus tectorum*; King et al. 2019) that facilitate increased frequency and severity of wildfire (Brooks et al. 2004, Chambers et al. 2014). Managed livestock, particularly cattle, are supplemented with salt, mineral, and water placement and graze during planned periods and locations, which allows direct management of land deferment and rest (Davies and Boyd 2019). Absent management action, where options are much more limited owing to the Wild Free-Roaming Horses and Burros Act (as amended), horses are not constrained to specific locations, often grazing continuously on preferred plant species and concentrating in riparian areas where ecological degradation is intensified (Kaweck et al. 2018). Collectively, the magnitude of these adverse effects is likely exacerbated as horse populations become increasingly overabundant relative to AML_{max} (i.e., exceed AML_{max}) and as horses move freely within the landscape uninhibited by fencing and other barriers. Additionally, previous research indicates that behavioral tendencies and interactions between horses and native ungulates can lead to displacement, even from the presence of a

single horse (Berger 1985), and exclusion from water sources (Gooch et al. 2017).

Overabundant horses will inevitably affect wildlife communities through modifications to their habitat (Davies et al. 2014, Hall et al. 2016), which is especially important to resource specialists that rely on specific habitat components during important life stages. One sagebrush-obligate species at the center of state and national land-use strategies (Stiver 2011), and potentially influenced by overabundant horse populations (Beever and Aldridge 2011), is the greater sage-grouse (*Centrocercus urophasianus;* sage-grouse). Sage-grouse require specific seasonal habitats within sagebrush ecosystems during important life-history stages, such as nesting, brood-rearing, and wintering (Patterson 1952, Schroeder et al. 1999). Accordingly, population viability for sage-grouse largely depends on a diversity of habitat conditions that occur across broad spatial extents, such that resulting population trends can serve as an indicator for the ecological integrity of sagebrush ecosystems at large scales (Rowland et al. 2006, Hanser et al. 2011). Sage-grouse are experiencing long-term population declines in semi-arid environments (Garton et al. 2015) and are facing a myriad of threats that include wildfire and invasive grass cycles (Chambers et al. 2014, Coates et al. 2016*b*), expansion of pines (*Pinus* spp.) and junipers (*Juniperus* spp.; Baruch-Mordo et al. 2013, Coates et al. 2017), anthropogenic development (Green et al. 2017), and increased drought (Coates et al. 2016*b*). Despite distributional overlap between sage-grouse and horses range-wide (Beever and Aldridge 2011), coupled with compelling evidence that most HMAs are exceeding set AML_{max} (BLM 2020*a*), studies that quantify relationships between horse abundance and sage-grouse population dynamics are notably missing. Such information can help validate and potentially refine setting and management of AMLs by estimating ecological thresholds of horse abundance that, when exceeded, have an additive negative influence on sage-grouse population dynamics.

Recommendations published by the National Academy of Sciences (National Research Council 2013) recently called for research designs to validate and refine estimates of AML with a focus on response by plants or wildlife to manage horse populations effectively. We chose sage-grouse as the study species to serve as a surrogate for effects to other wildlife species that rely on sagebrush ecosystems. Additionally, management actions that benefit sage-grouse habitat can benefit other species with similar life-history requirements such as the pygmy rabbit (*Brachylagus idahoensis*; Rowland et al. 2006), though potential benefits to other species becomes reduced as the amount and similarity of habitat overlap declines (Carlisle et al. 2018).

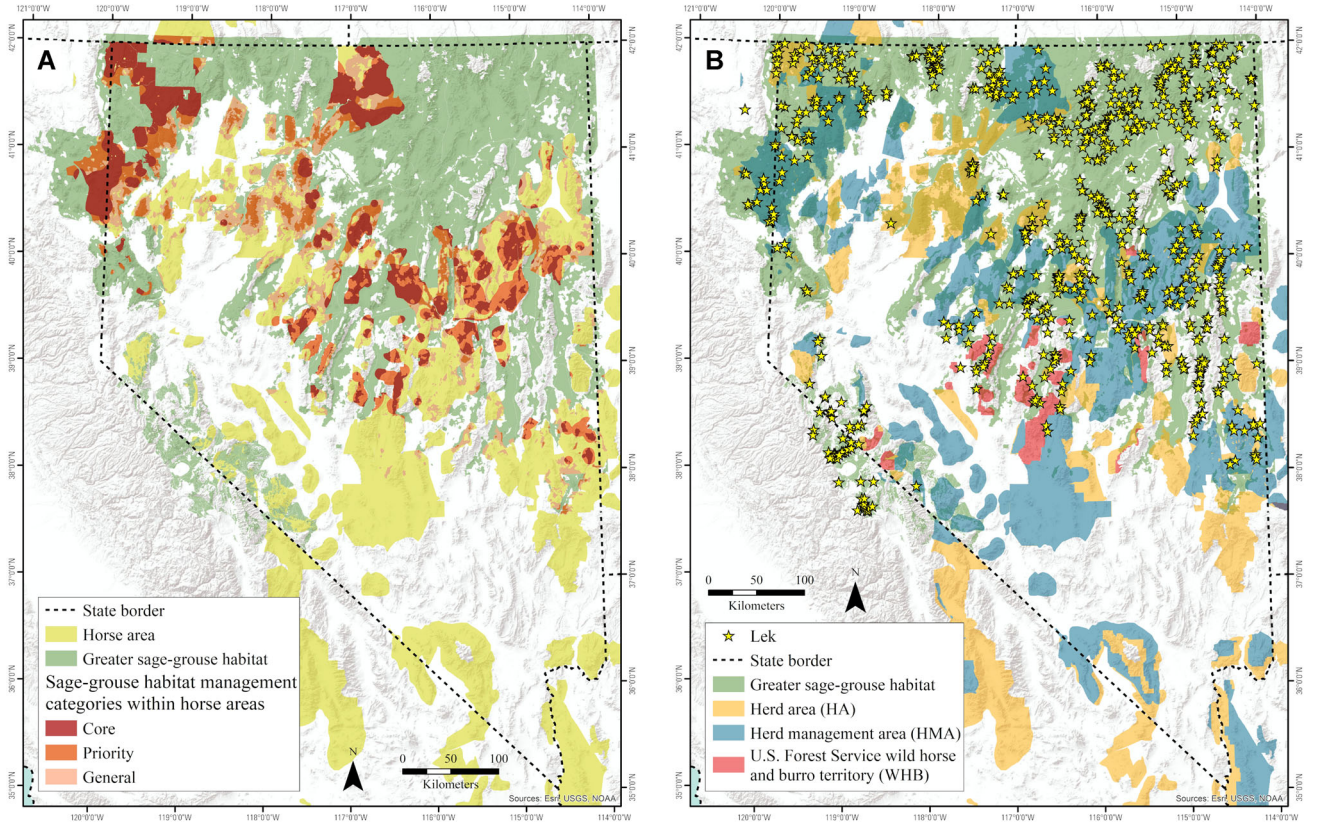


Figure 1. A) horse-occupied areas (i.e., Herd Management Areas, Herd Areas, and U.S. Forest Service Horse Territories) in relation to different habitat categories of greater sage-grouse (core, priority, and general; Coates et al. 2020*a*) and B) lek count locations used in Bayesian state-space models of greater sage-grouse rate of change in population abundance in relation to horse abundance and other environmental factors within sagebrush ecosystems of Nevada and California, USA, 2005–2019.

Importantly, in Nevada and northeastern California, increasing horse abundance represents a poorly quantified yet likely additional threat to sage-grouse populations because areas occupied by horses comprise ≥4,498,534 ha of sage-grouse habitat (Fig. 1A), of which 1,648,807 ha is considered priority habitat (31%) from recent sage-grouse habitat mapping (Coates et al. 2016*a*, 2020*a*).

Our goal was to conduct research to assist with horse management decisions, with 3 primary objectives. First, we aimed to model sage-grouse population rate of change (λ) as a function of covariates that represented free-roaming horse abundance, specifically population size over AML_{max} (%AML_{max}), while accounting for other known, potentially important environmental influences (i.e., wildfire, precipitation, % sagebrush, elevation). The second objective was to estimate changes in sage-grouse abundance over the next 15 years under 3 scenarios: horse population growth continues unabated, horse population rate of change is neutral (no growth) but current population abundance remains constant, and horse population numbers are reduced to current AML_{max} limits and maintained at those levels. Our third objective was to carry out an impact-control design by comparing estimates of sage-grouse population λ between areas occupied by horses (impact) relative to non-horse areas (controls). Impact areas included horse population sizes that were at or below AML_{max} and at different increments exceeding AML_{max} (exceeding by 1–3 times). We designed the last objective to validate the efficacy of AML_{max}, as a whole, in sustaining healthy sage-grouse populations.

STUDY AREA

Our study area spans the current sage-grouse distribution across Nevada and northeastern California, which comprises approximately 12.6 million ha of the Great Basin (Fig. 1A) and includes varied sagebrush communities. The Great Basin is a cold desert characterized by 4 seasons (spring, Mar–May; summer, Jun–Aug; fall, Sep–Nov, and winter, Dec–Feb) with hot, dry summers and cold, snowy winters and is topographically diverse with elevations ranging 600–3,100 m (Snyder et al. 2019). Precipitation was generally low and varied by elevation but primarily occurred as snow during the winter and as rain during spring and early summer (Snyder et al. 2019). Snowmelt provided water for the remainder of the year. The mean elevation across 726 lek sites (Fig. 1B) was 1,910 m (range = 1,374–2,778 m). Mean maximum temperatures ranged from 31.4°C to 33.1°C (Jul) and mean minimum temperatures ranged from −7.2°C to 1.6°C (Jan; Western Regional Climate Center, http://www.wrcc.dri.edu/, accessed 1 Jun 2020).

At relatively low elevations (<2,100 m), vegetation was dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*; Cagney et al. 2010), black sagebrush (*A. nova*), and low sagebrush (*A. arbuscula*). Cheatgrass is an invasive annual grass that was interspersed with sagebrush in many low-elevation areas and often replaced sagebrush following major disturbances like wildfire, especially in more xeric environments (Chambers et al. 2014). Mountain big sagebrush (*A. t. vaseyana*) dominated at higher elevations (>2,100 m). Single-leaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) are native conifers that were primarily present at mid to high elevations, but were expanding into sagebrush-dominated communities, likely because of a history of fire suppression over the last century in the Intermountain West (Miller and Rose 1999). Given the prevalence of sagebrush within the Great Basin, the faunal community was dominated by shrub-associated wildlife from various taxa including herptiles, raptors, passerines, and mammals (Rowland et al. 2006). Animals known to interact with sage-grouse or horses included common ravens (*Corvus corax*; Coates and Delehanty 2010), elk (*Cervus canadensis*; Perry et al. 2015), and pronghorn (*Antilocapra americana*; Gooch et al. 2017, Muñoz et al. 2021). Human enterprise including agriculture, energy development, mining, ranching, recreational activities, and transport infrastructure (e.g., roads, railways, water diversion) became commonplace following European settlement and have significantly altered Great Basin ecosystems (Morris and Rowe 2014).

METHODS

Data Collection

Lek count surveys.—Nevada Department of Wildlife (NDOW) and the California Department of Fish and Wildlife (CDFW) along with numerous personnel from private, non-profit, and governmental agencies (state and federal) administered and led collection of lek data. Lek counts followed standardized established protocols approved by interagency collaboration (Connelly et al. 2003, Western Association of Fish and Wildlife Agencies [WAFWA] 2015, Blomberg and Hagen 2020). Briefly, observers counted sage-grouse each spring during maximum lek attendance periods (Mar–Apr; Wann et al. 2019) from 2005–2019. At each survey, ground observers used binoculars or spotting scopes to count male sage-grouse at locations with a full view of the lek. They conducted surveys from 30 minutes before to 90 minutes after sunrise (Monroe et al. 2016). They conducted 3 counts per survey, and recorded the highest count. We used maximum male counts for leks receiving multiple surveys within the spring season to represent peak attendance, which indexed annual abundance (Blomberg et al. 2013, Monroe et al. 2016, Green et al. 2017). All lek count data underwent validation and quality control. For example, we included only lek counts that followed the data collection protocols defined by NDOW and CDFW and eliminated records that indicated unfavorable lekking conditions, including the presence of precipitation and wind speeds ≥16 km/hour (Christiansen 2012, Monroe et al. 2016, Edmunds et al. 2018). We also excluded leks if their time series did not include ≥2 consecutive counts of ≥2 males (i.e., lek classified as inactive), if the majority (>66%) of the time series contained missing values (i.e., leks not regularly counted), or if they occurred on private lands. We established the latter condition because our objectives were to evaluate feral horse effects on sage-grouse, and information

on horse presence or absence on private lands was unavailable.

Lek and feral horse datasets.—We used multiple publicly available datasets to categorize lek overlap with horse-occupied areas (HOAs) and to develop covariates that indexed horse density. We then related horse density covariates to changes in sage-grouse population abundance at the lek level using the lek count data described above. We overlayed lek locations with BLM's Wild Horse and Burro Herd Area and Herd Management Area layer (BLM 2020*b*) and the USFS's Wild Horse and Burro Territory layer (USFS 2020) using ArcMap 10.7 (Esri, Redlands, CA, USA). We assigned each lek as overlapping none or 1 of 3 types of HOAs: BLM HMA, BLM HA, or USFS Wild Horse and Burro Territory. We consolidated these into 3 management groups for use in our analysis: active management—lek overlaps HOA with set values for AML_{max} and horse population estimate data (e.g., HMAs); passive management—lek overlaps HOA that lacks set values of AML_{max} and may or may not have available horse population estimates (e.g., HAs and USFS Territories); and none—lek does not overlap any HOA and horses are assumed to be functionally absent because population estimates are lacking. We classified leks that overlayed an HMA and an HA as HMA because HMAs are associated with AMLs and annual horse population estimates. We classified leks that overlapped an HA and a USFS Territory as HA because territories lacked publicly available annual estimates or AML. We manually recategorized a few leks ($n = 7$) as overlapping an HMA rather than an HA when the lek fell on HA islands within HMAs. Burros (*Equus asinus*) are also present and populations monitored within some HOAs, but they are less widespread than horses within the Great Basin (Beever and Aldridge 2011). Additionally, few of the leks we monitored overlapped HOAs with burros and horses ($n = 17$, 2% of total) and no leks overlapped management areas with only burro populations. Therefore we did not index burro density for this study.

We used R package tabulizer (Leeper 2018) to extract annual AML_{max} and horse population estimates (i.e., horse abundance) within HMAs and HAs from BLM annual data summaries (BLM 2020*a*) for 2005–2019. For each lek during each year, we tabulated the AML_{max} and horse abundance for the corresponding HOA, if available. Missing data within HOAs were rare; in these cases, we imputed values from existing data and modeled trends where they existed.

Feral horse abundance indices.—We calculated indices that represented temporal changes in horse abundance relative to AML_{max} (e.g., $\%AML_{max}$) for each lek based on available BLM data. We consider these indices because true abundances were unknown, as numbers reported were not repeatable or corrected for imperfect detection (National Research Council 2013, Schoenecker et al. 2018). We calculated abundance relative to AML_{max} by dividing the BLM horse abundance estimate by the AML_{max} value for each year and multiplying by 100 to reflect a percentage ($\%AML_{max}$). To evaluate possible curvilinear pseudo-threshold relationships, we also considered log-transformed $\%AML_{max}$. To accommodate delayed effects of horse abundance on sage-grouse response, we created an index to reflect 1-year time lag for $\%AML_{max}$. Finally, we calculated the change (Δ) in $\%AML_{max}$ by dividing the index at time $t+1$ by the index at time t. As such, there were 6 candidate horse abundance indices considered in our models: $\%AML_{max}$, $\ln(\%AML_{max})$, lagged $\%AML_{max}$, lagged $\ln(\%AML_{max})$, $\Delta\%AML_{max}$, and $\Delta\ln(\%AML_{max})$.

Landscape covariates.—We considered several environmental predictors to account for landscape-scale habitat conditions explaining additional spatiotemporal variation in sage-grouse population rate of change. We modeled environmental predictors that accounted for sources of background variation in sage-grouse population trends along with estimation of any disturbance effects from horses to prevent potential confounding effects. We gathered these predictors from remotely sensed publicly available data sources typically developed with geographic information systems. We specified these predictors *a priori* based on environmental characteristics commonly known to explain distribution and population dynamics of sage-grouse. Predictors (Table S1, available online in Supporting Information) included sagebrush cover, sagebrush height, elevation, pinyon-juniper cover (Gustafson et al. 2018), proximity to water sources (water bodies, springs), cumulative burned area (Coates et al. 2016*b*), and precipitation indices (Palmer drought severity index [PDSI], Palmer Z index [PZI], standardized precipitation index [SPI], and standardized precipitation-evapotranspiration index [SPEI]; Kangas and Brown 2007, Daly et al. 2015, Abatzoglou et al. 2017).

We evaluated most predictors at 5- and 10-km radial buffers around each lek (Coates et al. 2016*b*), using zonal means to capture influences on sage-grouse population dynamics that are consistent with the spatial scale of sage-grouse breeding activity and space use across multiple life stages (Doherty et al. 2010, 2016). We modeled proximity to water sources as exponential distance-decay functions, $\exp(-d/\alpha)$, where d was the distance from each lek and candidate values for α were the 25th, 50th, and 75th percentile distances from all leks. Exponential decay functions allow a feature's influence to decline rapidly at large distances and we assumed they represented more biologically plausible relationships than if we treated distances as a continuous linear predictor (Coates et al. 2016*a*). To model precipitation influences, we evaluated 12 different precipitation indices characterized at both spatial scales (24; Table S1), ranging from immediate characterization of drought (e.g., PDSI, PZI) up to 2-year characterizations of precipitation patterns relative to long-term trends (e.g., 24-month SPI and SPEI; Abatzoglou et al. 2017). We treated vegetation predictors, water sources, and elevation as constant across the study's time series, whereas we updated cumulative burned area annually, and averaged precipitation indices for March–April of each annual breeding season when leks are counted (Table S1). Prior to modeling, we standardized all

candidate predictors to a common scale with mean = 0 and standard deviation = 1.

Statistical Analyses

State-space model.—We used Bayesian hierarchical state-space models (SSMs; Royle and Dorazio 2008, Kéry and Schaub 2011) to estimate lek-specific, interannual rate of change from lek count data gathered over the 15-year time series. The SSMs are advantageous over generalized linear models in this framework because they allow observation error to be modeled (i.e., detections are imperfect), and they are inherently Markovian, which is appropriate for modeling time series data (Kéry and Schaub 2011, Aeberhard et al. 2018). Thus, SSMs separate variance in the observation process from variance in the state process, which in this case is the change in abundance from year t to year $t+1$. We extended a general SSM framework, where the number of males (N) at each lek (lek = i), and for each year (time = t) was estimated as a function of the prior year N and intrinsic rate of change (r) in N with stochastic process error ($\sigma^2_{r_i}$) expressed as:

$$log(N_{i,t+1}) = log(N_{i,t}) + r_{i,t} \quad (1)$$

$$r_{i,t} \sim Normal(\mu_{r_{i,t}}, \sigma^2_{r_i}). \quad (2)$$

The observation component in our model was expressed as:

$$log(y_{i,t}) = log(N_{i,t}) + \varepsilon_i \quad (3)$$

$$\varepsilon_i \sim Normal(0, \sigma^2_{obs_i}). \quad (4)$$

We incorporated landscape covariates into the state process by modeling the mean rate of change ($\mu_{r_{i,t}}$) in N as a function of environmental predictors $x' = x_1, x_2, ..., x_k$ that were described above and expected to influence variation in the intrinsic rate of change:

$$\mu_{r_{i,t}} = \beta_0 + x'_{i,t}\beta. \quad (5)$$

In this case, β_0 was the population-level intercept with $x'_{i,t}\beta$ representing covariates x' multiplied by the vector of linear predictor coefficients β.

Latent indicator variable selection.—To choose a subset of informative independent predictors from groups of similar type (e.g., predictors measured at multiple scales or time lags), we implemented Bayesian variable selection using reversible jump Markov chain Monte Carlo (MCMC) methods (O'Hara and Sillanpää 2009, Tenan et al. 2014) with Bayesian latent indicator scale selection (BLISS; Stuber et al. 2017). Our *a priori* set of candidate predictors included groups of correlated predictors that were initially characterized at different spatial scales (5-km and 10-km buffers; Table S1) or different time lags (e.g., precipitation indices; Table S1), and multiple representations of horse abundance within HAs or HMAs. For instance, sagebrush cover and sagebrush height were highly correlated, and both were measured at 2 spatial scales, providing 4 representations of sagebrush vegetation. Similarly, we had 24 candidate precipitation indices involving spatial scales and multiple time lags. We also applied variable selection to the horse abundance indices representing $\%AML_{max}$.

We applied the BLISS method to identify a single predictor from each group based on probabilistic estimates from MCMC sampling. This method extends single-scale or single-variable approaches by introducing a latent categorical variable that is estimated along with the other quantities in a model (Stuber et al. 2017). For example, a single predictor variable x could have multiple candidate representations such as 2 spatial scales or 2 time lags, in which case $x_i \in \{x_{11}, x_{12}, x_{21}, x_{22}\}$, with sub-indices representing each unique combination of scale and time lag. A categorical distribution is then specified over all candidate representations with prior weights that sum to 1, $w_{i,1}, ..., w_{i,n_i}$; $\sum_{m=1}^{n_i} w_{i,m}$. A non-informative prior distribution is specified by setting equal prior weights across categories: $w_{i,m} = 1/n_i$ (Stuber et al. 2017). The posterior distribution is then estimated for each candidate representation for each predictor using MCMC, thus facilitating probabilistic selection of the most informative representations across all predictor types.

Density dependence.—We also investigated density-dependent influences on λ (Dennis et al. 2006, Hostetler and Chandler 2015) that have been described for sage-grouse population dynamics (Garton et al. 2015, Coates et al. 2016*b*, Edmunds et al. 2018). We specified density-dependent feedbacks with a 1-year time lag (Edmunds et al. 2018) that can yield cyclic patterns of λ displayed by sage-grouse in other areas (Fedy and Aldridge 2011, Coates et al. 2018). To prevent potential biases or overestimation of the density dependence term associated with substantial variation in lek size (counts ranging from <10 individuals to >250), we specified density for each lek as its count each year relative to an approximate maximum count after factoring in observation and process variance. The approximate maximum count is derived from the SSM structure itself rather than being calculated outside of the model and is included as a variable. Density dependence in this analysis thus took the form:

$$\frac{N_{i,t-1}}{k_i} = N_{i,t-1}/(max(N_i) + \sigma_i), \quad (6)$$

where k_i represented maximum N per lek, and σ_i was the standard deviation of all lek counts. We then included this representation of density in the linear predictor of intrinsic rate of change in N (eq 6), along with other environmental predictors.

Priors and model implementation.—Using BLISS, we selected 1 predictor from each of the following groups during the initial modeling stage: sagebrush vegetative cover and height, pinyon-juniper cover, elevation, cumulative burned area, drought or precipitation, proximity to water body, proximity to spring, and free-roaming horse abundance $\%AML_{max}$ indices. We specified non-informative prior

weights corresponding to $w = 1/4, 1/2, 1/2, 1/2, 1/24, 1/3$, and 1/6 for each of these groups, respectively. In addition, this model included whether a lek occurred outside of ($h = 0$) or within ($h = 1$) an HOA. Because horse estimates relative to AML_{max} were only available within HMAs, we included the horse abundance $\%AML_{max}$ index (Table S1) as a restricted interaction, such that its effect was conditioned on the subset of leks that overlapped HMAs. Under this constraint, we then selected the most informative horse abundance index from the set of candidate indices (Table S1).

In the second modeling stage, we selected the single predictor from each group that had the highest posterior probability of inclusion estimated from the model in stage 1. We carried each of these predictors forward into a new SSM with the selected predictor from each group. We used this method primarily so that each final predictor's posterior distribution was easily identified and interpretable. We obtained our final results from this second modeling stage, and based all inferences about free-roaming horse abundance influences on sage-grouse populations on this final model.

For both models, we specified Bayesian Lasso (double-exponential or Laplace) prior distributions for all predictor coefficients, $\beta_j \sim Laplace(0, \lambda)$, with an uninformative hyperparameter set for the tuning parameter, $\lambda \sim Uniform(0, 10)$. The Bayesian Lasso (Park and Casella 2008) protects against possible overfitting and predictor collinearity in a multivariate modeling framework by shrinking coefficient estimates toward zero when they are not well-supported by the data (Hooten and Hobbs 2015, Authier et al. 2017). A form of regularization (i.e., optimizing model fit by penalizing greater numbers of parameters), the Lasso results in better predictions and model stability in multiple regression models, particularly those with increasing numbers of candidate predictors (Tibshirani et al. 2012, Gerber and Northrup 2020).

We estimated model parameters in JAGS 4.2.0 (Plummer 2003) using packages rjags (Plummer 2018) and jagsUI (Kellner 2018) within R 3.6.3 (R Core Team 2019). We assigned vague prior and hyperprior distributions for the following parameters: process error $\sigma_{r_i} \sim Uniform(0, 1)$, $\tau_{r_i} = 1/\sigma_{r_i}^2$; observation error $\sigma_{obs_i} \sim Uniform(0, 2)$, $\tau_{obs_i} = 1/\sigma_{obs_i}^2$; and rate of change intercept $\sigma_{\beta_0}^2 \sim Uniform(0, 10)$, $\beta_0 \sim Normal(0, \sigma_{\beta_0}^2)$. We obtained 6,000 posterior samples from 3 independent chains (50,000 iterations) after a burn-in of 25,000 iterations, and thinned by a factor of 25. We determined convergence based on Gelman-Rubin $\hat{R} < 1.1$ for all model parameters (Brooks and Gelman 1998, Green et al. 2017), and assessed model fit using the Bayesian *P*-value (Kéry and Schaub 2011, Green et al. 2017). We evaluated predictor influence based on the proportion of the posterior distribution having the same sign as the mean (e.g., probability β_j greater or less than 0), and by graphically demonstrating the magnitude and uncertainty of predicted effects on the intrinsic rate of change parameter.

Future projections of sage-grouse population trends.—To help inform management decision and actions, we projected population trends over the next 15 years (i.e., 2020–2034) under 3 different simulated scenarios with the final SSM model: scenario 1 = horse abundance index continues at current rates of increase, scenario 2 = horse abundance index remains at values observed during the study (2005–2019), and scenario 3 = horse numbers are reduced to and maintained at AML_{max} for each HMA. We chose to project 15 years because this was the same number of years of which we acquired data to estimate parameters. We used the horse abundance index that garnered the most model support. For scenario 1, we fit a linear mixed model to estimate change in abundance index through time based on population and AML_{max} data from 2005 to 2019. The model took the form:

$$A = \zeta_j + \beta_j x_{j,t} + \varepsilon, \quad (7)$$

where we modeled the abundance index (A) as a linear function of random intercepts (ζ_j) for HMA j with a random slope coefficient per HMA (β_j) applied to a continuous covariate representing time (x_t, where t denotes years 2005–2019). Random slope coefficients were necessary because the trend in abundance varied by HMA, with a few decreasing and most increasing. We obtained an overall estimate of percent change in horse abundance by using model prediction for years 2005 and 2019 at each HMA and dividing the median difference by the median initial value. We calculated bootstrapped confidence intervals for this estimate by sampling with replacement among all HMAs 10,000 times. We derived posterior predictions of the abundance index at the HMA level for future years (2020–2034) by sampling from the posterior distribution of the linear mixed model for each HMA intercept and trend and projecting the trend over time.

To account for environmental stochasticity, for each iteration, we drew new precipitation values from a standard normal distribution (i.e., on the same scale as precipitation indices used in the model). This allowed for projections across a full range of future scenarios where climate conditions could range from low to high precipitation. We set burned area values to their last observed values, and held all other variables at their means for each lek. We then drew from posterior distributions of parameter estimates from the SSM to predict $\hat{N}$ of sage-grouse for each year. This technique accounted for uncertainty in changes in horse abundance index and uncertainty in the estimated effect of horse abundance index on sage-grouse population $\hat{N}$. We obtained the starting population size for sage-grouse population projections by sampling from the 2019 lek estimates derived from the SSM, and subsequent annual changes in population size were expressed as a proportion of the population in 2005 (the max. observed sage-grouse population size). For scenario 2, we followed similar methods but instead projected the proportional changes in population size through time given no change in the abundance index. For example, model projections over the next 15 years were

based on current %AML_{max} held constant. For scenario 3, we reset horse populations that were above AML_{max} back to 100% and again projected sage-grouse population changes through time. For illustrative purposes, we developed spatial maps depicting percent decrease in population λ between 2019 and 2034 across all leks in our study area using $\hat{N}$ from the SSM for each of the 3 scenarios.

Post hoc impact-control analysis.—In a final analysis, using predicted posterior distributions (*pD*) of sage-grouse population λ, we used our model to validate current AML_{max} settings and evaluate probability of sage-grouse population decline at different values of %AML_{max}. We estimated impact-control ratios based on methods modified from Conner et al. (2016). Specifically, we estimated predicted posterior distributions of population λ at HMA leks (e.g., impact leks) with %AML_{max} values of 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 times AML_{max}. These values corresponded to the majority observations of %AML_{max} at leks within our dataset, with the upper cutpoint coinciding with most recently observed %AML_{max} across Nevada. We also derived *pD* of λ at leks outside of HOAs (control leks). We developed distributions by averaging 5,000 iterations (MCMC samples) from the posterior probability distribution of each lek across all leks within and outside HOAs to account for uncertainty (variance) in the average λ at each percentile cutpoint. To estimate the probability of decrease in λ relative to controls at each cutpoint, we developed a distribution of ratios (impact:control), where 1.0 indicates an equivalent probability of increase or decrease relative to the control. After all iterations were completed, we then derived a predicted probability of decline under each defined threshold value by summing the number of iterations where the ratio was <1, divided by the number of iterations. These distributional ratios are advantageous as a post-processing technique to directly draw inference of effect size in terms of probability of declining λ at impact sites relative to controls (Conner et al. 2016). Additionally, full posterior predictions from MCMC sampling provide accurate estimates of variation for the ratios.

RESULTS

The lek count database (WAFWA 2015) contained 726 leks throughout Nevada (Fig. 1B). Of these leks, 213 (29%) overlapped with 59 HOAs and the remaining 513 (71%) did not overlap an HOA. Of the 213 leks that overlapped HOAs, 148 (69%) overlapped with 37 HMAs (63%), 61 (29%) with 19 HAs (32%), and 4 (2%) exclusively with 3 USFS WHB Territories (5%). We removed 65 leks from consideration because they occurred on private lands and horses could not be assumed present or absent. An additional 43 leks could not be used because of sparse information or lek inactivity during the study's time series. Our hierarchical SSMs thus incorporated 618 leks with usable count data, of which 193 (31%) overlapped with 55 HOAs and the remaining 425 (69%) did not. Of HOAs in modeled leks, 130 (67%) were designated as HMAs with set AML_{max}.

Latent Indicator Variable Selection

The BLISS approach identified the following predictor variables from each candidate group that we then used in our second stage SSM of sage-grouse population growth: percent sagebrush (5-km buffer), percent pinyon-juniper (5-km buffer), elevation (10-km buffer), cumulative burned area (10-km buffer), and standardized precipitation index (SPI; 12-month time lag, 10-km buffer). The horse abundance index that best explained sage-grouse population growth was abundance divided by AML_{max} (termed % AML_{max}). In addition, exponential decay functions representing proximity to springs ($\alpha = 1.28$ km, 25th percentile) and water bodies ($\alpha = 2.70$ km, 50th percentile), density dependence, and HOA (i.e., lek overlaps with any defined horse area) were included in the final model (Table S2).

State-Space Model

We obtained convergence on all model parameters ($\hat{R} < 1.1$), and the Bayesian *P*-value indicated strong goodness of fit ($P = 0.56$). Our final SSM suggested a declining population on average across all leks and years ($\hat{\lambda}$ [interquartile range] = 0.961 [0.730, 1.272]). Environmental predictors indicating strong evidence of positive influence on sage-grouse population growth (e.g., increasing λ with increasing predictor values) included elevation ($\hat{\beta} = 0.053$, $P > 0 = 1$; Fig. 2), previous 12-month precipitation at the lek (SPI; $\hat{\beta} = 0.029$, $P > 0 = 1$), and percent sagebrush ($\hat{\beta} = 0.019$, $P > 0 = 0.997$). Predictors evidencing strong negative influences (e.g., decreasing λ with increasing predictor values) included proximity to water body ($\hat{\beta} = -0.018$, $P < 0 = 0.997$) and horse %AML_{max} (effect given presence within HMA; $\hat{\beta} = -0.090$, $P < 0 = 1$). Notably, the proximity to water body effect implied reduced λ closer to water bodies because of the exponential decay transformation. Percent pinyon-juniper cover and cumulative burned area were also negatively associated with λ, with less evidence of effects ($\hat{\beta} = -0.006$, $P < 0 = 0.792$; and $\hat{\beta} = -0.002$, $P < 0 = 0.616$, respectively). We observed strong evidence for negative density-dependent feedback effects where counts were likely to decline when closer to their relative maximums, resulting in a negative influence on λ ($\hat{\beta} = -0.135$, $P < 0 = 1$). There was minimal evidence for influences of springs ($\hat{\beta} = -0.003$, $P < 0 = 0.632$), and weak evidence for an overall HOA effect after %AML_{max} was accounted for ($\hat{\beta} = -0.009$, $P < 0 = 0.762$).

Predicted λ was generally lower in HOAs ($\hat{\lambda} = 0.948$ [0.732, 1.241]), and declined further when summarized within HMAs ($\hat{\lambda} = 0.942$ [0.734, 1.225]). These declines were attributed to observed horse population sizes within HMAs being approximately 2 times AML_{max} on average during the time series ($\bar{x} = 2.30$, median = 1.92, 95% CI = 0.65–5.52), and increasing to 4.13 times AML_{max} (median = 3.61, 95% CI = 0.51–11.15) by the end of the study. Estimates from the linear mixed model of horse abundances reflected the trend across the time series for all HMAs but slightly underpredicted horse abundance for the

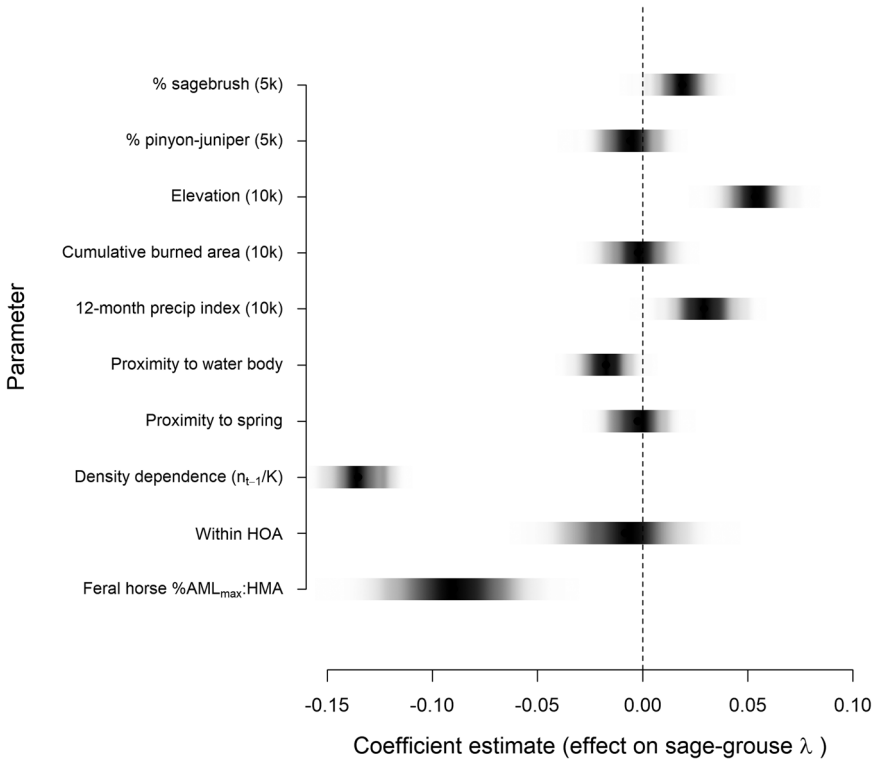


Figure 2. Estimated effects of environmental covariates with shaded 95% credible intervals used in Bayesian state-space models on annual greater sage-grouse rate of change (λ) in population abundance within Nevada and California, USA, 2005–2019. We selected scales and representations of environmental covariates using a latent indicator variable selection approach, and final representations included percent sagebrush (5-km buffer [5k]), percent pinyon-juniper (5-km buffer), elevation (10-km buffer [10k]), cumulative burned area (10-km buffer), standardized precipitation (precip) index (12-month time lag, 10-km buffer), proximity to water bodies, proximity to spring, prior year density-dependence effects (where K represents an estimate of maximum carrying capacity at each sage-grouse lek), within horse-occupied area (HOA) effect, and percent feral horse abundance relative to current maximum appropriate management level (AML_{max}) set by the Bureau of Land Management based on use rate and ecological capacity within horse management areas (HMAs).

last year (2019; Fig. 3A). Model estimates indicated that sage-grouse population $\hat{\lambda}$ decreased approximately 2.6% for every 50% increase in %AML_{max} (Fig. 3B).

Future Projections of Sage-Grouse Population Trends

Under scenario 1, we sampled from posterior probability distributions of the %AML_{max} trend model parameters to extrapolate future %AML_{max} over 15 more years. Sage-grouse populations were projected to decline by 70.9% (95% CI = 65.3–77.5%, precipitation at median; 95% CI = 45.4–90.9%, precipitation varied randomly) with 100% probability of decline by 2034 within HOAs under scenario 1 (Fig. 4). For scenario 2, in which horses reflected % AML_{max} observed in the study, our model predicted a 56.9% decrease (95% CI = 54.5–69.5%, precipitation at median; 95% CI = 11.2–87.5%, precipitation varied randomly) within HOAs, with 98% probability of decline. For scenario 3, with horses held to their current AML_{max}, we predicted an increase of 12.2% (95% CI = −25.9–1.8%, precipitation at median; 95% CI = −80.7–48.6%, precipitation varied randomly) within HMAs, with 62% probability of increase. For control areas, outside of HOAs, predictions indicated declines over 15 years of 21.2% (95% CI = 41.2–90.4%, precipitation at median; 95% CI = −45.0–65.6%, precipitation varied randomly), with 75% probability of decline.

Post Hoc Impact-Control Analysis

Our *post hoc* impact-control analysis revealed that current AML_{max} (e.g., horse abundance equal to established AML_{max}) resulted in little evidence that sage-grouse population λ for leks within HMAs was lower than control leks (outside HOA) when free-roaming horse populations were set at AML_{max} (i.e., 100% AML_{max}; Fig. 5A). Specifically, models predicted a 21% probability of population λ decline relative to controls at AML_{max} under this condition. At 1.5 times AML_{max}, the probability of decline increased to 46%. When horse populations were set to 2 times the AML_{max}, the probability of sage-grouse population λ decline was predicted to be 76% relative to controls, and at 2.5 and 3 times the relative AML_{max}, probabilities of decline increased to 97% and nearly 100%, respectively (Fig. 5).

DISCUSSION

Our study revealed new findings about adverse effects of horses on sage-grouse populations, especially where horse population estimates exceeded AML_{max}. Free-roaming horse populations have continued to grow (~20% annually; BLM 2020*a*) and have exceeded AML_{max} settings across most managed HMAs. Our models predicted a 70.9% reduction in sage-grouse numbers within HOAs by 2034 across approximately 4,500,000 ha of sage-grouse habitat in Nevada and northeastern California, assuming horse populations continue to

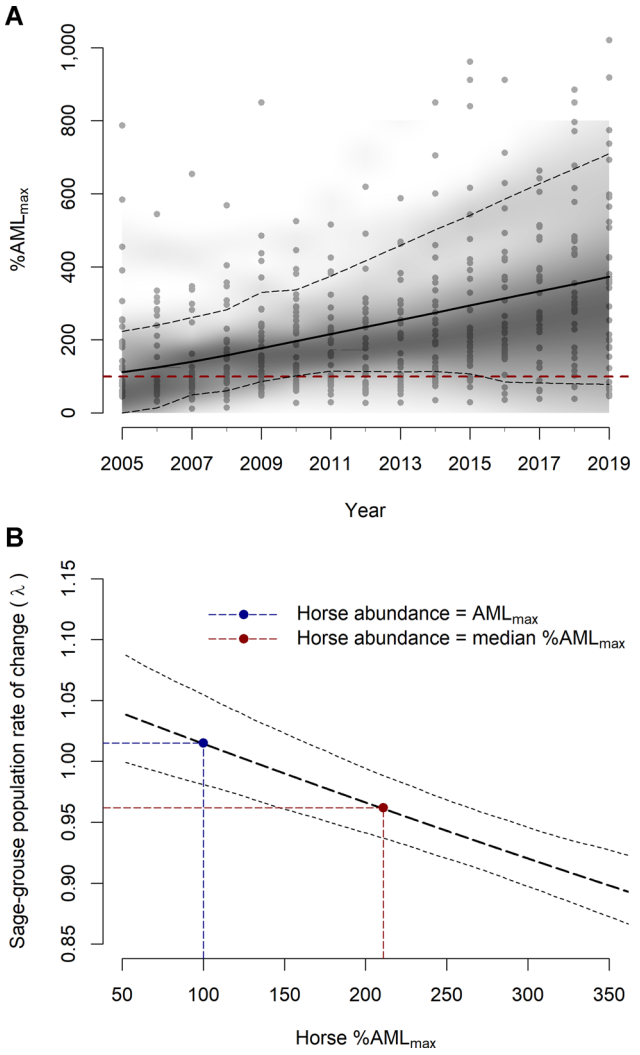


Figure 3. A) Trends in horse abundance relative to maximum appropriate management level (%AML$_{max}$) estimated from a linear mixed model at Horse Management Areas (HMAs) intersecting sage-grouse leks in Nevada and California, USA. The red dashed line indicates the defined maximum AML (100% AML$_{max}$), and black dotted lines above and below the main trend line show the 2.5th and 97.5th percentiles of the observed horse abundances relative to AML$_{max}$. B) Estimated effect of percent horse abundance over AML (%AML$_{max}$) with 95% credible intervals (black dotted lines) used in Bayesian state-space models on annual greater sage-grouse population rate of change (λ) within Nevada and California, USA, 2005–2019. The standardized linear effect is transformed to the original scale of %AML$_{max}$. Dashed vertical lines represent λ when horse population estimates are predicted to be at AML$_{max}$ (blue), as compared to the median estimated AML$_{max}$ across HMAs during the study (red).

increase at their current rates. If horse population growth was halted entirely, and numbers remained close to those observed during the previous 15 years, our model predicts a reduction in sage-grouse populations by 56.9% in areas affected by horses. Steep declines in sage-grouse populations are projected in this scenario because, as of 2020, horse populations were well above AML$_{max}$. Thus, sage-grouse populations are likely to experience continued decline in areas with overabundant horses. If horse herd sizes could be maintained at AML$_{max}$, an increase of 12.2% was predicted, suggesting there is a potential for rebound where sage-grouse populations have previously declined.

As recommended by the National Research Council (2013), we provide a novel example of using sage-grouse as an indicator species within sagebrush ecosystems (Hanser et al. 2011) to validate AML$_{max}$, which could help assist with an adaptive management framework that consists of multiple-use mandates intended to balance the presence of free-roaming horses with managed livestock and native sagebrush-dependent species. Successful adaptive management is contingent on the ability to evaluate outcomes that help validate management actions and suggest adjustments to management decisions (Schreiber et al. 2004). Although our study lends support to current AML$_{max}$ settings as a whole, well-designed local monitoring programs of other ecological responses such as the functionality of riparian systems, or the abundance and trends of plants or other key wildlife indicator species, will help ensure adequate rigor is built into validating and adjusting management decisions.

Spatiotemporal variation in %AML$_{max}$, including substantial increases within HMAs over 15 years, provided an opportunity to establish empirical links between variation in sage-grouse population λ and horse abundance relative to AML$_{max}$, and also facilitated evaluation of ecological thresholds based on modeled predictions. Model support for %AML$_{max}$ as a covariate for sage-grouse population λ indicated a decline in λ as horse abundance increased above AML$_{max}$. Current values set for AML$_{max}$ seemed adequate, as predicted sage-grouse population λ was similar within treatments and controls when horse population estimates were equal to or below AML$_{max}$, and also because λ was lower in treatments than controls when AML$_{max}$ was exceeded. The metric of %AML$_{max}$ was an informative predictor of sage-grouse population trends, which can likely be attributed to the establishment of AML$_{max}$ from information concerning the capacity of rangelands to meet target utilization rates and other factors (BLM 2010). For the purposes of this study, %AML$_{max}$ may be considered an overgrazing index under the assumption that AUMs of cattle did not change as horses increased within HMAs.

Previous research on ecological effects of horses has largely focused on vegetation and soils (Davies and Boyd 2019), but few studies have addressed effects on wildlife (Eldridge et al. 2020). Although interactions between horses and other ungulates have been investigated (Berger 1985, Ostermann-Kelm et al. 2008, Perry et al. 2015, Gooch et al. 2017, Hall et al. 2018), the effects to sensitive species are not well-understood (Cherubin et al. 2019). Our study corroborates hypothesized links between horses and sage-grouse populations (Beever and Aldridge 2011) by demonstrating reductions in sage-grouse population λ in response to increases in horse abundances relative to AML$_{max}$ settings. It is important to recognize that our response variable λ was largely a product of multiple population demographic rates related to reproduction (e.g., nest and chick survival) and adult survival (Taylor et al. 2012). Thus, it is logical to expect negative effects on sage-grouse population dynamics through indirect pathways associated with degradation of sage-grouse habitat across different demographic rates (Beever and Aldridge 2011, Davies

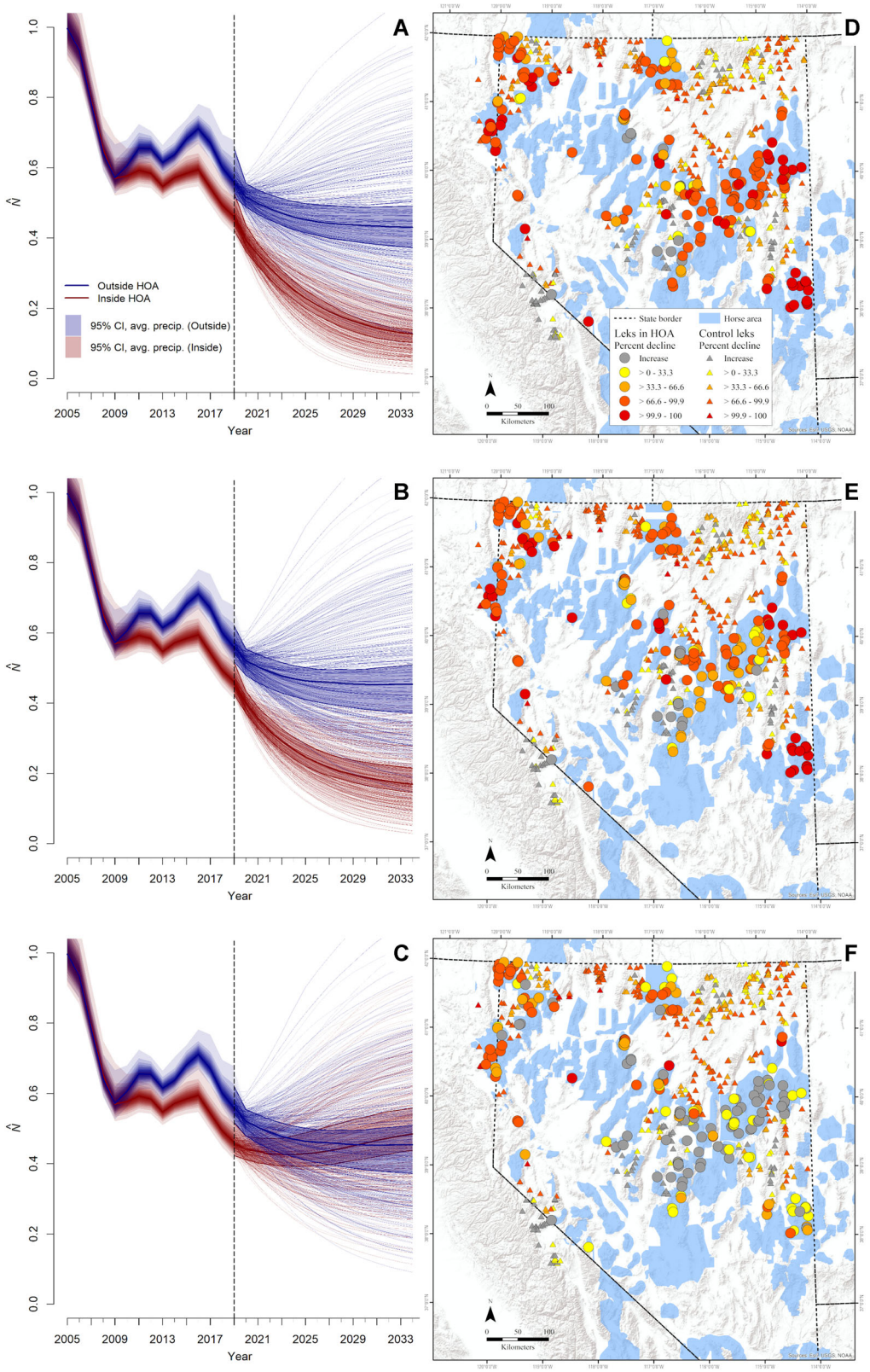


Figure 4. Bayesian state-space modeled estimates of annual predicted apparent abundance ($\hat{N}$) for greater sage-grouse populations within and outside horse-occupied areas (HOAs) in Nevada and California, USA, 2005–2019 (shaded areas represent samples from posterior distribution). We derived predictions of $\hat{N}$ during 2020–2035 from estimated parameters based on 3 scenarios: A) growth rate of horses continues unabated, B) growth rate of horses is neutralized but numbers remain constant, and C) numbers of horses are held at maximum appropriate management levels (AML_{max}). Shaded areas in 2020–2034 represented $\hat{N}$ under median (avg.) precipitation (precip.; e.g., $\%AML_{max}$ effect) and thin lines represented variation in precipitation sampled from its full distribution (e.g., $\%AML_{max}$ effect + environmental stochasticity), while other model parameters were held constant. Maps D–F illustrate spatial predictions of percent change in $\hat{N}$ (median precipitation) for sage-grouse under the same 3 scenarios, respectively.

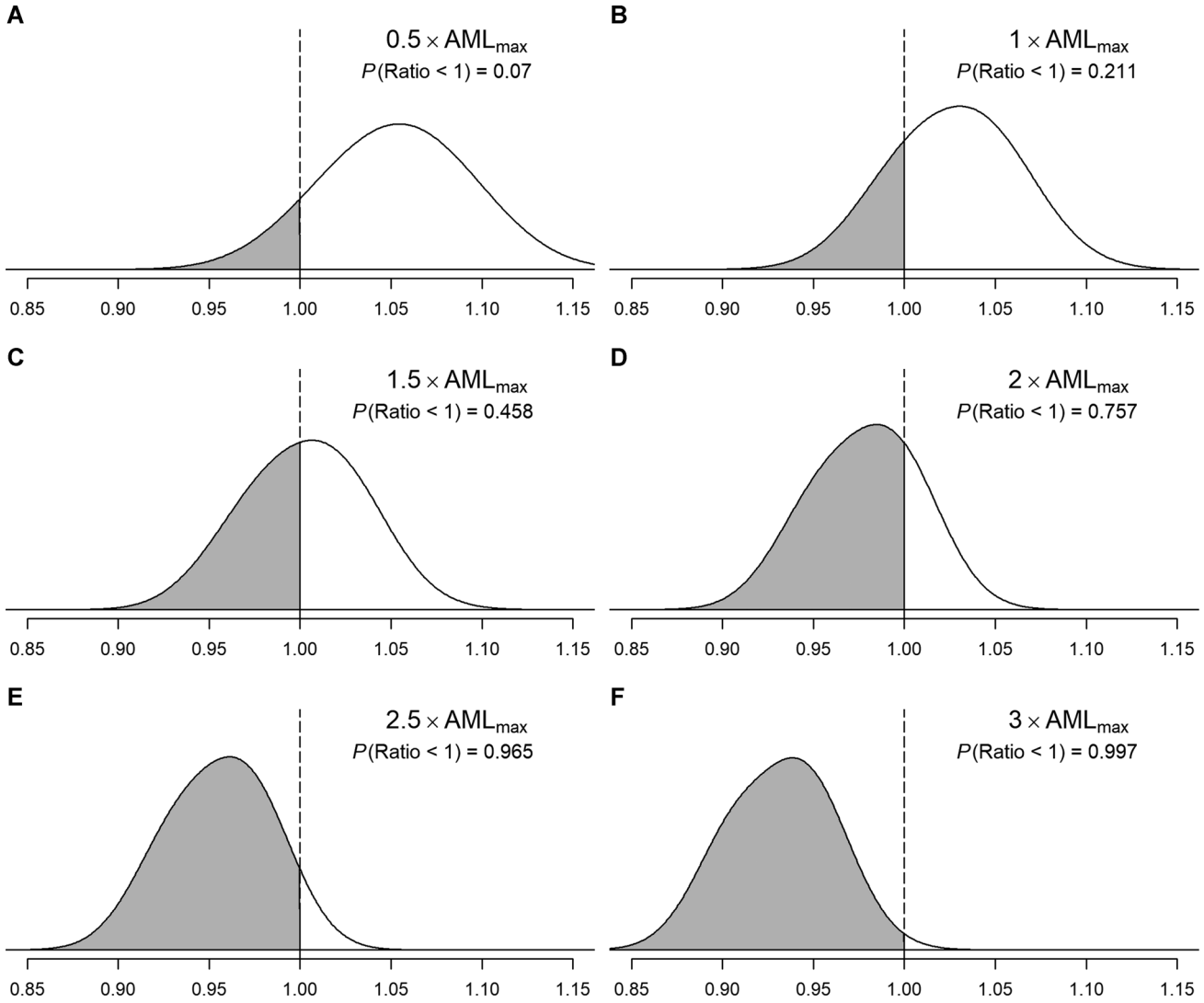


Figure 5. Ratio of greater sage-grouse population rate of change between impact (horse-occupied areas) and control (outside horse-occupied) leks in Nevada and California, USA, 2005–2019. Ratios were estimated at 6 levels of horse abundance relative to maximum appropriate management level (AML_{max}): A) 50% of current AML_{max}, B) AML_{max} (100%), C) 1.5 times AML_{max} D) 2.0 times AML_{max}, E) 2.5 times AML_{max}, and F) 3.0 times AML_{max}. The area under the curve below a ratio of 1.0 represented the probability of sage-grouse reduced population growth relative to control areas, which were assumed to have very few or no horses.

et al. 2014). Although identification of specific demographic mechanisms influencing changes in sage-grouse λ was beyond the scope of our study, horses likely affect multiple population vital rates such as nest and chick survival, leading to cumulative effects across life stages that can lead to reduced sage-grouse population growth and, ultimately, population viability (Taylor et al. 2012).

The importance of overstory shrub cover and density for sage-grouse is arguably the most consistent habitat component to influence nest survival in semi-arid environments of the Great Basin (Gregg et al. 1994, Kolada et al. 2009, Coates and Delehanty 2010, Coates et al. 2017). This habitat component provides concealment from nest predators (Schroeder and Baydack 2001, Coates and Delehanty 2010), which are responsible for the majority of nest failures (Moynahan et al. 2007, Lockyer et al. 2015). Grazing by free-roaming horses directly reduces shrub density (Davies et al. 2014, Beever and Brussard 2000) and continuity of shrub canopy (Beever et al. 2008). In one study, shrub canopy cover was 1.1–1.9 times greater in exclosures where free-roaming horses were removed (Beever et al. 2008), and this loss of shrub cover was attributed mainly to rubbing and trampling. Decreased shrub cover likely increases the ability of visually cued predators such as common ravens to find sage-grouse nests (Coates and Delehanty 2010), which is concerning given that raven abundance has also been increasing precipitously within the Great Basin since the 1970s (Sauer et al. 2017). A study in northeastern Nevada reported that a 1% decrease in shrub cover increased the probability of nest predation by ravens by 7.5% (Coates and Delehanty 2010). This may not be unique to the western United States because researchers of ground-nesting birds in Argentina reported that horse-grazed areas exhibited higher egg predation rates than horse-excluded areas (Zalba and Cozzani 2004).

Another important nest habitat component is structure and composition of herbaceous understory cover (Gregg et al. 1994, Doherty et al. 2010). Although the effects of herbaceous understory on nest survival may vary across sage-grouse range (Smith et al. 2020), the role of perennial grasses and forbs may be contingent on variation in primary productivity across the landscape (Coates et al. 2017). For example, grass height becomes more important in drier and warmer sagebrush environments where grasses are typically shorter and sagebrush shape is columnar (Coates et al. 2017). Additionally, relatively tall grasses and forbs immediately near the nest and within the shrub interspace might help conceal females from predators as they move to and from their nests during incubation recesses (Coates et al. 2008). Feral horse diet consists primarily of graminoids (80–95%; Hanley and Hanley 1982, Scasta et al. 2016) and areas occupied by horses have shorter perennial grasses with reduced cover relative to exclosures (Beever et al. 2008, Baur et al. 2018). Furthermore, sage-grouse tend to avoid nesting in areas with annual invasive grasses (Lockyer et al. 2015), and propagation and dispersal of invasive grasses by horses through intake and subsequent excretion of seeds (King et al. 2019) may decrease habitat suitability for nesting. Site-level mechanistic research that focuses on interactions among free-roaming horses, vegetation degradation, and nest predation by ravens is needed to identify proximate and ultimate causes of nest failure.

During the sage-grouse brood-rearing period, specifically later months in summer, riparian vegetation communities are important resources for chicks (Casazza et al. 2011, Gibson et al. 2016). These areas constitute a small proportion of western lands, but are some of the most productive and ecologically important areas of sagebrush ecosystems (Svejcar 1997, Donnelly et al. 2018). Feral horses within the Great Basin often relocate to higher elevations during the brood-rearing period from late spring to early fall (Pellegrini 1971, McInnis 1985) seeking riparian areas (Crane et al. 1997) because of the relatively higher water intake needs of horses compared to other ungulates (Groenendyk et al. 1988). They often concentrate at these sites throughout the day, especially during periods of high ambient temperatures and low precipitation (Hall et al. 2016). Grazing by horses can have severe effects on upland riparian areas (Boyd et al. 2017, Kaweck et al. 2018) by reducing the height of herbaceous cover, increasing bare ground, selective consumption, trampling of plants and soil, and the redistribution of nutrients and seeds on the landscape (King et al. 2019). In xeric regions of the Great Basin, sage-grouse select sites with greater perennial forb cover, also favoring taller forbs, increasing survival rates (Coates et al. 2017). These plants meet dietary needs (Sveum et al. 1998) and help to conceal chicks from predators while foraging (Casazza et al. 2011). Furthermore, detrimental effects of horses on hydrologic cycles of springs and riparian areas (Kaweck et al. 2018) limit water availability for sage-grouse, particularly chicks in late-summer habitat (Casazza et al. 2011). A recent study indicated that equids can dig wells to groundwater in arid environments to access water and, thereby, increase density of water features on the landscape for other wildlife species, and stimulate growth of riparian trees (Lundgren et al. 2021). But any benefits from well-digging by horses likely do not compensate for the substantial adverse effects of horses on riparian areas (Boyd et al. 2017, Kaweck et al. 2018), and such wells likely provide negligible to no benefit to sage-grouse. For example, water bodies included in our models were largely stock ponds and impoundments. Predicted negative effects of these features may be related to such areas attracting horses, livestock, and other species that might disturb or prey on sage-grouse, which likely also pertains to groundwater wells created by horses.

Although indirect effects from habitat degradation to specific vital rates offer the most logical explanation for reduced sage-grouse population λ, recent evidence also indicates that horses directly disrupt sage-grouse breeding behavior at lek sites (Muñoz et al. 2021). Specifically, the probability of sage-grouse being absent from lek sites was greatest (75.4%) when horses were present on leks relative to cattle and native ungulates. Because sage-grouse mating success is partly determined by the amount of time they spend displaying on the lek (Gibson and Bradbury 1985), disruption by feral horses potentially reduces reproductive activity. The frequency and scale at which this effect occurs is not well known, and research that disentangles potential bias in lek counts from effects on demographic rates related to disturbance would be beneficial.

In addition to strong evidence of negative horse effects, other covariates in our model corroborate a growing body of literature that sage-grouse population declines are attributed to cumulative and concomitant effects. Horses serve as another factor that can negatively influence sage-grouse populations, adding to other correlates of sage-grouse decline in this study region. For example, sagebrush habitat within the Great Basin has been declining since European settlement, and many native bunchgrasses and forbs have been replaced by introduced perennial and invasive annual grasses (Morris and Rowe 2014). Further exacerbating the loss of sagebrush and native vegetation components, wildfire destroys sagebrush and facilitates invasion of annual grasses that provide fine fuels such as cheatgrass (Chambers et al. 2014), which leads to an accelerated feedback loop of larger and more frequent fires (Brooks et al. 2015), with potentially negative responses by sage-grouse to wildfire (Coates et al. 2016*b*, Foster et al. 2019). Additionally, our model supported the conclusion that population λ was reduced when pinyon-juniper increased close to leks. One feasible explanation is that pinyon-juniper leads to greater movements by sage-grouse, which increases risk of predation (Prochazka et al. 2017) and leads to lower survival rates (Coates et al. 2017). Consequently, declines in sage-grouse population λ within and outside of HOAs were likely influenced by a combination of cumulative effects between several factors and the degree to which feral horses were above AML_{max}.

There were positive effects on sage-grouse λ in response to increased sagebrush cover, increasing elevation, and

increasing precipitation expressed as standardized precipitation index with a 12-month time lag. As expected, sage-grouse population λ was closely linked to sagebrush cover within 5 km of leks, which corroborates results from habitat suitability models for leks (Knick et al. 2013) and across individual sage-grouse at life stages in the Great Basin (Coates et al. 2017). Sage-grouse move to mesic areas at higher elevations during summer to access increased forb availability (Patterson 1952, Klebenow and Gray 1968, Connelly et al. 2004) that is directly linked to brood survival (Casazza et al. 2011, Coates et al. 2017). Lower elevation regions are more susceptible to invasion by cheatgrass (Chambers et al. 2007), are more readily grazed by cattle (Ganskopp and Vavra 1987), and often have greater raven occupancy and density (O'Neil et al. 2018, Coates et al. 2020). Lastly, independent of other environmental factors, precipitation can be a major influence of sage-grouse demographic rates by promoting plant production (Blomberg et al. 2012, Guttery et al. 2013). Because feral horse effects appear greatest in more arid environments where water is scarce (Eldridge et al. 2020), years with greater annual precipitation may mitigate the effects of horses on sage-grouse by diluting horse visitation to higher elevations and riparian areas used by sage-grouse or by masking the effects of horse herbivory through increased plant productivity. Additionally, our models corroborate findings of others that rate of change in sage-grouse populations exhibits strong negative density dependence (Garton et al. 2015, Coates et al. 2016*b*, Edmunds et al. 2018).

Our analysis did not explicitly model livestock (e.g., cattle) and large native ungulates as covariates, primarily because of challenges associated with compiling quality spatial data. We assumed that the amount of grazing pressure by these animals, particularly cattle, arises from the same distribution inside and outside areas occupied by free-roaming horses. We surmise that this assumption was met considering approximately 82.0% and 83.3% of leks within areas occupied by horses and those not occupied, respectively, were located within grazing allotments. We only expected competition for forage between cattle and horses, which primarily consume graminoids year-round, whereas smaller native ungulates such as pronghorn and mule deer (*Odocoileus hemionus*) primarily consume, browse, and move more freely across the landscape (Hanley and Hanley 1982, Scasta et al. 2016, King and Schoenecker 2019). Thus, our results should be interpreted as influences of $\%AML_{max}$ given current AUMs allocated to cattle. Research that investigates the influences of reducing cattle AUMs (e.g., lessening cattle grazing pressure) on estimated changes in the effects of $\%AML_{max}$ would be helpful. Cattle-induced effects on the landscape likely differ from horse-induced effects because of fundamental differences in physiology and behavior between the species (Beever 2003) and the year-round grazing pressure that free-roaming horses apply (Kaweck et al. 2018).

Multiple obstacles restricted our ability to compile precise information on horse occupancy and spatial distribution throughout our study area. For example, the horse abundance estimates we used for HMAs were likely underestimated because of failure to account for imperfect detection (National Research Council 2013, Schoenecker et al. 2018). If true, this should not influence estimated effects of $\%AML_{max}$ because this variable was an index of abundance above a set capacity point (AML_{max}). Because methodology used to determine AML_{max} does not consider imperfect detection, then estimates of $\%AML_{max}$ may in fact be lower than true values. For this reason, it would be valuable to know the extent to which true horse abundance exceeds estimated horse abundance to provide better calibration between AML_{max} and horse abundance estimates, but this should have little or no influence on the outcomes of this research. Survey methods that BLM has adopted since the report from the National Research Council (2013) appear to have relatively low bias in estimated herd sizes (Lubow and Ransom 2016). Additionally, lack of spatial movement data for free-roaming horses (Collins et al. 2014) meant that we could not account for horses moving outside of HOAs and into nearby control areas, which could introduce estimation error. Given the broad-scale scope of our study, potential error associated with movement of horses and horses occupying areas outside of HOAs was likely negligible. Finally, we had to exclude leks on tribal and private lands to reduce error in areas where horse data were not available, so inferences about horses and the influence of private and tribal lands is limited. In Nevada, because these lands account for a relatively small proportion of the entire study area, such error is likely negligible.

Interpretation of model projections is not without important considerations. First, because model projections did not consider sage-grouse habitat recovery times with simulated reductions in horses, and explicitly model mechanistic effects of horses to sage-grouse habitat, it is likely that predictions of immediate projected improvements in sage-grouse numbers derived from scenario 3 (i.e., horse numbers are reduced to and maintained at AML_{max} for each HMA) were optimistic. For example, sage-grouse habitat degradation attributed to overabundant horses, such as detrimental effects to riparian areas (Boyd et al. 2017, Kaweck et al. 2018), will likely require multiple years to recover following reduction in herd sizes and ultimately reverse negative effects on sage-grouse populations. Additionally, projected increases of sage-grouse numbers under the third scenario did not account for changes in other environmental factors influencing sage-grouse populations. For example, sage-grouse will likely still decline with additional losses of sagebrush as a result of continued increase in cumulative burned area associated with acceleration in wildfire-invasive grass cycles (Chambers et al. 2014, Coates et al. 2016*b*) and elevated nest predation from growing populations of ravens (Sauer et al. 2017, Coates et al. 2020*b*). Lastly, sage-grouse population abundance fluctuates with precipitation (Coates et al. 2018) and, thus, our predictive posterior distributions broaden as years progress to fully account for this environmental stochasticity.

In conclusion, we found sage-grouse populations in Nevada and northeastern California are declining at a rate

of approximately 3.9% annually ($\hat{\lambda} = 0.961$) with strong evidence that declines are associated with horse abundances that exceed the established AML_{max} for HMAs. These data garnered substantially more support for $\%AML_{max}$ as a predictor variable than other types of horse abundance indices on sage-grouse population λ, which suggests that effects are a likely result of overgrazing by horses that damage sage-grouse habitat. Exceeding current AML_{max}, or adjusting AML_{max} to higher values within the model, resulted in clear evidence of negative effects to sage-grouse population λ. In contrast, model predictions indicated that when horse populations did not exceed current AML_{max} values, there was no significant evidence of declines in sage-grouse population λ when compared to areas where horses were assumed absent. Sagebrush ecosystems are dynamic, undergoing changes in vegetation function, composition, and structure based on a variety of disturbances (e.g., wildfire, invasive plants) and different climatic conditions (e.g., drought), which affect the ecosystem's resilience (ability to recover) and resistance to invasive plants (Chambers et al. 2014). These processes necessitate periodic re-evaluation and modifications to AML_{max} to help prevent horses from exceeding the capacity of the ecosystem under these varying conditions. Our results indicate a need for appropriate science-based calculations of AML_{max} with continuous validation as additional ecological information is obtained. Studies that focus on disentangling use rates between horses and livestock, while linking grazing patterns to sage-grouse seasonal habitat and population vital rates, would provide valuable mechanistic pathways to help refine AML_{max} settings. Recent developments in telemetry of free-roaming horses have set the stage for investigations on movement patterns, habitat preferences, and resource uses that can address important research questions and help management and policy decisions at finer spatial scales (Collins et al. 2014, Schoenecker et al. 2020).

MANAGEMENT IMPLICATIONS

Effective management strategies for multiple-use landscapes with feral horse populations are likely to be those that target, reach, and hold horse abundance below or at AML_{max}. According to our models, this would neutralize negative effects of overabundant horses to sage-grouse populations, allowing for potential positive growth rates of sage-grouse assuming other threats were not increasing. Sage-grouse lek count data can be a useful environmental indicator for validation of AML_{max}. State-space population modeling frameworks can be periodically replicated by leveraging existing collaborations for lek data collection by state and federal agencies, universities, and private organizations. Although this SSM framework can be improved to help guide management decisions at finer spatial scales, it may not encompass the requirements of other key indicator species that may exhibit different responses to horse densities. Improved monitoring and information that helps to capture the broader community-level effects of horses will be key to validating and refining the designation of horse AML_{max} for the purpose of balancing multi-use landscape needs.

ACKNOWLEDGMENTS

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the United States Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank the countless biologists and technicians who counted sage-grouse leks over the course of 15 years and the Nevada Department of Wildlife and California Department of Fish and Wildlife for administering the lek count databases. Important geographical information system and administrative support were provided by K. A. Bollens and M. P. Chenaille. We thank K. McGowan, K. M. Andrle, and all members of the Sagebrush Ecosystem Council. Special thanks to P. C. Griffin, S. P. Espinosa, M. A. Ricca, S. J. Dettenmaier, B. E. Brussee, T. S. Kimball, and A. K. Miles for constructive comments on previous manuscript drafts. We thank K. A. Krause and K. L. Prentice for discussions and logistical support. This study was conducted to help address research needs identified through a National Research Council established for the BLM Wild Horse and Burro Program in 2013. Funding for this work was provided by federal partners as part of the Results Oriented Grazing for Ecological Resiliency collaborative between ranchers, organizations, the university, and state and federal agencies. Additional funding was provided by BLM and the United States Geological Survey Ecosystems Mission Area.

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Associate Editor: Sarah King.

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ECOGRAPHY 28: 37–48, 2005

Complementarity of epi- and endozoochory of plant seeds by free ranging donkeys

Martine Couvreur, Eric Cosyns, Martin Hermy and Maurice Hoffmann

Couvreur, M., Cosyns, E., Hermy, M. and Hoffmann, M. 2005. Complementarity of epi- and endozoochory of plant seeds by free ranging donkeys. – Ecography 28: 37–48.

Epizoochory and endozoochory are well-recognized long-distance seed dispersal mechanisms, yet their relative importance has hardly been studied before. Here, epi- and endozoochory were compared on donkeys foraging in a species-rich 100 ha coastal dune ecosystem, through in vitro germination of zoochorous material obtained by fur brushing and dung collection. We identified 6675 seedlings of 66 plant species, covering 20% of the species recorded in the study area. Of the 66 species, only 16 occurred in both epi- and endozoochory samples, demonstrating the complementarity of both dispersal mechanisms. The species composition in the zoochory samples reflected a strong seasonality, and seedling numbers were partly correlated with species abundance in the study area. The non-zoochorously dispersed species in the study area differed from the zoochorous species in seed size and weight, plant height, life span, dispersal strategy and seedbank persistence. Dispersal-relevant plant traits were used to derive dispersal-functional plant types for all species in the study area. Epizoochory showed to be more specific than endozoochory and was associated with a more narrow range of dispersal-functional plant types.

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Long-distance seed dispersal mechanisms have recently received much attention, especially in the context of understanding and predicting plant migration (Cain et al. 1998, Clark et al. 1998, Higgins and Richardson 1999, Pakeman 2001). The relevance of seed dispersal research has become increasingly clear given the problem of plant invasions, limited dispersal in fragmented habitats (Poschlod and Bonn 1998, Higgins et al. 2003), and the necessary plant migrations in response to global change (Watkinson and Gill 2002). Also the insight that seed limitation is a major ecological constraint in several ecosystems (Turnbull et al. 2000, Zobel et al. 2000, Dalling et al. 2002, Foster and Tilman 2003, Verheyen et al. 2003) has orientated research efforts towards dispersal.

Zoochory, the external and internal dispersal of plant seeds by animals, is an important dispersal mechanism. Epizoochory, on the one hand, is mainly associated with adhesive seed adaptations facilitating attachment to mammalian fur, although also species adapted to other dispersal modes or without obvious adaptations disperse epizoochorously (Fischer et al. 1996, Heinken and Raudnitschka 2002, Couvreur et al. 2004a, b, c). Endozoochory, on the other hand, covers the consumption of fleshy fruits by frugivores (Debussche and Isenmann 1989, Amico and Aizen 2000, Tabarelli and

Accepted 14 September 2004

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ISSN 0906-7590

Peres 2003) and the consumption of seeds of grasses and herbs by herbivorous mammals (Janzen 1984, Welch 1985, Gardener et al. 1993, Malo and Suárez 1995b, Pakeman et al. 1998, Heinken et al. 2001, Cosyns 2004, Cosyns et al. 2004). Edible vegetative plant parts (Janzen 1984) and seed resistance to digestion (Pakeman et al. 2002) are hypothesized to be adaptations to endozoochory by large herbivores.

Both epi- and endozoochory are key factors determining plant distribution (Welch 1985, Malo and Suárez 1995a, Fischer et al. 1996, Poschlod and Bonn 1998, Pakeman et al. 2002). Moreover, they may provide a means of "directed dispersal" for many species relying on disturbed habitats, which are frequented and even generated by herbivores through feeding, trampling or wallowing (Janzen 1984, Wenny 2001).

Recently, an increasing number of attempts to model zoochorous dispersal has been undertaken (Pakeman 2001, Higgins et al. 2003, Vellend et al. 2003). Yet, basic and reliable knowledge of which plants are dispersed zoochorously and which factors and plant traits direct zoochorous dispersal is still very limited. Several authors have therefore explicitly stressed the need for more data on the influencing factors of zoochory (Higgins and Richardson 1999, Bullock et al. 2002, Levin et al. 2003). Studies which fill this gap are scarce, especially comparative studies of epi- and endozoochorous dispersal. Both mechanisms have been studied simultaneously on sheep in calcareous grasslands (Fischer et al. 1995), on Galloway cattle in moorland pastures (Stender et al. 1997), and on wild boar and roe deer in a forest ecosystem (Heinken et al. 2002). However, the additive and/or complementary effects of epi- and endozoochory, as well as the role of dispersal-functional plant traits in facilitating epi- or endozoochory, remain largely unexplored.

In this paper, we compare epi- and endozoochorous seed dispersal by donkeys grazing in a species-rich coastal dune ecosystem. We test the following specific research hypotheses: 1) Different plant species are dispersed by epi- and endozoochory. 2) The species abundance in the study area influences the species abundance in the zoochory samples. 3) Morphological and ecological plant traits relevant for dispersal differ between species dispersed by zoochory and species not dispersed by zoochory.

Material and methods

Study area

The study was carried out in the coastal dune nature reserve "Houtsaegerduinen" (100 ha), in the west of Flanders, Belgium (51°05′N, 2°35′E). The variation in abiotic conditions and the historical land use in this coastal dune system led to a high plant species richness and a wide range of plant communities. Although the dune landscape is dominated by *Hippophae rhamnoides* and *Ligustrum vulgare* shrubs, grassland covers at least one third of the area. Part of the grassland is scattered within the scrub as small and mostly species poor remnants of dune grassland or as species poor *Calamagrostis epigejos*–*Arrhenatherum elatius* dominated patches, which established after scrub degradation. Flowering and fruiting of the plant species is concentrated from April to October. Six donkeys were released in the study area in 1997 for nature management purposes; the herd counted 15 animals at the time of data collection.

Data collection and treatment

The zoochory samples were collected in four different time periods between June and October 2000: early summer (9 June–19 July), mid-summer (20 July–19 August), late summer (20 August–19 September) and early autumn (20 September–19 October). In the case of epizoochory, 41 samples were collected. Respectively 8, 11, 15 and 7 donkeys were sampled in each of the four time periods, by brushing the entire fur of each individual with a very fine horse brush during 15 min. In the case of endozoochory, the number of sampled donkeys was 4 in early summer, and 8 in each of the three other periods. For practical reasons, the dung of two donkeys was pooled to one sample with a volume of 2.5 l, resulting in 28 sampled donkeys, pooled in 14 samples. Freshly deposited excrements were used, hereby avoiding the lowermost dung part to prevent contamination with seeds of underlying plants or from the soil seedbank.

In the laboratory, the samples were prepared for the seedling emergence method (Roberts 1981, Ter Heerdt 1996). The excess of hair was carefully removed from the dry epizoochory samples, while the endozoochory samples were air-dried in a greenhouse, then stored for two weeks at 4°C (without imbibition of the seeds), and subsequently softly homogenized in a Retsch mill (type SK 100) to allow easy spreading. All samples were sown in trays with sterilized potting soil, and kept in laboratory conditions with a daily light-exposure of 16 h, daily watering and occasional soil disturbance in order to light-expose buried seeds. During six months, species and seedlings were recorded, and immediately removed to prevent competition and flowering. Unrecognizable seedlings were grown separately until identification was possible. After six months, the epizoochory samples were stratified for 2 months at 4°C in imbibed conditions, after which the germination cycle was prolonged for another three months. However, no new species emerged during this second germination period.

The abundance of all plant species in the study area was recorded on several occasions between 1990 and 2000, using Tansley scaled ordinal abundance estimates for all species in the entire study area, in combination with percentage cover estimates in 1 m^2 quadrats. Plant species nomenclature follows Lambinon et al. (1998).

Data analysis

First, to explore overall differences in epi- and endozoochorous species composition, rank-abundance diagrams of the species dispersed by epizoochory and by endozoochory were designed. In addition, the log-transformed dataset of all zoochory samples together was used for Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980), using the program CANOCO 4.5 (ter Braak and Smilauer 2003). The sample-scores on the first four DCA-axes were then Spearman rank correlated (Siegel and Castellan 1988) with the date of sampling. The same ordination and correlation procedure was also used for the epizoochory and endozoochory samples separately.

Secondly, the species' abundance in the study area was Spearman rank correlated with the number of seedlings in the samples. This was done for the species in the combined "zoochorous" samples ($n = 66$), the species exclusively in the epizoochory samples ($n = 13$), the species exclusively in the endozoochory samples ($n = 37$), and the species in both epi- and endozoochory samples ($n = 16$), respectively.

Thirdly, morphological and ecological plant traits relevant for dispersal (Table 2, Appendix 1), were compared between a) species exclusively in epizoochory samples, b) species exclusively in endozoochory samples, c) species in both epi- and endozoochory samples, d) species in study area but not in zoochory samples. For this purpose, Kruskal Wallis tests and multiple comparisons (Siegel and Castellan 1988) were used for the continuous and ordinal variables, and Pearson χ^2 association tests (Siegel and Castellan 1988) for the categorical variables. All traits but plant height, strategy of dispersal and seedbank persistence (derived from Grime et al. 1988) originated from the BIOLFLOR database (Klotz et al. 2002), an elaborate database on biological and ecological traits of vascular plants in Germany.

Fourthly, all species in the study area were grouped into dispersal-functional plant types. These plant types were derived from cluster analysis, based on dispersal-relevant plant traits (Table 3), using Gower's Similarity Coefficient and the Sum of Squares method in the program Clustan Graphics 5.08 (Anon. 2001). The emergent clusters were tested for differences in these traits, using Kruskal Wallis tests with multiple comparisons for the continuous and ordinal variables, and Pearson χ^2 association tests for the categorical ones. The clusters were subsequently named by a dispersal-functional plant type, on the basis of their cluster profiles. Finally, the number of species identified in the samples of a) exclusively epizoochory, b) exclusively endozoochory and c) both epi- and endozoochory, was used to link the dispersal-functional plant types with epi- or endozoochorous dispersal. To check whether the species abundance in the study area, which might influence the probability of zoochorous dispersal, differed between the different clusters, a Kruskal Wallis test with multiple comparisons was used. All statistical analyses were performed using the program SPSS 10 (Anon. 1999), unless mentioned otherwise.

Results

Species composition

From all samples together, 6675 seedlings of 66 plant species germinated, covering 20% of all species in the study area (Appendix 1, 2). The endozoochory samples contained more species and seedlings, and had a higher diversity than the epizoochory samples (Fig. 1). The most abundantly germinating species were *Urtica dioica* (70% of the seedlings in the endozoochory samples), *Cynoglossum officinale* and *Galium aparine* (41 and 31% of the seedlings in the epizoochory samples, respectively). The epizoochory samples contained relatively more grasses than the endozoochory samples (Appendix 1). Of the 66 species, 16 occurred in both epi- and endozoochory samples, 13 were exclusively present in the epizoochory samples and 37 only in the endozoochory samples.

The dissimilarity in species composition between the epi- and endozoochory samples was clearly reflected in

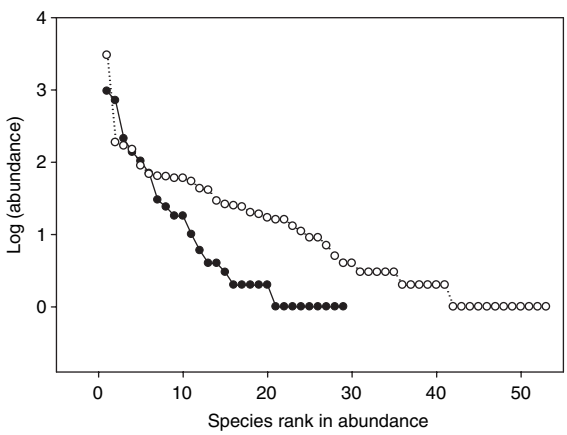


Fig. 1. Rank-abundance diagrams of dispersed plant species by epizoochory (filled symbols) and endozoochory (empty symbols). Species in each group are ranked from commonest (left) to rarest (right).

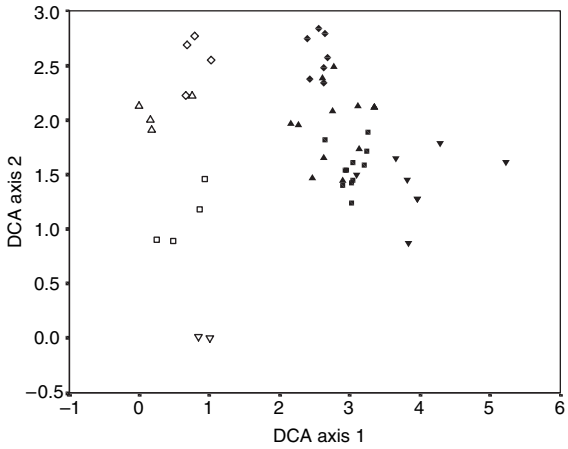


Fig. 2. First two axes of Detrended Correspondence Analysis (DCA) of all zoochory samples (filled symbols, epizoochory samples; empty symbols, endozoochory samples; downward pointing triangles, early summer; squares, mid-summer; upward pointing triangles, late summer; diamonds, early autumn). The percentages of explained variance are shown in Table 2.

the separation of both sample-groups along the first axis of the DCA-plot of all zoochory samples (Fig. 2). The second DCA-axis correlated strongest with date of sampling, indicating a seasonal variation in the species composition of the samples (Table 1). Also when the epi- and endozoochory samples were ordinated separately, the strong positive correlation of both first axes with date of sampling (Table 1) showed that time was a major factor explaining the variance within the epi- or endozoochory samples. The variation in axis scores among simultaneously collected samples illustrated the differences in species composition among seed loads of individual donkeys (Fig. 2).

Abundance in the study area

Species dominant in the study area (e.g. *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Rubus caesius*) as well as rare species (e.g. *Leontodon saxatilis*, *Myosotis arvensis*) were dispersed zoochorously. The overall seedling density in the zoochory samples was positively correlated with species abundance in the study area ($n = 66$, $r_S = 0.33$, $p = 0.006$). This correlation held true if only the species present in both epi- and endozoochory samples were regarded ($n = 16$, $r_S = 0.51$, $p = 0.045$), but not for the exclusively epizoochorous species ($n = 13$, $r_S = 0.49$, $p = 0.092$) and the exclusively endozoochorous species ($n = 39$, $r_S = 0.27$, $p = 0.101$).

Plant traits of zoochorous species and species in the study area

A number of plant traits differed between the species in the study area that were present in the zoochory samples and those that were not present in the samples (Table 2). The latter contained relatively more tall, woody perennials with larger and heavier seeds (more berries and ant- or wind-dispersed seeds) and a transient seedbank. The group of species exclusively in the epizoochory samples contained relatively more biennial species, with adaptations for adhesive seed dispersal. The species exclusively in the endozoochory samples were generally smaller, mostly herbs, with smaller and lighter seeds, and a more persistent seedbank. Finally, the species in both epi- and endozoochory samples, comprised relatively more grasses, often with "unspecialized" seeds or seeds with adaptations to adhesive dispersal. The most significant differences existed between the species exclusively in the study area on the one hand, and the species exclusively in the endozoochory samples on the other hand, but this was probably partly due to the small size of the other groups.

Dispersal-functional plant types associated with epi- and endozoochorous dispersal

Five dispersal-functional plant types were derived from cluster analysis of the 335 species in the study area on the basis of dispersal-relevant plant traits (Table 3, Appendix 2). Tall woody perennials (shrubs and trees) with large, heavy berries or wind-dispersed seeds and a transient seedbank were the main constituents of cluster 1. Cluster 2 predominantly consisted of biennial grasses and herbs with intermediately long seeds, adapted to

Table 1. Percentage of explained variance of the first four DCA axes and Spearman rank correlation coefficients (r_S) between sample scores and date of sampling, for (a) epi- and endozoochory samples together ($n = 55$), (b) epizoochory samples ($n = 41$) and (c) endozoochory samples ($n = 14$).

DCA axis	zoochory		epizoochory		endozoochory	
	% of expl. var.	r_S	% of expl. var.	r_S	% of expl. var.	r_S
1	14.6	−0.55***	18.3	0.94***	20.4	0.77**
2	6.1	0.81***	7.4	0.05 ns	9.7	0.51 ns
3	3.5	0.45**	3.8	−0.08 ns	5.7	0.25 ns
4	2.8	0.23 ns	1.8	0.29 ns	1.9	0.46 ns

***$p <= 0.001$; **$p <= 0.01$; ns, not significant.

Table 2. Overview of the traits associated with the following groups: (a) species in study area but not in zoochory samples; (b) species exclusively in epizoochory samples; (c) species exclusively in endozoochory samples; (d) species both in epi- and endozoochory samples.

		(a) exclusively study area	(b) exclusively epizoochory	(c) exclusively endozoochory	(d) epi+endo
number of species		269	13	37	16
seed weight (mg)	[k]18.6**	30.7 b	3.9 ab	1.1 a	0.9 ab
seed length (mm)	[k]16.2**	3.1 b	3.5 ab	1.7 a	2.0 ab
seed width (mm)	[k]22.4***	1.8 b	1.6 ab	0.9 a	0.8 a
plant height (ordinal 1–8)	8.5*	3.4 b	3.1 ab	2.4 a	3.2 ab
life span (ordinal 1–4)	[k]9.0*	3.3 b	2.3 a	3.0 ab	3.3 ab
dispersal strategy (categorical 1–6)	[c]47.3*** (15)	−12/7/−1/2/4/−1	7/−2/−1/−1/−1/−3	2/−3/3/−1/−2/1	2/−2/−1/0/−1/2
reproduction type (categorical 1–4)	[c]13.4 ns (12)	0/−4/1/3	0/6/−5/−1	0/−1/3/−1	0/0/1/−1
group (categorical 1–4)	[c]35.2*** (9)	−8/0/−5/13	2/−1/1/−3	0/1/5/−7	5/−1/−1/−3
seedbank persistence (ordinal 1–3)	[k]11.9**	2.2 a	2.2 ab	2.6 b	2.7 ab

Plant height (1, <100 mm; 2, 101–299 mm; 3, 300–599 mm; 4, 600–999 mm; 5, 1–3 m; 6, 3.1–6 m; 7, 6.1–15 m; 8, >15 m); life span (1, annual; 2, biennial; 3, annual/biennial to perennial; 4, perennial); dispersal strategy (1, adaptations for epizoochory; 2, ingested berries; 3, adaptations for anemochory; 4, adaptations for hydrochory; 5, adaptations for myrmecochory; 6, unspecialized); reproduction type (1, only by seed; 2, mostly by seed; 3, by seed and vegetative; 4, mainly or exclusively vegetative); group (1, grass; 2, sedge; 3, herb; 4, woody plant); seedbank persistence (1, transient; 2, short term persistent; 3, persistent).
[k] Kruskal Wallis test (values are group averages and groups that differ significantly are indicated by different letters); [c] Pearson χ^2 assosiation test (values are the differences between the observed and the expected values for the different categories. A positive value indicates an overrepresentation of the category in the cluster). ***$p <= 0.001$; **$p <= 0.01$; *$p <= 0.05$; ns, not significant. Values between brackets are degrees of freedom.

epizoochory. Cluster 3 mainly grouped biennial herbs with light seeds, often with seed adaptations for dispersal by wind or ants, and cluster 4 contained predominantly perennial herbs with short seeds and various dispersal strategies. Biennial or perennial grasses, sedges and herbs with unspecialized seeds, often also reproducing vegetatively, were the main constituents of cluster 5. There was no significant difference in mean abundance in the study area between the member species of the different clusters. The species identified exclusively in the epizoochory samples nearly all belonged to cluster 2, while the species identified in both epi- and endozoochory samples had a broader distribution range. This range was even broader for the species occurring exclusively in the endozoochory samples (Table 3).

Discussion

Zoochory in a coastal dune ecosystem

As demonstrated in this study, epi- and endozoochory are important dispersal mechanisms in coastal dune ecosystems grazed by large herbivores. At least one fifth of all species (66 of 335 species) in the study area were dispersed by the donkeys (Appendix 1). Probably even more species would have been revealed if more samples over a larger time span had been collected. In addition, the seedling emergence method may underestimate both species and seed numbers (Couvreur et al. 2004c). On the other hand, natural establishment rates of dispersed seeds may be considerably lower due to competition, predation and other environmental constraints (Edwards et al. 2000, Cosyns 2004).

The species composition of the epi- and endozoochory samples partially overlapped, but was clearly distinguishable in an ordination diagram (Appendix 1, Fig. 2). There was also a constant turnover in species composition of the zoochory samples in the course of the vegetation season (Table 1) (see also Malo and Suárez 1995b, Couvreur et al. 2004c), and the abundance of the species in the samples was correlated with the abundance in the study area, at least for those species occurring in both epi-and endozoochory samples.

Trees and shrubs seemed, with the exception of *Rubus caesius*, not to be dispersed zoochorously (Tables 2 and 3, see also Fischer et al. 1995, Stender et al. 1997, Heinken et al. 2002). Besides possibly unsuitable germination conditions, the relatively small amount of species with fleshy berries (e.g. *Rubus caesius, Solanum nigrum*) germinating from the donkey dung, may also suggest that these species are better adapted for dispersal by frugivorous birds than by large herbivores. Further investigation may elucidate this. A number of other plant traits differed between the species in the study area which were present in the zoochory samples, and those which were not (Table 2), and between the different clusters associated with the different types of zoochory (Table 3). Morphological seed properties such as seed size and seed weight seemed important indicators for

Table 3. Overview of the traits used to define dispersal-functional plant type clusters (named by their predominant profile). In addition, the abundance of the species in the study area is given, as well as the number of species identified in the exclusively epizoochory samples, the exclusively endozoochory samples, or in both. Finally, the last three rows show percentage of all cluster species in the former groups.

cluster number dispersal-functional type		1 Tall woody perennials with large, heavy seeds (berries or wind-dispersed) and a transient seedbank	2 Biennial grasses and herbs with intermediately long seeds adapted to epizoochory	3 Biennial herbs with light seeds adapted to dispersal by wind and ants	4 Perennial herbs with short seeds and various dispersal strategies	5 Biennial or perennial grasses, sedges and herbs with unspecialized seeds, often also reproducing vegetatively
number of species in cluster	total =335	74	63	51	77	70
seed weight (mg)	[k]58.6***	98.07 b	2.93 a	1.39 a	13.64 a	2.90 a
seed length (mm)	[k]62.0***	4.93 c	3.13 b	2.34 ab	1.90 a	2.33 ab
seed width (mm)	[k]66.3***	3.29 b	1.29 a	1.13 a	1.14 a	1.25 a
plant height (ordinal 1–8)	[k]144.7***	5.72 b	2.51 a	2.51 a	2.53 a	2.53 a
life span (ordinal 1–4)	[k]114.8***	4.00 c	2.61 ab	2.19 a	3.92 c	2.97 b
seedbank persistence	[k]35.4***	1.38 a	2.19 b	2.55 b	2.47 b	2.40 b
dispersal strategy (categorical 1–6)	[c]540.8*** (20)	−11/29/6/−1/−6/−17	36/−7/−14/−3/−4/−8	−10/−7/24/1/10/−18	−4/−5/4/4/2/−1	−11/−10/−19/−1/−3/44
reproduction type	[c]236.2*** (16)	1/−2/1/0	19/−16/−2/0	27/−23/−4/0	−44/47/−5/2	−2/−7/10/0
group (categorical 1–4)	[c]374.8*** (12)	−6/−1/−46/54	14/0/−4/−11	−6/−3/22/−13	−9/2/23/−16	7/3/5/−14
abundance in the study area	[k]7.0 ns	1.86 a	2.14 a	2.06 a	1.84 a	2.06 a
sp. excl. in epi		0	10	3	0	0
sp. excl. in endo		2	6	9	12	8
sp. excl. in epi+endo		0	5	3	2	6
% cluster sp. excl. in epi		0	16	6	0	0
% cluster sp. excl. in endo		3	10	18	16	11
% of sp. in epi+endo		0	8	6	3	9

Plant height (1, <100 mm; 2, 101–299 mm; 3, 300–599 mm; 4, 600–999 mm; 5, 1–3 m; 6, 3.1–6 m; 7, 6.1–15 m; 8, >15 m); life span (1, annual; 2, biennial; 3, annual/biennial to perennial; 4, perennial); seedbank persistence (1, transient; 2, short term persistent; 3, persistent); dispersal strategy (1, adaptations for epizoochory; 2, ingested berries; 3, adaptations for anemochory; 4, adaptations for hydrochory; 5, adaptations for myrmecochory; 6, unspecialized); reproduction type (1, only by seed; 2, mostly by seed; 3, by seed and vegetative; 4, mainly or exclusively vegetative); group (1, grass; 2, sedge; 3, herb; 4, woody plant); abundance in the study area (1, present; 2, occasional; 3, frequent; 4, codominant; 5, dominant). [k] Kruskal Wallis test (values are cluster averages and clusters that differ significantly are indicated by different letters); [c] Pearson χ^2 association test (values are the differences between the observed and the expected values for the different categories. A positive value indicates an overrepresentation of the category in the cluster). ***$p <= 0.001$; ns, not significant. Values between brackets are degrees of freedom.

zoochorous dispersal, as well as special dispersal adaptations. The latter seemed more indicative in the case of epizoochory than in the case of endozoochory. Still, a much wider range of dispersal adaptations was represented among the epi- and endozoochorously dispersed species than previously assumed (see Grime et al. 1988, Appendix). For endozoochory, small and light seeds, a small plant size and a persistent seedbank (see also Pakeman et al. 2002) seemed important determinants, while adhesive seed adaptations and a short life span seemed associated with epizoochory. The species identified in both epi- and endozoochory samples often possessed intermediate traits.

Pakeman et al. (2002) suggested that many species adapted to endozoochory by large herbivores might be hidden in the dispersal strategy category "unspecialized" (Grime et al. 1988). These species lack obvious seed adaptations and use their edible vegetative parts as ecological "fruits" to attract herbivores as seed dispersers. Janzen (1984) formulated this "foliage is the fruit" hypothesis in the context of endozoochory. However, the presence of many grasses with unspecialized seeds in our epizoochorory samples (Appendix 1 and 2, see also Couvreur et al. 2004c) may suggest that the "foliage is the fruit" hypothesis might not only apply to endozoochory, but also to epizoochory. Apparently, not only specialized seed adaptations increase the chance of dispersal in the fur of herbivores, but also increasing the chance that animals come into contact with the seeds, by providing a food source. The fact that the inflorescence of many grasses is physically separated from the edible leaves by a tall stem, may further enhance the probability of adherence of the seeds to the fur of grazing herbivores. Edibility might thus enhance both forms of zoochory.

Complementarity of epi- and endozoochory

The differences in species composition between the epi- and endozoochory samples, as well as the different association of dispersal-functional plant types with either of the mechanisms demonstrate the complementarity of epi- and endozoochory. This complementarity seemed to be more pronounced than the additive effect of epi- and endozoochory, since only 16 species were dispersed by both mechanisms and 50 species by only one of the mechanisms. In addition, the different association of epi- and endozoochory with the dispersal-functional plant types revealed an increasing degree of specificity from endozoochory towards epizoochory, since the endozoochorously dispersed species covered many more dispersal-functional plant types than those dispersed by epizoochory. Although endozoochory is supposed to have a greater impact than epizoochory on vegetation dynamics in terms of quantity of seed dispersal (Janzen 1984), both mechanisms are ecologically important and complementary. The combination of epi- and endozoochory results not only in a larger number of dispersed seeds, but, more importantly, in a larger spectrum of dispersed species. This is a consequence of the different constraints of both mechanisms. Whereas e.g. grooming behaviour of animals can limit epizoochory (Sorensen 1986, Kiviniemi 1996), endozoochorous dispersal is constrained by seed survival in the digestive tract (Neto and Jones 1987, Gardener et al. 1993, Cosyns 2004) and by feeding preferences of herbivores. Yet, the general relative ecological significance of both dispersal modes as compared to each other but also compared to other possible long-distance seed dispersal modes needs further investigation.

Consequences for nature mangement

As large herbivores have always been part of natural ecosystems, their complementary role as epi- and endozoochorous dispersal vectors may be important for maintaining species richness. Grazing by livestock has recently become an important nature management tool for conservation and restoration of many habitats in northern temperate regions (see also Couvreur et al. 2004c). Until now, much attention was given to the contribution of livestock to plant diversity patterns, both at the local and landscape scale, through their activities of selective grazing, trampling and defecating, which influence processes that enhance local extinction rates. Yet herbivores may also influence plant diversity through processes that affect colonisation rates (Olff and Ritchie 1998). The results of this paper clearly show the importance of large herbivores as long-distance seed dispersal vectors for much more plant species than could be assumed from their morphological seed characteristics (see also Couvreur et al. 2004a, b, c). Retention times of seeds in the fur (see Couvreur et al. 2004b) and in the digestive tract of large herbivores (Cosyns 2004) allow dispersal over distances of metres to kilometers, hence covering the entire 100 ha study area. The growing evidence for the role of large herbivores in the seed dispersal process urges for a well-considered nature management policy which not only focuses on amelioration of habitat conditions, but also considers the spatial arrangement of suitable but still unoccupied patches for critical plant species. If plants can bridge gaps in space and time, this may favour a sustainable conservation of critical plant populations. It is shown here that the use of large herbivores like donkeys as managers, might help to reach this goal, through the epi- and endozoochorous dispersal of plant seeds.

Acknowledgements – This research was supported financially by a Research Assistant grant from the Fund for Scientific Research, Flanders (F.W.O.). We are grateful to Kris Verheyen for statistical advice and useful comments on an earlier version

of the manuscript. We thank the Ministry of the Flemish Community, AMINAL, Dept of Nature for permitting this research project in their nature reserve, and to Bert Delanoeije, Marc Leten and Stefaan Theuninck for their kind help in data collection.

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Appendix 1. Overview of the species in the zoochory samples and their relevant traits.

Species	presence in epi/endo	plants in epi samples	plants in endo samples	number of epi samples	number of endo samples	abundance in study area	seed weight (mg)	seed length (mm)	seed width (mm)	plant height	life span	dispersal strategy	reproduction type	group	seedbank persistence	cluster number dispersal – functional plant type
Achillea millefolium	2	0	4	0	3	3	0.13	2	0.86	2	4	3	2	3	1	4
Agrostis capillaris	12	3	29	2	8	2	0.06	1.00	0.38	2	4	6	2	1	3	5
Agrostis stolonifera	2	0	41	0	5	2	0.08	1.08	0.45	2	4	6	2	1	3	5
Aira praecox	2	0	3	0	2	2	0.18	2.52	0.48	1	1	1	1	1	2	2
Anthriscus caucalis	12	211	1	14	1	4	1.3	3.77	0.96	3	1	1	1	3	.	2
Arctium minus	1	137	0	6	0	2	7.38	5.73	2.24	5	2	1	1	3	3	2
Arenaria serpyllifolia	2	0	13	0	6	4	0.05	0.6	0.44	1	1	3	1	1	3	3
Arrhenatherum elatius	1	30	0	9	0	5	3.29	3.81	1.22	5	4	1	1	1	1	2
Artemisia vulgaris	12	1	68	1	4	2	0.13	1.46	0.44	5	4	6	1	3	3	5
Bidens tripartita	1	1	0	1	0	1	2.61	6.36	2.18	3	1	1	1	3	.	2
Bromus hordeaceus	1	2	0	1	0	3	3.48	6.08	1.51	3	1	1	1	1	1	2
Calamagrostis epigejos	2	0	26	0	5	5	0.10	1.25	0.4	4	4	3	2	1	.	1
Capsella bursa-pastoris	2	0	1	0	1	3	0.13	0.95	0.47	1	1	3	1	3	3	3
Carex arenaria	2	0	187	0	14	4	0.78	1.83	1.08	2	4	6	3	2	.	5
Cerastium fontanum	2	0	3	0	2	3	0.12	.	.	1	4	6	2	3	3	4
Cerastium semidecandrum	1	4	0	3	0	3	0.04	0.45	0.41	2	1	3	1	3	3	3
Chelidonium majus	2	0	2	0	2	3	0.83	1.36	0.81	3	4	5	1	3	3	3
Chenopodium album	2	0	1	0	1	2	1.5	1.17	1.17	5	1	6	1	3	3	5
Conyza canadensis	2	0	2	0	2	3	0.05	1.21	0.34	3	1	3	1	3	.	3
Crepis capillaris	2	0	2	0	2	4	0.26	2.20	0.53	2	1	3	1	3	3	3
Cynoglossum officinale	1	957	0	32	0	3	26.05	6.78	5.6	3	3	1	1	3	2	2
Dactylis glomerata	1	1	0	1	0	2	0.99	2.77	0.99	3	4	6	1	1	1	2
Epilobium ciliatum	12	1	1	1	1	1	0.07	1.13	0.4	4	4	3	2	3	2	4
Epilobium hirsutum	2	0	2	0	1	2	0.14	0.98	0.44	5	4	3	2	3	3	4
Epilobium montanum	2	0	1	0	1	2	0.12	1.18	0.48	3	4	3	2	3	3	4
Eupatorium cannabinum	2	0	4	0	3	3	0.27	2.97	0.52	5	4	3	2	3	3	4
Festuca rubra	12	4	2	2	2	3	1.30	3.83	1	2	4	6	2	1	1	5
Galium aparine	12	712	60	19	13	4	8.34	3.2	2.63	4	1	1	1	3	1	2
Galium mollugo	2	0	54	0	2	2	0.53	1.22	1.13	3	4	1	1	3	.	2
Galium verum	2	0	60	0	6	4	0.44	1.42	1.2	2	4	6	2	3	1	4
Geranium molle	2	0	5	0	2	3	1.24	1.54	1.09	2	1	6	1	3	2	5
Geum urbanum	1	1	0	1	0	2	2.45	4.54	1.75	3	4	1	1	3	2	2
Holcus lanatus	12	10	89	9	9	4	0.47	2.35	0.84	3	4	6	2	1	3	5
Hypochaeris radicata	2	0	2	0	1	2	.	6.00	0.75	1	4	3	1	3	2	3
Juncus articulatus	2	0	17	0	7	2	0.02	0.57	0.27	3	4	1	2	2	3	4
Juncus bufonius	2	0	16	0	7	2	0.02	0.39	0.31	1	1	1	1	2	3	2
Koeleria albescens	2	0	3	0	2	3	.	.	.	2	4	6	2	1	.	5
Leontodon saxatilis	2	0	1	0	1	1	.	.	.	2	4	3	2	3	2	4

Appendix (Continued.)

Species	presence in epi/endo	plants in epi samples	plants in endo samples	number of epi samples	number of endo samples	abundance in study area	seed weight (mg)	seed length (mm)	seed width (mm)	plant height	life span	dispersal strategy	reproduction type	group	seedbank persistence	cluster number dispersal – functional plant type
Lythrum salicaria	12	6	25	2	4	2	0.05	1.03	0.4	4	4	4	1	3	3	3
Myosotis arvensis	1	24	0	11	0	1	0.29	1.43	0.89	2	2	1	1	3	3	2
Oenothera biennis	1	70	0	6	0	3	0.44	1.7	1.25	4	2	3	1	3	.	3
Oenothera glazioviana	2	0	19	0	3	3	0.6	1.51	1.24	4	2	3	1	3	.	3
Phleum arenarium	1	2	0	2	0	3	0.18	1.03	0.6	1	1	1	1	1	.	2
Phleum pratense	12	2	63	2	13	1	1.00	1.48	0.91	3	4	1	1	1	3	2
Plantago coronopus	2	0	1	0	1	2	.	1.1	0.65	1	3	1	1	3	3	2
Plantago lanceolata	2	0	16	0	4	2	1.81	2.84	1.39	2	4	1	1	3	3	2
Plantago major	12	1	43	1	3	3	0.26	1.5	0.81	2	4	1	1	3	3	2
Poa annua	12	2	24	2	7	3	0.30	1.86	0.7	2	3	6	1	1	3	2
Poa pratensis	12	1	149	1	14	3	0.30	1.60	0.52	3	4	6	2	1	3	5
Poa trivialis	12	18	168	11	12	4	0.17	1.52	0.5	3	4	6	2	1	3	5
Ranunculus repens	2	0	1	0	1	2	1.82	3.09	2.27	2	4	4	2	3	3	4
Rubus caesius	2	0	3	0	3	5	3.61	3.13	1.93	4	4	2	2	4	2	1
Rumex crispus	2	0	1	0	1	2	2.93	2.51	1.58	3	4	6	2	3	3	4
Rumex obtusifolius	1	1	0	1	0	2	2.70	2.29	1.4	3	4	1	1	3	3	2
Sagina procumbens	2	0	1	0	1	3	0.02	0.43	0.27	1	4	6	1	3	3	5
Senecio jacobaea	12	18	9	7	5	4	0.39	2.02	0.5	4	3	3	1	3	3	3
Silene latifolia subsp. *alba*	2	0	3	0	2	3	0.81	1.35	1.1	4	4	3	1	3	3	3
Solanum nigrum	2	0	1	0	1	2	0.74	1.92	1.36	2	1	2	1	3	.	3
Sonchus asper	1	1	0	1	0	2	0.34	2.70	1.06	3	1	3	1	3	3	3
Sonchus oleraceus	12	2	9	2	6	2	0.53	2.86	0.91	3	1	3	1	3	3	3
Stellaria media	2	0	7	0	5	4	0.48	1.13	1.05	2	1	6	1	3	3	5
Trifolium dubium	2	0	11	0	3	3	0.36	1.25	0.86	2	1	1	1	3	3	2
Trifolium repens	2	0	20	0	3	2	0.59	1.17	1.02	1	4	1	2	3	3	4
Urtica dioica	12	103	3010	17	10	3	0.19	1.19	0.77	4	4	1	2	3	3	4
Veronica chamaedrys	2	0	64	0	10	3	0.22	1.18	1	1	4	6	2	3	3	4
Vicia cracca	2	0	1	0	1	4	14.29	2.89	2.81	4	4	6	1	3	1	5

Presence in epi/endo samples (1, epizoochory samples; 2, endozoochory samples; 12, both epi- and endozoochory samples); abundance in the study area (1, present; 2, occasional; 3, frequent; 4, codominant; 5, dominant); plant height (1, <100 mm; 2, 101–299 mm; 3, 300–599 mm; 4, 600–999 mm; 5, 1–3 m; 6, 3.1–6 m; 7, 6.1–15 m; 8, >15 m); life span (1, annual; 2, biennial; 3, annual/biennial to perennial; 4, perennial); dispersal strategy (1, adaptations for epizoochory; 2, ingested berries; 3, adaptations for anemochory; 4, adaptations for hydrochory; 5, adaptations for myrmecochory; 6, unspecialized); reproduction type (1, only by seed; 2, mostly by seed; 3, by seed and vegetative; 4, mainly or exclusively vegetative); group (1, grass; 2, sedge; 3, herb; 4, woody plant); seedbank persistence (1, transient; 2, short term persistent; 3, persistent); cluster number (see legend of Appendix 2).

Appendix 2. All plant species in the study area, clustered in dispersal-relevant functional plant types. The species are represented by the first four letters of genus resp. species name (first four letters in capitals, species identified exclusively in epizoochory samples; last four letters in capitals, species identified exclusively in endozoochory samples; all letters in capitals, species identified both in epi- and endozoochory samples).

Cluster 1		Cluster 2		Cluster 3		Cluster 4		Cluster 5	
acerpseu	rosarugo	agrieupa	trifcamp	ancharve	ConyCANA	AchiMILL	mentaqua	aegopoda	stelpall
popucand	sympalbu	CYNOoffi	TrifDUBI	fumaoffi	sisyoffi	vincmajo	apiurepe	allivine	gerapusi
tiliplat	cotohori	GEUMurba	BIDEtrip	lamipurp	senevisc	epillanc	ranuflam	fallaube	veropers
fraxexce	RubuCAES	ranuacri	GALIAPAR	mercannu	senevulg	sedurupe	RanuREPE	cardprat	vicilath
carpbetu	rubufruc	helinumm	ARCTminu	verohede	SONCaspe	ceratome	carepani	convarve	anagarve
ulmmino	cotosimo	ballnigr	arctpube	clayperf	SONCOLER	LeonSAXA	hydrvulg	lemnmino	StelMEDI
betuspp	ribeuvac	RUMEobtu	MYOSarve	lamiampl	lactserr	orobcary	lysivulg	potacris	matrmatr
pinunigr	hedeheli	GaliMOLL	torijapo	lamihybr	senesylv	pyrorotu	dantdecu	ranutric	vicihirs
popualba	rosapimp	PlanLANC	erodlebe	anchoffi	carlvulg	hierpilo	luzucamp	orniumbe	fallconv
popubals	mahoaqui	PLANMAJO	myosramo	ChelMAJU	cirspalu	seduacre	JuncARTI	ranufica	polypers
popucans	prunspin	ranubulb	myosstric	theshumi	pastsati	veroanag	juncsubn	AGROCAPI	fumamura
salialba	cratmono	thympule	PlanCORO	polyserp	SENEJACO	epilangu	scirseta	KoelALBE	ChenALBU
pinusylv	prunsero	juncinfl		polyvulg	cirsvulg	hierumbe	bellpere	AgroSTOL	chenrubr
clemvita	pyrucomm	PHLEPRAT		violcani	crepbien	pulidyse	poteanse	HOLCLANA	vicisati
salimult	prunaviu	anthodo		violcurt	OENObien	EPILCILI	nastoffi	milieffu	anthsylv
salicapr	pruncera	avenpube		bryodioi	OenoGLAZ	seneeruc	RumeCRIS	POAPRAT	chaetemu
ammoaren	euoneuro	ARRHelat		SolaNIGR	verbthap	cirsarve	thalminu	POATRIV	centthui
phraaust	rosacaes	triseflav		erigacer	dipltenu	sapooffi	poteerec	elumobtu	rumeprat
CalaEPIG	franalnu	holcmoll		tragprat	taraspp	EpilHIRS	poterept	elymath	lathprat
humulupu	rosacani	DACTglom		heraspho	silenuta	EupaCANN	cardhirs	glycnota	ViccCRAC
salirepe	vibulant	festarun		LYTHSALI	HypoRADI	EpilMONT	ceraarve	glycflui	lithoffi
syrivulg	malusylv	festgiga		rumecong	siledioi	hypeperf	CeraFONT	poapalu	aquivulg
poputrem	sorbauc	festfili		myoscaesp	silevulg	lychflos	rumeacet	festjunci	centjace
salifrag	liguvulg	lolipere		ranuscel	SileLATI	epiphell	VeroCHAM	FESTRUBR	centnigr
saliatro	rosatome	molicaer		rumemari		hypetetr	verooffi	CareAREN	ARTEVULG
salicine	rosaobtu	POAANNU		arabthal		inucony	potester	careflacc	aspecyna
alnuglut	rosarubi	AiraPRAE		gnaplute		arumital	saginodo	elymrepe	SagiPROC
alnuinca	ribealpi	bromthom		CapsBURS		aspaoffi	galaniva	leymaren	lotucorn
cladmari	ribenigr	PHLEaren		centeryt		sambebul	lamigale	caredist	arabhirs
eleopalu	ribeodor	JuncBUFO		saxitrid		soladulc	lamialbu	carehirt	jasimont
coluarbo	riberubr	aperinte		centpulc		groendens	lamimacu	caretrin	moehtrin
labuanag	ribesang	BROMhord		CERAsemi		calysepi	glechede	careviri	
ononrepe	sambnigr	hordmuri		sileconi		hemespp	violhirt	allipeti	
rhushirt	prundome	bromtect		CrepCAPI		galiulig	myosscor	chenmura	
robipseu	querrobu	bromster		centlitt		rheum	prunvulg	GeraMOLL	
cornsang		ANTHCAUC		diplmura		GaliVERU	TrifREPE	gerarober	
lycibarb		urtiuren		eropvern		thalflav	zannpalu	ceradiff	
rubuidae		erodcicu		ArenSERP		apiunodi	URTIDIOI	veroarve	
hipprham		myosdisc		corycane		galipalu		cochdani	

Cluster legend: 1, predominantly tall woody perennials with large, heavy seeds (berries or wind-dispersed); 2, predominantly biennial grasses and herbs with intermediately long seeds, adapted to epizoochory; 3, predominantly biennial herbs with light seeds, adaptated for dispersal by wind and ants; 4, predominantly perennial herbs with short seeds and various dispersal strategies; 5, predominantly biennial or perennial grasses, sedges and herbs with unspecialized seeds, reproducing by seed or vegetatively.

Applied Vegetation Science 7: 229-236, 2004
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Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal

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Abstract

Question: Do large herbivores contribute to the dispersal of plant seeds between isolated habitats by epizoochory?

Location: Nature reserves in Flanders, Belgium.

Methods: Epizoochory was studied by brushing plant seeds from the fur of 201 domesticated large herbivores (Galloway cattle, donkeys and horses), grazing in 27 Flemish nature reserves. Several herbivores were examined after transport between different nature reserves as part of the seasonal grazing system in Flanders, allowing detection of seed dispersal both within and between reserves. The seedling emergence method was used to identify the dispersed plant species.

Results: In total, 6385 epizoochorous seeds from 75 species germinated, yet the real seed quantity was underestimated by the seedling emergence method. A wide variety of seed morphology, seed weights and plant heights was represented among the dispersed species, many of which had a transient seed bank. There was a gradual turnover in epizoochorous species composition in the course of the vegetation season, and seed dispersal occurred both within and between different nature reserves.

Conclusions: Domesticated large herbivores, as models for wild mammals in the present and the past, are important dispersers of many plant species. Through seasonal grazing, the herbivores function as 'mobile link organisms', connecting isolated nature reserves through seed dispersal, possibly influencing vegetation development and long-term survival of plant populations. As such, large herbivores are important instruments in ecological restoration, especially in fragmented ecosystems.

Keywords: Cattle; Donkey; Epizoochory; Grazing; Horse; Long-distance seed dispersal; Nature management; Plant trait.

Nomenclature: Lambinon et al. (1998).

Introduction

Long-distance plant dispersal has recently received much attention, mainly because of its importance for migration in a rapidly changing landscape. The fitness of isolated plant populations depends on successful dispersal between populations, as do the creation and maintenance of a metapopulation (Eriksson 1996; Cain et al. 2000) and the necessary species migrations in response to environmental changes (Watkinson & Gill 2002).

In postglacial times, wild animals were probably key long-distance dispersal vectors through external (epizoochory) and internal (endozoochory) seed dispersal (Poschlod & Bonn 1998; Pakeman 2001). Nowadays, however, their movement and migration patterns are dramatically restricted, particularly in the present western European fragmented landscape. In semi-natural systems, most dispersal processes have disappeared with the abandonment of traditional agricultural techniques (Poschlod & Bonn 1998; Bruun & Fritsbøger 2002), e.g. transhumant sheep shepherding in calcareous grasslands (Fischer et al. 1996; Poschlod et al. 1998). Seed dispersal has now become a bottleneck for vegetation development and restoration of isolated (semi)-natural relicts (e.g. Strykstra et al. 1998; Pywell et al. 2002), particularly for species with short-lived seed banks. Detection of long-distance dispersal in the present day landscape, which is subject to climate change, habitat destruction and fragmentation, is therefore crucial (Cain et al. 1998, 2000; Pakeman 2001). More data on long-distance dispersal are also indispensable for improving present models, which fail to explain observed plant migration rates (Higgins & Richardson 1999; Greene & Calogeropoulos 2002; Levin et al. 2003). Tracing long-distance dispersal, however, is intrinsically difficult. Because genetic approaches (Cain et al. 2000) are, in practice, only feasible for detecting seed movement if it results in successful recruitment (Nathan & Muller-Landau 2000), direct field observations of long-distance seed dispersal remain invaluable for understanding plant migration.

Epizoochory is one of the most important long-distance dispersal mechanisms. It has recently been documented by Fischer et al. (1996), Kiviniemi (1996), Stender et al. (1997), Kiviniemi & Telenius (1998), Kiviniemi & Eriksson (1999), Heinken (2000), Heinken & Raudnitschka (2002), Graae (2002) and Couvreur et al. (2004, In press a, b). The need for more data on occasional long-distance dispersal events has been stressed (Levin et al. 2003), especially with respect to the number of animals followed, and for longer distances (Greene & Calogeropoulos 2002).

In this study, we examine epizoochory on several herbivore species and long-distance seed movement, albeit human induced. We focus on domesticated large herbivores, grazing in nature reserves in Flanders, Belgium. Grazing is a major management measure to maintain the semi-natural vegetation types in these reserves. Domesticated herbivores are therefore introduced at low densities, as a substitute for the extinct natural herbivores. Several species, mostly cattle (often Galloway cattle), horses and sheep, but also donkeys and goats, do currently graze in Flemish nature reserves. Due to the small area, and therefore limited food supply, of most reserves parts of the herds are regularly transported to other nature reserves. Many herbivores spend the winter on a central farm and return to the reserves in spring. These 'nomadic' animals sometimes travel the whole area of Flanders in their life span. Anecdotal observations of seeds in the fur of these transported herbivores suggested that they function as 'mobile link organisms' (Lundberg & Moberg 2003), providing not only seed transport within individual nature reserves, but also seed exchange between suitable habitats at long distances. Therefore, we examined the epizoochorous seed loads of Galloway cattle, donkeys and horses in actual nature management situations in Flanders. The following questions were addressed:

- What are the species and quantity of seeds dispersed epizoochorously by large herbivores?
- Which dispersal relevant plant traits are represented among the epizoochorously dispersed seeds?
- Do the three herbivore species differ in their epizoochorous dispersal capacity?
- Does the epizoochorous species composition change during the vegetation seasons? Finally, the consequences for nature conservation and management are discussed.

Material and Methods

Study areas

Studies were carried out in 27 nature reserves in Flanders, Belgium (Fig. 1; App. 1), ranging in size from a few to more than 300 ha. The reserves are isolated relicts of former species-rich, semi-natural landscapes, which are now heavily fragmented as a result of land use changes. The vegetation consists mainly of species-rich grasslands, sometimes interspersed with areas of tall herbage or woody vegetation.

Sampling method

Between May 2000 and February 2001, epizoochorous seeds were collected from 201 large herbivores (125 Galloway cattle from 23 different reserves, 30 horses from six reserves and 46 donkeys from three nature reserves) (App. 1). These numbers reflect the ratio between the different herbivore species in Flemish nature reserves. The epizoochorous seeds were collected by brushing the fur of each animal for 15 minutes with a very fine horse brush. For practical reasons, the sampling mostly coincided with capture events for veterinary control or transport. Although this resulted in an 'unbalanced' sampling, it allowed us to intercept epizoochorous seeds which would actually be displaced over long distances. Of the 201 sampled animals, 82 were brushed after transport from a 'donor' reserve to a 'receptor' reserve (Fig. 1; App. 1). This allowed us to witness and quantify seed dispersal between different nature reserves.

Seed germination

After removal of hair, the samples were sown in trays with sterilized potting soil (seedling emergence method; ter Heerdt et al. 1996). The trays were kept in laboratory conditions, with a daily light exposure of 16 h, daily watering and occasional soil disturbance to expose buried seeds to light. The easily recognizable seeds of seven taxa (see Fig. 2) were counted before being sown, to estimate their germination success. Over a period of six months, seedling numbers and species were recorded, and removed to prevent competition. Unrecognizable seedlings were transplanted to separate pots until identification was possible. So that germination of very short-lived seeds was not compromised, a cold treatment of two months at 4°C was only given after six months, when germination had ceased. Subsequently, germination was followed up for another three months.

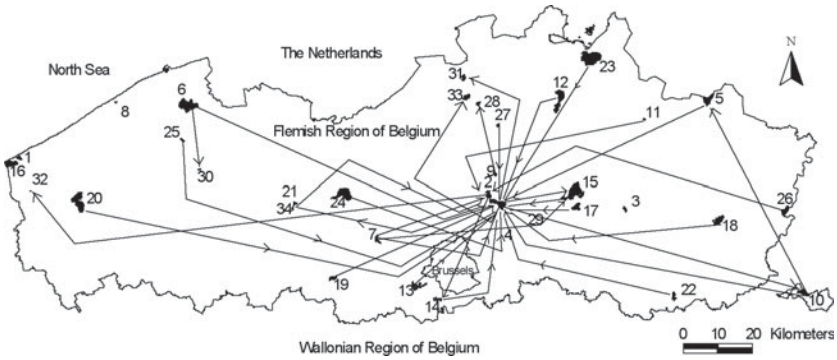


Fig. 1. Flemish nature reserves where epizoochory by large herbivores was investigated. Arrows represent transport routes for seasonal grazing of the sampled herbivores. In all reserves except 1, 3, 8, 16, 19 ('no transport'), at least part of the samples were collected after transport of the herbivores from a 'donor' reserve (2, 4-7, 9-10, 11-15, 17-18, 20-27) to a 'receptor' reserve (2, 4, 5, 10, 14-15, 28-34) (see App. 1 for reserve names).

Data analysis

Given the nature of the data, non-parametric statistics were used and relevant data were selected according to the question posed.

Firstly, the germination success of seven taxa was evaluated by comparing the number of sown seeds with the number of seedlings germinated during the pre- and post-chilling germination cycle.

Secondly, to assess the variety of some dispersal relevant plant traits represented among the epizoochorous species, we recorded their 'dispersal agency' category and the rank of plant height and seed weight (Grime et al. 1988). A Kruskal-Wallis test (Siegel & Castellan 1988) was used to test whether the mean seed weight was higher in certain dispersal-agency categories. Since species with short-lived seed banks depend on dispersal in space more than species which can also disperse in time through seed bank formation, we calculated each species' seed bank longevity index (Thompson et al. 1997; Bekker et al. 1998).

Thirdly, the quantity of species and seedlings in the epizoochorous samples was compared between the herbivore species. However, a comparison between herbivores sampled in different reserves or different months was considered to be biased by vegetation variations. Therefore, we limited the statistical comparison (Mann-Whitney U-test; Siegel & Castellan 1988) to the data from 'Hageven', the reserve from which most simultaneously collected samples from Galloway cattle and horses were available. Data on donkeys were insufficient to include them in the statistical comparison.

Fourthly, the species composition of the samples was screened for a temporal gradient. To obtain balanced data sets with respect to the number of samples and different sampling months, we selected five reserves with at least 10 non-empty samples collected in at least three different sampling months (Table 2). For each of these reserves, the epizoochorous samples were ordinated on the basis of their species composition, using Detrended Correspondence Analysis (DCA; Hill & Gauch 1980), after logarithmic transformation, in CANOCO 4.0 (ter Braak & Šmilauer 1998). To check if the ranking of the epizoochorous samples along the major DCA axis reflected the moment of sampling, which would suggest a gradual turnover (temporal gradient) in species composition, Spearman rank correlation coefficients (Siegel & Castellan 1988) were calculated between the sample scores on the first DCA axis and the sampling month (ranked from May 2000 to February 2001).

Finally, the samples from the 82 transported large herbivores were used to assess the scale of long-distance seed movement between different nature reserves.

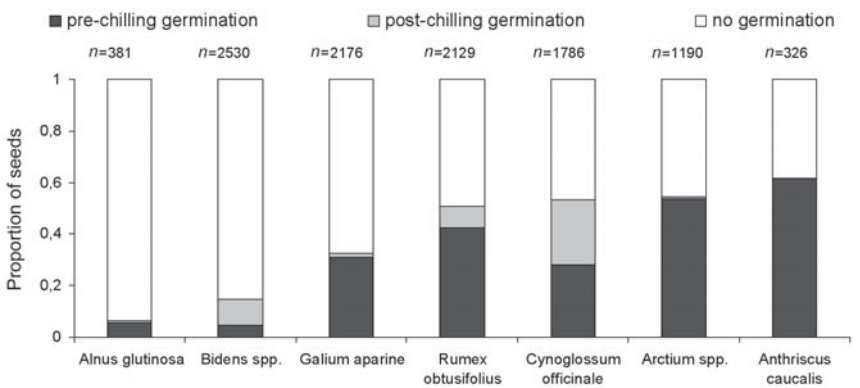


Fig. 2. Germination success of seven species in the pre- and post-chilling germination cycle (n = total number of sown seeds).

Results

Species and seedlings

A total of 6385 seedlings of 75 plant species germinated in the epizoochorous samples of all herbivores (Table 1, Fig. 3). The chilling treatment enhanced germination of 29 species (21% of the seedlings). For the seven seed species which were counted before being sown, the overall germination success ranged from 6.3% to > 50%, and the post-chilling germination accounted for < 5% to 70% of the germinated seeds (Fig. 2). Among the species, 23 plant families were represented, *Asteraceae* and *Poaceae* containing most species (both 24%), and 14% respectively 42% of the seedlings. Except for *Alnus glutinosa* and *Salix cinerea*, all identified species were herbaceous. Of all seedlings, 67% belonged to only five species and 90% to 10 species (Table 1).

Plant traits

Eight 'dispersal agency' categories were distinguished (Table 1). 32% of the species (62% of the seedlings), had adaptations for epizoochory (ANIMa, b, m). Most of these species possessed awns or spiny calyx teeth (ANIMa), but most individuals had burrs (ANIMb). Wind dispersal adaptations, mainly plumes or woolly hairs, occurred in 29.4% of the species (23% of the seedlings). Water dispersal was the main strategy of 10.6% of the species (but only < 1% of the seedlings), and 26.6% were unspecialized dispersers (13%). Seed weight ranged from < 0.2 mg to > 10 mg, and was highest in the category ANIMb (Kruskal Wallis test, KW = 25.5; df = 7; $P = 0.001$). Plant height ranged from < 10 cm to > 15 m, with over 30% of the species < 30 cm. The seed bank longevity index, calculation of which was possible for 77% of the species, indicated that 45% of the species and 52% of the seedlings lacked seed bank formation (longevity index < 0.35; Strykstra et al. 2002).

Herbivore species

Seedling and species numbers per sample are summarized in Fig. 3. In the non-empty samples (81%), few seedlings and species germinated, while only a few animals transported many seedlings (maximum 685) and species (maximum 10). At Hageven, in the January samples, the Galloway cattle dispersed more species and seedlings than the horses: mean 16 seedlings; 2.7 species vs. 0.33 seedlings; 0.33 species (Mann-Whitney U, $P = 0.015$ and $P = 0.014$, respectively).

Temporal gradient

A temporal gradient (turnover) in epizoochorous species composition could be detected for three of the five nature reserves where sufficient samples collected in several months were available (Table 2). This species turnover was demonstrated by the fact that DCA ordination of the epizoochorous samples, on the basis of their species composition, resulted in a ranking of the samples according to the month in which they were collected (indicated by a significant correlation between sample scores on the first DCA axis and month of sampling).

Long-distance seed movement

The dispersal distances within nature reserves were restricted to the size of the reserves where the herbivores grazed, ranging from 100-200 m to a few km. However, the exchange of large herbivores between different reserves, as part of the nature management system, regularly increased these distances significantly. The germination of 2522 seedlings of 52 plant species (Table 1) from the epizoochorous material of the 82 herbivores, which were brushed after transport between reserves, revealed the existence of a long-distance seed dispersal pathway between distant and isolated reserves. The travel routes of these seed carrying herbivores ranged from 2 to 160 km in our study (Fig. 1).

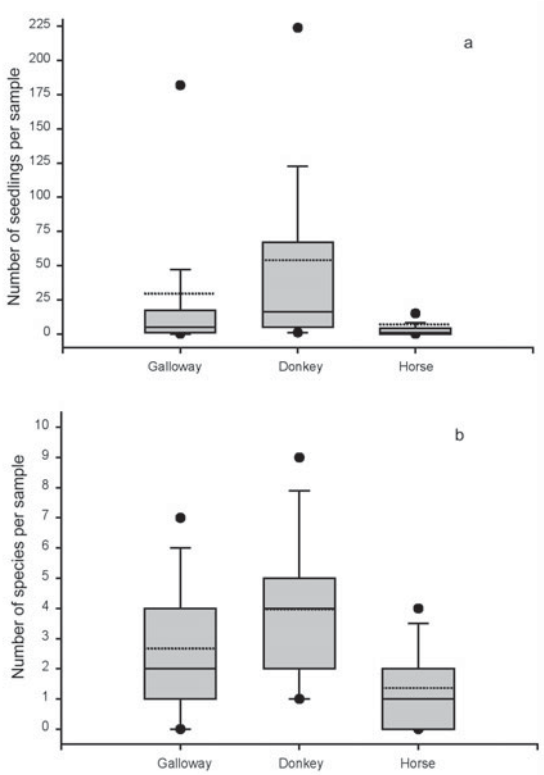


Fig. 3. The number of (**a**) epizoochorous seedlings and (**b**) species per sample, for Galloway cattle (n=125), donkey (n = 46) and horse (n = 30). The full horizontal lines in the grey boxes show the median, the 25th and 75th percentile, and the 10th and 90th percentile. The dashed line represents the mean, and the dots indicate the 5th and 95th percentile.

Table 1. Plant species identified in the fur of 201 large herbivores (*: in samples of herbivores transported between reserves). Columns 1-3: seedling numbers of species identified at least twice on herbivores (the number of samples containing the species are between brackets). Col. 4: number of reserves (n = 27) with the species present in at least one sample. Col. 5: number of months (n = 10) with the species present in at least one sample. Col. 6: dispersal agency (Grime et al. 1988): ANIM= adhesively dispersed by animals (a: dispersule with awn or spiny calyx teeth; b = adhesive burr; m = adhesive through mucilage secretion); AQUAT = water-dispersed; WIND = wind-dispersed (p = dispersule plumed or wrapped in woolly hairs; c = seeds small and shed from a capsule from above the surrounding vegetation; w = seeds winged or strongly flattened); UNSP = unspecialized disperser. Col. 7: dispersule weight: 1 = < 0.2 mg; 2 = 0.21 - 0.5 mg; 3 = 0.51 -1 mg; 4 = 1.01 - 2 mg; 5 = 2.01 - 10 mg; 6 = > 10 mg. Col. 8: plant height: 1 = < 100 mm; 2 = 101 - 299 mm; 3 = 300 - 599 mm; 4 = 600-999 mm; 5 = 1 - 3 m; 6 = 3.1 - 6 m; 7 = 6.1 - 15 m; 8 = > 15 m; Col. 9: seedbank longevity index. Col. 10: percentage of seedlings germinated after chilling treatment.

	1 Galloway (n = 125)	2 Donkey (n = 46)	3 Horse (n = 30)	4 No. of reserves	5 No. of months	6 Dispersal agency	7 Diaspore weight	8 Plant height	9 Seed bank longevity	10 % post chilling
*Senecio jacobaea**	1129 (4)	158 (9)	1 (1)	4	3	WINDp	1	4	0.14	26.4
Cynoglossum officinale	0	957 (32)	0	1	3	ANIMb	6	3	0.28	47.4
Arctium spp.*	634 (6)	137 (6)	0	5	3	ANIMb	6	5	0.11	1.7
*Galium aparine**	18 (5)	712 (19)	0	6	4	ANIMb	5	5	0.52	4.9
*Bidens frondosa/tripartita**	541 (9)	1 (1)	0	6	6	ANIMb	5	4	0.25	59.6
*Agrostis capillaris**	453 (43)	3 (2)	7 (4)	14	9	UNSP	1	2	0.59	5.8
*Urtica dioica**	184 (33)	104 (18)	137 (3)	16	7	ANIMa	1	5	0.06	5.4
*Poa trivialis**	186 (35)	22 (14)	12 (4)	14	9	UNSP	1	1		1.4
Anthriscus caucalis	0	211 (14)	0	1	4	ANIMb	4	3	0	0
*Rumex obtusifolius**	127 (27)	1 (1)	25 (6)	16	8	ANIMa	4	5	0.39	35.3
Oenothera spp.	0	70 (6)	0	1	1	WINDc	2	4	0.88	54.3
*Alnus glutinosa**	54 (7)	0	0	3	3	AQ/WIw	4	8	0.38	5.6
*Holcus lanatus**	41 (21)	11 (10)	1 (1)	13	8	UNSP	2	3	0	3.8
*Lythrum salicaria**	39 (4)	6 (2)	5 (3)	4	4	AQUAT	1	4	0.54	12
Epilobium spp.*	46 (16)	1 (1)	1 (1)	9	7	WINDp	1	3	0.08	2.1
*Arrhenatherum elatius**	5 (2)	30 (9)	0	3	3	ANIMa	5	5	0.14	0
*Myosotis arvensis**	1 (1)	24 (11)	0	2	4	ANIMa	2	2	0.83	0
*Agrostis stolonifera**	23 (10)	0	0	5	3	UNSP	1	2	0.38	4.3
*Juncus effusus**	23 (4)	0	0	2	2	ANIMm	1	5	0	0
Salix cinerea	21 (2)	2 (2)	0	1	1	WINDp	1	7	0.19	0
*Poa pratensis**	15 (6)	2 (2)	1 (1)	8	6	UNSP	2	2	0.05	5.6
*Juncus bufonius**	14 (3)	0	1 (1)	2	4	ANIMm	1	1	0.49	0
*Plantago major**	11 (10)	1 (1)	2 (2)	8	5	ANIMm	2	2	1	7.1
*Eupatorium cannabinum**	7 (3)	4 (2)	0	2	2	WINDp	2	5	0.12	63.6
*Lolium perenne**	10 (7)	0	1 (1)	4	4	UNSP	4	2	0.25	0
*Senecio vulgaris**	7 (3)	0	4 (4)	3	2	WINDp	1	2	0.67	54.5
*Artemisia vulgaris**	8 (5)	1 (1)	0	5	5	UNSP	1	5	0.33	0
*Polygonum mite**	7 (4)	2 (1)	0	4	3	UNSP	4	2		100
*Deschampsia cespitosa**	8 (2)	0	0	1	1	ANIMa	2	3	0.88	37.5
*Festuca rubra**	4 (2)	4 (2)	0	2	2	ANIMa	3	2	0.04	0
*Dactylis glomerata**	5 (4)	2 (2)	0	6	4	UNSP	3	3	0.91	0
Matricaria spp.*	7 (5)	0	0	3	3	UNSP	1	2	0.22	28.6
Hypericum perforatum	4 (3)	0	2 (1)	2	2	WINDc	1	3	0.03	0
Poa annua	4 (3)	2 (2)	0	4	4	UNSP	2	2	0.24	0
*Sonchus oleraceus**	3 (3)	2 (2)	1 (1)	5	4	WINDp	2	5	1	0
Chenopodium album	5 (3)	0	0	1	1	UNSP	4	5		0
*Lycopus europaeus**	5 (4)	0	0	3	2	AQ/AN	2	4	0.5	0
Polygonum persicaria	5 (2)	0	0	1	1	UNSP	5	4	0.33	0
Cerastium semidecandrum	0	4 (3)	0	1	1	WINDc	1	2	0.89	0
Trifolium repens	0	0	4 (2)	1	1	ANIMa	3	1	0	0
Anthriscus sylvestris	0	1 (1)	2 (2)	2	2	UNSP	5	3	0.44	0
*Bromus hordeaceus**	1 (1)	2 (1)	0	2	2	ANIMa	5	3	0.89	0
Echinochloa crus-galli	3 (1)	0	0	1	1	ANIMa	5	4	0.89	0
Gnaphalium uliginosum	2 (2)	0	1 (1)	1	2	WINDp	1	2	0.76	0
*Carex disticha**	2 (1)	0	0	1	1	UNSP	4	3	0.77	0
Digitalis purpurea	2 (2)	0	0	1	1	WINDc	1	4	0.33	100
*Festuca pratensis**	2 (2)	0	0	2	2	ANIMa	4	4	0.11	0
*Galinsoga quadriradiata**	2 (2)	0	0	2	2	WINDp	1	3	0.58	50
Phleum arenarium	0	2 (2)	0	1	2	ANIMa	2	2	0.75	0
Phleum pratense	0	2 (2)	0	1	2	ANIMa	2	3		0
*Plantago lanceolata**	2 (1)	0	0	1	1	ANIMm	4	2	0.25	0
*Ranunculus repens**	2 (2)	0	0	2	2	AQ/AN	5	2	0.11	0
*Scrophularia auriculata**	2 (1)	0	0	1	1	AQ/WIc	1	3	0.12	0

Species identified only once in samples of (1) **Galloway cattle**: *Cardamine pratensis**, *Centaurea nigra*, *Cerastium glomeratum**, *Chaerophyllum temulum**, *Cirsium vulgare**, *Conyza canadensis**, *Crepis capillaris**, *Glyceria fluitans**, *Hieracium umbellatum*, *Hypericum tetrapterum**, *Juncus articulatus**, *Mentha aquatica**, *Myosotis cespitosa*, *Phalaris arundinacea**, *Polygonum aviculare**, *Rumex acetosa**, *Taraxacum* spp.*, *Trifolium pratense**; (2) **Donkey**: *Geum urbanum*, *Sonchus asper*; (3) **Horse**: *Phacelia tanacetifolia*, *Tanacetum vulgare*.

Table 2. Temporal gradient (turnover) in epizoochorous species composition, indicated by significant Spearman rank correlations between DCA sample-scores (axis 1) and sampling months (last column), for reserves with at least 10 non-empty samples collected in at least three different months. Month numbers reflect the vegetation season, from May (5) till January (13).

Reserve	Herbivore species	No. of samples (non-empty)	No. of species	No. of seedlings	Sampling months	Correlation DCA1/sampling month	
Houtsaegerduinen	D	41	30	2335	6-7-8-10	0.94	***
Oude Stadswallen	GD	10	15	1384	5-8-11	0.87	**
Mechels Broek	GHD	27	37	1068	5-6-7-9-10-11-13	0.80	***
Webbekomsbroek	H	13	17	193	8-9-12	0.19	ns
Mispeldonk	G	12	17	92	5-6-7-9-11	0.05	ns

G = Galloway cattle ; H = horse; D = donkey; *** = $P \leq 0.001$; ** = $P \leq 0.01$; ns = not significant.

Discussion

This study demonstrates that large herbivores disperse considerable quantities of viable seeds from a wide range of plant species in their fur (Tables 1 and 2). Given the number of herbivores used in Flemish nature reserves, the numbers of seeds dispersed within or between reserves may be hundreds of thousands, while the highly variable and relatively low germination performance of some species (Fig. 2) suggests that the actual number of dispersed seeds and species is much higher (cf. Stender et al. 1997). It is not clear whether some of the seeds were not viable, or whether germination conditions were suboptimal. However, germination in natural conditions (see Turnbull et al. 2000) is probably much lower than suggested by the seedling emergence method, in spite of the possibilities for 'directed dispersal' provided by zoochory (Janzen et al. 1989; Wenny 2001).

Plant traits

A wide variety of dispersal adaptations (adhesive, wind, water, unspecialized) was represented among the epizoochorously dispersed species, but seeds with fleshy fruits (typically dispersed by frugivores) and ant-dispersed seeds were absent from the samples (Table 1). Thus, epizoochory is not restricted to seeds with obvious adhesive adaptations, despite the efficiency of these structures (see also Couvreur et al. 2004, In press b). The combination of the wide range of plant heights (small species can be picked up by lying or wallowing animals; see Fischer et al. 1996) and seed weights (heavy seeds may possess more adhesive properties; see Kiviniemi & Telenius 1998) among the dispersed species, suggests that most grassland species are, theoretically, capable of adhesive dispersal (see also Fischer et al. 1996).

Herbivore species

Galloway cattle seem better dispersers than horses, probably due to their longer hair (see also Couvreur et al. 2004, In press b) and 'bulldozer' behaviour. Horses can still be effective seed dispersers over shorter distances (Couvreur et al. 2004b), as illustrated by the following observation in the 'Webbekomsbroek' reserve: 1080 *Rumex obtusifolius* seeds (from 2129 counted seeds) germinated from three horse samples (not included in the data set), which were collected after the horses walked through seed bearing *Rumex obtusifolius* vegetation following a 'normal' sampling (resulting in almost-empty samples). The donkeys were not included in the statistical comparison because they did not share their main home reserve (Houtsaegerduinen) with other large herbivores. The vegetation in this coastal dune reserve was also quite different from most other reserves. This may explain the relatively high numbers of seedlings and species in the donkey samples (Fig. 3), including a few very adhesive species (e.g. *Cynoglossum officinale*, *Galium aparine* and *Anthriscus caucalis*).(see also Couvreur et al. In press a).

Temporal gradient

The epizoochorous species composition gradually changed in time, as demonstrated by the high correlations between the month of collection of the samples and their scores on axis 1 of the ordination based on the species composition of the samples (Table 2). Such a turnover (see also Fischer et al. 1996; Heinken 2000) results from the fact that seed setting periods vary with species and retention times of seeds in fur are usually short (cf. Couvreur et al. 2004b). A temporal gradient in epizoochorous species composition could not be shown for two of the five examined reserves, possibly due to insufficient data (Table 2) or to the (accidental) lack of species with a sufficiently delineated seed shedding period in the samples. Several of the abundant epizoochorous species occurred indeed in samples of at least seven different months (e.g. *Urtica dioica*, *Rumex obtusifolius*, *Holcus lanatus*), and 25% of all 75 species were observed to be dispersed at least in four different months.

Plant migration, nature management and conservation

The examined herbivores serve as models for wild mammals and for herbivores currently used in agriculture and nature management. Similar seed dispersal mechanisms must have occurred in the past, when natu-

ral populations of large mammals still populated these regions. Our results may, therefore, help to understand the role of epizoochory in former plant migrations. In the present western European landscape most natural populations of large mammals have vanished or have been greatly reduced. Habitat loss and fragmentation has limited the migration of animals and the distances over which they disperse seeds (Higgins et al. 2003). We showed that the actual role of domesticated large herbivores may still be considerable in nature reserves, where grazing is an important management measure. Although potential dispersal distances are restricted by the size of the reserves, regular animal transport between reserves (up to 200 km), such as in the seasonal grazing system in Flanders, increase the herbivores' artificial home ranges and thus the seed movement distances (Fig. 1). We observed 2522 viable seeds of 52 plant species dispersing between different reserves; since we examined only a fraction of the herbivores transferred annually between Flemish reserves, the actual total seed flow must be considerable. In addition, herbivores also disperse seeds by endozoochory (Janzen 1984; Pakeman 2001; Pakeman et al. 2002), generally with higher seed quantities per herbivore (Cosyns et al. in press), and a complementary set of plant species (Couvreur et al. In press a). Given the importance of long-distance dispersal (Clark et al. 1998), these transfers may be (besides seed dispersal by man and mowing machinery; Couvreur & Hermy 2002) the only remaining 'link' between isolated reserves, in terms of genetically connecting plant populations and of supplying seeds of 'new species'.

Domesticated large herbivores may, thus, partly adopt the role of extinct wild animals in seed dispersal. Consequently, they could be an important instrument in ecological restoration projects, which are often confronted with seed dispersal limitations (Strykstra et al. 1998; Bakker & Berendse 1999; Pywell et al. 2002). In a restoration context, herbivore movement could be strategically directed in space and time, from target seed sources towards insufficiently developed vegetation. The long-haired Galloway cattle seems suited for this purpose (see also Stender et al. 1997; Couvreur et al. 2004, In press b). Without animals as 'mobile links' (see also Poschlod et al. 1996; Lundberg & Moberg 2003), vegetation development may be much more restricted and slower as a result of dispersal limitation, particularly in new nature reserves established on former agricultural land (see also Briers 2002). The presence of many species lacking seed bank formation (in contrast to endozoochory; Pakeman et al. 2002) is also important in a nature restoration point of view, since the loss of species with short-lived seeds can only be counteracted by successful dispersal.

Herbivores as dispersal promoting mobile links could partly counteract the catastrophic effect on biodiversity of the disappearance of free-ranging wild animals and migrating herds. Moreover, the herbivores enhance the dispersal opportunities of plants over distances which might be crucial in the face of climate change (see also Watkinson & Gill 2002; Higgins et al. 2003).

Acknowledgements. Research was supported by a Research Assistant Grant from the Fund for Scientific Research, Flanders (F.W.O.). We thank Bert Delanoeije, Natuurpunt and the Ministry of the Flemish Community, AMINAL, Department of Nature for cooperation in data collection, and Eric Van Beek, Matylda Strojnowska and Slawomira Wojtas for help with seedling identification. Bea Bossuyt and Olivier Honnay provided useful comments on an earlier version of the manuscript.

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Received 31 October 2003;
Accepted 1 July 2004.
Co-ordinating Editor: K. Thompson.

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App. 1. List of nature reserves where samples of epizoochorous material were collected (the codes correspond to Fig. 1). Columns 3-5 show the sampled herbivore species (G = Galloway cattle; H = horse; D = donkey), the number of samples (in the case of several herbivore species, numbers are given in the same order as in column 3), and the number of different sampling months. In columns 6-9, the total number of plant species and seedlings identified in the samples of each reserve is given, as well as the mean species and seedling number per sample. In all reserves except those with 'no transport' in column 10, at least part of the samples were collected after transport of the herbivores from a 'donor' reserve to a 'receptor' reserve (transport routes depicted in Fig. 1).

Code	Nature reserve	Herbivore species	Number of samples	Number of sampling months	Total species number	Total seedling number	Mean number of species per sample	Mean number of seedlings per sample	Herbivore transport
1	Houtsaegerduinen	DH	41+1	5	30	2335	4	55.6	no transport
2	Mechels Broek	GDH	24+1+4	7	37	1068	3.2	36.8	donor + receptor
3	Webbekomsbroek	H	18	3	17	193	1.8	10.7	no transport
4	Mispeldonk	G	16	5	17	92	2	5.8	donor + receptor
5	Hageven	GH	10+3	2	9	148	2.2	11.4	donor + receptor
6	Oude stadswallen	GD	8+4	3	15	1384	2.8	115.3	donor
7	Wellemeersen	G	9	3	8	55	1.9	6.1	donor
8	D'heye-Blutsyde	G	8	1	2	14	0.8	1.8	no transport
9	Hondsbossen	G	7	2	10	39	2.7	5.6	donor
10	Altembroek	G	6	3	16	145	6	24.2	donor + receptor
11	Sluismeer	G	4	1	5	30	2.3	7.5	donor
12	Visbeek-Kindernauw	G	4	1	10	28	3.5	7	donor
13	Zuunvallei	G	4	1	4	6	1	1.5	donor
14	Kesterbeekvallei	G	4	1	0	0	0	0	donor + receptor
15	Langdonken	G	4	1	6	93	2.5	23.3	donor + receptor
16	De Westhoek	H	3	1	4	0	0	0	no transport
17	Demerbroeken	G	3	1	0	4	1	1.3	donor
18	Maten	G	3	1	6	12	2.3	4	donor
19	Moenebroek	G	2	1	10	584	7	292	no transport
20	Blankaart	G	2	1	1	1	0.5	0.5	donor
21	Scheldemeersen	G	2	1	12	120	8	60	donor
22	Gelinden	G	1	1	2	2	2	2	donor
23	Hoogmoerheide	G	1	1	0	0	0	0	donor
24	Kalkense Meersen	G	1	1	2	2	2	2	donor
25	Leiemeersen	G	1	1	6	26	6	26	donor
26	Maaswinkel	H	1	1	0	0	0	0	donor
27	Zevenbergen	G	1	1	3	4	3	4	donor
	Sum		**201**		**75**	**6385**			

App. 1. Internet supplement to: Couvreur M.; Christiaen B.; Verheyen K. & Hermy M. 2004. Large herbivores as mobile links within and between isolated nature reserves through adhesive seed dispersal. *Appl. Veg. Sci.* 7: 229-236.

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Author(s): Kelly K. Crane, Michael A. Smith, Doug Reynolds
Source: *Journal of Range Management*, Vol. 50, No. 4 (Jul., 1997), pp. 374-380
Published by: Allen Press and Society for Range Management
Stable URL: http://www.jstor.org/stable/4003303
Accessed: 14/09/2009 16:57

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J. Range Manage.
50:374–380

Habitat selection patterns of feral horses in southcentral Wyoming

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Abstract

Feral horse habitat selection patterns and forage attributes on available habitats were studied on public rangelands of southcentral Wyoming. Environmental assessments preceding roundup of excess horses requires resource data to justify the number of horses removed. Randomly selected bands of horses were followed for 24-hour observation periods during the spring and summer to determine if they utilized habitats in proportion to their abundance. We also determined if forage abundance, succulence (an index to forage palatability), percent utilization, and dietary composition were related to habitats selected. Streamsides, bog/meadows, and mountain sagebrush habitats were preferentially selected ($p \leq 0.05$). Lowland sagebrush habitats were avoided and no apparent selection behavior was shown for grassland and coniferous forest habitats. Forage abundance, palatability, and percent utilization were higher ($p \leq 0.05$) in streamside and bog/meadow habitat classes. Diet composition indicated that sedges (*Carex* sp.), common in streamsides and bog/meadows, were an important forage of feral horses. Palatability and abundance of graminoid vegetation and proximity to preferred habitats seemed to be the primary influences on habitat selection by feral horses.

Key Words: forage abundance, succulence, utilization

Resúmen

Se estudiaron la selección del hábitat y los atributos asociados del forrajear en cada hábitat disponible a los caballos silvestres en las dehesas públicas de la zona sur central del estado de Wyoming. Las evaluaciones del medio ambiente que preceden el rodeo de los caballos determinados de ser en exceso requieren la acumulación de datos de los recursos para justificar el número de caballos que se van a reubicar. Se observaron unas bandas de caballos elegidas al azar por períodos de veinticuatro horas durante la primavera y el verano para determinar si utilizaban cada hábitat en proporción con su abundancia. También se investigó si la abundancia del forraje, la suculencia (un índice del aspecto de deseo del forraje), el porcentaje de la utilización, y la composición dietética se relacionaron con cada hábitat elegido. Las orillas de los arroyos, las ciénagas/los prados, y el hábitat donde crece la artemisa de la montaña se destacaron por ser preferibles ($p \leq .05$). La abundancia del forraje, el deseo del forraje, y el porcentaje de utilización eran los variables más altos ($p \leq .05$) en las dos clases de hábitat de las orillas de los arroyos y las ciénagas/los prados. La investigación de la composición de la dieta indicó que las juncias (*Carex* sp.), una planta común en las orillas, las ciénagas y los prados, eran un forraje importante de los caballos silvestres. El deseo del forraje, la abundancia de la vegetación herbácea, y la cercanía de cada hábitat preferido parecían ser las influencias más importantes en la elección de hábitat por parte de los caballos silvestres.

Management of rangeland is contingent upon understanding the influences of each species of herbivore on the system. The impact of feral horses (*Equus caballus*) on plant communities and physiographic areas must be determined to provide a basis for the planned herd size, to quantify numbers to remove, and potential impacts on other species.

A recently completed census estimated that over 46,000 feral horses inhabit federally owned rangelands in the western United States (USDI-BLM and USDA-FS 1993). The potential for rapid population growth (Eberhardt et al. 1982, Boyd 1980, Cook 1975) coupled with the management constraints of the Wild Free-Roaming Horse and Burro Act of 1971, has lead to excessive feral horse densities in important habitats on many public rangelands (Krysl et al. 1984, Cook 1975).

Krysl et al. (1984), Denniston et al. (1982), Rittenhouse et al. (1982), Salter and Hudson (1979) suggest similarities in habitat selection and diet composition, thus a potential for interspecific competition between feral horses and other domestic and wild herbivores. Most feral horse habitat selection studies in the western U. S. were conducted in sagebrush steppe or desert areas (Ganskopp and Vavra 1986, Denniston et al. 1982, Miller 1983) ecosystems with a relatively low diversity of habitats, where water is often the determining factor in habitat selection. The area of the study described here has diverse habitats and abundant water sources. In such an area, Salter and Hudson (1979) found that forage attributes including standing crop and quality were the most important factors influencing habitat selection by horses and other large herbivores (Smith et al. 1992, Pinchak et al. 1991, and Senft et al. 1985).

Research was funded by Rangeland Ecology and Watershed Management Department, Cooperative Extension Service, and Carbon County Cooperative Extension office, University of Wyoming; and Wyoming State Grazing Board. The study was conducted in cooperation with the Sun Ranch, the Sun Ranch Stewardship Committee, and the Lander Resource Area of the Rawlins District, BLM. Authors wish to thank Drs. Fred Lindzey and Bill Laycock for assistance with study design and editing.

Manuscript accepted 18 Aug. 1996.

Our research was initiated to address the lack of information regarding feral horse habitat selection and activity patterns in an area of southcentral Wyoming. We hypothesized that greater standing crop and quality of forage would be positively related to habitat selection by feral horses, and that this would result in their preference for riparian plant communities over uplands. Explicitly tested hypotheses were that proportions of horses using each of the various habitat classes in the study area would not be the same as the proportion of the study area occupied by each habitat class, and that vegetation abundance, palatability (quality), and utilization, would not be equal for all habitat classes. We also nonstatistically evaluated the diet composition of feral horses to ascertain if feral horse diet composition was consistent with observed habitat selection patterns.

Materials and Methods

Study Area

The study area is located in the Sweetwater River valley of southcentral Wyoming, and includes the Willow, Cooper, and Spring Creek drainages on the north slope of Green Mountain (Fig. 1). To meet the assumptions of our statistical analysis, the study area was defined by the smallest convex polygon enclosing all horse relocation points (Johnson 1980). The study area is within the 28,633-ha Whiskey Peak grazing allotment administered by the Bureau of Land Management. Elevations on the allotment range from 1,976 to 2,812 meters. Thirty-year average annual precipitation (1951–1980) was 25.4 cm at the Muddy Gap Junction of highways US287 and WY220, one-half occurring as snowfall. Average annual high and low temperatures at the same station were 13.4 and 0.33°C, respectively (Martner 1986). The frost free period varies elevationally from 114 to <60 days (BLM 1990).

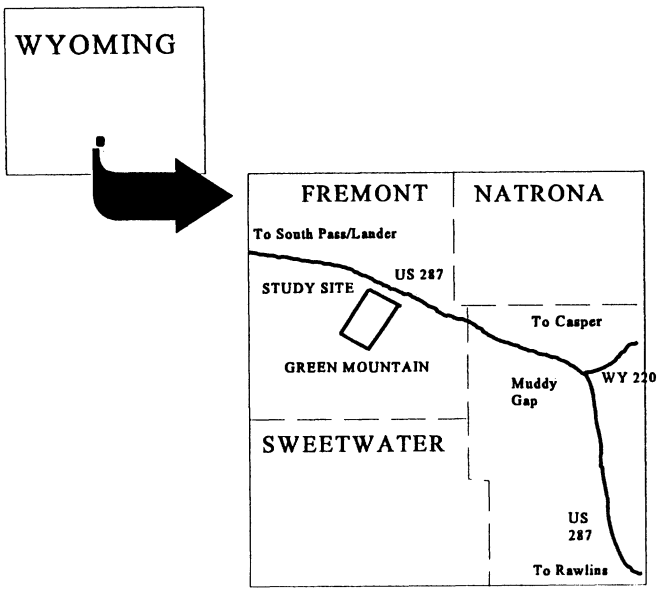


Fig. 1. Study area location in southcentral Wyoming.

Topographic features of the study area include outwash plains, gently rolling hills, forested and open ridges, canyons, and rock outcrops. Soils are generally well developed and of loamy texture, with the occurrence of some coarse sandy and skeletal, very gravelly, or very cobbly soils (BLM 1990).

Plant communities and associated physiographic habitats occurring on the Whiskey Peak allotment were designated for our purposes as streamside, bog/meadow, mountain sagebrush, lowland sagebrush, grassland, and coniferous forest. The delineation of these habitat classes was based on dominant vegetation, topographic position, and geographic location. Streamside habitats were areas within 5 m of a water course with a willow (*Salix* spp.)/graminoid plant community. Bog/meadow habitats were low-lying areas associated with surface and/or subsurface water (other than streamsides) which supported a more mesic graminoid plant community than surrounding areas. Lowland sagebrush habitats were generally alluvial plains dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. var. *wyomingensis* (Beetle and Young) Welsh) and graminiods situated geographically north from and not interspersed with other habitats. Coniferous forest habitats had a 50–90% canopy coverage of limber pine (*Pinus flexilis* James), lodge pine pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats.) and other conifers and usually supported understory graminoid/forb communities different from adjacent non-forested habitats. The mountain sagebrush habitat class was largely non-forested slopes and ridges of Green Mountain and Owl Hills dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. var. *vaseyana* Rydb.) and graminoids, and intermingled with coniferous forest habitat. Grasslands were dominated by graminoids and usually occurred on high elevation, wind-swept slopes. Area estimates from digitized orthophoto maps (1:24,000 scale) indicate approximately 0.05, 0.06, 28, 59, 0.07, and 12% of the study area were streamside, bog/meadow, mountain sagebrush, lowland sagebrush, grassland, and coniferous forest, respectively.

The Whiskey Peak allotment supported approximately 75% of the 500 feral horses within the Green Mountain Wild Horse Herd Management Area prior to 1993. A roundup during the summer and fall of 1993 reduced the population to planned management levels of between 170 and 300 horses (BLM 1993). In addition to horses, the area also supports populations of pronghorn antelope (*Antilocarpa americana americana* Ord), elk (*Cervus elaphus nelsoni* Bailey), and mule deer (*Odocoileus hemionus hemionus* Rafinesque). Seasonal cattle (*Bos taurus*) use (7,723 animal unit months) occurs annually but did not occur in 1993 until after the conclusion of this study.

Habitat Selection

Habitat selection patterns of feral horses were observed in 1992 and 1993. During the June-August 1992 field season, habitat selection was estimated from 320 repeated observations of 20 individually identified horses of different sex and age classes. Daily surveys during daylight hours were conducted to relocate these individuals and determine their activity and habitat selection from independent, instantaneous observations. After the season, we suspected a visibility sampling bias in the 1992 observations resulting from potentially lower probabilities of horse relocation in wooded streamside and coniferous forest habitats.(Oedekoven and Lindzey 1987, Neu et al. 1974).

To reduce potential bias in 1993, 23 randomly selected bands of undisturbed horses were followed and visually observed during daylight hours. Scan sampling (Altmann 1974) at 30-minute

intervals was used to determine the proportion of horses in the band in each habitat class, activity class (feeding, idling, or traveling), and time of day class (1=0500-0900 hours, 2=0901-1300 hours, 3=1301-1700 hours, 4=1701-2200 hours). Feeding included harvesting forage, drinking, and travel <5 steps while feeding. Idling included resting and minor movements. Traveling was directed movement of more than 5 steps. Geographic locations were recorded to allow determining distance to water and minimum convex polygon enclosing the study area.

Observation periods began during daylight hours, terminated at dark, resumed at daylight, and continued until the same time as the initial observation the previous day. Band relocations at daylight were usually close to where they were last seen at dark the previous evening. Horses were observed from a distance (≈200m) that would not disrupt "normal" habitat selection and activity patterns with the aid of a 10 to 20 power spotting scope and binoculars. Horse bands were followed on horseback.

Habitat selection data from 1992 were summarized by determining the proportion of total observations occurring in each habitat. All 1993 observations were summarized by calculating the proportion of animals in each activity by habitat and time of day class.

Vegetation Utilization, Palatability, and Abundance

Percent utilization and percent moisture (succulence) were determined for the most abundant graminoid plant species on each habitat. Feral horses select primarily graminoid species (Krysl et al. 1984, Salter and Hudson 1979, Hansen 1976). Utilization will be indicative of the potential detriment of grazing on plant health. Utilization of plant species was determined through sequential biweekly late May through August 1993 estimates (n=7) of dry weight standing crop of 30 individually marked bunch grass plants or 0.01 m^2 quadrats containing one rhizomatous species along 3 transects (30m) in each habitat class (Smith et al. 1992). The difference between the average ending weight of grazed and ungrazed plants and ungrazed plants was used to calculate total percentage of herbage removal (utilization) for each habitat class. Bi-weekly utilization was not calculated because we observed relatively low levels of total utilization, and found no seasonal variation in feral horse habitat selection patterns with which to correlate seasonal utilization.

Forage succulence appears to be correlated with quality and palatability as herbivores usually graze plants with higher succulence, quality, and palatability (Smith et al. 1992, Pinchak et al. 1991, Senft 1985). Vegetation succulence was used as an index to forage palatability and quality. Randomly selected whole plant samples were collected from each habitat class (50 to 100 plants including major species with about 200-g total of plant material/habitat) at bi-weekly May–August intervals coinciding with utilization sampling. Green weights of these samples minus oven-dried (50°C, 36 hours) weights were divided by oven-dried weights to determine percent moisture (succulence).

Forage abundance as indicated by standing crop biomass of all herbage, above a minimum weight, was determined using visual obstruction measurements (following Robel et al. 1970). Biweekly May–August measurements were taken at 50 random points in each habitat class. The relationship between Robel readings and actual above-ground oven dry biomass was determined by taking the visual obstruction measurement in and harvesting 30 quadrats (0.25 m^2), followed by determining coefficients by simple linear regression in each habitat class.

Diet Composition

Fecal samples from feral horses were collected during the spring, summer, and winter of 1991 and 1992. A minimum of 5 samples were collected by searching the vicinity of 4–6 sites (depending on seasonal access) on the allotment. Only fecal material determined by freshness and color to have been deposited during the seasonal period was collected. Fecal piles were subsampled, material was mixed and 5 subsamples taken. Subsamples were sent to a commercial lab (AFAB Laboratories in Ft. Collins, Colo.) for identification of plant species in feces. The relative frequency of fragments of each plant species in each sample were quantified by microhistological procedures outlined by Sparks and Malechek (1968). Plant epidermal characteristics determined from reference slides are used to identify species in microscope slides of fecal materials. Twenty fields per slide and 5 slides per sample were examined. Data were summarized by sites within seasons.

Statistical Analyses

Chi-square analyses (Neu et al. 1974) of 1992 and 1993 data separately were employed to determine whether feral horses utilized all habitat classes in proportion to their availability. Calculated χ^2 statistics may be biased if expected values are very low (eg. streamside, bog/meadow, and grassland habitat classes),thus creating an artificially large χ^2 and making the probability of a type I error greater than apriori p (Zar 1984). However, we did not combine these habitat classes because the mean (over all classes) expected value exceeded the minimum suggested by Roscoe and Byars (1971).

If χ^2 analyses indicated a significant difference existed between habitat selection and availability, relative preference for individual habitat classes was determined using the Bonferroni Z simultaneous confidence interval (CI) approach described by Neu et al. (1974) and revised by Byers et al. (1984). If the availability of a habitat class was less or greater than the CI, the habitat was considered to be preferred or not preferred respectively.

A General Linear Model analysis of variance (AOV) (Hicks 1973) was used to test for significant differences in vegetation attributes between habitat classes. If a significant difference was observed, a Scheffe mean separation test was employed. A factorial AOV design was used to evaluate the influence of time of day class, month, habitat class, and horse activity on proportions of horses in habitats. The 1993 data summary experimental unit for analysis was a monthly mean (n=3) proportion of horses for each time of day (n=4), habitat (n=6) and activity (n=3) class. The data assumptions of independence, normality of residuals, and equal variances necessary for AOV were evaluated prior to hypothesis testing.

Analyses were performed using the Statistical Analysis System (SAS Institute 1988) and Statistix (Statistix 1988) statistical software packages. All statistical tests were evaluated at the $p \leq 0.05$ level of significance.

Results and Discussion

Habitat Selection

Overall expected usage and observed usage (Table 1) were significantly different ($p \leq 0.05$) in 1993. Comparison of simultaneous confidence intervals to proportion of the area in each habitat (Table 1) indicated that the proportional use of streamside,

Table 1. Total area, relative area, expected use, and observed use by feral horses for 6 habitat classes on a study area within the Whiskey Peak Allotment, southcentral Wyoming, 1993.

Habitat Class	Total Area	Relative Area (P_{io})	Relative Usage (U_{io})	Expected Use ($E_i = n^1p_{io}$)	Observed Use (O_i)[2]	Bonferroni Intervals for U_{io}	Apparent[3] Selection Behavior
	(ha)						
Streamside	31	0.005	0.09	0.43	7.7	$0.008 \le P_1 \le 0.17$*	+
Bog/Meadow						$0.029 \le P_2 \le 0.22$*	+
	39	0.006	0.12	0.53	11.7		
Mtn. Sagebrush						$0.37 \le P_3 \le 0.65$*	+
	1699	0.28	0.51	24.92	45.4		
Low. Sagebrush						$0.03 \le P_4 \le 0.30$*	-
	3620	0.59	0.17	52.51	15.1		
Grassland						$0 \le P_5 \le 0.12$	=
	44	0.007	0.05	0.62	4.5		
Coniferous Forest	750	0.12	0.07	10.68	6.2	$0 \le P_6 \le 0.14$	=

[1] n=86 for streamside and 89 for other habitat classes
[2] $X^2 5 = 441$, p=0.00; $X^2_{(5,\ \alpha=0.05)} = 11.07$
[3] + use greater than expected, p≤0.05
= use not different from expected, p≤0.05
- use less than expected, p≤0.05

bog/meadow, and mountain sagebrush habitats was significantly greater ($p \le 0.05$) than the proportion of the study area occupied by these habitat classes. In contrast, lowland sagebrush habitats (Table 1) were used significantly less ($p \le 0.05$) than the extent of these habitats within the study area. Feral horses used the coniferous forest and grassland habitat classes in similar ($p \le 0.05$) proportion to their relative abundance on the study area.

Our suspicion of a visibility bias in the method of observing horses during 1992 appeared to be confirmed by the reduced proportion of horses observed in the streamside (1992=0.02, 1993=0.09) (Tables 1 and 2). Otherwise the 1992 results generally support the results of 1993 since (Byers et al. 1984) the observed proportions of habitat use in 1992 (Table 2) occur within the confidence intervals of proportional use in 1993 (Table 1). Many streamside habitats support dense stands of willow, cottonwood, and aspen which obscure horses. This problem was mitigated with the 1993 sampling method, likely increasing the proportion of streamside observations.

A feral horse monitoring program, independent of our study, was conducted in 1992 in the general vicinity of our study area, by the Lander Resource Area of the Bureau of Land Management (unpublished). These results lend support to our overall conclusions that feral horses show a preference for riparian habitats.

The degree of selection for riparian habitats by unmanaged feral horses on this study area seems noteworthy considering the widespread concern for the condition of riparian vegetation; the streamside and bog/meadow habitats combined account for slightly over 1% of the study area, but received 21% of the use by feral horses. The preference of large herbivores for riparian habitats is well documented (Smith et al. 1992, Pinchak et al. 1991, Roath and Krueger 1982), yet this selection behavior in feral horses has not been widely reported in the literature. Ganskopp and Vavra (1986) reported that feral horses in the northern sagebrush steppe exhibited no preference for a particular plant community, and instead made the greatest use of the most prevalent habitat. In contrast, the results of Salter and Hudson (1979) and Hubbard and Hansen (1976) indicate that *Carices* were the major dietary constituent of feral horses, suggesting that horses select more mesic communities in their foraging behavior if they are available. Our findings are consistent with Salter's (1979) observations that feral horses utilized certain meadow types more heavily on a year-long basis. Berger (1986) also reported that

Table. 2. Total area, relative area, expected use, and observed use by feral horses for 6 habitat classes on a study area within the Whiskey Peak Allotment, southcentral Wyoming, 1992.

Habitat Class	Total Area	Relative Area (P_{io})	Relative Usage (U_{io})	Expected Use ($E_i = n^1p_{io}$)	Observed Use (O_i)[2]	Bonferroni Intervals for U_{io}	Apparent[3] Selection Behavior
	(ha)						
Streamside	31	0.005	0.02	1.6	6.4	$0 \le P_1 \le 0.041$	=
Bog/Meadow	39	0.006	0.12	1.92	38.4	$0.072 \le P_2 \le 0.17$*	+
Mtn. Sagebrush	1699	0.28	0.59	89.6	188.8	$0.52 \le P_3 \le 0.66$*	+
Low. Sagebrush	3620	0.59	0.17	189.0	54.4	$0.12 \le P_4 \le 0.23$*	-
Grassland	44	0.007	0.04	2.24	12.8	$0.01 \le P_5 \le 0.07$*	+
Coniferous Forest	750	0.12	0.06	38.0	19.2	$0.25 \le P_6 \le 0.10$*	-

[1] n=320
[2] $X^2 5 = 320.4$, p=0.00
[3] + use greater than expected, p≤0.05
= use not different from expected, p≤0.05
- use less than expected, p≤0.05

Table 3. Herbaceous vegetation standing crop (g/0.25m^2 ± SE[1]) of 4 habitat classes on Whiskey Peak Allotment in southcentral Wyoming, 1993.

	Herbaceous Standing Crop Sampling Period					
Habitat Class	6/30	7/7	7/20	8/4	8/17	Average
	(g/0.25m^2 ± SE[1])					
Streamside	24 ± 1.84	22 ± 1.27	33 ± 1.97	43 ± 2.40	21 ± 1.27	29 ± 4.02a[3]
Bog/Meadow	30 ± 1.84	33 ± 1.97	41 ± 1.84	66 ± 5.94	52 ± 3.68	44 ± 5.81b
Grassland	8 ± 1.27	48 ± 13.29	15 ± 1.84	13 ± 1.56	21 ± 2.12	20 ± 6.26c
Coniferous Forest	<4[2]	5 ± .424	4 ±.424	5 ± .57	6 ± .57	5 ± 0.22d

[1]SE = Standard error N=5 dates, 50 observations within dates
[2]Standing crop below the minimum detectable amount
[3]Means followed by the same letter were not significantly different, p≤0.05

meadows received the greatest use in proportion to their availability, when compared to all other habitats.

Forages in the streamside and bog/meadow habitat classes had the greatest ($p < 0.05$) vegetation standing crop (Table 3) and were high ($p \leq 0.05$) in succulence (Table 4) compared to other habitats. Habitat selection by large herbivores is reported to be positively associated with forage biomass and succulence (Smith et al. 1992, Pinchak et al. 1991, Senft et al. 1985). Salter and Hudson (1979) found that seasonal variability in diet composition of feral horses was related to forage palatability and abundance. Utilization levels (Table 5) on these habitats, while not high because of the herd reduction, was significantly higher ($p \leq 0.05$) than on all other habitats. Higher horse numbers would undoubtedly result in these habitats having the greatest potential to receive overuse of the vegetation resource.

The later growth initiation by forage species at higher elevations may partially explain the preference of horses for the mountain sagebrush habitat class over the lowland sagebrush habitats during the months of this study. Forage abundance (Table 3) was low for both habitats, being below the minimum measurable with the Robel et al. (1970) technique (≈ 4 g/0.25m^2) but succulence (Table 4) was higher ($p \leq 0.05$) in mountain sagebrush areas. Topographic diversity and proximity to other preferred habitat offer a better explanation of why feral horses may prefer mountain sagebrush habitats. Feral horses may select the open ridges and slopes of this habitat class for refuge from insects (Keiper and Berger 1982), or to enhance their visual assessment of threats (Ganskopp and Vavra 1986). Miller (1983) also found that the proximity to ridges was a significant factor in the habitat selection of feral horses in the Red Desert of Wyoming. The preference for these habitats may also be related to the close proximity of many mountain sagebrush habitats to streamside and bog/meadow habitats. Following feeding or watering in riparian habitat classes, horses moved into the adjacent mountain sagebrush habitats. However, the preference for the more abundant mountain sagebrush habitats was not reflected in significantly higher ($p \leq 0.05$) utilization (Table 5) because of the large area relative to animal numbers.

The lower use than availability of lowland sagebrush habitats may be related to low ($p \leq 0.05$) forage productivity (Table 3) and succulence (Table 4) compared to higher elevation habitats.

Table 4. Forage succulence (% moisture, dry weight basis4) of 6 habitat classes on Whiskey peak Allotment in southcentral Wyoming, 1993.

	Sampling Period[2]							
	5/27 SD[1]	6/10	6/24	7/7	7/20	8/4	8/17	Mean ± SE[1]
Habitat Class	(% moisture)							
Streamside	70	72	70	65	68	64	62	67 ± 1.47a[3]
Bog/Meadow	75	71	65	65	64	63	54	65 ± 2.49ab
Mtn. Sagebrush	74	64	62	58	54	49	42	58 ± 3.93bc
Low. Sagebrush	65	62	56	54	48	41	33	51 ± 4.27c
Grassland	72	69	65	59	42	47	36	56 ± 5.32c
Coniferous Forest	84	75	66	70	67	58	52	67 ± 4.08a

[1]SE = Standard deviation
[2]Bi-weekly sampling from 5/27 to 8/18
[3]Means followed by the same letter were not significantly different, p ≤ 0.05
[4]((wet weight-dry weight)/dry weight × 100=% moisture on a dry weight basis)
% moisture of fresh samples = ((%moisture dry basis/(% moisture dry basis + 100)) × 100

The avoidance of lowland sagebrush habitats by feral horses in this study illustrates seasonal movements from lower to higher elevations in summer. Area ranchers and agency personnel have observed that feral horses on the Whiskey Peak Allotment winter on lowland sagebrush sites where access to feed is less hampered by snow accumulation. We did observe a larger proportion of horses using the lowland sagebrush habitats during the early spring prior to initiation of observations. This selection behavior may also be a result of earlier growth initiation by forage species on these lower elevation sites. Miller (1983) and Salter and Hudson (1979) also concluded that areas which remained snow-free or had reduced snow depth throughout the winter were exploited as feeding habitat by feral horses. Salter (1979) also suggested that habitat selection during early spring was related to stage of forage growth and that areas which "green-up" first were most heavily used for grazing. Although water is abundant on the study area as a whole, during the summer distance to water from the northern reaches of the lowland sagebrush area may exceed 1.5 km. This distance to water may be sufficient to discourage feral horse use of these sites.

Table 5. Utilization (% ± SE[1]) of annual forage growth in 6 habitat classes on Whiskey Peak Allotment in southcentral Wyoming, as of 18 Aug. 1993.

Habitat Class	Utilization
	- - - (% + SE[1]) - - -
Streamside	7.5 ± 1.5 a[2]
Bog/Meadow	11.0 ± 2.9 a
Mtn. Sagebrush	2.3 ± .83 b
Lowland Sagebrush	2.0 ± 1.09 b
Grassland	2.2 ± 1.02 b
Coniferous Forest	2.9 ± 1.02 b

[1]SE = Standard Error N=5
[2]Means followed by the same letter were not significantly different, $p \leq 0.05$

No apparent selection behavior was observed for grassland habitats even though the abundance of forage (Table 3) on these sites was relatively high. Forage succulence (Table 4) was lower ($p \leq 0.05$) than on preferred habitats. The steep topographic position of grassland habitats and the distance to preferred riparian habitats may also have made these sites less attractive for foraging.

Coniferous forest habitats, used in proportion to their availability, had higher ($p \leq 0.05$) forage succulence (Table 4) but lower ($p \leq 0.05$) biomass (Table 3) than other habitats. This indicates that the influence of forage succulence on habitat selection is initiated above some minimum level of forage productivity. This habitat, as with all other abundant but less preferred habitats had lower ($p \leq 0.05$) utilization (Table 5) than the less abundant preferred habitats.

Horse Activities

The proportion of horses feeding, idling, or traveling did not differ significantly ($p \leq 0.05$) between habitat class or monthly categories. This lack of seasonal variation in habitat selection was also observed by Ganskopp and Vavra (1986) and Denniston et al. (1982).

Feral horses spent 61, 32, and 7% of their diurnal hours feeding, idling, and traveling, respectively. We observed a significant difference in feeding and loafing activities between different time classes (Fig. 2). Generally, horses spent morning and evening hours feeding and loafed during mid-day. Traveling was not significantly different between time classes. These results are consistent with observations reported by Salter and Hudson (1979). We found no significant interaction between diurnal activity patterns and habitat selection which suggests that feral horse activity patterns are independent of habitats used.

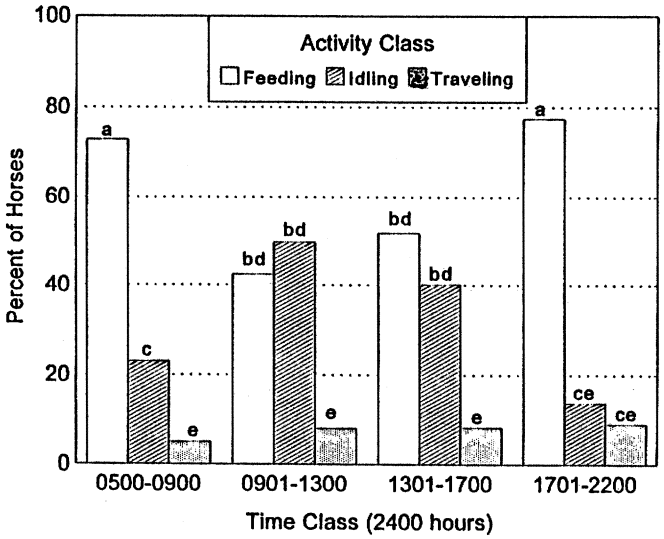


Fig. 2. Activity % in each time of day class in 1993.

Diet Composition

The annual diet of feral horses on this study area was comprised mostly of graminoid species with a relatively small and highly variable forb and shrub component (Table 6), similar to findings of Salter and Hudson (1979) and Hubbard and Hansen (1976). Forage species of the *Agropyron, Stipa,* and *Carex* genera were major dietary constituents during all seasons. The proportional intake of each forage species was relatively constant between seasons, except for *Carex* which increased in the spring and *Festuca* which increased in the summer consistent with the seasonal availability and use of habitats where these species occur. Microhistological analyses cannot distinguish between upland and mesic/aquatic *Carices*, however the increase in *Carices* consumption early in the growing season may reflect horses selection of upland species of this genus (threadleaf and needleleaf sedge, *C. filifolia* Nutt. and *C. stenophylla* Wahl., respectively) because of their early growth and high palatability in the spring. *Festuca* occurs on higher elevation sites of the study area that are only used in summer.

In general, *Carices* are the most important forage genus to feral

Table 6. Major dietary components (mean % ± SE[1]) of feral horses on the Whiskey Peak Allotment in southcentral Wyoming.

Plant Name	Winter 1991 (n=5)	Spring 1991 (n=5)	Summer 1991 (n=4)	Winter 1992 (n=6)	Spring 1992 (n=6)	Summer 1992 (n=4)
Graminoids			- - - - - - - - - - - - - - - - (% Relative Density ± SD[1]) - - - - - - - - - - - - - - - -			
Agropyron	13 ± 2.68	12 ± 2.23	14 ± 2	10 ± 1.22	8 ± 1.63	8 ± 2
Carex	24 ± 5.8	62 ± 7.15	31 ± 2.5	26 ± 4.49	41 ± 5.71	23 ± 5
Festuca	4 ± 1.34	< 1	18 ± 1.5	6 ± 2.44	8 ± 1.63	24 ± 12
Juncus	2 ± .89	1 ± .89	2 ± 1	1 ± .408	3 ± .816	< 1
Poa	< 1	1 ± .357	< 1	4 ± .816	9 ± 1.63	3 ± .5
Stipa comata	22 ± 7.15	18 ± 2.68	19 ± 1.5	28 ± 4.89	27 ± 4.49	32 ± 9
Oryzopsis	1 ± .89	2 ± .447	7 ± 3.5	1 ± .244	3 ± 1.22	1 ± .3
Forbs and Shrubs						
Total	23 ± 14.31	< 1	<1	19 ± 6.53	< 1	< 1

[1]SE=Standard error of n sites. Data were averages of pooled samples within sites.

horses in this study area. Although a portion of the total *Carex* intake is from upland species, selective preference of horses for streamside and bog/meadow habitats indicate that mesic and aquatic species of this genus represent a significant proportion of feral horse diets compared to other forage species. Dietary composition generally follows patterns of habitats selected by horses.

Conclusions

Selectivity, diets, and utilization observed in this study indicate any detrimental impacts from excessive numbers of feral horses would first be apparent in the streamside, bog/meadow, and secondarily in mountain sagebrush habitats of this study area. These habitats were preferentially selected by feral horses during the growing season on the study area, the most probable season of negative grazing impact. The streamside and bog/meadow habitats represent a small portion of the study area and the allotment as a whole, yet these are also the habitats preferred by wildlife (Dealy et al. 1981, Leckenby et al. 1982, Collins 1980, Hubbard 1977) and livestock (Smith et al. 1992, Pinchak et al. 1991, Hart et al. 1991, Roath and Krueger 1982). Further evidence of potential for spatial overlap between feral horses and elk occurs with their common preference for the open ridges of the mountain sagebrush habitats (Hart et al. 1991, Oedekoven and Lindzey 1987, Thomas and Toweill 1982, Julander and Jeffery 1964).

Feral horse numbers must be kept at appropriate levels to mitigate the potential for detrimental impacts to habitats. Feral horses should also be managed with the knowledge that there appears to be a potential for interspecific competition between horses and other large herbivores.

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Science Framework for Conservation and Restoration of the Sagebrush Biome: Linking the Department of the Interior's Integrated Rangeland Fire Management Strategy to Long-Term Strategic Conservation Actions

Part 2. Management Applications



Forest Service

Rocky Mountain Research Station

General Technical Report RMRS-GTR-389

April 2019

Crist, Michele R.; Chambers, Jeanne C.; Phillips, Susan L.; Prentice, Karen L.; Wiechman, Lief A., eds. 2019. Science framework for conservation and restoration of the sagebrush biome: Linking the Department of the Interior's Integrated Rangeland Fire Management Strategy to long-term strategic conservation actions. Part 2. Management applications. Gen. Tech. Rep. RMRS-GTR-389. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 237 p.

Abstract

The Science Framework is intended to link the Department of the Interior's Integrated Rangeland Fire Management Strategy with long-term strategic conservation and restoration actions in the sagebrush biome. The focus is on sagebrush (*Artemisia* spp.) ecosystems and sagebrush dependent species with an emphasis on Greater sage-grouse (*Centrocercus urophasianus*). Part 1 of the Science Framework, published in 2017, provides the scientific information and decision-support tools for prioritizing areas for management and determining effective management strategies across the sagebrush biome. Part 2, this document, provides the management considerations for applying the information and tools in Part 1. Part 2 is intended to facilitate implementation of resource management priorities and use of management strategies that increase ecosystem resilience to disturbance and resistance to nonnative invasive annual grasses. The target audience of Part 2 is field managers, resource specialists, and regional and national-level managers. The topics addressed in this volume include adaptive management and monitoring, climate adaptation, wildfire and vegetation management, nonnative invasive plant management, application of National Seed Strategy concepts, livestock grazing management, wild horse and burro considerations, and integration and tradeoffs. Geospatial data, maps, and models for the Science Framework are provided through the U.S. Geological Survey's ScienceBase database and Bureau of Land Management's Landscape Approach Data Portal. The Science Framework is intended to be adaptive and will be updated as additional data become available on other values and species at risk. It is anticipated that the Science Framework will be widely used to: (1) inform emerging strategies to conserve sagebrush ecosystems, sagebrush dependent species, and human uses of the sagebrush system; and (2) assist managers in prioritizing and planning on-the-ground restoration and mitigation actions across the sagebrush biome.

Keywords: sagebrush habitat, Greater sage-grouse, resilience, resistance, conservation, restoration, monitoring, adaptive management, climate adaptation, wildfire, nonnative invasive plants, National Seed Strategy, livestock grazing, wild horses and burros

Front cover photo. Sagebrush ecosystem in the Toiyabe Range, Nevada (photo: Jeanne Chambers, USDA Forest Service). Inset: Greater sage-grouse chick (photo: USDOI Fish and Wildlife Service).

Rear cover photo. Tail feathers of a Greater sage-grouse (photo: USDOI Fish and Wildlife Service).

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Acknowledgments

We thank the Bureau of Land Management for financial assistance and the numerous other agencies that provided in-kind support for this effort. We received comments from over 40 reviewers from State and Federal agencies, nongovernmental organizations (NGOs), and private individuals during two review processes that helped to improve the manuscript.

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8. WILD HORSE AND BURRO CONSIDERATIONS

Paul Griffin, Jared Bybee, Hope Woodward, Gail Collins, Jacob D. Hennig, and Jeanne C. Chambers

Introduction

Wild horses (*Equus caballus*) and wild burros (*E. asinus*), like domestic livestock, can alter sagebrush ecosystem structure and composition and affect habitat quality for sagebrush dependent species (Beever and Aldridge 2011). The presence of Federally protected wild horses and wild burros can also have substantial effects on the capacity for habitat restoration efforts to achieve conservation and restoration goals. In the Conservation Objectives Team Report (USDOI FWS 2013), the presence of wild horses and burros was considered a threat to Greater sage-grouse (*Centrocercus urophasianus*; hereafter, GRSG) habitat quality, particularly in the sage-grouse's western range (USDOI FWS 2013). Four years after the Conservation Objectives Team Report was published, wild horse population sizes on Bureau of Land Management (BLM) and Forest Service lands have almost doubled (USDOI BLM 2017).

Lands with Federally protected wild horses and burros are managed for multiple uses, so it can be difficult to separate their ecological effects. However, scientific studies designed to isolate the effects of various land uses lead to the conclusion that landscapes with greater wild horse and burro abundance tend to have lower resilience to disturbance and resistance to invasive plants than similar landscapes with herds at or below target levels (Beever and Aldridge 2011; Chambers et al. 2017 [hereafter, Part 1], section 5.3.8). Many studies corroborate the general understanding that wild horses can lead to biologically significant changes in sagebrush ecosystems, particularly when their populations are overabundant relative to forage and water resources. In the Great Basin, areas without wild horses had higher shrub cover, plant cover, species richness, native plant cover, and overall plant biomass, and lower cover of grazing-tolerant, unpalatable, and invasive plant species such as cheatgrass (*Bromus tectorum*), when compared to areas with horses (Beever et al. 2008; Boyd et al. 2017; Davies et al. 2014; Smith 1986; Zeigenfuss et al. 2014). There were also measurable increases in soil penetration resistance and erosion, decreases in ant mound and granivorous small mammal densities, and changes in reptile communities (Beever et al. 2003; Beever and Brussard 2004; Beever and Herrick 2006; Ostermann-Kelm et al. 2009).

Top: Wild horses at Cherry Spring in the Maverick-Medicine Herd Management Area, Nevada (photo: USDOI Bureau of Land Management). Middle left: Wild horses in Divide Basin Horse Management Area, Wyoming (photo: USDOI Bureau of Land Management). Middle right: Wild burros at Wood Hills spring in the Elko, Nevada, BLM District (photo: USDOI Bureau of Land Management). Bottom left: Wild Horses at Victoria spring in the Antelope Triple B complex (photo: USDOI Bureau of Land Management). Bottom right: Wild horse gather by the BLM (photo: USDOI Bureau of Land Management).

Wild horses can have severe impacts on water source quality, aquatic ecosystems, and riparian communities (Barnett 2002; Beever and Brussard 2000; Earnst et al. 2012; Kaweck 2016; Nordquist 2011; USDOI FWS 2008, 2012) and can sometimes exclude native ungulates from water sources (Gooch et al. 2017; Hall et al. 2016; Ostermann-Kelm et al. 2008; Perry et al. 2015; USDOI FWS 2008). Bird nest survival may be lower in areas with wild horses (Zalba and Cozzani 2004), and bird populations have recovered substantially after livestock or wild horses, or both, have been removed (Batchelor et al. 2015; Earnst et al. 2005, 2012). Wild horses can spread nonnative plant species, including cheatgrass, and may limit the effectiveness of reseeding projects (Beever et al. 2003; Couvreur et al. 2004; Jessop and Anderson 2007; Loydi and Zalba 2009). Even after domestic livestock are removed, continued wild horse use above appropriate management levels can cause ongoing detrimental ecosystem effects (Davies et al. 2014; USDOI FWS 2008), which may require several decades for recovery (e.g., Anderson and Inouye 2001).

Wild burros can have grazing and trampling impacts that are similar to wild horses (Carothers et al. 1976; Douglas and Hurst 1983; Hanley and Brady 1977) and can substantially affect riparian habitats (e.g., Tiller 1997) and native wildlife (e.g., Seegmiller and Ohmart 1981). Where wild burros and GRSG co-occur, year-round use by burros in low elevation habitats may lead to a high degree of overlap between burros and GRSG (Beever and Aldridge 2011).

In contrast to managed domestic livestock grazing (see section 7), neither the seasonal timing nor the intensity of grazing by Federally protected wild horses and burros can be managed, except through efforts to manage their numbers and distribution. Wild horses roam freely on the range year-round, and wild horse populations have the potential to grow 15 to 20 percent or more per year (Dawson 2005; Eberhardt et al. 1982; Garrott et al. 1991; Roelle et al. 2010; Scorolli and Cazorla 2010; Wolfe 1980). Although annual growth rates may be marginally lower in some areas where mountain lions (*Puma concolor*) can take foals (Turner 2015; Turner and Morrison 2001), horses tend to favor use of more open habitats (Schoenecker et al. 2016) that are dominated by grasses and shrubs and where ambush is less likely. For the majority of wild horse herds, there is little evidence that population growth is significantly affected by predation. As a result of the potential for wild horse populations to grow rapidly, impacts of wild horses on water, soil, vegetation, and native wildlife resources can increase exponentially unless there is active management to limit their population sizes.

On lands administered by the BLM, there were an estimated 72,674 BLM-administered, Federally protected wild horses and burros as of March 1, 2017, not including foals born in 2017 (USDOI BLM 2017). Approximately 60 percent of those are present within 13 million acres (5 million hectares) of GRSG habitat. Federal protections exist for an estimated 7,100 wild horses and 900 wild burros that occupy approximately 2 million acres (800,000 hectares) of Forest Service-administered lands. Approximately 446,065 acres (180,523 hectares) of active Territories administered by the Forest Service contain GRSG habitat, which is occupied by an estimated 3,400 wild horses and burros. Some wild horses also inhabit other Federal lands in the sagebrush biome, including lands administered by the National Park Service, U.S. Fish and Wildlife Service, or Department of Defense, and Native American reservations and tribal lands.

Although wild horses and burros can present challenges to achieving desired habitat conditions, wild horse management is a necessary requirement of planning for long-term sagebrush ecosystem and GRSG conservation. This section relates to management of Federal lands and the terms “wild horses”

and "wild burros" are used throughout. However, the specific legal status for any given wild horse or burro population has a large influence on management objectives and the ability to manage wild horse and burro impacts.

In the biological sense, all free-roaming horses and burros in North America are feral, meaning that they are descendants of domesticated animals brought to the Americas by European colonists. Horses went extinct in the Americas by the end of the Pleistocene, about 10,000 years ago (MacFadden 2005; Webb 1984). Burros evolved in Eurasia (Geigl et al. 2016). The published literature refers to free-roaming horses and burros as either feral or wild. In the ecological context the terms are interchangeable, but the term "wild" horse is associated with a specific legal status. Wild and free-roaming horses and burros under the jurisdiction of the BLM and Forest Service are designated "wild" as legally defined by the Wild Free Roaming Horses and Burros Act of 1971 (WFRHBA) as amended (Public Law 92–195), and are under the protection, management, and control of the BLM and Forest Service. Only those horses whose unbranded and unclaimed ancestors were present on BLM and Forest Service lands at the time of the passage of the WFRHBA are managed in accordance with the WFRHBA, and only those lands where wild horses and burros were found when the WFRHBA was passed can be managed to maintain Federally recognized wild horse and burro populations.

Other populations of feral horses and burros on Federal lands (i.e., those on lands administered by the U.S. Fish and Wildlife Service, National Park Service, or Department of Defense; and Native American reservations and tribal trust lands) are generally subject to other Federal regulations and relevant State laws, but are not subject to provisions of the WFRHBA. This section draws on scientific studies of feral horses and burros, some of which also have wild horse or wild burro legal status. Clarification of which horses and burros are considered Federally protected is provided in the BLM regulation (43 CFR 4700 [FR 2011]), BLM wild horse and burro management handbook and manuals (USDOI BLM 2010a,b,c,d), Forest Service manual (FSM 2260.5), and Forest Service regulation (36 CFR 222.20(b)(13), 36 CFR 222.63 [FR 2012]). The legal designation of a particular herd is not expected to change the animals' ecological effects, but it will influence management options. Discussions about management in this section reflect constraints for Federally designated wild horses and burros.

This section begins with information on wild horse and burro management structure, population estimates and spatial distribution, and management actions to maintain wild horses and burros at appropriate management levels. Then it discusses using resilience and resistance concepts to inform management of wild horses and burros. It concludes with management considerations at the project scale. This section refers mainly to wild horses because wild burros are not nearly as numerous as wild horses in most areas of the sagebrush biome.

Wild Horse and Burro Management Structure

For lands administered by the BLM, Herd Areas (HAs) are defined as areas where wild horses and burros existed at the time of passage of the WFRHBA. Herd Management Areas (HMAs)—the subset of lands designated for active management of wild horses and burros as part of multiple use management—can be designated only within HAs during land use planning activities. In most cases, each HMA is intended to support only wild horses or wild burros, but there are some HMAs that contain both. For HAs that do not have an HMA designation, it generally has been determined that resources are limiting and that wild horse and

burro populations cannot be maintained for the long term. The Forest Service-administered Wild Horse Territories (WHTs), Wild Burro Territories (WBTs), and Wild Horse and Burro Territories (WHBTs) are designated according to the species that occupy the Territory. There are some Territories without any wild horses or burros that are considered "inactive," where it has been determined that there are not sufficient resources to maintain wild horses and burros, or where wild horses and burros no longer exist. The numbers of wild horses and burros in HMAs, WHTs, WBTs, or WHBTs and the overlap with GRSG habitat are in text box 8.1.

When two or more HMAs, WHTs, WBTs, or WHBTs are located close to one another, with the potential for wild horses and burros to move freely among them, those areas may be managed collectively as a "complex" (or "joint management area"). Complexes sometimes cross administrative boundaries between BLM field or district offices and Forest Service districts.

The spatial scales of wild horse management are the entire population at the West-wide scale; complexes or groups of HMAs or WHTs, WBTs, and WHBTs with interchange for the regional scale; and individual herds for the local scale. A National Academies of Science report (National Research Council 2013) suggested that wild horse management should be focused more broadly on meta-populations, in which HMAs, WHTs, WBTs, and WHBTs are grouped where interchange occurs, regardless of administrative boundaries. Thus, relative to the spatial scales presented in section 1 of this report, the BLM and Forest Service manage wild horses between the regional and local project levels. The actual spatial scale for any given wild horse population should be determined in consultation with the local staff that manages those populations (i.e., BLM wild horse and burro specialist; Forest Service rangeland management specialist).

Importantly, each HMA, WHT, WBT, and WHBT has an established target population size range for wild horses (and a separate target for wild burros, if they are present), known as the appropriate management level (AML). The BLM and Forest Service view AML as a target population size range which, if maintained, should allow for a thriving ecological balance and multiple use relationship (43 CFR 4710.3-1 [USDOI BLM 2010b]; 43 CFR 4770.3(c) [USDOI 2012]; 36 CFR 222.60(b)(3), 36 CFR 222.61(a)(1), 36 CFR 222.69(a)

Text Box 8.1—Wild Horse and Burro Population Sizes

The BLM manages wild horses and burros within a total of 177 Herd Management Areas (HMAs), which range in size from 3.0 square miles (777 hectares) to 2,033.8 square miles (526,754.2 hectares). As of March 1, 2017, the estimated number of wild horses and burros managed by BLM was 72,674. A total of 105 HMAs overlap with approximately 13 million acres (5 million hectares) of GRSG habitat.

The Forest Service manages 34 active and 19 inactive wild horse and burro administrative units that include: Wild Horse Territories (WHTs; 27 active, 16 inactive), Wild Burro Territories (WBTs; 4 active, 3 inactive), and Wild Horse and Burro Territories (WHBTs; 3 active). These range in size from 5.4 square miles (1,398.6 hectares) to 530.4 square miles (137,373.6 hectares). The Forest Service manages approximately 8,000 wild horses and burros. Thirteen active Territories overlap with approximately 446,000 acres (180,000 hectares) of GRSG habitat.

One thousand or more wild horses on three WHTs and five HMAs live on or near Bi-State GRSG habitat (about 70,000 Forest Service acres [28,000 hectares] and 82,403 BLM acres [33,348 hectares]) (Bi-State Technical Advisory Committee 2012). The Bi-State population has been identified as a Distinct Population Segment of GRSG and is managed under a separate conservation Action Plan.

[FR 2012]). This view reflects an assumption that wild horse and burro populations at AML should allow for land health standards to be met (USDOI BLM 2010a). The AML generally is a range between a low and high value, to allow for some variability in population size across years (USDOI BLM 2010a). The AML is typically determined at the activity planning level through site-specific analysis or, in some cases, through the land use planning process. Monitoring information that couples data on wild horse and burro populations and rangeland status and trends is used to establish or adjust AMLs (text box 8.2). Progress toward attainment of site-specific and landscape-level management objectives or multiple use objectives is also considered. Future studies at local scales could test the assumption that wild horse and burro populations at AML allow for land health standards to be met.

Text Box 8.2—Monitoring Considerations for Wild Horses and Burros

Reliable estimates of population sizes and habitat data provide the basis for management decisions regarding wild horses and wild burros. Understanding the annual growth rates of wild horse and burro populations and the status and trends of rangelands occupied by wild horses and burros is essential for making informed management decisions.

Inventory (monitoring) data for wild horse and burro populations include information on the numbers of animals, their use patterns, and spatial distribution. Habitat data include grazing utilization, range ecological condition and trend, actual use, and climate (weather) data. Habitat monitoring data collection should be coordinated with other resource programs (e.g., range, watershed, wildlife) to maximize efficiency and minimize duplication.

Data and analyses of populations and habitats are used in concert to:

- Establish or adjust Appropriate Management Levels (AMLs);
- Make a determination of excess wild horses or burros (i.e., establish the need to gather and remove excess animals in order to reach and stay at AML);
- Develop or revise Herd Management Area (HMA) boundaries; and
- Evaluate conformance with Land Health Standards, Land Use Plan goals and objectives, or other site-specific or landscape-level objectives.

Data and methods used to inform decisions should be scientifically defensible. The public should be able to understand the methods used and how they are implemented and also to access the data used to make decisions.

Data on Population Estimates and Spatial Distribution of Wild Horses and Burros

Population estimates for each HA and HMA are reported annually in the Public Land Statistics (http://www.blm.gov/public_land_statistics/); spatial data are available via the BLM GeoCortex, which is available to managers for analyses and planning and is useful in determining the number of excess animals present on the range (https://webmaps.blm.gov/Geocortex/Html5Viewer/Index.html?viewer=whb). The Forest Service reports population estimates for each territory on the Forest Service wild horse and burro program website (https://www.fs.fed.us/wild-horse-burro/territories/index.shtml). The BLM and Forest Service have recently adopted a statistically valid, standardized methodology for estimating wild horse population sizes (Lubow and Ransom 2009, 2016; Ransom 2012) that accounts for animals that were present, but not seen by observers. In

most cases, reported population estimates are based on the statistical analysis of aerial survey data; BLM policy calls for each HMA (and complexes that include both BLM lands and Forest Service WHTs, WBTs, or WHBTs) to be surveyed at least once every 2 years (USDOI BLM 2010e). For both agencies, population size estimates are projected for intervening years based on the best available information about expected population growth rates for each area. As previously discussed, wild horse growth rates can typically be assumed to be about 15 percent to 20 percent per year (National Research Council 2013) unless there is a contraceptive project to limit reproduction. However, in some places the annual growth rate may be greater than 20 percent. The range-wide population estimates are used to develop BLM geospatial data (accessible at the BLM GeoCortex site) and the status of a population relative to high AML within a particular HMA.

Although it is the intended management goal that wild horses remain only on HMAs, WHTs, or WHBTs, the current reality is that Federally protected wild horses are also present on many HAs and on other Federal, State, tribal, and private lands outside of these administrative boundaries. As a result, the user must be cautiously aware that the data representing boundaries of and populations within HMAs, HAs, WHTs, WBTs, and WHBTs may not portray the actual spatial distribution of all wild horse and burro populations. Continued increases in wild horse and burro populations, relative to AML, will result in a more widespread distribution of herds, including into areas outside designated boundaries. In areas where road or trail access allows for observations and on-the-ground documentation of horse sign (e.g., trailing, scat piles, evidence of horse grazing and browsing), the local designated staff is likely to have a broad understanding of where the animals tend to go in different seasons, which water sources they rely on, and the general pattern of their movements.

Management Actions to Maintain Wild Horses and Burros at Appropriate Management Levels

The 1971 WFRHBA directs the BLM and Forest Service to remove excess animals from the range (43 CFR 4720.1 and 36 CFR 222.69, respectively) to maintain a thriving natural balance. The number of wild horses or burros greater than a designated high AML for a HMA, WHT, WBT, or WHBT is considered to be the number of "excess" animals in the area. In order to take management action, the agencies must make two determinations: (1) that an overpopulation exists, and (2) whether or not it will be necessary to remove excess animals.

Historically, the BLM and Forest Service reduced herd population sizes to the low value of AML. This was accomplished by removing excess animals from the range. The population would then typically grow to reach the high value of the AML range within 3 to 4 years, unless some form of contraception was used to limit population growth rates. Natural regulation via starvation or dehydration is generally not acceptable to many members of the public (National Research Council 2013).

After removal, animals were placed in holding facilities, offered to the public for adoption, and then kept in holding facilities indefinitely if there was no adoption demand. However, removing all excess wild horses and holding them in off-range facilities for the remainder of their lives would be prohibitively expensive (Garrott and Oli 2013). In many recent years, the BLM has not had the budgetary capacity to remove more than approximately 3,500 animals per year

from the range. Further, the more than 45,000 BLM-administered, captive wild horses currently in long-term holding (of which about 850 are horses from Forest Service Territories) require over $50 million per year to maintain. As a result, populations of wild horses and burros across all BLM-administered lands (and on some Forest Service Territories) have not been gathered so frequently. Average population sizes are now more than three times greater than the high end of the total AML and these populations are growing.

In 2015, the BLM, the Forest Service, and other agencies identified certain areas as the most important habitats for GRSG and other sagebrush obligates. None of those areas overlapped with Forest Service-administered wild horse or wild burro populations. The BLM developed a 5-year gather schedule to achieve AML by 2020 in 22 HMAs that overlapped areas identified as the most important habitats for GRSG and other sagebrush obligates. However, under budget projections made in FY2017, the BLM will not have the fiscal capacity to conduct gathers within GRSG Priority Habitat Management Areas until 2020 or later, and has no capacity to manage wild horse populations that overlap with GRSG General Habitat Management Areas. Unless there are Congressionally directed changes to the BLM program, it is expected that the number of wild horses within GRSG habitat could surpass 65,000 horses in 2019. Furthermore, maintaining any wild horse population at or below AML will require an active and ongoing program of population growth suppression or scheduled removals (or both) of excess animals. Without such a program, habitat restoration will quickly be at risk as wild horse populations again grow to exceed AML.

Currently used population growth suppression methods include gelding and the immunocontraceptives porcine zona pellucida (PZP) and GonaCon (National Research Council 2013). Both vaccines may be effective for only 1 year, unless booster doses are given (National Research Council 2013). Repeated PZP boosters require annual darting or recapture of the vast majority of wild horses under BLM or Forest Service management, which is infeasible on many HMAs and Territories, would be prohibitively expensive to apply across the range of wild horses and burros, and may lead to more stress for wild horses as a result of frequent capture. The BLM is supporting ongoing research initiatives to develop and test longer-term contraception for wild horses and burros and to improve contraceptive efficacy and production (USDOI BLM 2015). However, planning decisions that propose to remove excess horses or utilize population growth suppression on any BLM lands are often appealed and litigated by interested members of the public. This results in a high degree of uncertainty about the ability of designated Federal agencies to maintain wild horse populations within AML.

Using Resilience and Resistance Concepts and the Science Framework to Inform Management of Wild Horses and Burros

Information on relative ecosystem resilience to disturbance and resistance to invasive annual grasses can be used to help understand the responses of sagebrush ecosystems, species at risk, and other resources to wild horse and burro use and to the interactions of wild horse and burro use with other potential disturbance factors such as wildfire and invasive plants. Information on resilience and resistance to invasive annual grasses, coupled with information on current

and projected wild horse and burro population sizes relative to AML and other predominant threats and disturbance factors, can be used to inform conservation and restoration strategies in sagebrush ecosystems across scales.

Part 1 of the Science Framework provides an approach based on an understanding of ecosystem resilience to disturbance and resistance to invasive annual grasses that uses assessments at the mid-scale (ecoregional or GRSG Management Zone) (fig. 1.1) to help prioritize areas for management and determine effective management strategies (Chambers et al. 2017). The approach is based on: (1) the likely response of an area to disturbance or stress due to threats or management actions (i.e., resilience to disturbance and resistance to invasive annual grasses), (2) the capacity of an area to support target species or resources, and (3) the predominant threats. The geospatial data layers and analyses used in the approach are described in Part 1, sections 8.1 and 8.2. The process involves overlaying key data layers including resilience and resistance to invasive annual grasses as indicated by soil temperature and moisture regimes (Maestas et al. 2016), sage-grouse breeding habitat probabilities (Doherty et al. 2016), the densities or distributions of other sagebrush dependent species, and the primary threats for the ecoregions or Management Zones in the assessment. The maps and analyses that managers derive from this process are an essential component of prioritizing areas for management actions and developing management strategies.

Wild horse and burro densities and AMLs can be used similarly to other threats and disturbance factors in the analyses. Managers can devise categories to evaluate the degree to which wild horse and burro populations are within or exceed AMLs for HMAs, WHTs, WBTs, and WHBTs. Here, three abundance categories relative to AML were developed based on available abundance estimates for BLM lands and Forest Service lands: within AML, more than 100 percent to 200 percent of AML, and more than 200 percent of AML. The wild horse HMAs were overlaid with these three abundance categories (fig. 8.1). Note that this figure also depicts HAs where the target population for wild horses is zero, but where wild horses are present.

The three abundance categories were overlaid with: (1) the three resilience and resistance categories derived from soil temperature and moisture regime information, and (2) GRSG breeding habitat probabilities (see Part 1, sections 8.1 and 8.2). This analysis does not include areas outside the boundaries of HMAs, HAs, WHTs, WBTs, and WHBTs where horses and burros have expanded their use. The data used in the analyses can be found at: https://www.sciencebase.gov/catalog/item/576bf69ce4b07657d1a26ea2.

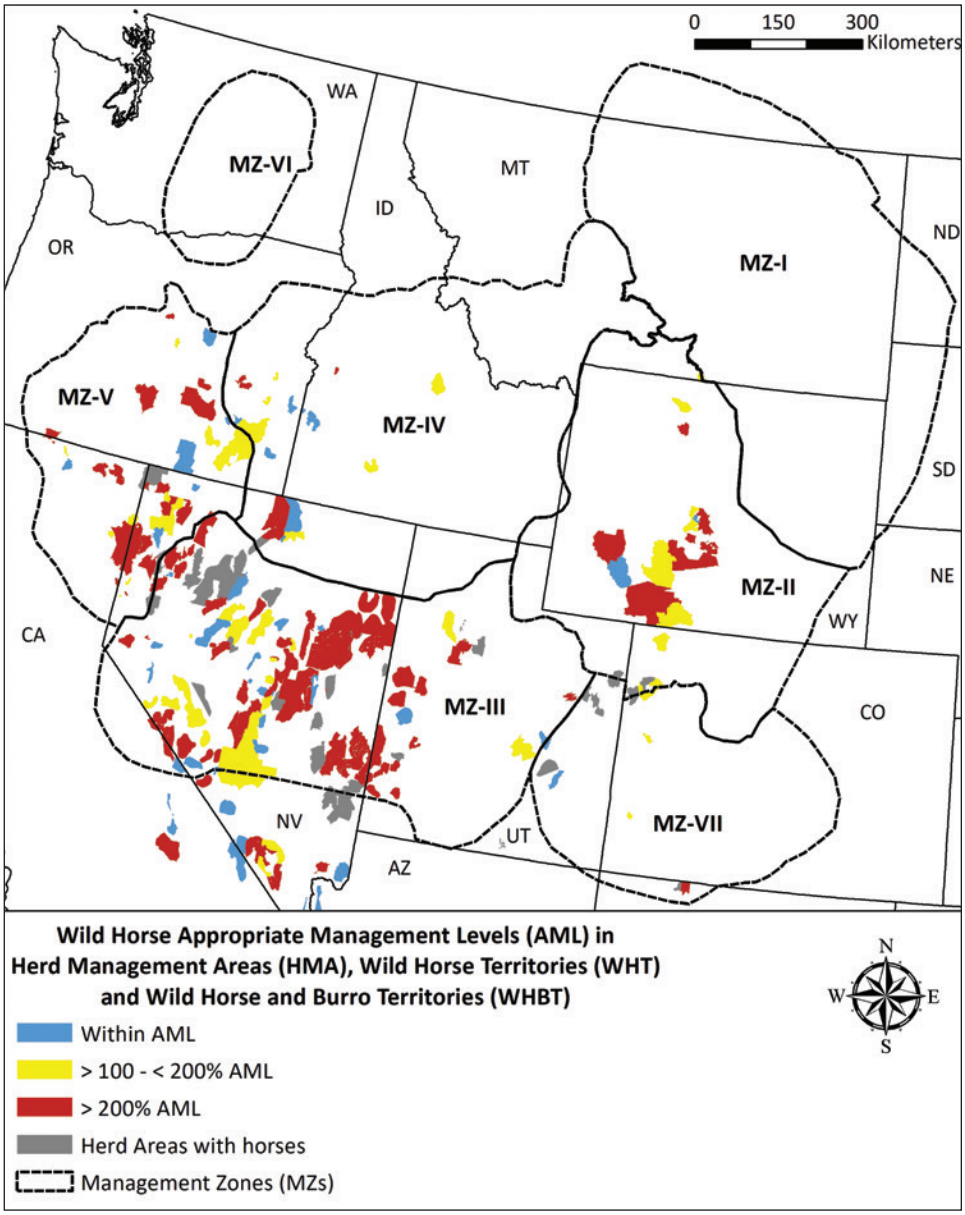


Figure 8.1—Categories of estimated wild horse abundance as of March 1, 2017 relative to Appropriate Management Level (AML) for wild horse Herd Management Areas (HMAs) on BLM lands and Wild Horse Territories (WHTs) and Wild Horse and Burro Territories (WHBTs) on Forest Service lands. Gray polygons indicate Herd Areas where the target population for wild horses is zero, but where wild horses are present. Estimated wild horse abundance exceeds AML in most HMAs, WHTs, and WHBTs.

Analyses of Appropriate Management Levels, Ecosystem Resilience and Resistance, and Breeding Bird Habitat Probabilities

Sixty percent of HMAs, WHTs, and WHBTs managed by the BLM and Forest Service are in areas categorized as having low resilience and resistance (fig. 8.2, table 8.1). In contrast, 33 percent have moderate resilience and resistance and only 7 percent have high resilience and resistance. In the area with low resilience and resistance, 60 percent has wild horse abundance that exceeds 200 percent of the horse AML.

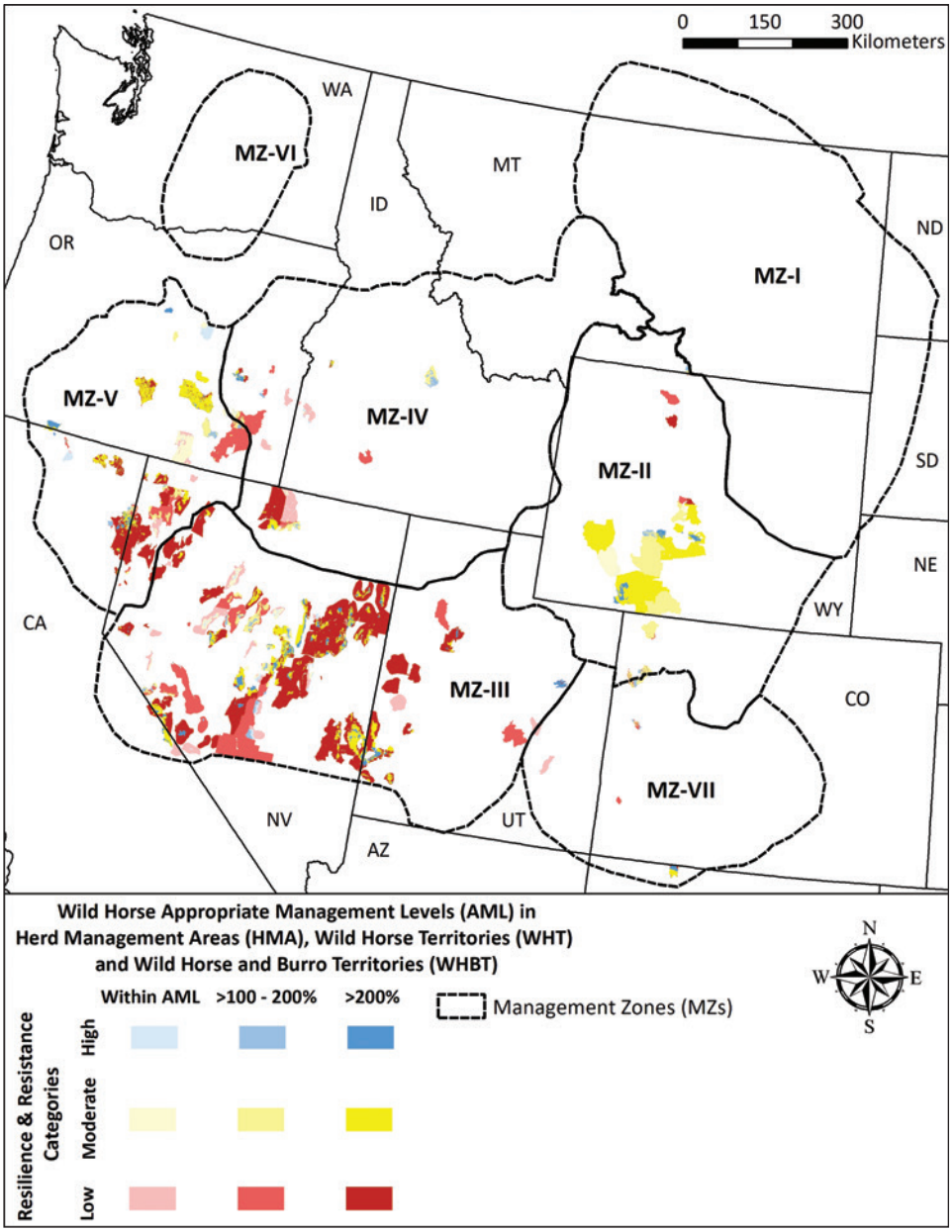


Figure 8.2—Categories of estimated wild horse abundance as of March 1, 2017 relative to Appropriate Management Level (AML), overlaid with the resilience and resistance classes within wild horse Herd Management Areas (HMAs) on BLM lands and Wild Horse Territories (WHTs) and Wild Horse and Burro Territories (WHBTs) on Forest Service lands. Most HMAs, WHTs, and WHBTs are in low to moderate resilience and resistance categories and exceed AML.

Table 8.1—The area and percentage of Herd Management Areas, Wild Horse Territories, and Wild Horse and Burro Territories for the Bureau of Land Management and Forest Service by wild horse Appropriate Management Level (AML) class and resilience and resistance class. Percentages within a Management Zone (MZ) add to 100.

	Resilience and resistance					
Percent Horse	Low		Moderate		High	
AML class	Acres	%	Acres	%	Acres	%
MZ I						
<100	0	0	0	0	0	0
>100–200	0	0	4,326	57	3,200	43
>200	0	0	0	0	0	0
Total	0	0	4,326	57	3,200	43
MZ II						
<100	0	0	414,831	8	2,204	1
>100–200	182,045	4	1,578,883	31	68,236	1
>200	108,086	2	2,548,764	50	166,862	3
Total	290,131	6	4,542,478	89	237,302	5
MZ III						
<100	1,161,465	8	233,713	2	146,235	1
>100–200	2,965,677	19	368,132	2	168,363	1
>200	7,916,216	52	1,743,470	11	618,498	4
Total	12,043,358	79	2,345,315	15	933,096	6
MZ IV						
<100	560,601	27	67,981	3	19,771	1
>100–200	490,895	23	198,977	9	89,076	4
>200	560,706	27	90,401	4	49,144	2
Total	1,612,201	77	357,359	16	157,991	7
MZ V						
<100	193,058	4	426,958	8	186,252	4
>100–200	942,681	18	336,100	6	85,331	2
>200	1,618,840	31	1,119,312	22	276,522	5
Total	2,754,579		1,882,370		548,105	
MZ VII						
<100	130,987	38	0	0	0	0
>100–200	47,132	13	64,758	19	29,502	8
>200	8,427	2	40,236	12	27,286	8
Total	186,546	53	104,994	31	56,788	16
All MZs						
<100	2,046,111	7	1,143,483	4	354,462	1
>100–200	4,628,430	17	2,551,176	9	443,708	2
>200	10,212,274	36	5,542,187	20	1,138,311	4
Total	16,886,815	60	9,236,846	33	1,936,481	7

Differences in both resilience and resistance and the abundance categories exist among Management Zones for wild horses (fig. 8.2, table 8.1). In Management Zone III, where the majority of wild horses are found, lands managed for wild horses are primarily within low resilience and resistance areas (79%). In the area with low resilience and resistance, 52 percent has wild horse abundance in excess of 200 percent of the horse AML. In Management Zones IV and V, lands managed for wild horses also are primarily within low resilience and resistance areas: 77 percent and 53 percent, respectively. In both of these areas, most lands managed for wild horses have horse abundance greater than 100 to 200 percent of the horse AML.

For wild burro populations, most of the land area in HMAs, WBTs, and WHBTs included in this analysis is in low resilience and resistance areas (80 percent), followed by moderate resilience and resistance areas (18 percent) (fig. 8.3, table 8.2). Moreover, 73 percent of the lands managed for wild burros in this analysis have wild burro abundance in excess of 200 percent of the burro AML.

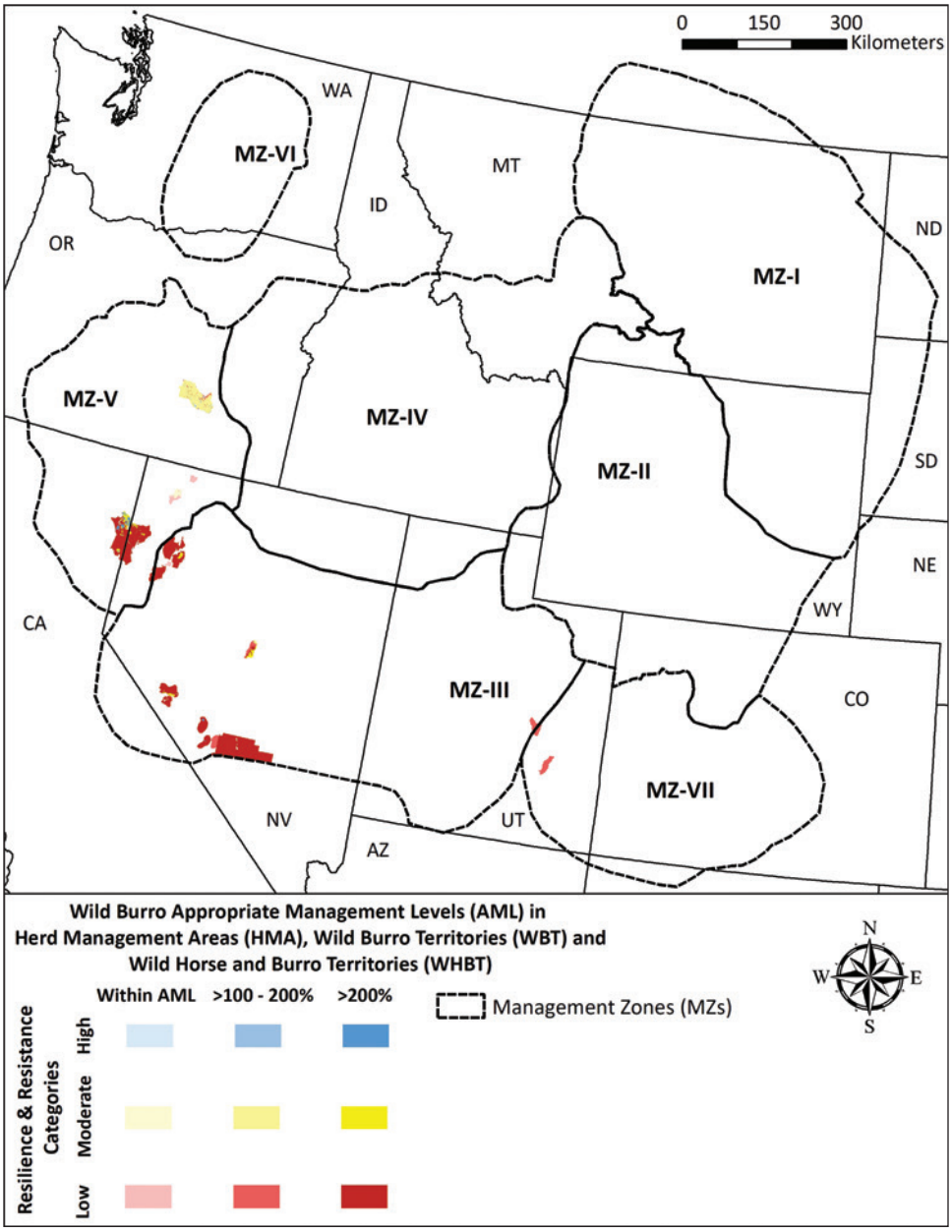


Figure 8.3—Categories of estimated wild burro abundance as of March 1, 2017 relative to Appropriate Management Level (AML), overlaid with the resilience and resistance classes within wild burro Herd Management Areas (HMAs) on BLM lands and Wild Burro Territories (WBTs) and Wild Horse and Burro Territories (WHBTs) on Forest Service lands. Estimated wild burro abundance exceeds AML in most HMAs, WHTs, and WHBTs.

Table 8.2—The area and percentage of Herd Management Areas, Wild Burro Territories, and Wild Horse and Burro Territories for the Bureau of Land Management and Forest Service by wild burro Appropriate Management Level (AML) class and resilience and resistance class. Percentages within a Management Zone (MZ) add to 100.

Percent Burro AML class	Resilience and resistance					
	Low		Moderate		High	
	Acres	%	Acres	%	Acres	%
MZ III						
<100	18,063	1	0	0	0	0
>100–200	162,160	8	9,563	1	0	0
>200	1,655,499	87	59,095	3	4,076	0
Total	1,835,722	96	68,658	4	4,076	0
MZ V						
<100	77,478	5	44,492	3	0	0
>100–200	30,008	2	442,165	29	20,651	1
>200	795,307	52	80,589	5	51,215	3
Total	902,793	59	567,246	37	71,865	4
MZ VII						
<100	0	0	0	0	0	0
>100–200	130,987	100	0	0	0	0
>200	0	0	0	0	0	0
Total	130,987	100	0	0	0	0
All MZs						
<100	95,541	3	44,492	1	0	0
>100–200	323,155	9	451,728	13	20,651	1
>200	2,450,806	68	108,351	4	55,290	1
Total	2,869,502	80	635,940	18	75,941	2

In Management Zones III and V the highest percentage of land is in low resilience and resistance areas with wild burro abundance more than 200 percent of the burro AML. Most of the burros managed by the BLM are located in Arizona and southern Nevada (USDOI 2017), which is outside of the sagebrush biome and the area of this analysis.

Overlaying the categories of wild horse abundance relative to AMLs with the sage-grouse breeding habitat probabilities shows that 42 percent of the lands managed for wild horses occur in the low, 40 percent in the moderate, and 18 percent in the high GRSG breeding habitat probability (fig. 8.4, table 8.3). In the high breeding habitat probability areas, which are the highest priority for protection, and in the moderate breeding habitat probability areas, which often provide opportunities for conservation actions, about two-thirds of the lands managed for wild horses have horse abundance in excess of 200 percent of the horse AML.

Analysis of the sage-grouse breeding habitat probabilities overlaid on categories of wild burro abundance relative to AML shows that 46 percent, 46 percent, and 8 percent of those GRSG breeding habitats managed for wild burros and included in this analysis occur in the low, moderate, and high breeding habitat probability areas, respectively (table 8.4). Within low, moderate, and high GRSG breeding habitat probability areas, 69 percent, 72 percent, and 38 percent, respectively, of the lands managed for wild burros have burro abundance greater than 200 percent of the burro AML. Management Zone V has a higher land area managed for wild burros with GRSG breeding habitat than Management Zone III, and a higher percentage of the wild burro population is in moderate and high GRSG breeding habitat probability areas.

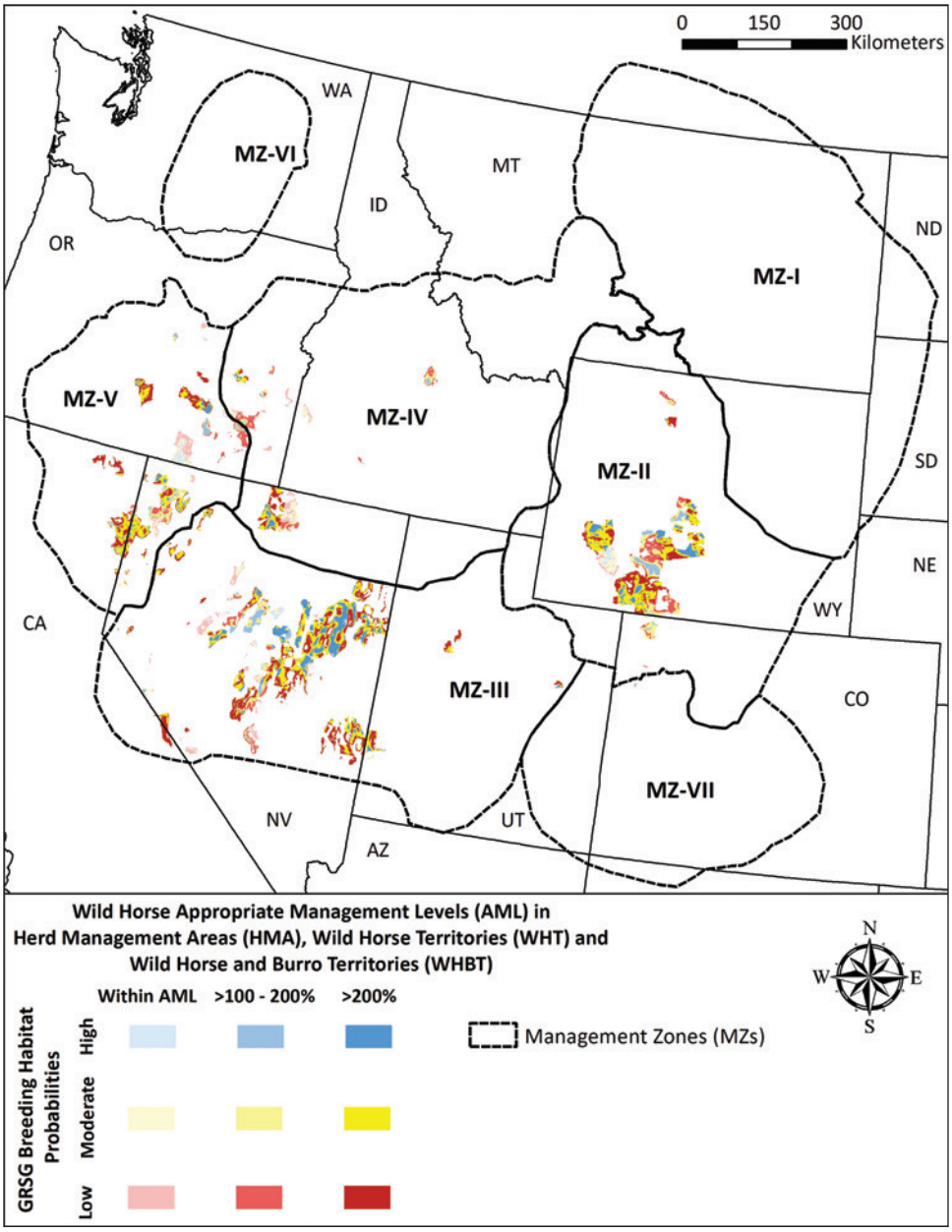


Figure 8.4—Categories of estimated wild horse abundance as of March 1, 2017 relative to Appropriate Management Level (AML), overlaid with the GRSG breeding habitat probabilities within wild horse Herd Management Areas (HMAs) on BLM lands and Wild Horse Territories (WHT) and Wild Horse and Burro Territories (WHBTs) on Forest Service lands. Estimated wild horse abundance exceeds AML in many areas with moderate to high GRSG breeding habitat probabilities.

Table 8.3—The area and percentage of Herd Management Areas, Wild Horse Territories, and Wild Horse and Burro Territories for the Bureau of Land Management and Forest Service by wild horse Appropriate Management Level (AML) class and Greater sage-grouse (GRSG) breeding habitat probability class. Percentages within a Management Zone (MZ) add to 100.

Percent Horse AML class	GRSG breeding habitat probability					
	Low		Moderate		High	
	Acres	%	Acres	%	Acres	%
MZ II						
<100	92,230	2	198,329	4	77,042	2
>100–200	573,836	13	557,183	13	255,275	6
>200	924,545	21	1,298,137	29	462,370	10
Total	1,590,610	36	2,053,649	46	794,686	18
MZ III						
<100	353,147	5	148,052	2	85,319	1
>100–200	312,594	4	319,359	5	273,905	4
>200	2,319,075	33	2,028,561	29	1,185,258	17
Total	2,984,816	42	2,495,972	36	1,544,482	22
MZ IV						
<100	234,091	16	208,371	14	10,955	1
>100–200	293,756	20	160,647	11	33,053	2
>200	212,954	14	224,679	15	95,330	7
Total	740,802	50	593,697	40	139,338	10
MZ V						
<100	281,312	9	161,838	5	94,638	3
>100–200	334,833	10	320,755	10	142,127	4
>200	867,460	27	832,302	26	178,115	6
Total	1,483,605	46	1,314,895	41	414,880	13
MZ VII						
<100	0	0	0	0	0	0
>100–200	252	3	2,494	29	5,748	68
>200	0	0	0	0	0	0
Total	252	3	2,494	29	5,748	68
All MZs						
<100	960,780	6	716,590	4	267,954	2
>100–200	1,515,271	9	1,360,438	8	710,108	4
>200	4,324,034	27	4,383,679	27	1,921,073	12
Total	6,800,085	42	6,460,707	40	2,899,135	18

Using the Science Framework to Inform Management Decisions

Primary considerations for wild horse and burro management from the Science Framework approach are presented next (see tables 1.3, 1.4).

- In general, areas that support medium to high sage-grouse breeding habitat probabilities or other important resources are high priorities for management (table 1.3: cells 2A, 2B, 2C, 3A, 3B, 3C), especially low resilience and resistance categories that lack the potential to recover from disturbances such as excessive wild horse and burro use without significant intervention (table 1.3: cells 2C, 3C). These areas could be considered priorities for wild horse and burro gathers and fertility control where horse and burro abundance exceeds target AMLs and the area is not highly degraded.
- Areas with moderate and, especially, high resilience and resistance often have the potential to recover through successional processes (table 1.3: cells 1B, 1C, 2B, 2C).

Table 8.4—The area and percentage of Herd Management Areas, Wild Burro Territories, and Wild Horse and Burro Territories for the Bureau of Land Management and Forest Service by wild burro Appropriate Management Level (AML) class and Greater sage-grouse (GRSG) breeding habitat probability class. Percentages within a Management Zone (MZ) add to 100.

Percent Burro AML class	GRSG breeding habitat probability					
	Low		Moderate		High	
	Acres	%	Acres	%	Acres	%
MZ III						
<100	107	1	0	0	0	0
>100–200	9,882	3	12,082	4	8,717	3
>200	168,963	58	86,373	30	2,943	1
Total	178,952	62	98,455	34	11,660	4
MZ V						
<100	23,217	2	68,662	7	18,022	2
>100–200	147,908	14	91,557	8	50,412	5
>200	263,516	24	364,745	34	44,423	4
Total	434,640	40	524,964	49	112,857	11
All MZs						
<100	23,217	2	68,662	5	18,022	1
>100–200	157,790	12	103,638	8	59,130	4
>200	432,479	32	451,118	33	47,366	3
Total	613,486	46	623,418	46	124,518	8

    - These areas represent significant opportunities to improve habitat and could also be considered priorities for wild horse and burro gathers and fertility control where horse and burro abundance exceeds target AMLs and removals are likely to result in habitat improvement.
    - In areas where wild horses and burros exceed target AMLs (including occupied areas outside of HMAs, HAs, WHTs, WBTs, and WHBTs), managers should carefully consider the current spatial extent and growth potential of any nearby wild horse herds and their potential effects on management actions to improve habitat.
- New postfire rehabilitation areas and areas that provide sagebrush habitat connectivity for GRSG and other species at risk are conservation priorities and, thus, could be priorities for wild horse and burro gathers, where abundance exceeds AMLs.

Ecological type or ecological site descriptions and their associated state-and-transition models (STMs) can be used to help evaluate potential effects of wild horse and burro use and the likely success of conservation and restoration actions. In the Science Framework, generalized ecological types and STMs have been developed for the range of environmental conditions in the eastern and western portions of the sagebrush biome (see Part 1, Appendices 5 and 6). The ecological types and STMs are characterized according to their resilience to disturbance and resistance to invasive annual grasses based on soil temperature and moisture regimes and other biophysical characteristics such as plant community composition. They provide information on the alternative states, ranges of variability within states, and processes that cause plant community shifts within states as well as transitions among states. These ecological types and STMs can be used to: (1) identify the different ecological types that exist within the HMA or Territory and determine their relative resilience to disturbance and resistance to invasive annual grasses; (2) evaluate the current ecological dynamics of the

ecological types or ecological sites and, where possible, their restoration pathways; (3) increase understanding of the potential effects of wild horse and burro use; and (4) determine the likelihood of conservation and restoration actions succeeding given ongoing wild horse and burro use (Part 1, section 9).

Section 7 uses these STMs to illustrate potential livestock management strategies for ecological types that support GRSG populations and that may benefit from improved livestock grazing management. Information on how to use these resilience-based ecological types and STMs for managing ecosystem threats across the sagebrush biome is in Part 1, section 9.2. Information on how to use resilience-based ecological types and STMs for selecting appropriate treatments for assessing postwildfire recovery and restoration decisions in sagebrush and juniper-piñon ecosystems in the Great Basin is in Miller et al. (2014, 2015) and Pyke et al. (2017), respectively.

Management Considerations at the Project Scale

An assessment of the ecological sites in the project area and their relative resilience to disturbance and resistance to invasive annual grasses can help determine the potential for conservation and restoration treatments to succeed. More detailed information can be obtained from ecological site descriptions for those areas where they have been developed (see http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/). Ecological type and ecological site descriptions provide basic information on the climate and soil characteristics of an area and the potential of the area to support a dynamic set of plant communities. The associated STMs provide information on the current states and the potential transitions among them due to disturbances and other drivers such as wild horse and burro use as well as management treatments. Assessing the states and the plant communities within the states based on STMs provides information on both the disturbances and the drivers that have led to the current state and the potential restoration pathways. For example, plant communities within the reference state or within states that have feasible restoration pathways may respond favorably to conservation and restoration actions if the wild horse population can be managed at or below AML. However, plant communities in other states, such as an invaded state or annual state (see figs. 7.2, 7.6) may not respond favorably to conservation and restoration actions if the wild horse population cannot be managed at or below AML. Ecological types or ecological sites with relatively low resilience and resistance to invasive annual grasses often require more than one intervention for restoration efforts to succeed and wild horse and burro use can have significant effects on project success.

Effects of wild horses and burros on project success depend on the number of wild horses and burros that can reach the site. If the project site is located within an HMA, WHT, WBT, or WHBT, then grazing and trampling pressure from wild horses should be expected in most cases. Even if the project area is outside any HMA, WHT, WBT, and WHBT, managers should carefully consider the current spatial extent, and growth potential, of any nearby wild horse population. Higher population sizes tend to lead to an expanded spatial area used by the wild horse population. If the number of wild horses is at AML, and there are measures in place to limit the population's growth rate, then wild horse use across the landscape may be distributed enough that a conservation or restoration project could achieve habitat quality goals. Thus, managers should carefully evaluate the likelihood of success of planned conservation and restoration activities if a local or adjacent wild horse population cannot be kept at AML.

Project success is also likely to be influenced by distance to the nearest drinking water source for wild horses. The greater the distance, the lower the grazing pressure that can be expected. Horses require access to large amounts of water; an individual can drink an average of 7.4 gallons [28.0 liters] of water per day (Groenendyk et al. 1988). Despite a general preference for habitats near water (e.g., Crane et al. 1997), wild horses will routinely commute long distances (e.g., 10+ miles [16 kilometers] per day) between water sources and palatable vegetation (Hampson et al. 2010). Managers should expect that any restoration project less than 5 miles [8 kilometers] from water will be subject to use by wild horses in the area. Riparian and wildlife habitat improvement projects that intend to increase the availability of grasses, forbs, riparian habitats, and water are likely to attract and be subject to heavy grazing and trampling by wild horses that live near the project.

Managers need to understand and consider the potential effects of wild horses and burros on conservation and restoration projects and plan accordingly. For certain habitat restoration projects, managers may want to consider installing fencing to discourage use by wild horses, particularly around riparian areas. On BLM and Forest Service lands, temporary fencing for habitat rehabilitation is generally acceptable on HMAs, HAs, WHTs, WBTs, and WHBTs. But permanent fencing often requires a more in-depth environmental assessment or land use plan revision, and should be designed in a way that allows for wild horse and burro movement throughout the rest of the HMA or Territory. The Forest Service also requires National Environmental Policy Act analysis for fence installation. Fencing that excludes wild horses and burros from riparian areas or water development projects that are designed to disperse both riparian and upland use by wild horses and burros are important management tools to protect riparian habitat. Fencing riparian areas to exclude wild horses and burros is generally acceptable as long as water from the area continues to be available to them, and solid pipe fencing is used that can withstand pressure from wild horses and burros. Continued monitoring to assess changes in plant communities and wild horse and burro abundance should be part of any conservation or restoration project where these animals are found.

If AML cannot be achieved, it may be more reasonable to forego a habitat restoration project entirely instead of spending time and resources on projects with a low probability of success. Managers deciding about any project that is near a wild horse or burro population should consider population sizes of wild horses and burros relative to the AML, including explicit schedules for wild horse and burro removals or population growth suppression treatments that are adequate to limit population growth. Unfortunately, high populations of wild horses or burros can substantially affect the ability of land managers to implement conservation measures in some areas. A potential project area with high current wild horse or burro population sizes may become suitable for restoration if the manager can influence priorities and policies such that wild horse and burro populations in the project area are reduced to and maintained at or below high AML.

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BioScience

A Forum for Integrating the Life Sciences

July 2019 American Institute of Biological Sciences Vol. 69 No. 7



Free-Roaming Horses

How to Make a Weed Degraded or Just Dusty?

OXFORD UNIVERSITY PRESS

Ecological Effects of Free-Roaming Horses in North American Rangelands

KIRK W. DAVIES AND CHAD S. BOYD

Free-roaming horses are a widespread conservation challenge. Horse use (grazing and related impacts) is largely unmanaged, leading to concerns about its impact on native plant communities and ecosystem function. We synthesized the literature to determine the ecological effects of free-roaming horses in North American rangelands. Largely unmanaged horse use can alter plant community composition, diversity, and structure and can increase bare ground and erosion potential. Free-roaming-horse use has also been linked to negative impacts on native fauna. Horses have repeatedly been shown to limit and even exclude native wildlife's use of water sources. These effects would likely be greatly reduced if the horse populations were better managed, but sociopolitical factors often preclude improved management. Using rigorous ecological research to educate politicians and the general public may facilitate the development of science-based management of free-roaming horses; however, ecological effects may have to become more severe before such changes can be realized.

Keywords: conservation, grazing, herbivory, trampling, wild horses, wildlife

Free-roaming horses in North America are a management challenge and conservation concern (Turner 1987, Beever 2003, Girard et al. 2013, Beever et al. 2018). Wild horses (*Equus* sp.) went extinct in North America approximately 10,500 (Guthrie 2003, 2006) to 13,000 (Grayson 2006) years ago. Self-sustaining populations of free-roaming domestic horses (*Equus caballus*) in North America established in the sixteenth and seventeenth centuries from domestic stock introduced by Spanish explorers (Haines 1938). Both accidental and intentional releases of domestic horses associated with the agricultural industry also augmented free-roaming horse populations and genetics (Young and Sparks 2002). At times, livestock producers used nearby free-roaming-horse populations as brood stock and would occasionally release stallions to alter the free-roaming-horse genetics for their purposes (Bowling 1994, Hyslop 2017, Idaho BLM 2018). These practices largely ended with the passage of the Wild Free-Roaming Horses and Burros Act (WFRHBA) of 1971, although the abandonment of domestic horses in free-roaming-horse-occupied areas still occurs, particularly during economic downturns or when feed costs increase substantially.

The management of free-roaming horses is a contentious topic, with pressure from multiple special interest groups (e.g., wildlife enthusiasts, hunters, animal-rights groups, ranchers, conservationists, environmental groups, and horse advocates and enthusiasts) with divergent demands. A large part of the challenge is that humans often have a strong emotional connection to horses, because horses have been ingrained in human cultures for centuries (Beever et al. 2019). Free-roaming horses are viewed as a symbol of freedom and strength, as well as an icon of the American West (Beever 2003), but the modern free-roaming horse is also an exotic species in North America that may influence ecosystem function and integrity if the population is left unmanaged. An additional concern is that most of the free-roaming horses on public lands in the United States occur in the driest state, Nevada (BLM 2018), which, similar to other arid and semiarid environments, is composed of plant communities and ecological sites that are sensitive to disturbance and mismanagement. The management of free-roaming horses, however, is often challenged and criticized by special interest groups (Symanski 1996, Linklater et al. 2002).

Free-roaming horses are a serious conservation concern, because the use (grazing and related impacts) by this species is largely unmanaged and continuous, suggesting that its effects may be large, even in areas with low animal populations (Beever 2003). In contrast, domestic livestock are more intensively managed through planned periods of grazing deferment and rest; herding; and salt, mineral, and water placement (Beever 2003). Therefore, unlike domestic species under managed grazing, free-roaming horses have the potential to continuously graze preferred plants and locations, such as riparian areas. The ecological effects of free-roaming horses would likely be similar to the effects that have been documented for largely unmanaged use by other large herbivores, such as historic livestock grazing in the western United States (Davies et al. 2014b) or free-roaming

BioScience 69: 558–565. Published by Oxford University Press on behalf of American Institute of Biological Sciences 2019. This work is written by (a) US Government employee(s) and is in the public domain in the US.
doi:10.1093/biosci/biz060

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camels in Australia (Edwards et al. 2010). Therefore, free-roaming horses may pose a threat to the sustainability of these ecosystems and the services they provide, including wildlife habitat, ecohydrologic function, and forage production.

Free-roaming horses have the potential to affect large tracts of rangeland. They occupy 31.6 million acres of federal land in the United States (BLM 2018). The population estimate of free-roaming horses and burros ranging on Bureau of Land Management (BLM)–administered lands was 81,951 animals and exceeded the appropriate management level (AML) by more than 55,000 animals in 2018 (BLM 2018). The BLM is required to determine the AML by the 1971 WFRHBA, and AML reflects the number of horses allowable, given consideration of ecological factors and other uses and values, including wilderness, wildlife, recreation, and livestock grazing. The number of horses on US rangelands will likely continue to grow; free-roaming horse populations are estimated to increase at a mean annual rate approaching 20% (National Research Council of the National Academies 2013), and the federal government has been unable to remove even a substantial portion of this increase in recent years (BLM 2018). Free-roaming-horse–occupied areas also overlap with habitat for many species of conservation concern, including sage-grouse and other sagebrush obligate species. There is a critical need to determine the ecological effects of free-roaming horses on North American rangelands.

However, determining the ecological effects of free-roaming horses has proven difficult, because domestic livestock frequently uses the same landscapes as free-roaming horses. Domestic livestock, particularly cattle, and free-roaming-horse diets overlap substantially (Krysl et al. 1984, Scasta et al. 2016). Therefore, domestic livestock grazing often confounds the ecological effects of free-roaming-horse grazing, giving rise to considerable uncertainty regarding the full extent and degree of impact of horses on rangeland ecological processes.

A synthesis of the literature is needed to more fully comprehend the ecological effects of free-roaming horses and to separate their effects from those of domestic livestock. Our objective in this article is to synthesize the ecological effects of free-roaming horses on North American rangelands and to provide science-based suggestions for minimizing those effects. We will determine the state of the science and its application potential in the management of free-roaming horses.

Free-roaming-horse effects on vegetation

Unrestricted free-roaming-horse use affects vegetation in uplands and riparian areas. In general, horse use alters the structural characteristics and, at times, the abundance of native vegetation (figure 1). Areas from which horses had been excluded compared with horse-occupied areas in Great Basin uplands had two to three times greater native grass cover and frequency (Beever et al. 2008). In riparian areas, free-roaming-horse use decreased herbaceous vegetation cover and height (Beever and Brussard 2000, Boyd et al. 2017). Grass cover was lower in areas occupied by horses over a long term than those from which horses had been excluded for short or long terms in Montana and Wyoming (Fahnestock and Detling 1999). In contrast, Davies and colleagues (2014a) found greater native perennial grass cover in sagebrush communities from which horses had been excluded than in those with heavy horse use but found no difference between areas from which horses had been excluded and those that showed light to moderate use by horses. One limitation with the Davies and colleagues (2014a) study was that the horses were only excluded for 4–5 years, and therefore, the exclusion areas may have still been recovering from prior horse use. Sagebrush communities often require several decades for recovery to become detectable after the removal of a disturbing agent (Sneva et al. 1980, West et al. 1984, Anderson and Inouye 2001). Beever and colleagues (2008) found that horse use can shift plant community composition toward greater abundance and cover of grazing-tolerant and unpalatable herbaceous species, but others have not detected an effect on composition (with a small sample size and confounding grazing effects from other large herbivores; Baur et al. 2017).

In shrub-occupied riparian and upland habitats, the exclusion of free-roaming horses increased shrub density (Beever and Brussard 2000, Davies et al. 2014a, Boyd et al. 2017). Horses also consumed riparian shrubs and thereby greatly decreased the shrubs' height. Although the difference was not significant, the juvenile sagebrush density in areas from which horses had been excluded was 7.8 times greater than that in horse-occupied areas (Davies et al. 2014a). Juvenile sagebrush density was not significantly different between occupied and unoccupied areas because of large variability, and one of the replicates essentially had no juveniles because it was fully occupied by mature sagebrush. The results from Davies and colleagues (2014a) and Boyd and colleagues (2017) suggest that free-roaming horses limit the recruitment of shrubs and thereby prevent their recovery. Mature sagebrush was twice as dense in areas from which horses had been excluded than in those horses occupied (Davies et al. 2014a). Shrub cover was also generally greater in areas from which horses had been excluded than in those horses occupied (Beever et al. 2008, Davies et al. 2014a). The exclusion of unmanaged use by other large herbivores also increased shrub cover in shrub-steppe communities in the Rocky Mountains (Manier and Hobbs 2006).

Free-roaming-horse use may also decrease plant species diversity and richness in Intermountain West plant communities. Species richness was lower in free-roaming-horse–occupied sites than in those from which the horses had been removed in the Great Basin and declined as grazing disturbance increased (Beever et al. 2008). Diversity increased with free-roaming-horse exclusion in sagebrush communities in northern Nevada (Davies et al. 2014a). In riparian

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Figure 1. Free-roaming-horse–grazed upland on the right and horse excluded upland on the left on Sheldon National Wildlife Refuge, in Nevada, in early June 2012. Horse use at this location was heavy and should not be interpreted to represent horse use across the entire area occupied by horses, because their forage use is highly heterogeneous.

areas, species richness increased with free-roaming-horse exclusion (Beever and Brussard 2000). However, plant diversity declined in Montana and Wyoming with free-roaming-horse exclusion (Fahnestock and Detling 1999). The reduced cover of dominant grasses probably allowed subordinate species to increase in horse-occupied areas (Fahnestock and Detling 1999). No difference in diversity or species richness was detected across five study sites spanning a wide diversity of ecosystems (from the Great Basin Desert to mixed-grass prairie; Baur et al. 2017). The effects of herbivory on diversity and richness likely vary with use levels and frequency (de Villalobos and Zalba 2010), plant community composition, environmental characteristics (Olff and Ricthie 1998), and the degree to which plant communities evolved with herbivory. Therefore, limited free-roaming-horse use likely increases diversity when it reduces dominant vegetation where light competition is a driving force in the composition of the plant community. However, when horse use is heavy or in a moisture-limited system, it likely reduces diversity and richness.

Postfire restoration is likely hampered by free-roaming-horse use. In southeast Oregon, free-roaming-horse use was a major factor leading to the failure of a postfire seeding project. The free-roaming horses pulled first-year grass seedlings out of the ground, resulting in high mortality of perennial bunchgrass and, subsequently, much lower grass density than in adjacent areas that did not have horses. Compounding this problem is the reality that grazing animals may preferentially use burned areas in larger landscapes (Clark et al. 2014). Similar issues have been observed with domestic livestock use of grass seedlings (Salihi and Norton 1987), and it is therefore a standard practice to defer grazing until after grass seedlings are of sufficient maturity to not be readily pulled from the ground. Grazing is also not recommended immediately after fire in areas that are not seeded, because it will likely decrease recovery by adding

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more stress to already stressed plants (Bates et al. 2009). Therefore, free-roaming horses are an added challenge to postfire restoration of rangelands.

The effects of free-roaming-horse use on exotic plant abundance are not clear. Cheatgrass (*Bromus tectorum* L.), an exotic annual grass causing ecological damage across the western United States, was generally more frequent in horse-occupied sites, but its cover was not significantly greater on these sites (Beever et al. 2008). Short-term horse exclusion did not decrease annual grasses (largely composed of exotic species) relative to those in horse-occupied sites (Davies et al. 2014a), although it's unlikely that short-term grazing cessation would allow native vegetation to recover to a high enough abundance to limit exotic annual grasses (Davies et al. 2014b). However, because free-roaming-horse grazing can decrease native perennial grasses (Beever et al. 2008), it may increase the risk of exotic annual grass invasion. Perennial grasses are a plant functional group crucial to limiting exotic annual grasses in the Great Basin (Chambers et al. 2007, Davies 2010). In other systems, feral-horse-driven changes in the abundance of native plant functional groups have decreased biotic resistance to exotic plant invasion (de Villalobos and Schwerdt 2017). Better knowledge of the effects of free-roaming horses on exotic plants would improve the understanding of their ecological effects and potentially improve resource management in horse occupied areas.

Free-roaming-horse effects on soils

One of the more concerning impacts of unmanaged horse use may be its effects on soils and erosion potential, because these affect site productivity and ecosystem function. Unrestricted free-roaming-horse use can result in high levels of bare ground, particularly in areas they repeatedly select (figure 2). Similar impacts were observed with other large herbivores when they were allowed to repeatedly use preferred areas (Dobkin et al. 1998, Bescta and Ripple 2009, Batchelor et al. 2015). Bare ground was approximately seven times greater in riparian areas occupied by free-roaming horses than in areas from which horses were excluded (Boyd et al. 2017). Bare ground was quantitatively greater in horse-occupied sagebrush communities than in those from which horses had been excluded; however, the difference was not statistically significant (Davies et al. 2014a). Combined, these results suggest the potential for free-roaming horses to increase bare ground.

The trampling effect of horses on soils is a destructive component of unmanaged use by free-roaming horses (Turner 1987). Horse use decreased soil aggregate stability and increased soil surface penetration resistance (i.e., an index of compaction) in uplands (Beever and Herrick 2006, Davies et al. 2014a), likely largely because of trampling and unrestricted grazing. In some instances, the effects of compaction may be limited to established trails; however, the area covered by such trails can be extensive (Ostermann-Kelm et al. 2009). Water infiltration rates decrease with increased soil penetration resistance, leading to increased runoff risk (Maestre et al. 2002, Aksakal et al. 2011). Declines in aggregate stability increase the risk of soil movement with wind and water (Herrick et al. 2001). Bare ground is also more exposed to erosional forces than ground covered by litter or vegetation and can increase the probability of exotic plant invasion. The combined effect of these alterations to soils from unmanaged horse use is an elevated risk of soil erosion, potentially affecting ecohydrologic function. Furthermore, soil erosion has the potential to cause irreversible declines in plant community productivity and stability (Pimentel et al. 1995); therefore, free-roaming-horse use over time could permanently affect the productivity and function of some areas.

Free-roaming horse effects on wildlife

It is well established that free-roaming horses can alter vegetation and soils in rangeland ecosystems (e.g., Beaver and Herrick 2006, Beever et al. 2008, Davies et al. 2014a), and this can negatively affect wildlife habitat (Beever and Aldridge 2011). Free-roaming-horse use has also been linked to negative impacts on insects (Beever and Herrick 2006), small mammals (Beever and Brussard 2004), birds (Zalba and Conzzani 2004), and estuarine fauna (Levin et al. 2002).

Shrubs are a critical habitat component for many wildlife species, and therefore, horse use limiting the recovery of shrubs could negatively affect these species. In particular, unmanaged horse use may negatively affect sagebrush-associated wildlife. The results from recent horse-exclusion studies (Davies et al. 2014a, Boyd et al. 2017) support the prior conclusions that free-roaming-horse effects may negatively influence sagebrush-associated wildlife (Beever and Brussard 2004, Beever and Aldridge 2011). Altered vegetation structure and composition in riparian areas can affect the availability and suitability of habitat for a variety of wildlife species. Avian species often select particular vegetation characteristics in riparian habitats (Ammon and Stacey 1997); therefore, horse effects may negatively influence some species and positively influence other species, depending on their habitat requirements.

In moisture-limited ecosystems, horses may cause additional stress on native wildlife through competition for water. Free-roaming horses frequently prevented water acquisition by elk at a natural water source in Colorado (Perry et al. 2015) and pronghorn in Nevada (Gooch et al. 2017). Pronghorn and mule deer also used water sources less often where horse activity was high (Hall et al. 2018). Free-roaming-horse use of water sources was also associated with decreased native wildlife species richness and diversity (Hall et al. 2016). Native wildlife also visit and spend less time at water sources used by free-roaming horses, indicating that horses further constrain access to a limited resource (Hall et al. 2016, 2018). Clearly, free-roaming horses displace native wildlife at water sources. How this affects wildlife populations, demographics, and fitness is unknown (Berger 1985), but further loss of water in these water-limited environments from competition with free-roaming horses could amplify conservation challenges for native wildlife.

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Figure 2. Free-roaming-horse–grazed riparian area on Sheldon National Wildlife Refuge, in Nevada, in September of 2009. Note the high degree of trampling. Domestic livestock have been excluded from the Sheldon National Wildlife Refuge since the mid-1990s, and wild ungulates were not abundant. Unrestricted use by other large herbivores in areas that have a similar disparity in the timing between riparian vegetation and upland vegetation senescence will produce similar results.

We agree with Beever and Aldridge (2011) that the effects of free-roaming-horse use in sagebrush uplands and riparian areas (Beever and Brussard 2000, Beever et al. 2008, Davies et al. 2014, Boyd et al. 2017) on the conservation of sage-grouse and other sagebrush-associated wildlife need to be considered in developing wildlife management plans and conservation strategies. Free-roaming horses are an additional stressor on the wildlife species of conservation concern in North America, particularly in water-limited ecosystems. Therefore, horse effects likely need to be considered when developing wildlife plans and conservations strategies for any species with a range that substantially overlaps with horse-occupied areas.

Management implications

The management of free-roaming horses is a complicated social and legal issue. It is controversial, with many special interest groups issuing competing demands. Furthermore, management is constrained by the WFRHBA and politicians with faulty or incomplete knowledge of the issue (Beever 2003). In particular, the "minimal management strategy" set forth by the act restricts the application of scientifically validated management options.

Managing free-roaming horse populations is needed, because most herd management areas are over AML (BLM 2018). The overpopulation of free-roaming horses is a widely recognized problem, and limitations to resolving this issue are largely sociopolitical, because there are well-defined strategies for animal population management (Gaillard et al. 1998, Garrott 2018, Norris 2018). Unmanaged herbivores will repeatedly defoliate preferred vegetation, causing ecological damage over time (Engle and Schimmel 1984, Launchbaugh and Howery 2005, di Virgilio and Morales 2016). Repeated defoliation that continuously removes photosynthetic tissue can place grazed plants at a competitive disadvantage with ungrazed plants and prevents the grazed

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plants from completing their life cycle (Caldwell et al. 1987, Briske and Richards 1995, Holechek et al. 1998). Dissimilar to free-roaming-horse use, use by domestic livestock is managed so that defoliation only occurs for a set period of time; defoliation is limited during the periods of use; and periods of no use (deferment or short-term rest from herbivory) occur, which allows plants to periodically complete their life cycle without the physiological stress of defoliation (Davies et al. 2014b). Ecological damage is exacerbated with increasing free-roaming-horse populations, because larger areas experience repeated use. Therefore, purposeful management to reduce horse populations should be practiced, because the management strategies often used for domestic livestock (e.g., rotational grazing, periodic rest) are generally not allowed under the WFRHBA or are not feasible with horses.

Where competition for water from horses negatively affects native wildlife access to water, the full or partial exclusion of horses from water sources may be needed, perhaps with a concomitant development of off-site water sources. Horses may also need to be excluded from sensitive areas, such as riparian areas, or other areas they overuse. However, the exclusion of horses from any resources will need to be carefully applied, because exclusion may increase horse use in other areas. This, again, points to the need for diligent management of horse populations.

A reevaluation of AMLs is needed, because climate change, invasive plants, and woody plant encroachment have potentially altered forage production, plant community composition, and water availability since the WFRHBA was written. Reevaluating AMLs is particularly needed in areas in which federal agencies have frequently had to supplement forage or water or have had to conduct emergency gathers to prevent horse deaths. Clearly, AMLs need to be reevaluated if herd management areas cannot meet the needs of horses year-round. AMLs may need to be lowered in areas in which free-roaming-horse use causes substantial ecological damage or negatively affects species of conservation concern.

Conclusions

Unmanaged free-roaming-horse use can cause changes in plant community structure, composition, and diversity, which can affect both ecological processes and the quality and availability of wildlife habitat. When they are largely unmanaged, other animals, including camels, cattle, and pigs cause similar ecological degradation (Gallacher and Hill 2006, Cole and Litton 2014, Davies et al. 2014b). Free-roaming horses also appear to directly affect other wild species by potentially limiting their access to water sources. Providing wildlife with access to water without the presence of free-roaming horses may entail excluding the horses from at least a portion of the water sources in water-limited environments. Unmanaged horse use increases the risk of soil erosion in both riparian and upland plant communities (Davies et al. 2014a, Boyd et al. 2017) and may, at some sites, decrease ecosystem productivity and function. Unrestricted use over time may cause stream channel incision and a drop in the water table in riparian areas, particularly if the banks were made unstable by a loss of deep-rooted plant species (e.g., *Carex* spp.). Soil compaction from unrestricted free-roaming-horse use likely limits herbaceous vegetation, because soil compaction can restrict water infiltration and root growth (Ehlers et al. 1983, Bengough and Mullin 1991, Villamil et al. 2001). Collectively, the body of literature on unrestricted free-roaming-horse grazing demonstrates that horses have a substantial ecological impact in native upland and riparian plant communities. The ecological effects are probably greater than these studies suggest, because ecosystem recovery can be slow and because most exclusion studies are short term relative to the speed at which ecological properties are recovered following a disturbance (e.g., Davies et al. 2014a, Boyd et al. 2017). Longer-term evaluation of the response of soil, vegetation, and wildlife to free-roaming-horse exclusion is needed in order to better understand the magnitude of these effects. However, the magnitude of horse effects will likely vary substantially across the landscape, because horse use intensity and frequency is variable. The ecological effects of free-roaming horses need to be considered in restoration efforts and conservation plans for native fauna and flora. Some restoration and conservation goals may not be achievable in areas that free-roaming horses occupy and should therefore not be attempted, because resources would be wasted.

Limiting the ecological effects of free-roaming-horse use will require the successful navigation of a complex and emotionally charged sociopolitical environment. We currently have sufficient ecological literature to inform management decisions regarding free-roaming horses. However, science-based ecosystem conservation is confounded by human psychology and the politics and sociology of horse advocacy groups (Sysmanski 1996).

We would like to believe that change in the sociopolitical arena around free-roaming horses can be stimulated by rigorous ecological research and using that research to inform scientifically sound management of free-roaming horses, as well as educating politicians and the public. However, we recognized that science is often ignored and, in some cases, blatantly discounted because of people's emotional connection to horses. People's emotional connections to other animals cause similar issues around the world. In Dubai, camel use is unrestricted because of a cultural reverence for them, even though it is the single greatest threat to inland deserts (Gallacher and Hill 2006). Introduced feral pigs cause ecosystem degradation in Hawaii, but eliminating them is strongly opposed by native Hawaiians because of their cultural tradition of pig hunting (Cole and Litton 2014, Beever et al. 2019). The ecological impacts of free-roaming horses will likely have to become more severe before the sociopolitical environment surrounding this issue changes sufficiently to alter management. That said, the status quo of largely not managing free-roaming-horse populations is neither ecologically tenable nor compatible with the conservation of North American rangelands and their native fauna.

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Acknowledgments

We appreciated thoughtful reviews of earlier versions of the manuscript by David Ganskopp and two reviewers who wished to remain anonymous because of the sociopolitical environment surrounding this issue. We are also grateful to the associated editor and three anonymous reviewers for their constructive reviews of the manuscript. The US Department of Agriculture is an equal opportunity provider and employer. Mention of a proprietary product does not constitute a guarantee or warranty of the product by the USDA or the authors and does not imply its approval to the exclusion of other products that may also be suitable.

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Effects of feral free-roaming horses on semi-arid rangeland ecosystems: an example from the sagebrush steppe

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Citation: Davies, K. W., G. Collins, and C. S. Boyd. 2014. Effects of feral free-roaming horses on semi-arid rangeland ecosystems: an example from the sagebrush steppe. Ecosphere 5(10):127. http://dx.doi.org/10.1890/ES14-00171.1

Abstract. Feral horses (*Equus caballus*) are viewed as a symbol of freedom and power; however, they are also a relatively unmanaged, non-native grazer in North America, South America, and Australia. Information about their influence on vegetation and soil characteristics in semi-arid rangelands has been limited by confounding effects of cattle (*Bos taurus*) grazing and a lack of empirical manipulative studies. We compared vegetation and soil surface characteristics in feral horse grazed areas and ungrazed exclosures at five sagebrush (*Artemisia*) steppe sites in northern Nevada. Horse grazed areas had lower sagebrush density and plant diversity, greater soil penetration resistance, and lower soil aggregate stability than ungrazed areas. Herbaceous cover and density generally did not differ between grazed and ungrazed treatments, with the exception of heavily grazed sites in which perennial grass cover was reduced. The cumulative effect of feral horses on soil characteristics suggests that they may affect the ecological function of semi-arid rangelands by increasing the risk of soil erosion and potentially decreasing availability of water for plant growth. The two-fold increase in sagebrush density with horse exclusion suggests that feral horses may limit sagebrush recruitment and thereby negatively impact Greater Sage-grouse (*Centrocercus urophasianus*) and other sagebrush associated wildlife. The effects of feral horses on sagebrush and other semi-arid ecosystems should be considered when developing conservation plans for these ecosystems and associated wildlife.

Key words: *Artemisia*; *Equus caballus*; exclosures; grazing; herbivory; soil aggregate stability; trampling; wild horses.

Received 4 June 2014; revised 16 August 2014; accepted 18 August 2014; final version received 11 September 2014; **published** 22 October 2014. Corresponding Editor: R. R. Parmenter.

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INTRODUCTION

Free-ranging horses (*Equus caballus*) are a management and conservation concern in North America (Turner 1987, Beever 2003, Girard et al. 2013) and other locations around the globe (e.g., Rogers 1991, Zalba and Cozzani 2004, Nimmo and Miller 2007, de Villalobos and Zalba 2010). Management of free-ranging horses in the United States is contentious because they are viewed as a symbol of freedom and strength and an icon of the American West (Beever 2003), but they are also a non-native, feral grazer. The concern with feral horses is that unmanaged and poorly managed non-native grazers can have substantial impacts on ecosystem integrity as seen with poorly managed livestock in the western United States (Fleischner 1994, Jones 2000). The potential

for feral horse effects may be large in some areas even with low populations because feral horse grazing is largely unmanaged and on the landscape year round; where, in contrast, domestic livestock grazing is much more intensively managed through fencing, rotation grazing, herding, salt and mineral supplementation, and water sources (Beever 2003). A large portion of the western United States has the potential to be affected by feral horses as there are currently over 40,000 free-ranging horses and burros occupying 12.8 million ha (BLM 2014).

It is well established that ungulates affect ecosystems and can modify plant community composition and structure (Hobbs 1996, Augustine and McNaughton 1998). The effects of herbivory depend on the complex interaction of the characteristics of the ungulate, plant community, soil, climate, and landscape (Hobbs 1996). Thus, some of the controversy regarding feral horses is the result of a limited number of studies investigating their effects, especially in arid and semi-arid ecosystems such as the sagebrush (*Artemisia* L.) ecosystem. Beever et al. (2003) found that disturbance sensitive variables could collectively be used to separate feral horse occupied areas from horse removed areas in multivariate ordination space, despite indistinguishability of the two types of sites using data on 'key' forage species monitored by the Bureau of Land Management. Horse removed areas had greater shrub, native grass, and total plant cover and species richness than horse occupied sites (Beever et al. 2008). Penetration resistance of the soil surface (an indicator of soil compaction) was less where feral horses had been removed compared to horse occupied sites (Beever and Herrick 2006). Though these studies (Beever et al. 2003, 2008, Beever and Herrick 2006) provide valuable information regarding horse occupied and horse removed areas, they do have some limitations. Horse occupied and horse removed areas occurred in separate mountain ranges, though they had similar slope, aspect, dominant shrub, fire history, and grazing pressure by cattle (*Bos taurus*; Beever et al. 2003, 2008, Beever and Herrick 2006). Without rigorous experimental control there are undoubtedly some unaccounted for confounding variables and cause and effect relationships cannot be determined. When treatments are not randomly assigned and before and after treatment data in both control and experimental plots are not acquired, it is not possible to attribute differences to the treatments (Beever and Brussard 2000). Though grazing pressure by cattle was estimated to be minimal to none across their study sites (Beever et al. 2003, 2008, Beever and Herrick 2006), cattle presence may obscure some of the horse effects or make it difficult to separate. Therefore, there is a critical need to evaluate feral horse effects in areas without domestic livestock. Though covering large landscapes, all these studies (Beever et al. 2003, 2008, Beever and Herrick 2006) also used the same study sites. Thus, there is a need for further analysis of feral horse effects in sagebrush rangelands to broaden the scope of research to other areas occupied by feral horses.

In grasslands in Argentina, feral horses reduced grass seed density and richness in the seedbank (Loydi et al. 2012) and decreased plant species richness and grass abundance and biomass production (de Villalobos and Zalba 2010). Feral horse use decreased biomass production in marshes (Turner 1987, 1988) and islands (Rogers 1991, Seliskar 2003). In contrast, Fahnestock and Detling (1999) reported feral horses did not have consistent effects on plant cover and that abiotic factors were more important than feral horse use in determining plant community dynamics in the Pryor Mountain Wild Horse Range in southern Montana and northern Wyoming. In addition, plant species diversity was slightly greater in horse grazed compared to ungrazed sites in the Pryor Mountain lowlands (Fahnestock and Detling 1999). The inconsistency in the reported effects of feral horse grazing suggests that vegetation response likely varies by site characteristics. Furthermore, feral horse effects in more mesic habitats may contribute little to our understanding of feral horse effects in sagebrush (Beever and Aldridge 2011) and other arid and semi-arid ecosystems.

The purpose of this study was to develop a better understanding of feral horse effects in semi-arid rangeland ecosystems. We compared mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Rydb.) Beetle) steppe communities where feral horses were excluded for 5 years with adjacent continuously grazed areas on the Sheldon National Wildlife Refuge in northern Nevada. Cattle were excluded from the refuge

since the early 1990s. We hypothesized that: (1) perennial herbaceous and sagebrush cover and density would be lower in feral horse grazed compared to ungrazed areas, (2) plant species richness and diversity would be less in grazed compared to ungrazed areas, and (3) soil surface penetration resistance would be higher and soil aggregate stability less in grazed compared to ungrazed areas.

Materials and Methods

Study area

We conducted this study from 2008 to 2013 on Sheldon National Wildlife Refuge in northern Nevada. The study area is mountainous with elevations at the study sites ranging around 1900 m above sea level. Climate is typical of the northern Great Basin with cool, wet winters and hot, dry summers. Average annual precipitation was between 300 and 400 mm at the study sites (NRCS 1998). Annual precipitation in 2008, 2009, 2010, 2011, 2012, and 2013 was 68%, 88%, 148%, 110%, 70%, and 69% of average at the Winnemucca, NV weather station, respectively (Weather Underground 2014), approximately 180 km southeast of Sheldon National Wildlife Refuge. Feral horse populations at Sheldon National Wildlife Refuge from 2004–2013 ranged from 700 to 1200 individuals. The study area within Sheldon National Wildlife Refuge was 80,300 ha with feral horse population ranging from 387 to 673 horses with an average of 528 horses between 2007 and 2013. The study area is an unfenced area in southern portion of the refuge (Fig. 1) and horses can travel into and out of the study area. All study sites were mountain big sagebrush steppe. However, two of the study sites were lacking a sagebrush overstory because they were in the interior of the 1999 Badger Fire. Common perennial grasses included bluebunch wheatgrass (*Pseduoroegneria spicata* (Pursh) A. Löve), Idaho fescue (*Festuca idahoensis* Elmer), Thurber's needlegrass (Achnatherum thurberianum (Piper) Barkworth), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Common perennial forbs included milkvetches (*Astragalus* L.), fleabanes (*Erigeron* L.), biscuitroots (*Lomatium* Raf.), hawksbeards (*Crepis* L.), phloxes (*Phlox longifolia* Nutt. and *P. hoodii* Richardson), and lupines (*Lupinus* L.).

Experimental design and measurements

A randomized complete block design was used to determine the response of mountain big sagebrush steppe communities to feral horse use and exclusion. Five blocks, dispersed within the 80,300 ha study area, were selected for this experiment. Blocks were separated by up to 20 km and varied by elevation, slope, aspect, and soil. The different blocks included north, south, east, and west aspects. Elevation of blocks ranged from 1856 to 1914 m above sea level. Prior to treatment herbaceous and shrub cover and density varied by block, but treatments within a block were similar ($P > 0.10$). Each block consisted of two adjacent 50 × 60 m plots separated by a 10-m buffer. Each block was within 0.1 km of a riparian area with a perennial spring or small creek. Both treatment plots were the same distance from the riparian area at each block. Treatments were randomly assigned to one of the plots at each block and were: (1) feral horse grazing exclosure (ungrazed) and (2) unrestricted (free-roaming) feral horse grazing. Exclosures were metal pipe buck-and-pole fences constructed in 2008 to prevent feral horse use. Exclosures were constructed with three poles with the bottom and top pole placed 43 cm and 107 cm above the ground, respectively. Wildlife were not excluded from the exclosures and motion sensor cameras recorded no difference in visits by native ungulates inside compared to outside exclosures.

Vegetation cover and density was measured in mid-June 2012 and 2013, the fourth and fifth year after exclosures were constructed. Herbaceous cover and density was measured by species in 60 0.2-m^2 quadrats in each treatment plot. The 0.2-m^2 quadrats were placed at 3-m intervals on four 50-m transects (starting at 3 m and ending at 45 m) in each plot (15 quadrats per transect). The four 50-m transects were placed parallel to each other at 5-m intervals. Cover of biological soil crust, bare ground and litter were also measured in the 0.2-m^2 quadrats. Shrub cover by species was measured on the four 50-m transects using the line-intercept method (Canfield 1941). Shrub density by species was measured by counting plants rooted inside 2 × 50-m belt transects laid over the 50-m transects. Sagebrush density was separated into juvenile and mature sagebrush. Sagebrush was considered to be mature if

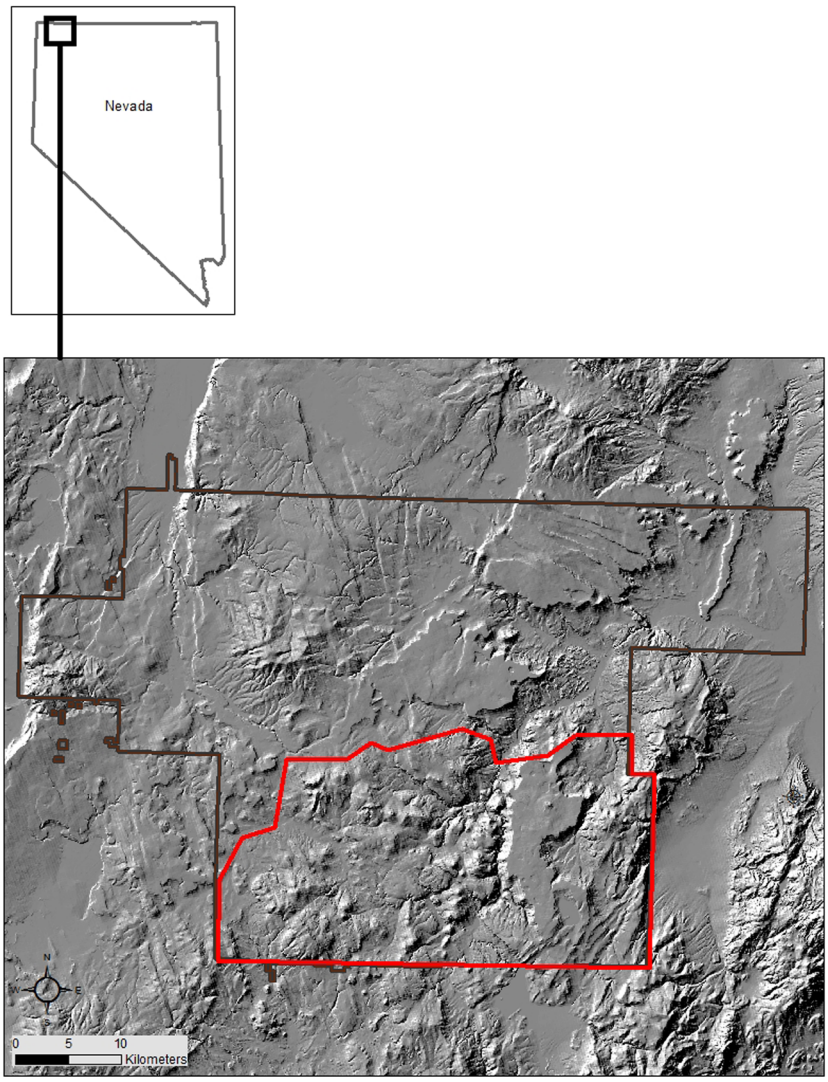


Fig. 1. Map of the study area (red perimeter polygon) inside of Sheldon National Wildlife Refuge (brown perimeter polygon) with the location of the refuge identified on a map of Nevada, USA.

reproductive stems were present and juvenile if it did not have reproductive stems. Density data was used to calculated plant species richness and diversity. We calculated plant diversity as the Shannon Diversity Index (H) (Krebs 1998). Forage utilization was measured in late September of 2009–2013 following the method described in Anderson and Curreir (1973) to quantify the level of horse use at each block. Soil aggregate stability and penetration resistance of the soil surface were measured in June 2013. Soil aggregate stability was measured at five locations in each treatment in each block with a Soil Stability Test Kit (Synergy Resource Solutions, Belgrade, MT). Penetration resistance of the soil surface was measured at five locations in each treatment in each block with a Geotester Pocket Penetrometer (Novatest, Italy).

Statistical analyses

We used repeated measures analysis of variance (ANOVA) models in PROC MIXED in SAS v.9.2 (SAS Institute, Cary, NC) with year as the repeated variable to evaluate the response of variables that were repeatedly measured with feral horse grazing and exclusion. Blocks and

Table 1. Average herbaceous utilization by feral horses at each site measured in September each year using the method described in Anderson and Curreir (1973). Sites grouped into grazing levels based on average utilization levels: low-moderate, <40%; high, >40%.

	Utilization		
Site (block)	Mean (%)	SE (%)	Grazing level
Tenmile	14	5	low-moderate
Buckaroo	61	8	high
Corral	53	4	high
Smith	48	10	high
Cottonwood	29	5	low-moderate

block by treatment interactions were treated as random variables. We also analyzed level of grazing influence on treatment response. Level of utilization was separated into two categories based on average utilization measured in September of 2009–2013: low-moderate (<40% utilization; n = 2) and high (>40% utilization; n = 3) (Table 1). Our categorization of utilization level was based on Holechek et al. (1999) synthesis of grazing studies. Covariance structures used in the repeated measure ANOVAs were selected using the Akaike's Information Criterion (Littell et al. 1996). Response variables that were not repeatedly sampled (soil aggregate stability and penetration resistance) were analyzed with ANOVAs in PROC MIXED in SAS v. 9.2 (SAS Institute, Cary, NC). Data that violated assumptions of ANOVAs were log-transformed prior to analyses. All figures and text report original data (i.e., non-transformed). For analyses, herbaceous cover and density were grouped into five functional groups: perennial grasses, Sandberg bluegrass, annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was treated as a separate functional group from the other perennial grasses because it is much smaller in stature and matures earlier (Davies 2008). Cheatgrass (*Bromus tectorum* L.) was the only annual grass detected at the study sites. Total herbaceous cover was the sum of all the herbaceous species cover. Shrub cover and density was separated into sagebrush and other shrubs. The other shrub category included all shrubs except for sagebrush. The two blocks that did not contain sagebrush were excluded from analyses of treatment effects on sagebrush. Differences between treatment means were considered significant at $P \leq 0.05$. Means are reported with one standard error.

Results

Perennial grass cover response to grazing treatments varied by grazing level (Fig. 2; $P = 0.047$). In areas with high levels of grazing, perennial grass cover was half of ungrazed exclosures ($P = 0.02$). We did not find evidence that perennial grass cover varied between areas with low-moderate levels of grazing and ungrazed exclosures ($P = 0.682$). Perennial grass density did not varied by treatment (Fig. 3) and did not vary by grazing level ($P = 0.227$ and 0.291, respectively). We also did not find any evidence that density (Fig. 3) or cover (Fig. 4) of any other herbaceous plant functional groups varied between grazed and ungrazed treatments or was influenced by grazing level or year ($P > 0.05$). Total herbaceous cover, bare ground, and litter did not vary between grazed and ungrazed treatment ($P = 0.195$, 0.304, and 0.979). Cover of biological soil crust did not differ between treatments ($P = 0.332$). Grazing level and year had no effect on total herbaceous cover, bare ground, litter, and biological soil crust cover ($P > 0.05$).

Sagebrush and other shrub cover did not differ between grazed and ungrazed treatments (Fig. 5) or among years ($P > 0.05$). In sagebrush occupied blocks, density of mature sagebrush was 2-fold greater in ungrazed exclosures compared to the grazed treatment (Fig. 6; $P = 0.005$). Sagebrush juvenile density followed a similar pattern, but statistically there was no difference between treatments (Fig. 6; $P = 0.124$). Other shrub density did not differ between treatments ($P = 0.768$). Grazing level and year had no effect on any of the shrub cover and density responses ($P > 0.05$).

Plant species richness did not differ between ungrazed exclosures (22.6 ± 1.2) and grazed treatments (22.5 ± 1.3) ($P = 0.990$). Plant species diversity (H) was 1.2-fold greater in exclosures (1.8 ± 0.2) compared to the grazed treatment (1.5 ± 0.2) ($P = 0.042$). Grazing level and year did not influence plant species richness or diversity ($P > 0.05$).

Soil aggregate stability averaged 1.5 greater in

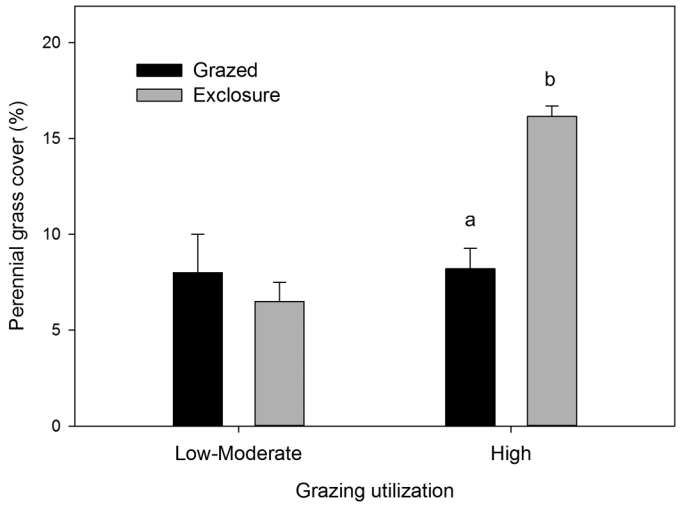


Fig. 2. Perennial grass cover (mean + SE), excluding Sandberg bluegrass, in feral horse grazed (grazed) and ungrazed (exclosure) treatments split by average grazing utilization levels: low-moderate, <40% utilization; high, >40% utilization. Utilization was determined in September in each year. Data presented from the fourth and fifth years after exclosures were constructed. Lowercase letters indicate difference between treatments ($P \leq 0.05$) at that grazing level.

ungrazed exclosures compared to the grazed treatment (Fig. 7; $P = 0.002$), but was not affected by grazing level ($P = 0.724$). Averaged across blocks, the grazed treatment required 2.5-fold more force to penetrate the soil surface compared to ungrazed exclosures ($P < 0.001$). Grazing level did not affect treatment response ($P = 0.200$).

Discussion

Our results suggest that feral horse grazing can affect some aspects of semi-arid ecosystems.

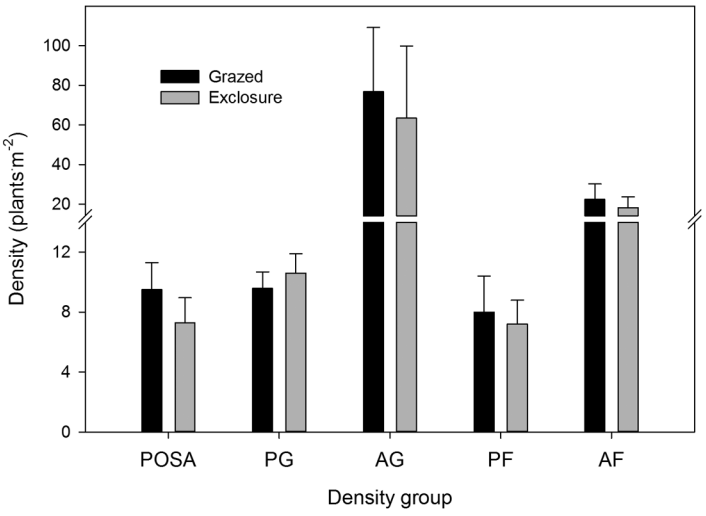


Fig. 3. Density (mean + SE) of different plant functional groups in feral horse grazed (grazed) and ungrazed (exclosure) treatments. POSA, Sandberg bluegrass; PG, perennial grasses excluding POSA; AG, annual grasses; PF, perennial forbs; and AF, annual forbs. Data presented from the fourth and fifth years after exclosures were constructed. Lowercase letters indicate difference between treatments ($P \leq 0.05$).

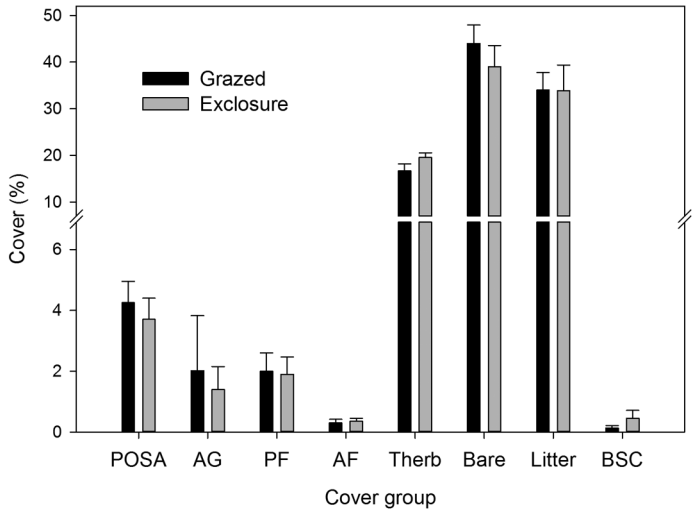


Fig. 4. Cover (mean + SE) of different cover groups in feral horse grazed (grazed) and ungrazed (exclosure) treatments. POSA, Sandberg bluegrass; AG, annual grasses; PF, perennial forbs; AF, annual forbs; Therb, total herbaceous; Bare, bare ground; Litter, ground litter; and BSC, biological soil crusts. Data presented from the fourth and fifth years after exclosures were constructed. Lowercase letters indicate difference between treatments ($P \leq 0.05$).

Similar effects have been reported for other large herbivores (Hobbs 1996, Augustine and McNaughton 1998, Olff and Ritchie 1998). Although previous research (Beever et al. 2003, 2008, Beever and Herrick 2006) suggested that feral horse use affects the sagebrush ecosystem, our results are the first study that empirically measured effects of free-roaming feral horses on the sagebrush steppe. One limitation of our study was that our study sites were relatively close to riparian areas with permanent springs or small creeks that can concentrate horse use (Crane et al.

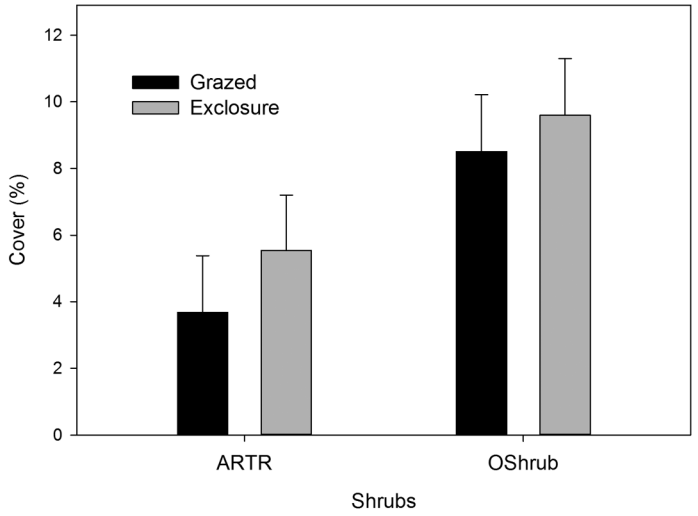


Fig. 5. Cover (mean + SE) of different shrub groups in feral horse grazed (grazed) and ungrazed (exclosure) treatments. ARTR, big sagebrush; Oshrub, shrubs other than ARTR. Data presented from the fourth and fifth years after exclosures were constructed. Lowercase letters indicate difference between treatments ($P \leq 0.05$).

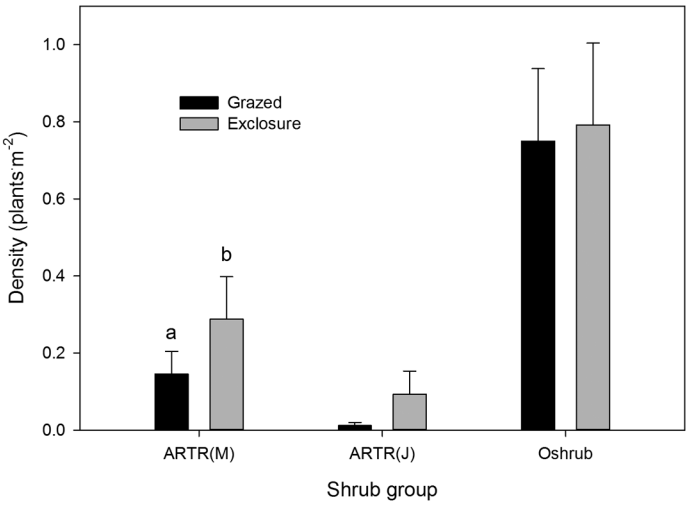


Fig. 6. Density (mean + SE) of different shrub groups in feral horse grazed (grazed) and ungrazed (exclosure) treatments. ARTR(M), mature big sagebrush; ARTR(J), juvenile big sagebrush; Oshrub, shrubs other than ARTR. Big sagebrush data are only from the three blocks that contained big sagebrush. Data presented from the fourth and fifth years after exclosures were constructed. Lowercase letters indicate difference between treatments ($P \leq 0.05$).

1997) and thus, horse effects may dissipate further from water sources. However, Ganskopp and Vavra (1986) reported that feral horses rapidly vacate watering areas after drinking. Feral horses will also travel long distances (up to 55 km) from water if forage is scarce and even disperse up to 8 km from water when forage is plentiful (Hampson et al. 2010). Herbaceous use at our study sites spanned a wide range of utilization levels (Table 1). Thus, our results can likely be extrapolated to a broad array of different feral horse use scenarios in arid and semi-arid ecosystems.

At higher levels of horse use there was about half the perennial grass cover in grazed compared to ungrazed exclosures; however, herba-

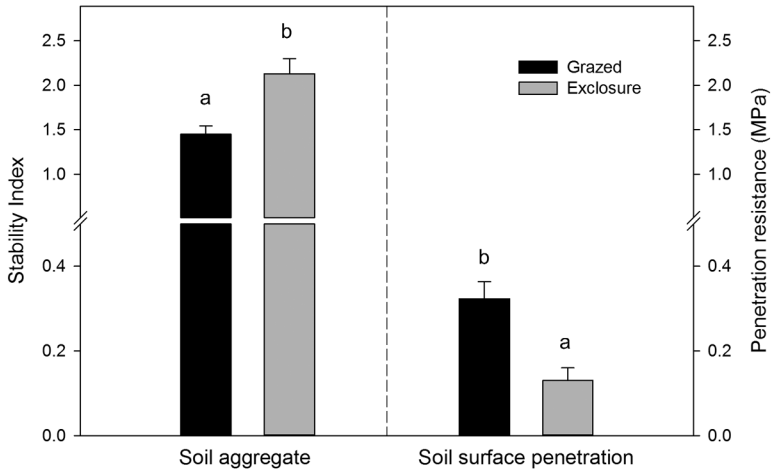


Fig. 7. Soil aggregate stability (left) and soil surface penetration resistance (right) in the feral horse grazed (grazed) and ungrazed (exclosure) treatments five years after exclosures were constructed. Lowercase letters indicate difference between treatments ($P \leq 0.05$).

ceous cover and density were generally not different between horse grazed and ungrazed areas in our study. In contrast, Beever et al. (2008) reported herbaceous cover and abundance generally varied between horse removed and horse occupied areas. Contrasting our results of no difference in perennial grass density, abundance of perennial grasses was greater in horse excluded areas in grasslands in Argentina (de Villalobos and Zalba 2010). In our study feral horses may have been affecting herbaceous cover and density, but recovery of herbaceous plant communities may not be rapid enough to detect differences with short-term exclusion of horses. Arid and semi-arid plant communities can be relatively slow to recover from disturbances. For example, sagebrush steppe plant communities can take several decades once a disturbing agent is removed for even partial recovery (Sneva et al. 1980, West et al. 1984, Anderson and Inouye 2001). Our study sites had less than half and about a third the density of perennial grasses and perennial forbs reported for relatively intact mountain big sagebrush communities in Davies and Bates (2010); further suggesting these plant communities may need more time to recover. Horses had been removed for two to three times longer in areas evaluated by Beever et al. (2008), thus over a longer time period we may see a similar herbaceous response to feral horse exclusion in our study area. De Villalobos and Zalba (2010) were also comparing longer term (7 years) horse exclusion to continuous feral horse grazing. Differences between de Villalobos and Zalba's (2010) and our results could also have been the result of different plant community and site characteristics.

In contrast to the lack of measured effects of feral horse grazing exclusion on herbaceous vegetation abundance, sagebrush density was two-fold higher in horse exclosures suggesting sagebrush recruitment may be limited by feral horses, probably though physical damage of sagebrush. Consumption of sagebrush may also be influencing its recruitment as feral horses will consume small quantities of sagebrush, though they primarily consume grass (Krysl et al. 1984, McInnis and Vavra 1987). In contrast to our results, Beever et al. (2008) did not find a difference in sagebrush frequency between horse grazed and horse removed areas. However, sagebrush density at our plots was low, about half of the density Davies and Bates (2010) reported for relatively intact mountain big sagebrush communities, suggesting that sagebrush was recovering from past disturbances. Feral horse effects on sagebrush density may be more evident when sagebrush is recovering from a disturbance event; thus, potentially explaining why we found a difference is sagebrush density between feral horse grazed and ungrazed areas and Beever et al. (2008) did not. Beever et al. (2008) also measured the frequency of sagebrush using a line-intercept, which may produce a different result than counting individual plants in a belt transect as we did.

Non-sprouting shrubs, such as sagebrush, usually do not recover before herbaceous vegetation after a disturbance (e.g., Davies et al. 2007, Bates et al. 2011). However, this type of research has primarily investigated the recovery of plant communities after fire, not the removal of an herbivore. Fire often completely removes non-sprouting shrubs, but not herbaceous vegetation (Davies et al. 2007, Bates et al. 2011). In contrast, areas where an herbivore was removed may have a residual population of the non-sprouting shrub to expedite its recovery. Anderson and Holte (1981) reported that with the cessation of heavy grazing by sheep and cattle in areas with sagebrush that sagebrush cover increased 42% in the next 15 years while no detectable change occurred in perennial grass cover, however, 10 years later perennial grass cover had increased more than 20-fold. Similar to our results, Manier and Hobbs (2006) found that the long term exclusion of large herbivores in shrub-steppe communities in the Rocky Mountains resulted in increased shrub cover, but did not affect grass cover. Thus our research and the results from Anderson and Holte (1981) suggest that sagebrush, if present in the community, may recover faster than perennial herbaceous vegetation or alternatively, some herbaceous plant groups may not change much with herbivore exclusion (Manier and Hobbs 2006). Additional research would be valuable to determine the mechanisms underlying these varying responses to herbivore removal.

We did not measure a statistically significant difference in juvenile sagebrush density, which seems to contradict our results of higher densities

of mature sagebrush. However, average density of juvenile sagebrush in ungrazed areas was 7.8-fold greater than in horse grazed areas (Fig. 6). Thus, juvenile sagebrush density results are similar to mature sagebrush density, but not statically significantly different due to large variability. This may be due to the episodic nature of sagebrush recruitment (Perryman et al. 2001). The lack of a statistically significant difference may have also been due, in part, to the way we classified juvenile and mature sagebrush. Sagebrush was considered mature if it had reproductive stems, which can occur by the second growing season (Davies et al. 2014). Thus, relatively small, young sagebrush were classified as mature because they had reproductive stems. We saw a similar pattern in sagebrush cover, where we did not measure a statistically significant difference in sagebrush cover between grazed and ungrazed areas, but average sagebrush cover was 1.5-fold greater in grazed compared to ungrazed areas. Many of the sagebrush plants were relatively small and thus, we suspect as sagebrush grows larger that its cover may increase in ungrazed exclosures because of the higher density of sagebrush and become statistically different between ungrazed and grazed areas. The first year mountain big sagebrush produces reproductive stems plants are only about half the height and their canopy cover is less than a fourth of what they will grow to in the next couple of years (K. W. Davies, *unpublished data*). In support of our speculation, Beever et al. (2008) found that sagebrush cover was 1.1 to 2.2 times greater in long term (10–14 yr) horse removed areas compared to horse occupied areas.

Our results suggest effects of feral horses on species richness and diversity may vary by plant community and site characteristics (grazing-plant coevolution, climate, soils, etc.). Plant species diversity was greater in exclosures than feral horse grazed areas in our study. Beever et al. (2008) reported that species richness was greater in feral horse removed compared to horse occupied areas, but they found no difference in diversity between areas. Plant species richness and diversity response to excluding feral horses has been mixed. Species richness and diversity were greater in mountain grasslands in Argentina after seven years of feral horse exclusion (de Villalobos and Zalba 2010). Other studies have found that feral horse grazing exclusion promoted a decline in species richness in montane grasslands in Argentina (Loydi et al. 2012) and plant diversity in the Pryor Mountain Wild Horse Range (Fahnestock and Detling 1999). Variation in intensity and persistence of feral horse grazing likely also correlates to differences in diversity responses (de Villalobos and Zalba 2010). Similarly, Olff and Ritchie (1998) in synthesis of the literature reported that herbivore effects on plant diversity vary by abundance and type of herbivore, plant community composition, and environment characteristics.

Greater penetration resistance of the soil surface in feral horse grazed areas suggests that horse trampling compacted the soil. Beever and Herrick (2006) reported that penetration resistance of the soil surface was 3–15 times higher in horse occupied compared to horse removed areas. This difference was greater than we observed, but exclosures in our study had only excluded horses for half to a third of the time that horses had been absent from horse removed areas used by Beever and Herrick (2006). The greater penetration resistance of the soil surface in feral horse grazed areas than ungrazed exclosures may be a concern, because the soil environment influences many ecosystem processes (Beever and Herrick 2006). We found that soil aggregate stability was 1.5 times greater in feral horse exclosures compared to grazed plots, further demonstrating that feral horses were affecting important soil characteristics. In the Mojave Desert, removal of feral burros (*Equus asinus* L.) and domestic cattle did not produce a consistent soil aggregate stability response (Beever et al. 2006). However, Beever et al. (2006) only investigated soil aggregate stability with one to two years of grazing removal. Soil aggregate stability may take longer to respond and this likely explains why we found a difference with five years of feral horse exclusion.

Horse grazed areas are likely at an elevated risk of soil erosion compared to horse excluded areas. Infiltration rates are slower in areas with higher soil penetration resistance leading to increased runoff risk (Maestre et al. 2002, Aksakal et al. 2011). Similarly, a decline in aggregate stability increases the risk of erosion (Herrick et al. 2001). Soil erosion has the potential

to result in irreversible declines in site productivity and stability and high environmental and economic costs (Pimentel et al. 1995). This suggests that the effects of feral horse trampling may have as much or even more influence on ecosystems than their selective consumption of plants. In support of this argument, Turner (1987) reported in marshes in Georgia that trampling, as it altered the soils, may be the more destructive component of grazing by feral horses.

Our results suggest that soil characteristics may need to recover to facilitate an herbaceous response. Alternatively, herbaceous vegetation may not have been substantially affected by feral horse grazing and a significant change in herbaceous vegetation with feral horse exclusion should not be expected. Other authors have also found that the exclusion of herbivores did not generally increased herbaceous cover and density (e.g., West et al. 1984, Manier and Hobbs 2006, Davies et al. 2009). However, Manier and Hobbs (2006) cautioned that their results should not be interpreted as evidence that herbivory had not influenced the herbaceous plant community because herbivory effects could be long lasting. Our study sites had less than half the density of perennial grasses found in relatively intact mountain big sagebrush communities (Davies and Bates 2010), thus, feral horses may have significantly influenced the herbaceous communities at our sites. Soil recovery may have to occur first because increased soil penetration resistance and decreased aggregate stability can reduce the amount of water available for plant growth (Boxell and Drohan 2009). In addition, high soil penetration resistance can restrict root growth (Ehlers et al. 1983, Bengough and Mullin 1991, Villamil et al. 2001). Soil compaction and trampling by large herbivores can also inhibit plant diversity (Olff and Ritchie 1998).

Our research agrees with previous research (Beever et al. 2003, 2008, Beever and Herrick 2006) that suggested feral horse grazing can cause significant ecological effects in sagebrush steppe and that these effects on sagebrush may influence sagebrush associated wildlife species (Beever and Brussard 2004, Beever and Aldridge 2011). Similarly, feral horses have been reported to negatively impact native wildlife in Argentina (Zalba and Cozzani 2004). Our research suggests that feral horse grazing is limiting the recruitment of sagebrush which likely prolongs the time that the plant community is unsuitable habitat for sagebrush associated wildlife species. This is especially concerning because sagebrush habitat is already limited for many sagebrush associated wildlife, such as Greater Sage-grouse (*Centrocercus urophasianus*) (Connelly et al. 2000, Crawford et al. 2004, Davies et al. 2011) and that fires, which remove sagebrush, are expected to become larger and more frequent with global climate change (Fulé 2008). The role feral horse grazing plays in limiting sage-grouse and other sagebrush associated wildlife conservation needs to be considered (Beever and Aldridge 2011). Additional research investigating sagebrush recruitment and longer term evaluation of the response of sagebrush and herbaceous cover and density to feral horse exclusion is needed to fully understand potential effects of feral horses on habitat for sagebrush associated wildlife.

Conclusions

Feral horse exclusion increased sagebrush density and plant species diversity and promoted recovery of important soil surface characteristics. Collectively, these results suggests that feral horse grazing at the utilization levels occurring in this study can affect the ecological function of semi-arid rangelands and may degrade the habitat value of these communities for associated wildlife. Feral horse grazing elevates the risk of soil erosion by increasing soil penetration resistance and decreasing soil aggregate stability. However, our study demonstrated that relatively short-term feral horse exclusion can initiate recovery of some variables. Other variables (e.g., perennial grass density and forb cover and density) may increase with extended horse exclusion, but long term studies are needed for verification. Though feral horse effects likely vary by intensity and frequency of use as well as a host of other factors, our results suggest that feral horses have some ecological impacts on semi-arid rangelands across a range of levels of utilization. Our results agree with Beever and Aldridge (2011) assertion that feral horses' value to society must be weighed against their ecological costs. The collective results from our study suggest that the effects of feral horses should be considered when developing conservation plans for sagebrush steppe rangelands and other semi-

arid and arid ecosystems.

Acknowledgments

The authors thank the staff at the Sheldon-Hart Mountain National Wildlife Refuge Complex for allowing this research to be conducted on lands they administer and providing the labor and materials to build the exclosures. The authors also appreciate Aleta Nafus, Urban "Woody" Strachan, and all the summer students for assistance with data collection. We are also grateful to Erik Beever, Marty Vavra, Rob Sharp and Dave Ganskopp for reviewing earlier versions of this manuscript. United States Department of Agriculture is an equal opportunity provider and employer. Mention of a proprietary product does not constitute a guarantee or warranty of the product by the USDA or the authors and does not imply its approval to the exclusion of other products that may also be suitable.

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The Population Ecology of Feral Horses in the Australian Alps

Management Summary

Prepared for the Australian Alps Liaison Committee

April 2005

by Michelle Dawson



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Introduction

From 1999-2002 I studied the population ecology of wild (feral) horses in the Australian Alps for my Doctorate through the Applied Ecology Research Group, University of Canberra (under my maiden name 'Walter'). The Australian Alps Liaison Committee (AALC) funded most of the field work and many parks staff from across the Alps were involved. In 2005, the AALC commissioned me to summarise my thesis into a version suitable for park managers and this is the result. It provides a synthesis of the work and its key findings. If people are after details of any component of the research, I refer them to the thesis and other references mentioned in the text. There have been numerous developments in wild horse management since 2002, as well as a very large fire. I have not dealt with them here.

This study was the first of its kind in the Australian Alps, and therefore has a broad focus. It stemmed from a need to improve our understanding of this controversial species and aims to provide interested parties with information to determine the best approach to management. It also contributes to broader knowledge on survey techniques for large mammals and horse population dynamics in general and examines brumby-running for the first time. The only previous study of wild horses in the Australian Alps was on their impact in sub-alpine and montane environments (Dyring 1990).

Horses were first introduced into Australia in 1788 (Dobbie *et al.* 1993). They adapted well to conditions and numbers rose rapidly. Between 1830 and 1850 they increased from an estimated 14 000 to 160 000 largely by natural increase and were first recognised as feral pests in Australia in the 1860's. Australia has the highest number of wild horses in the world (Dobbie *et al.* 1993). They occur mostly in remote, usually rugged, semi-arid areas. The largest populations are on unfenced pastoral country in the Northern Territory and Queensland. The major concentration of wild horses in New South Wales and Victoria are found in the Australian Alps (Dobbie *et al.* 1993).

Wild horses are an introduced species in the Australian Alps. They are a large and hard-hoofed animal occupying an environment that evolved without similar species. There is concern that they have a negative impact on the Alps environment. Wild horses were

seen to be a problem during last century (Helms 1890 in Dyring 1990) and many scientists (Costin 1954, Walters & Hallam 1992, Dobbie *et al.* 1993, Green & Osborne 1994) have expressed concern about the threat of increasing numbers of wild horses to environmental values of the Alps. In the Australian Alps, Dyring (1990) identified track formation, soil compaction, change in vegetation structure and streambank disturbance as impacts of wild horses on sub-alpine and montane environments.

There is a considerable amount of folklore associated with wild horses in the Australian Alps and many people see them as having cultural value. They even feature on the Australian ten dollar note. These contradictory views of wild horses will always make them a sensitive management issue. The aim of this research is to provide people with information so that we can better understand wild horses and how they are interacting with the Alps environment with the hope of aiding more effective management.

Improving our understanding of wild horses in the Australian Alps national parks has been on the agenda for some time. In 1992, a review of wild horses in the Australian Alps national parks recommended that an action plan for feral horses be developed and implemented at the earliest opportunity (Walters & Hallam 1992). The action plan was to be preceded by two key studies: 1) a study of wild horse demography and their ecology, and 2) a study of wild horse impact on vegetation communities and the environment of the Australian Alps national parks. This study addressed the first point.

Distribution

Keeping track of the distribution of wild horses over time helps us to monitor the effect of control programs (or no control) and environmental events such as severe winters or fire. We can learn from past changes in distribution and its causes, and will assist future land managers by keeping records of changes in distribution especially in response to control programs. In this section I present a revised distribution map of wild horses in the Australian Alps national parks and discuss reasons for current and historical distribution.

Dyring (1990) produced a distribution map of wild horses in the Australian Alps. The main features of her maps were: 1) the absence of horses in the ACT, 2) small isolated populations in northern Kosciuszko at Peppercorn, Wild Horse and Nungar Plains, and in nearby Bago and Maragle State Forests, 3) a small population at Botherum Plain near Lake Jindabyne, 4) a large continuous population south of Thredbo River extending through southern Kosciuszko to the Victorian border, 5) a continuation of the same population in Victoria, in the Cobberas-Tingaringy National Park (now part of the Alpine National Park), and 6) a population on the Bogong High Plains near Omeo and smaller populations at Mount Willis (west of Lake Dartmouth) and on the Moroka and Caledonia Rivers.

I revised the wild horse distribution maps between 1999-2002 by searched NSW and Victorian wildlife atlases, holding discussions with local managers and park users to determine current boundaries and factors influencing past distribution, and visiting a lot of the range. Wild horses are found in Kosciuszko National Park, NSW (Figure 1) and

the Alpine National Park, Victoria (Figure 2) and were present on the border of the Australian Capital Territory.

The maximum observed rate of spread of wild horses in the Australian Alps between Dyring's (1990) study and the maps presented here is remarkably low (< 4 km per year). The areas where they appear to have spread is in northern Kosciuszko National Park, and into alpine areas near Mount Kosciuszko. They now do not occupy the full extent of their potential range (for example they used to be present in Namadgi National Park, ACT). Horses are adaptable to a wide range of environments, and are present from the highest to lowest elevations in the Australian Alps so they have the potential to have a much greater distribution than at present.

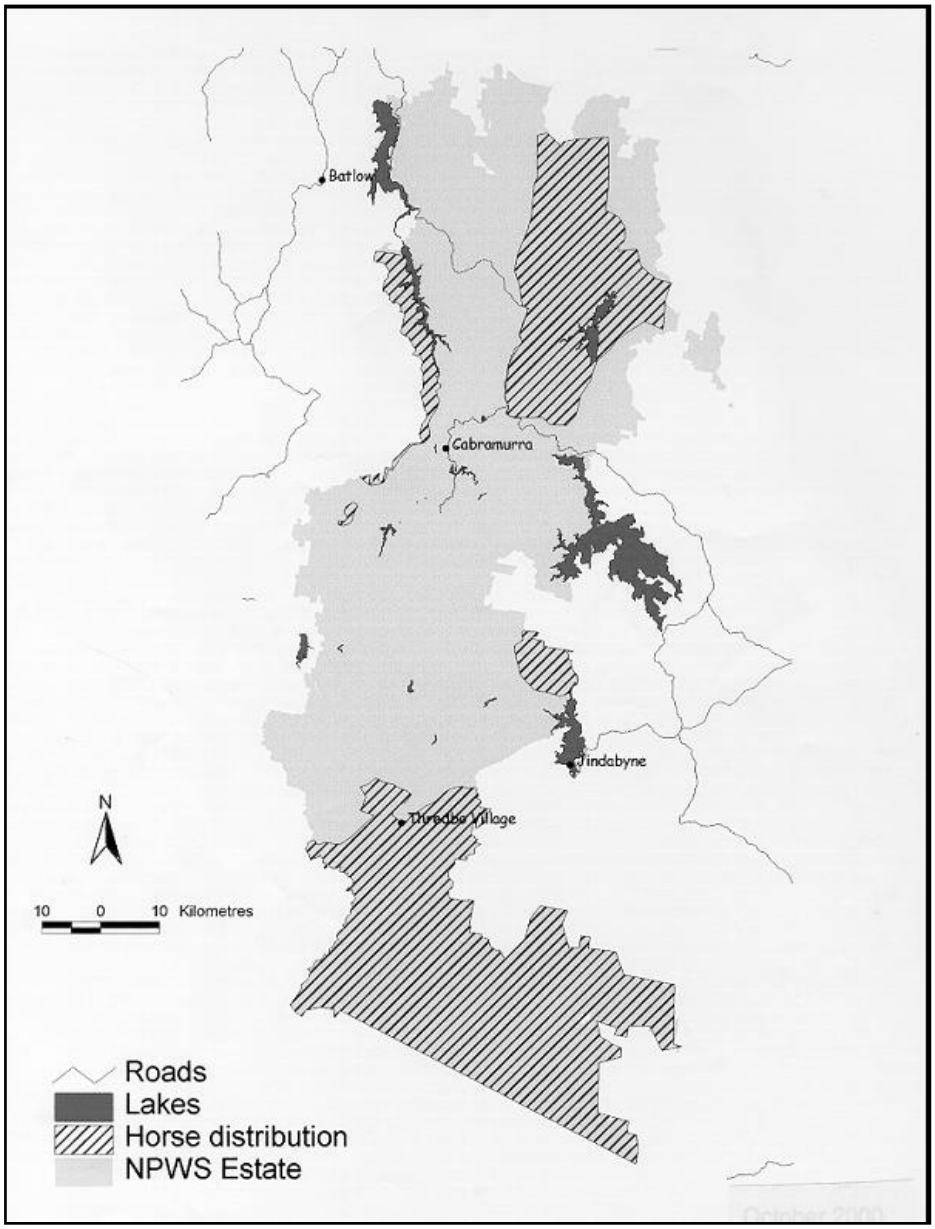


Figure 1: Distribution of wild horses in Kosciuszko National Park. Map produced courtesy of NSW NPWS.

Humans appear to be the most important factor influencing wild horse distribution. The presence of horses in an area can usually be traced back to an introduction event, and control efforts have removed them or reduced their range. Other factors that appear to influence wild horse distribution include geographical barriers, severe snow events, drought and possibly behaviour.

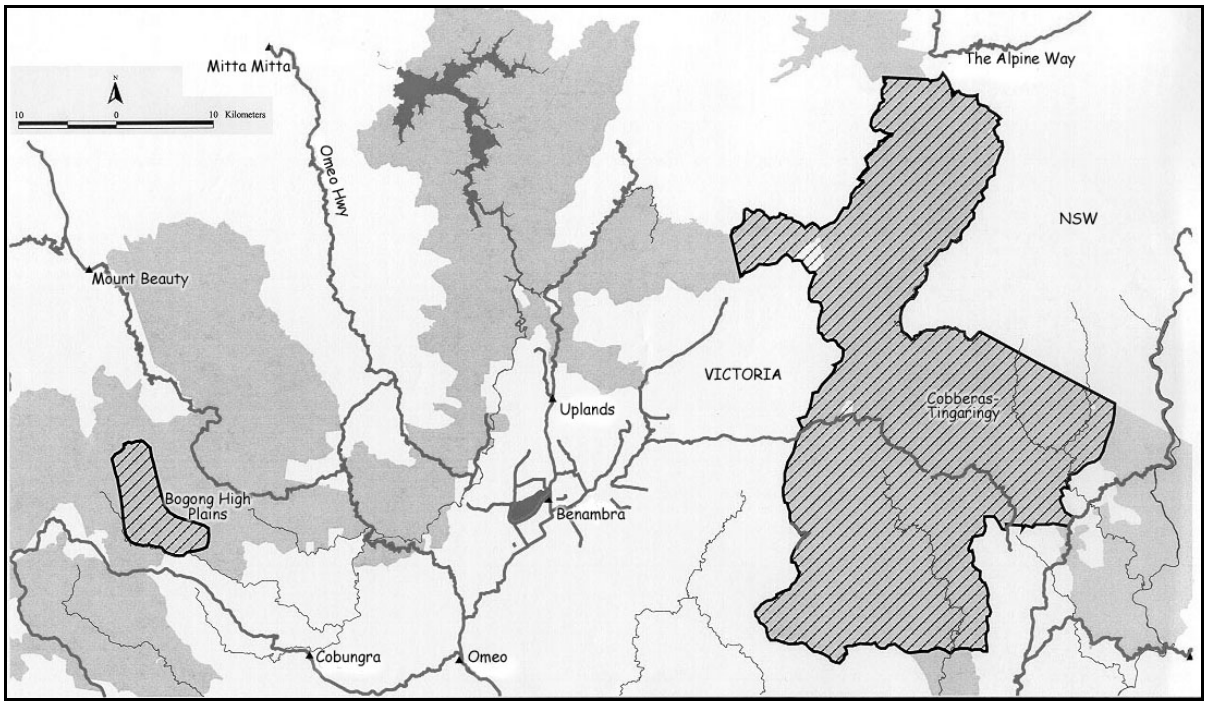


Figure 2: Distribution of wild horses in the Alpine National Park, Victoria. Map produced courtesy of the Department of Natural Resources and Environment. Refer to Figure 1 for legend.

Graziers controlled the distribution of wild horses in much of the Australian Alps from the mid-1800s to as late as the 1960s. Different graziers had different approaches to wild horses; some eradicated them locally and others were responsible for their release into new areas. With the area subsequently reserved as national parks humans continue to influence wild horse distribution. For example wild horses were successfully eradicated from Namadgi National Park in the 1980s (Higgins 1994). However no management action appears to contribute to the spread of horses, as do the occasional illegal reintroduction. (small populations (less than 10 animals) are less likely to establish after introduction than larger ones).

Barriers of dense vegetation and steep slopes appear to prevent horses from colonising new areas in the short term. The question in these cases is whether horses will eventually overcome these barriers. The effectiveness of a barrier will depend on the form of the barrier and the pressure on it from the wild horse population.

Heavy snow events can cause mortality of wild horses. These events appear to be rare and only affect populations at higher elevations. For example, wild horses in the ACT suffered a large reduction in numbers in the early 1960s due to heavy snowfalls (Higgins

1994). In the longer-term, heavy snow events may become less frequent if global warming raises mean temperatures in the Australian Alps (Whetton 1998). Such changes may facilitate the expansion of the distribution of wild horses.

Drought influences the distribution of wild horses in the rainshadow area on the eastern side of the Australian Alps south of Jindabyne. There is very little water available in this environment in contrast to the rest of the Alps where water is freely available. In 1982-83 drought killed off most of the horses in the area and kangaroo, wallaby and rabbit populations also suffered massive losses.

The potential of behaviour to limit the distribution of wild horses is difficult to assess. They are highly social animals and there is a general belief that they are strongly tied to their home range. Behaviour, environmental events (e.g. drought, snow, fire) and other species (eg wild dogs) may have acted in conjunction with humans to restrict the expansion in range of wild horses by keeping them below a threshold density. If wild horses are similar to wood bison in that they are pulse dispersers, they must reach a threshold density before they disperse and colonise a new area.

It will be interesting to see the patterns of wild horse distribution in the Australian Alps in the future. It is likely to depend heavily on the approach to management. If they are not actively managed they may disperse into new areas. Alternatively, management may result in a range reduction. The low rate of spread of wild horses in the Australian Alps should make them relatively easy to manage compared to other introduced species such as the European rabbit which spread at 64km per year (Caughley 1977).

Abundance

The goals of managing wild animal populations are usually expressed in terms of population size. For endangered species, managers try to increase population size, for pest species they try to reduce population size and for harvested populations they try to maintain a population size to optimise harvest. Population estimates are particularly useful if they are repeated through time. Population trend data is useful for assessing the success of management actions or response of the population to natural events. I used aerial survey to estimate the size of the wild horse population in the Australian Alps national parks in 2001. I repeated this survey in 2003 after the fires (refer to Walter 2003 for details).

Despite the obvious advantages of using aerial survey to estimate abundance and density of animals, it has many shortcomings. One of the challenges is to improve accuracy, which is a measure of how close a population estimate is to true population size. Undercounting is the rule in aerial surveys, so results usually are negatively biased. Some of the main factors contributing to bias are vegetation cover, species being surveyed, survey specifications (e.g. height above ground, speed, strip width), weather conditions and observer experience. There are several analysis techniques frequently used for aerial survey including strip surveys (used extensively in kangaroo surveys), mark-recapture models (used on emus and mule deer), and line transect models (a newer technique which is proving to be very useful). In this study I used all three

methods simultaneously and assessed the best method. For full details, refer to Walter and Hone (2003).

The area surveyed follows the distribution maps presented in Figures 1 and 2 and are summarised in Table 1. It excluded the area adjacent to Talbingo Reservoir and east of the Snowy River in Byadbo as these areas were considered to be too rugged and population densities too low to provide accurate estimates.

Table 1: Regions surveyed in the Australian Alps national parks during the wild horse aerial survey in 2001.

Region	Area (km2)	No. of transects	Total transect length (km)
North Kosciuszko	795	25	412
Snowy Plain	77	6	42
South Kosciuszko	758	22	379
North Victoria	1069	30	587
Bogong High Plains	90	8	54
TOTAL	2789	91	1474

The average size of groups observed from the air was 4.91 (± 0.61 SE, n = 34) and 3.79 (± 0.57 SE, n = 4) for observer 1 and 2 respectively. This is in contrast to the group size observed from ground surveys done as part of the population dynamics study (below) of 5.65 (± 0.51 SE, n = 34). The smaller group sizes observed from the air is probably a result of not seeing all individuals in a group from the air. Two observers were used in the aircraft to improve the accuracy of estimates. Interestingly, observer 2 saw more singletons and pairs than observer 1.

We found that the number of horses sighted dropped rapidly with increasing distance from the aircraft. This meant that strip and mark-recapture estimates resulted in an underestimate of abundance. We cannot know what the most accurate survey method is because true population size was not known. However the line transect analysis for both observers combined appears to account for bias the most effectively. It also gave a higher level of precision.

Population estimates using the line transect method equated to 1.86 horses per km^2 and a population estimate of 5200 horses (coefficient of variation = 31%) (Walter and Hone 2003). The average density of wild horses across the entire Australian Alps national parks would be lower than the survey estimates because areas where there were no horses present and of lower horse abundance were not included in the surveys. Density was not uniform across the areas surveyed (if they were the coefficient of variation would be zero). No horses were seen in the southern section of north Victoria (lower Buchan River), but horses were seen frequently on the high plateau country on the NSW/Victoria border, and in the open plains in north Kosciuszko.

Dyring (1990) estimated the number of horses in the Australian Alps based on anecdotal evidence. She suggested that there were 1500-1700 horses in the area covered in her survey in Victoria, which is slightly lower than the estimates obtained in the current study for Victorian Alps parks, and for NSW she suggested there were several hundred

horses in south Kosciuszko and approximately 100 in northern Kosciuszko. We have no way of knowing how accurate these estimates are, but they are much lower than the current study and suggest a 3 fold increase in the population in Kosciuszko National park over 10 years.

Population dynamics

The options available to managers of any wildlife species are either to make the population increase, to make it decrease, harvest it for a continual yield or leave it alone. All of these options are greatly assisted by an understanding of the underlying dynamics of the population. Population dynamics are the variations in the sizes and densities of populations reflecting a change in demographic parameters including birth and death rates. Estimation and modelling of demographic parameters provides information on the state of the population, such as whether it is likely to be stable, increasing or declining, and possible causes. The aim of this section of the study was to examine the population dynamics of three populations of wild horses across the Alps, determine what factors are likely to be limiting the populations if any, and assess the sensitivity of population growth rate to change in key demographic parameters (which can be used to help make decisions on what component of the population to target if undertaking control).

Studies on other wild horses around the world give us a good basic understanding of typical population dynamics and social organisation of wild horses. Linklater (2000) reviewed feral horse populations in North America, South America, Europe and Australasia and found that comparison across different populations showed that horses had remarkably similar social and spatial organisation and that group sizes (range 1 – 28) and home range size (range 0.8 – 303km^2) varied as much between as within populations (Linklater 2000). The density of populations ranged from 0.1 to 35.4 horses per km^2, and adult sex ratios varied from 0.03 to 1.85 males per female. Variation in densities and sex ratios were often the result of management practices such as removal of animals. The maximum rate of increase observed for any wild horse population to date is 30% per year (Duncan 1992), however values of 21% per year are more common (Garrott *et al.* 1991). Horses have an annual breeding season with generally 80-90% of adult females (over 2 years) producing one foal each year (Garrott *et al.* 1991). Survivorship is high in adults with little annual variation and generally lower and more variable earlier in life (Garrott & Taylor 1990).

Variability in wild horse population dynamics occurs at different locations due to the fact that different limiting factors are operating on the various age and sex classes of the population. For example, mountain lion predation can drastically reduce juvenile survival, and food limitation reduces juvenile survival, delays age at first reproduction and reduces fecundity. Management practices can potentially limit populations by reducing fecundity (birth rate) using fertility control or reducing survival rates of adults and/or juveniles by culling.

The population dynamics of wild horses were studied in detail at three sites each spring and autumn between spring 1999 and autumn 2002. The sites were Big Boggy near Mount Kosciuszko in central Kosciuszko National Park, Cowombat on the border of

Kosciuszko National Park and the Alpine National Park near The Pilot, and Currango in northern Kosciuszko National Park southwest of Mount Bimberi (Table 2). These sites were chosen to sample a range of habitats, because they were areas of interest for park managers, wild horses could readily be found at all of the sites, and they are independent of each other (too far apart for horses to move between). There was no management of these populations for the duration of the study.

Population estimates through time at each site showed different patterns. The Big Boggy population showed seasonal patterns with higher numbers in autumn than in spring, and the spring estimates were more precise than the autumn estimates (range 57 ± 1 SE to 86 ± 6 SE horses). This trend is probably related to snow in the area over winter. Cowombat population estimates also showed seasonal trends but not as clearly as the Big Boggy, and were generally less precise than Big Boggy estimates (range from 64 ± 6 SE to 101 ± 10 SE horses). There was no clear seasonal trend in population estimates for Currango, and precision varied between occasions (range from 69 ± 4 SE to 109 ± 6 SE horses). The variability in estimates of the Currango population was probably due to immigration and emigration. The highest average density of horses was observed at Cowombat, while the Big Boggy and Currango populations had similar lower densities (Table 3).

Table 2: Population dynamics study area descriptions

Site	Area (km^2)	Elevation (m)	Vegetation
Big Boggy	35.5	1500-2228	Alpine, sub alpine woodland, cold air drainage shrub and herbfield
Cowombat	12.7	1000-1540	Montane and mixed open forest, subalpine woodland, tall gum and alpine ash forest
Currango	41.4	1220-1370	Cold air drainage shrub and herbfield, montane mixed open forest, subalpine woodland, tall gum and alpine ash forest

The demographics of the populations were similar to those of other wild horse populations with high adult survival rates, lower survival in the first 3 years of life and fecundity rates of about 0.25 (number of females born per female per year) (Table 3). All sites had a positive rate of increase but the only site where the rate of increase was significantly different to a stable population was Currango. Cowombat had the lowest rate of increase.

Table 3: Summary of key demographic variables for the three study sites 1999-2001. Fecundity is half juveniles per adult female per year, survival rates are annual, and rate of increase (λ) is the annual finite growth rate (with coefficient of variation in the estimate).

Site	Average density (horseskm^{-2})	Fecundity	Survival 0-3 years	Adult survival	Rate of increase (CV %)
Big Boggy	2.01	0.24	0.75	0.91	1.07 (3.5)
Cowombat	6.40	0.21	0.63	0.91	1.03 (3.4)
Currango	2.13	0.31	0.67	0.91	1.09 (4.2)

Horses at Cowombat had the poorest average body condition of the three sites, and horses at Currango had the highest body condition score. This trend of body condition was reflected in the trend in food available (Table 4). The body condition of females was poorer than males, overall however, the body condition of females at Currango was not significantly different to that of males.

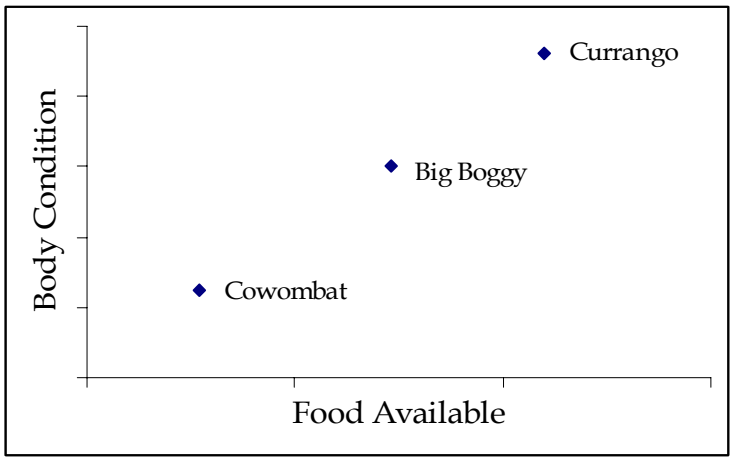


Figure 3: Average body condition scores and food availability scores for the three study sites between 1999 and 2001.

The trend in body condition and food availability (Figure 3) and rate of increase (Table 3) across the three sites suggests that the population at Cowombat is food limited and relatively stable while the population at Currango is not limited by food and increasing. The Big Boggy is in between the two. The implications of this for management is that the Currango population is likely to continue to increase if no control actions are taken, although the relative impact of the horses at Currango on vegetation is lower. At the other end of the scale, the population at Cowombat appears to be stable and in equilibrium with its environment and unlikely to increase in size in the absence of management, although the impact of the wild horses in the area on the vegetation is higher. The Cowombat site was burnt by intense wildfire in 2003 and it would be beneficial to revisit the sites to reassess the populations.

Managers that target adults (survival or removal) in any control measure will yield the most significant result, followed by fertility control then targeting 0-3 year olds. This is because the rate of increase of the wild horse populations were most sensitive to changes in adult survival. The next most influential parameter is fecundity, which has half the weighting of adult survival. Survival in the first 3 years of life has less influence receiving only 1/5th the weighting of adult survival, and age of first reproduction had a negligible effect on population growth rate.

Brumby-running

Management of wild horses in the Australian Alps is not based purely in the context of an introduced species but also as one with cultural value. Brumby-running is an activity that began soon after the arrival of horses in the Australian Alps and is closely tied to the culture of wild horses. At the time of the study, the only active management of wild horses in the Australian Alps national park was brumby-running in the Victorian Alps. Brumby-running is a form of harvesting where horse-riders rope wild horses and remove them from the population; it is thought to have a limiting effect on the wild horse population in Victoria, but it has never been examined empirically. The purpose of this section of the study was to gain an understanding of the influence of brumby-running on the wild horse population in Victoria. In particular to describe the demography of wild horses removed by brumby-runners, assess the behaviour of brumby-runners relevant to the type and quantity of wild horses caught, and predict the likely effect of brumby-running on the wild horse population.

Demographic data on wild horses caught and removed from the Alpine National Park, Victoria was supplied by the Alpine Brumby Management Association (ABMA) and Parks Victoria from 1998 to 2002. Brumby-runners recorded the general location, number and type (stallion, colt, mare, filly) of all horses caught each financial year. The quality of information supplied improved over time. The data for 2000-2001 and 2001-2002 are the most detailed including the month of capture and estimated age. I gave body condition scores to 176 horses caught between autumn 1999 and spring 2001 inclusive based on photographic records kept by one brumby-runner (BR1). Body condition and demography of horses caught were compared to the wild horses studied in the population dynamics component of the study to see if the brumby-runners were selectively harvesting. I also used records kept by BR1 on trips made between January 2000 and January 2001 on number of brumby-runners, length of trip and capture rate to get an insight into the effectiveness of brumby-running. Finally, I used logistic growth models to assess whether the number of horses removed by brumby-runners is likely to be limiting the population.

About 200 horses were caught each year between 1998 and 2002 (Table 4). The majority of horses caught were young (colts and fillies). More females (mares and fillies) than males (stallions and colts) were caught in all years (ratio 0.67:1). The difference is due mostly to the fact that so few stallions were caught. Most horses were caught in autumn and least in summer with similar amounts being caught in winter and spring.

Table 4: Summary of horses caught by brumby-runners in the Alpine National Park, Victoria. *Not all horses caught were recorded in 1999-2000.

Year	Total caught	Stallions (%)	Colts (%)	Mares (%)	Fillies (%)
1998-1999	224	9.4	29.9	43.8	17
1999-2000	78*	7.7	37.2	41	14.1
2000-2001	174	9.8	25.9	36.2	28.2
2001-2002	207	7.7	36.2	33.3	22.7

The assignment of wild horses caught into categories of stallion, mares, colts and fillies can be misleading for interpreting age of horses, particularly males because males (3-6 years old) can be called colts while the classification of 3-year-old females and older as fillies is less common. I would recommend that any data collection should include an estimation of age in the future to address this. This was done between 2000 and 2002 and the data was used in comparisons with the Cowombat, Big Boggy and Currango wild populations.

Brumby-runners did not select for males or females when all age classes were combined for the analysis, however they did select for adult females over adult males. They also showed a preference for younger animals (<3 years old) than were present in the wild. 49% of all horses caught between July 2000 and June 2002 were younger than three while the average proportion of horses under the age of three at Cowombat, Currango and Big Boggy were 28%. Brumby-runners did not select horses in poorer condition. These findings suggest that the brumby-runners are not targeting the 'doomed surplus' (the old, young or weak).

The average trip length for BR1 was 2.93 days, and the majority of trips were 2 days in duration (weekends). He was accompanied by other brumby runners on most trips with a total effort of all brumby-runners n this sample being 172 days. The mean catch per unit effort for BR1 was 1.16 horses/day. All other riders combined had a mean catch per unit effort of 0.55 horses per day. So there is an effect of skill on catch per unit effort. Catch per unit effort did not vary across seasons. Mean catch per unit effort was highest when brumby-runners were in a group of three.

Predictive modelling for the wild horse population assuming logistic growth shows that brumby-running is likely to have a limiting effect on the population. The predicted effect of different levels of brumby-running on the population into the future are shown in Figure 4. The model assumes that the population size is 2000 (based on aerial survey results) and 200 horses have been removed annually prior to the present. The model assumes a stable environment. Note that the 2003 wildfires reduced the population size significantly (Walter 2003) so harvesting at a rate of 200 horses per year post-fire would drive the population to extinction.

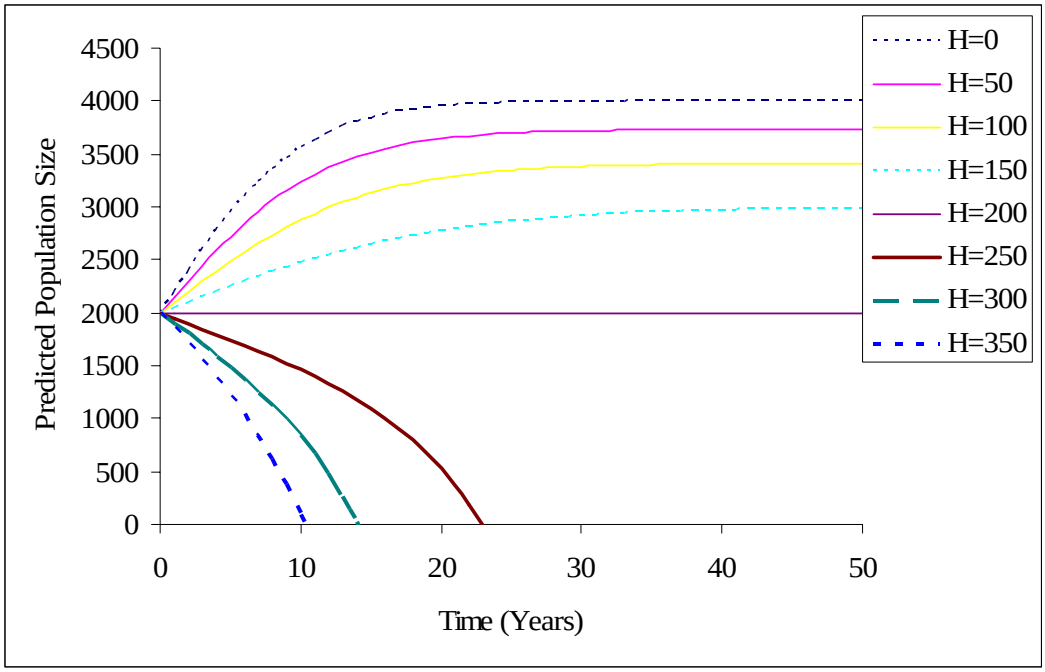


Figure 4: Predicted size of the Alpine National Park wild horse population at different levels of harvest (H) per year. The model assumes logistic growth with intrinsic rate of increase = 0.2, initial population size = 2000 and carrying capacity = 4000.

This model assumes a non-selective harvest. Harvesting that targets younger animals means that more animals have to be removed to achieve the same population reduction, while selectively harvesting adult females will lead to a sex bias in the population and less animals would have to be removed to achieve the same target.

Modelling shows that although brumby-running is a form of recreational harvesting, it can suppress populations below carrying capacity and can be used as a management tool. Its effectiveness as a management tool will depend on the management objectives in each circumstance. I recommend that if it is used as a management tool in the future it should be accompanied by population and/or impact monitoring, as should any form of management.

Key management messages

- The maximum observed rate of spread of wild horses in the Australian Alps between Dyring's (1990) study and the maps presented here is remarkably low (< 4 km per year).
- Wild horses do not occupy the full extent of their potential range.
- Humans appear to be the most important factor influencing wild horse distribution. The presence of horses in an area can usually be traced back to an introduction event, and control efforts have removed them or reduced their range.

- Population estimates in the survey area using the line transect method equated to 1.86 horses per km² and a population estimate of 5200.
- There is some evidence to suggest that the wild horse population in Kosciuszko increased 3-fold in Kosciuszko National park over 10 years.
- Management practices can potentially limit populations by targeting reducing fecundity (birth rate) using fertility control or reducing survival rates (by removal or culling) of adults and/or juveniles. Managers that target adults will yield the most significant results, followed by fertility control then targeting 0-3 year olds.
- Across the three populations studied (Currango, Big Boggy and Cowombat) trends in population rate of increase, body condition and food availability suggest that the population at Cowombat is food limited and relatively stable while the population at Currango is not limited by food and increasing. The Big Boggy is in between the two.
- Brumby-runners in the Alpine National park, Victoria caught approximately 200 horses annually between 1998 and 2002. The majority of horses caught were young and more females than males were caught. The discrepancy between the sexes is because so few adult males (stallions) were caught.
- Modelling shows that brumby-running can suppress wild horse populations below carrying capacity and can be used as a management tool.

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Carbon sequestration and rangelands: A synthesis of land management and precipitation effects
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Journal of Soil and Water Conservation; Mar/Apr 2007; 62, 2; SciTech Premium Collection
pg. 77

Carbon sequestration and rangelands: A synthesis of land management and precipitation effects

J.D. Derner and G.E. Schuman

Abstract: Management of rangelands can aid in the mitigation of rising atmospheric carbon dioxide concentrations via carbon storage in biomass and soil organic matter, a process termed carbon sequestration. Here we provide a review of current knowledge on the effects of land management practices (grazing, nitrogen inputs, and restoration) and precipitation on carbon sequestration in rangelands. Although there was no statistical relationship between change in soil carbon with longevity of the grazing management practice in native rangelands of the North American Great Plains, the general trend seems to suggest a decrease in carbon sequestration with longevity of the grazing management practice across stocking rates. The relationship of carbon sequestration to mean annual precipitation is negative for both the 0 to 10 cm (0 to 3.9 in) and 0 to 30 cm (0 to 11.8 in) soil depths across stocking rates. The threshold from positive to negative carbon change occurs at approximately 440 mm (17.3 in) of precipitation for the 0 to 10 cm soil depth and at 600 mm (23.6 in) for the 0 to 30 cm soil depth. We acknowledge that largely unexplored is the arena of management-environment interactions needed to increase our understanding of climate-plant-soil-microbial interactions as factors affecting nutrient cycling. Continued refinement of estimates of terrestrial carbon storage in rangelands will assist in the development of greenhouse gas emissions and carbon credit marketing policies, as well as potentially modifying government natural resource conservation programs to emphasize land management practices that increase carbon sequestration.

Key words: grazing—legumes—nitrogen inputs—precipitation gradient—soil organic carbon (SOC)

Atmospheric carbon dioxide concentrations have varied historically, but they have substantially increased from 270 µmol mol^{-1} in 1870 prior to the Industrial Revolution to current levels greater than 365 µmol mol^{-1} (Morgan et al. 2004a). Land management practices, however, offer opportunities to mitigate the rise in atmospheric CO_2 concentration through sequestration of this additional carbon via storage in plant biomass and soil organic matter in a process termed terrestrial C sequestration (Izaurralde et al. 2001). Carbon sequestration also provides associated ecosystem co-benefits such as increased soil water holding capacity, better soil structure, improved soil quality and nutrient cycling, and reduced soil erosion.

Rangelands have a large potential to sequester C because they occupy about half of the world's land area and store greater than 10% of terrestrial biomass C and 10 to 30% of global soil organic carbon (SOC) (Schlesinger 1997; Scurlock and Hall 1998). It is estimated that rangelands globally sequester C in soil at a rate of 0.5 Pg C yr^{-1} (Schlesinger 1997; Scurlock and Hall 1998). Although soil C sequestration rates are low on rangelands relative to those reported for croplands and improved pastures, increases in terrestrial C on rangelands resulting from management account for a significant amount of C sequestration given the large geographical area of this land resource and generally require minimal inputs. This implies that modest changes in C storage in rangeland ecosystems have the potential to modify the global C cycle and indirectly influence climate (Schimel et al. 1990; Ojima et al. 1993; Conant et al. 2001). Despite its significance, our understanding of land use effects on the storage of C in rangelands remains limited (Schuman et al. 2001; Reeder and Schuman 2002). In addition, research addressing C sequestration in rangelands is still in its infancy when compared to cropland and forestry.

Soil C sequestration on rangelands is influenced by biome, climate (Conant et al. 2001), management practices, and environmental factors (Jones and Donnelly 2004). Even though C dynamics on rangelands involve complex interactions involving climate, soils, plant communities and management, we currently only have a rudimentary knowledge of these interactions as controlling drivers influencing soil C sequestration (Schuman et al. 2001). There is, however, emerging evidence that the relative contribution of management practices can be lower compared to climatic drivers (e.g., Schuman et al. 2005). Nevertheless, there remains a paucity of basic ecological information that is needed to improve understanding of why, when and where rangeland ecosystems function as C sinks or sources.

Here we provide a review of current knowledge on the effects of land management practices (grazing, N inputs via fertilization and interseeding of N-fixing legumes, and restoration of degraded lands) on C sequestration in rangelands. Because of the limited information on C sequestration in dry lands including deserts and desert grasslands (e.g., Gardner 1950; Rasmussen and Brotherson 1986; Lal 2004a; Vagen et al. 2005), this paper primarily addresses semi-arid (250 to 500 mm annual precipitation) and mesic (500 to 1000 mm) rangeland ecosystems where the vast majority of research has been conducted. These data are synthesized to determine relationships of changes in soil C to length of time a rangeland management practice has been in place and to gradients in mean annual precipitation as C sequestration rates increase from arid (0.02 to 0.08 Mg C ha^{-1} yr^{-1}) to semi-arid (0.03 to 0.12 Mg C ha^{-1} yr^{-1}) to semi-humid and sub-humid (0.08 to 0.20 Mg C ha^{-1} yr^{-1}) environments (Lal 2000). Differences in above-ground versus below-ground constraints on plant growth (Burke et al. 1998), root/shoot ratios

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Table 1
Management effects on soil organic carbon sequestration rates of rangelands across ecosystems.

Management practice/ecosystem	Location	SOC sequestration	Citation
Grazing			
Shortgrass prairie	Colorado	0.12 Mg C ha^{-1} yr^{-1}	Derner et al. 1997
	Colorado	0.07 Mg C ha^{-1} yr^{-1}	Reeder and Schuman 2002
Northern mixed-grass prairie	Wyoming	0.30 Mg C ha^{-1} yr^{-1}	Schuman et al. 1999
	North Dakota	0.29 Mg C ha^{-1} yr^{-1}	Frank 2004
Southern mixed-grass prairie	Oklahoma	No change	Fuhlendorf et al. 2002
Nitrogen fertilization			
Tallgrass prairie	Kansas	1.6 Mg C ha^{-1} yr^{-1}	Rice 2000
Conservation Reserve Program	Wyoming	0.41 to 1.16 Mg C ha^{-1} yr^{-1}	Reeder et al.1998
	Saskatchewan	Increases of 5.4 to 9.3 Mg C ha^{-1} yr^{-1}	Nyborg et al. 1994
Legume interseeding			
Northern mixed-grass prairie	South Dakota	0.33 to 1.56 Mg C ha^{-1} yr^{-1}	Mortenson et al. 2004
Restoration			
Southern mixed-grass prairie	Oklahoma	No difference 0 to 10 cm with moderate grazing, but 65% decrease with heavy grazing	Fuhlendorf et al. 2002
	Sudan	Restored soil C to 80% of native rangeland in 100 yr	Olsson and Ardö 2002
Semiarid savanna	Argentina	466% increase	Abril and Bucher 2001
Tallgrass prairie	Texas	Average 0.45 Mg C ha^{-1}, estimated 100 years to achieve native rangeland level	Potter et al. 1999
Conservation Reserve Program	Texas, Kansas, and Nebraska	0.8 to 1.1 Mg C ha^{-1} yr^{-1}	Gebhart et al. 1994
	Texas to North Dakota	Average 0.9 Mg C ha^{-1} yr^{-1}	Follett et al. 2001
Mined lands	Wyoming	400% increase over 30 years	Stahl et al. 2003

Note: Data from Schuman and Derner 2004; Follett and Schuman 2005.

(Sims et al. 1978; Derner et al. 2006), root C/SOC ratios (Derner et al. 2006), and productivity potential (Knapp and Smith 2001) have been previously demonstrated across precipitation gradients.

Land Management Effects on Carbon Sequestration

Grazing. Grazing facilitates the physical breakdown, soil incorporation and rate of decomposition of residual plant material (Naeth et al. 1991; Shariff et al. 1994; Schuman et al. 1999). Grazing intensity and frequency are thought to cause the primary effects on C storage across rangelands (Bruce et al. 1999), although these effects are often inconsistent and difficult to predict (Milchunas and Lauenroth 1993; Schuman et al. 2001; Reeder and Schuman 2002).

Grazing-induced changes in plant community composition are likely responsible for many of the changes in C sequestration observed with stocking rates. For example, moderate and heavy stocking rates during the grazing season employed in a shortgrass steppe and a northern mixed-grass prairie modified the plant community composition by reducing the proportion of cool-season (C3) perennial grasses while increasing the predominant warm season (C4) perennial grass, blue grama (Frank et al. 1995; Schuman et al. 1999; Derner et al. 2006). This change in plant community composition reduces the production potential of these rangelands by up to one-third (Schuman et al. 1999) but increases SOC because of the greater transfer of C to belowground plant parts in blue grama (Coupland and Van Dyne 1979). Grazing at moderate and heavy stocking rates in a shortgrass steppe increased SOC in the surface 30 cm (11.9 in) compared to adjacent nongrazed exclosures (Derner et al. 1997, 2006; Reeder and Schuman 2002; Reeder et al. 2004), resulting in estimated C sequestration rates of 0.12 Mg C ha^{-1} yr^{-1} (108.78 lbs ac^{-1} yr^{-1})for the moderate stocking rate and 0.07 Mg C ha^{-1} yr^{-1} (63.46 lbs ac^{-1} yr^{-1}) for the heavy stocking rate (table 1).

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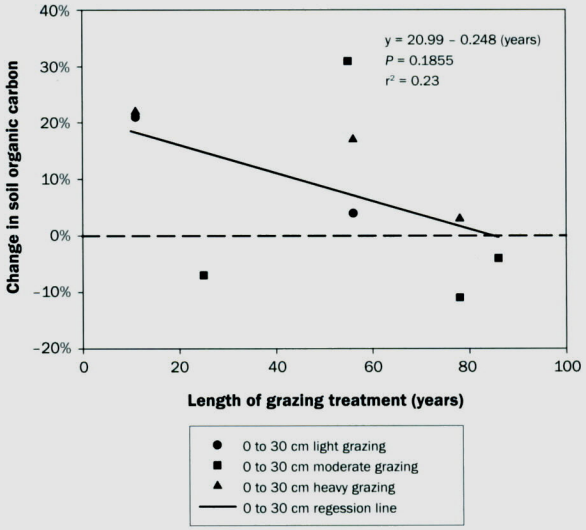
Also, grazing at light or heavy stocking rates in northern mixed-grass prairie increased SOC in the surface 30 cm of the soil compared to nongrazed exclosures (Schuman et al. 1999), resulting in a C sequestration rate of 0.30 Mg C ha^{-1} yr^{-1} (271.96 lbs ac^{-1} yr^{-1}) (table 1). Carbon sequestration rates, calculated using CO_2 flux data, on a northern mixed-grass prairie were similar at 0.29 Mg C ha^{-1} yr^{-1} (262.89 lbs ac^{-1} yr^{-1})(Frank 2004). Long-term (81 years) moderate and heavy grazing in northern mixed-prairie increased soil C by 19% and 34%, respectively, in the surface 5 cm (1.9 in) of soil compared to nongrazed exclosures (Wienhold et al. 2001). Grazing strategy did not affect C sequestration in a northern mixed-grass prairie as no differences were evident among short-duration rotational grazing, rotationally-deferred grazing, and continuous season-long grazing at heavy stocking rates (Manley et al. 1995).

There is a paucity of information addressing the interactions of management and environment on C sequestration. One recent study, however, sheds considerable light into the complexity of these interactions and the limitations in extending data from relatively short-term investigations to long-term predictions. Severe drought and heavy grazing can result in significant losses of SOC that was previously stored during normal to above-normal production years in northern mixed-grass prairie (Schuman et al. 2005). Loss of SOC during these drought years concurs with CO_2 flux data results during the same time period in a nearby shortgrass prairie (Morgan et al. 2004b). Microbial community shifts and activity were also observed in the heavy stocking rate of the northern mixed-grass prairie that exhibited significant losses in soil C during the severe drought period (Ingram et al. 2004, Stahl et al. 2004). These data suggest that additional information is needed to assess the importance and processes associated with dramatic fluctuations in climatic factors, such as drought, that may induce losses of C in rangeland ecosystems (Breshears and Allen 2002). Drought may change rangelands from sinks to sources of atmospheric CO_2 because limiting soil water proportionally affects photosynthetic rates more than total respiration (Balogh et al. 2005.)

Nitrogen Inputs. Many rangelands are N deficient and have been shown to exhibit increased production (Samuel and Hart 1998; Berg and Sims 2000) and water-use-efficiency in response to N addition (Power and Alessi 1971). Addition of N fertilizer increased soil C in a tallgrass prairie (Rice 2000), in CRP lands (Reeder et al. 1998), in rangelands in Saskatchewan, (Nyborg et al. 1994) and in Alberta (Malhi et al. 1991) (table 1).There are, however, substantial C emissions associated with the production, packaging, storing and distribution of N fertilizers (Lal 2004b). Changes in SOC on "WW-Spar" Old World bluestem (*Bothriochloa ischaemum* L.) pastures in Oklahoma after five years of annual N fertilizer applications were greater for the intermediate application rate (68 kg N ha^{-1} yr^{-1}) compared to lower (34 kg N ha^{-1} yr^{-1}) and higher (102 kg N ha^{-1} yr^{-1}) application rates (Berg and Sims 2000). Application of other nutrients, where they are deficient, can also enhance SOC storage (Nyborg et al. 1998, 1999; Conant et al. 2001). The benefits of increased SOC sequestration with N-fertilization are offset, however, by emissions of CO_2 and N_2O in the fertilizer process (Schlesinger 1999, 2000), as well as the enhancement of NO_x (nitric oxide plus nitrous oxide) emissions and reduction of CH_4 uptake in soils (Mosier et al. 1998).

The introduction of N-fixing legumes into rangelands has been the subject of research for decades to provide an alternative to N-fertilization (Tesar and Jakobs 1972; Heinrichs 1975; Kruger and Vigil 1979; Berdahl et al. 1989). For example, interseeding yellow-flowered alfalfa (*Medicago sativa* ssp. *falcata*) into northern mixed-grass prairie increased SOC by 4% to 17% across three interseeding dates (Mortenson et al. 2004), resulting in C sequestration rates of 1.56, 0.65, and 0.33 Mg C ha^{-1} yr^{-1}, for 3-, 14-, and 36-year post-interseeding, respectively (table 1). N fixation by the yellow-flowering alfalfa also significantly increased soil total N, aboveground production, and N forage quality (Mortenson et al. 2004, 2005). This increase in production accounts for the enhanced SOC storage and does not represent any "C costs" in the production of N. An initial report by Schuman et al. (2004)

Figure 1
Percent change (grazed vs. nongrazed) in soil organic carbon with respect to length of grazing treatment in the North American Great Plains.



Note: Data from Frank et al. 1995; Schuman et al. 1999; Reeder and Schuman 2002; Derner et al. 2006.

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indicated no increase in the emission of the greenhouse gas nitrous oxide from rangeland soils on which yellow-flowered alfalfa had been interseeded.

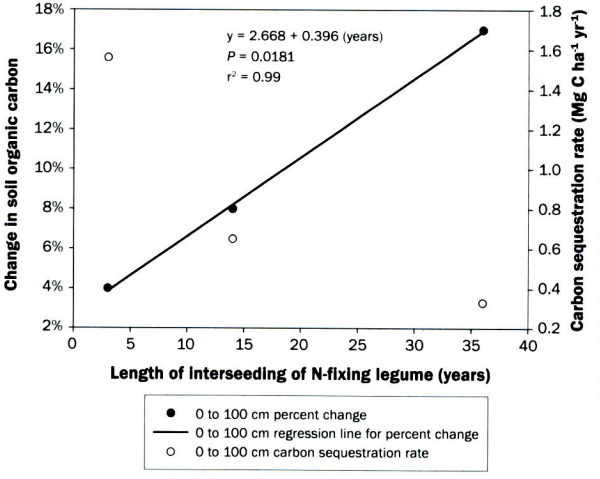
Restoration of Degraded Lands

Cultivated Lands. Cultivation of rangeland soils dramatically reduces SOC (Haas et al. 1957). For example, shortgrass steppe soils cultivated for 60 years had 62% less SOC in the upper 15 cm (5.9 in) of the soil profile compared to native rangeland (Bowman et al. 1990). Abandoning cultivation of the shortgrass steppe soils, without re-establishing permanent vegetation, has increased SOC by 20% in the surface 10 cm (3.9 in) over 50 years (Burke et al. 1995); yet these soils contained only 67% of the SOC found in native shortgrass steppe, suggesting that there is a considerable capacity to sequester C in these degraded soils. This capacity may be tempered, however, by limitations associated with the loss of soil productivity due to historic erosional losses of topsoil while these lands were under cultivation.

Restoring permanent vegetation on formerly cultivated lands offers opportunities to store substantial amounts of SOC. For example, Post and Kwon (2000) report an average soil C sequestration rate for grassland establishment on formerly cultivated lands of 0.33 Mg C ha^{-1} yr^{-1} (299.15 lbs ac^{-1} yr^{-1}), although they acknowledge there is considerable variation. Grazing can alter the recovery of these restored sites and affect C sequestration as heavy grazing can reduce the rate of C accumulation (Fuhlendorf et al. 2002). Predicted recovery of soil C on cultivated fields to pre-cultivation levels without restoration efforts is 230 years (Knops and Tilman 2000). Model estimates indicate that conversion of marginal agricultural lands to rangeland in Sudan would restore SOC levels to 80% of those found in native savannas in 100 years (Olsson and Ardö 2002). Potter et al. (1999) estimated restoration efforts in a tallgrass prairie would require 158 years for the restored site to have a similar C pool as native prairie.

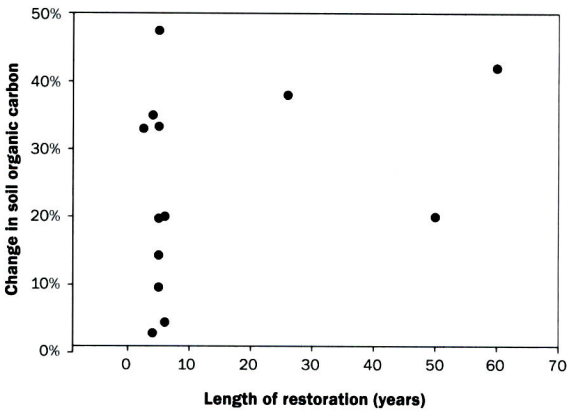
Carbon sequestration rate estimates for restored lands range from 0.28 Mg C ha^{-1} yr^{-1} (253.83 lbs ac^{-1} yr^{-1}) in the surface 20 cm (7.9 in) on highly restored sites in a semi-arid savanna in the western Chaco of Argentina (Abril and Bucher 2001) to 0.90 Mg C ha^{-1} yr^{-1} for Conservation Reserve Program lands from Texas to North Dakota

Figure 2
Percent change (interseeded vs. noninterseeded) in soil organic carbon and carbon sequestration rate with respect to length of interseeding of N-fixing legume in a northern mixed-grass prairie.



Note: Data from Mortenson et al. 2004.

Figure 3
Percent change (restored vs. nonrestored) in soil organic carbon with respect to length of restoration of formerly cultivated lands in North American Great Plains.



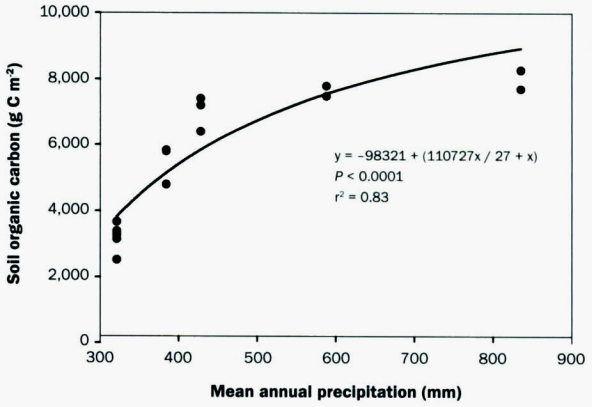
Note: Data from Gebhart et al. 1994; Burke et al. 1995; Reeder et al. 1998; Karlen et al. 1999; Potter et al. 1999.

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(Follett et al. 2001) (table 1). Similarly, C sequestration rates in the 0 to 40 cm (0 to 15.7 in) and 0 to 300 cm (0 to 118.1 in) soil depths were estimated to be 0.8 to 1.1 Mg C ha^{-1} yr^{-1} (725.22 to 997.17 lbs ac^{-1} yr^{-1}) for Conservation Reserve Program lands in Texas, Kansas and Nebraska (Gebhart et al. 1994). Restored tallgrass prairie in Texas was estimated to have a C sequestration rate of 0.45 Mg C ha^{-1} yr^{-1} (407.93 lbs ac^{-1} yr^{-1}) in the upper 60 cm (23.6 in) of the soil profile (Potter et al. 1999).

Mined Lands. Restoration of rangelands disturbed by surface mining represent a minor fraction of the land area in the United States. Only 2.3 M ha (5,683,423 ac) of land was permitted for surface coal mining in the United States between 1977 and 2001 (Galetovic 2005), but these lands have great potential for high rates of C sequestration because of the soil salvage process. Soil salvage generally results in the collection of the two surface soil horizons and in some cases stockpiling of this material for several years. This process results in the dilution of the SOC pool by mixing of the soil organic matter (SOM) rich surface horizon with subsoil horizons that have lower amounts of SOM (Woods and Schuman 1986; Schuman 2002). The resulting soil material has similar levels of SOM to those found in dryland cropland soils that were cultivated for > 50 years (Haas et al. 1957; Tiessen et al. 1982; Burke et al. 1989; Bowman et al. 1990); therefore, these soils have a SOC sequestration potential similar to marginal, highly erodible croplands that have been restored to grasslands. Stockpiling soil also greatly diminishes the quality of the soil through enhanced organic matter degradation/decomposition, loss of plant residue inputs and general loss of much of the microbial functions (Severson and Gough 1983; Harris et al. 1989, 1993). Alternative plant growth materials are also sometimes used in place of topsoil resulting in subsoil or mine spoil material with very low levels of SOC and limited nutrient cycling potential (Schuman and Taylor 1978; Woods and Schuman 1986). Reclaimed mine soils (0 to 15 cm depth) in Wyoming have exhibited increases in SOC of about 400% over a 30-year period (Stahl et al. 2003) (table 1). These authors hypothesized that the decomposition rates are reduced in reclaimed mine soils due to low microbial activity, thereby accounting for the larger than expected increase in C.

Figure 4
Soil organic carbon pools to 30 cm depth across a mean annual precipitation gradient in the North American Great Plains.



Note: Data from Frank et al. 1995; Schuman et al. 1999; Reeder et al. 2004; Derner et al. 2006.

Synthesis of Land Management Effects on Carbon Sequestration in Rangelands

Length of Practice. Although there was no statistical relationship between change in SOC with longevity of the grazing management practice in native rangelands of the North American Great Plains, the general trend seems to suggest a decrease in C sequestration with longevity of the grazing management practice across stocking rates (figure 1). This trend in linear reduction in C sequestration of the top 30 cm (11.8 in) of the soil profile is consistent with the understanding that the ecosystem will reach a 'steady-state' and a change in management and/or inputs would be required to sequester additional C (Conant et al. 2001, 2003; Swift 2001).

In contrast to grazing, the general relationship of change in SOC to longevity of the interseeding of a N-fixing legume is positive with time (figure 2). It should be noted, however, that this relationship is based on a single study. Nevertheless, interseeding of an N-fixing legume in rangelands likely has the potential to continue to increase inputs of C, and illustrates the importance of N in C sequestration. Management practices that maintain or slightly increase soil N, such as grazing (Johnston et al. 1971; Smoliak et al. 1972; Manley et al. 1995; Dormaar and Willms 1998; Burke et al. 1999; Schuman et al. 1999; Verchot et al. 2002; but see Frank et al. 1995; Frank and Evans 1997), will likely result in limited C sequestration. Management practices that reduce soil N will result in net C losses from the system.

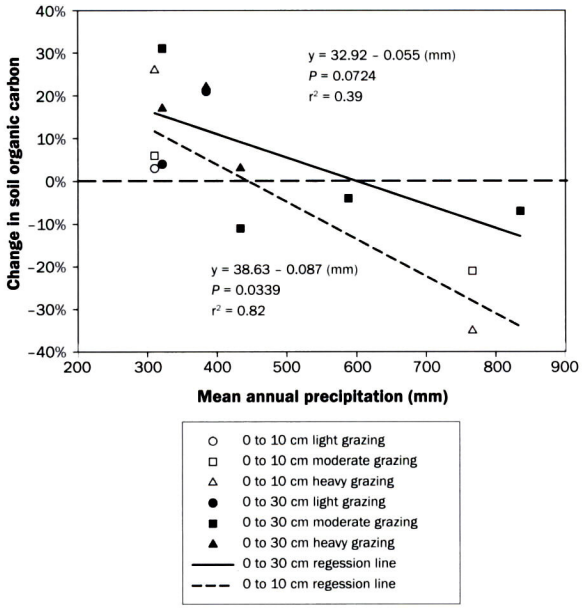
The lack of a general relationship between C sequestration and longevity of restoration of perennial grass on formerly cultivated lands results from the high variability in changes in C reported for numerous studies where the length of restoration is less than 10 years (figure 3). This lack of a relationship is in contrast with increasing changes in SOC with length of restoration reported in central Texas by Potter et al. (1999) for the 0 to 60 cm (0 to 23.6 in) soil profile.

Mitigation of increasing atmospheric CO_2 is partially achievable through proper land management on rangelands. Additional data is needed to further develop the relationship between N-fixing legumes and length of treatment to increase our degree of confidence. Land management practices that increase soil N, such as interseeding of N-fixing legumes have the potential to continue sequestering C for longer time periods, and without the "C-costs" associated with the production of inorganic N fertilizers.

Precipitation Gradients. In rangelands of the North American Great Plains, SOC pools to a depth of 30 cm (11.8 in) have been shown to increase with increasing precipitation (figure 4). Pools of SOC are two to three

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Figure 5
Percent change (grazed vs. nongrazed) in soil organic carbon with mean annual precipitation with grazing in North American Great Plains.



Note: 0 to 10 cm data from Smoliak et al. 1972 and Fuhlendorf et al. 2002; 0 to 30 cm data from Frank et al. 1995, Schuman et al. 1999, Reeder and Schuman 2002, Derner et al. 2006.

times lower in semi-arid than mesic rangelands (Derner et al. 2006). The same absolute change in SOC pools in semi-arid and mesic rangelands would result in a greater relative change in SOC pools for the semi-arid rangeland. Differential responses of SOC between semi-arid and mesic rangelands in the Great Plains to grazing are thought to be a result of 1) lower SOC pools, 2) greater root C/soil C ratios, and 3) a grazing-induced compositional shift to greater C4 dominance in the semi-arid shortgrass steppe (Derner et al. 2006). These authors hypothesized that the primary driver linking grazing-induced compositional changes in species composition to the C changes in shortgrass steppe was the magnitude and proportion of fine root mass in the upper soil profile (Derner et al. 2006).

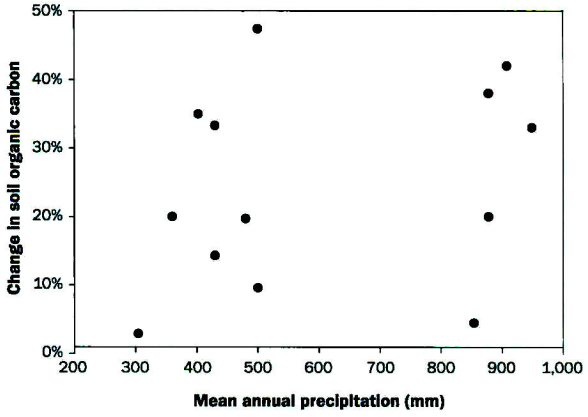
The relationship of C sequestration to mean annual precipitation is negative for both the 0 to 10 (0 to 3.9 in) and 0 to 30 cm (0 to 11.8 in) soil depths across stocking rates (figure 5). The threshold from positive to negative C change occurs at approximately 440 mm (17.3 in) of precipitation for the 0 to 10 cm soil depth and at 600 mm (23.6 in) for the 0 to 30 cm soil depth. Above these threshold precipitation values, C sequestration does not increase and may actually decrease SOC. The observed relationship for the 0 to 10 cm soil depth along this precipitation gradient is in general agreement with Sims et al. (1978) and Sala et al. (1988) in identifying the 370 to 400 mm (14.6 to 15.8 in) precipitation range as the region in which a transition in aboveground ecosystem responses to grazing occurs, and this aboveground difference may also be manifested belowground. Not surprisingly, no differences for SOC were observed between nine long-term grazed and ungrazed (20 to 71 years) sites along a precipitation gradient of 330 to 480 mm (13.0 to 18.9 in) in Canada (Henderson et al. 2004). A potential mechanism responsible for the transition in C sequestration from semi-arid to more mesic environments may be the control of precipitation on N turnover and in interaction with N availability in controlling C gain (Austin and Sala 2002). The reduction in C sequestration in relatively wet environments can be explained by greater microbial biomass C and N and labile organic matter pools which increase nutrient cycling (Zak et al. 1994).

A relationship of C sequestration to mean annual precipitation for interseeding N-legumes cannot be assessed at this time because of a lack of data. Several interseedings of yellow-flowering alfalfa across Wyoming and adjacent states in the past two years should provide the opportunity to develop such a relationship in coming years. In addition, there is also a lack of any general relationship of C sequestration to mean annual precipitation for restoration of perennial grass on formerly cultivated lands (figure 6). The high variability in change in SOC to mean annual precipitation may be, in part, because of differences in the length of time sites were cultivated prior to restoration efforts, intensity of cultivation efforts, and types of species used in the restoration efforts.

Constraints to Synthesis. We note that the high degree of variability in soils and vegetation at multiple spatial scales ranging from plant community interspaces (Hook et al. 1991; Vinton and Burke 1995; Derner et al. 1997) to the landscape (Burke et al. 1999) necessitates that researchers select appropriate and comparable sampling sites across treatments for initial and subsequent sample collection to facilitate field data estimates of C sequestration rates (Schuman and Derner 2004). Furthermore, the concentration of SOC near the soil surface in rangelands (Weaver et al. 1935; Gill et al. 1999) has resulted in many studies addressing only responses of the uppermost portion of the soil profile (Burke et al. 1999). Deeper depths have also been shown to sequester C (Schuman et al. 1999), and C turnover is influenced by decomposition rates of roots which decrease with increasing soil depth (Gill and Burke 2002).

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Figure 6
Percent change (restored vs. nonrestored) in soil organic carbon change with mean annual precipitation with restoration of formerly cultivated lands in North American Great Plains.



Note: Data from Gebhart et al. 1994; Burke et al. 1995; Reeder et al. 1998; Karlen et al. 1999; Potter et al. 1999.

Summary and Conclusions

Future Research Arenas involving Carbon Sequestration. Research is needed across multiple locations addressing key ecological processes and mechanisms to determine the principal drivers affecting C sequestration. The continued development of sophisticated in situ and laboratory equipment to accurately detect small but ecologically-important changes in soil C and its components will open new horizons for future experimentation and verification of C change due to management options or climatic variances. Newly emergent fields of soil microbial ecology should provide additional insight into microbial function and processes that affect C sequestration under normal and the widely fluctuating precipitation patterns found in arid and semi-arid environments. There is a need to move from the basic approach of soils and soil ecology to a more fundamental and functional understanding of the processes and mechanisms that affect SOC dynamics and how they are influenced by land management, environment and their interaction. For example, management strategies may offer opportunities to enhance soil fungal activity and C storage (Bailey et al. 2002). Largely unexplored is the arena of management-environment interactions that will increase our understanding of climate-plant-soil-microbial interactions as control factors affecting nutrient cycling within the context of determining costs and benefits (i.e., risk assessment) associated with varying land management practices. Management-environment interaction investigations should emphasize greater recognition of complete greenhouse gas budgets, thereby determining C storage and sequestration, as well as greenhouse gas emissions.

Existing long-term grazing studies, initially set up to evaluate livestock performance and vegetation change, provide excellent field laboratories to overlay additional contemporary treatments (e.g., prescribed fire and results of global climate change such as increased temperatures, altered precipitation patterns, carbon dioxide enrichment, N fixation/deposition) to more fully understand how and which best management practices affect greenhouse gas budgets (C sequestration and global warming). These efforts can be conducted within the established scientific missions of the USDA Agricultural Research Service, Agricultural Experiment Stations, and the Long-Term Ecological Research Network. Of paramount interest is the causal role that grazing-mediated changes in vegetation composition, productivity and diversity have in the interpretation of SOC responses. These efforts should be conducted within the framework of ecological sites, with particular attention directed at those vegetation states which are 'at-risk' of transitioning to another vegetation state.

Policy Implications. Estimates of soil C storage and rates of C sequestration for rangelands are being used by scientists and policymakers to estimate the potential of these lands to help mitigate the elevated atmospheric levels of CO_2 (Lal et al. 2003). Considerable interest is being generated in terrestrial C storage and marketing of stored C (Williams et al. 2004). Economic benefits from C sequestration programs have the potential to significantly contribute to household economies (Olsson and Ardö 2002). Continued refinement of estimates of terrestrial C storage in rangelands will assist in the development of greenhouse gas emissions and C credit marketing policies.

Existing U.S. government policies related to private land management are increasingly conservation-oriented as evidenced by programs within the 2002 Farm Bill relevant for rangelands which include the (1) Conservation of Private Grazing Land Program, (2) Conservation Security Program, (3) Environmental Quality Incentives Program, (4) Grassland Reserve Program, (5) Wildlife Habitat Incentives Program, and (6) Wetlands Reserve Program. Collectively, these programs emphasize monetary incentives for private land managers to adopt/maintain conservation practices, but these programs may be modified to emphasize land management practices that increase C sequestration.

Acknowledgements

We appreciate the insightful review comments from Joel Brown, Mark Liebig, and three anonymous reviewers.

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The National Park Service and the University of Nevada signed a Master Agreement on November 4, 1971 that provided for the establishment and operation of this Unit on the Las Vegas Campus. The Unit, although located in the Department of Biological Sciences, is geared to provide a multidisciplinary approach that utilizes all talents on the University Campus to natural resources studies in areas administered by the National Park Service. Primary attention of this Unit is directed to Death Valley National Monument, California/Nevada; Lake Mead National Recreation Area, Nevada/Arizona; and Joshua Tree National Monument, California.

Through the direction and coordination of the Unit Leader, projects are undertaken in these areas that are designed to provide scientific facts upon which the park managers may make appropriate decisions and formulate and implement effective management action plans. Through close association with faculty members and through guidance of graduate students, a greater awareness of problems and needs of the Service are recognized and academic interests are channelized to participate with the National Park Service in studies of mutual interest and concern.



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REVIEW and ANNOTATED BIBLIOGRAPHY of FERAL BURRO LITERATURE

by

Charles L. Douglas and Thomas L. Hurst

December, 1993

NATIONAL PARK SERVICE/UNIVERSITY OF NEVADA, LAS VEGAS
NPS/WRUNLV/NRTR-93/3 D40
Contribution Number CPSU/UNLV 044/02

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"...wild free-roaming horses and burros are living symbols of the historic and pioneer spirit of the West...[and] they are to be considered in the area where presently found, as an integral part of the natural systems of the public lands."

Wild Free-Roaming Horse and Burro Act of 1971

Literature Review

Introduction

Domesticated Somalian and Nubian wild asses (*Equus asinus*) were introduced into Mexico by Spaniards in the 1530's, and spread northward into what is now the United States as a consequence of Spanish colonization. These hardy, desert adapted animals provided transportation for people and equipment in this country for more than 3 centuries. Domesticated asses, or burros, were introduced into areas that became National Parks more than 100 years ago by miners; burros were released into the wild following the decline of mining, the advent of the railroad, and the availability of motorized vehicles (see Woodward [1976] for an excellent history, and Clutton-Brock [1981] for a history of domestication).

The control of feral burros was curtailed in California in 1953 when the state provided them with official protection. In 1959 Congress halted the pursuit of wild horses and burros from motorized vehicles by passing the "Wild Horse Annie Act", after the nickname of Mrs. Velma Johnston of Reno, NV, who lobbied almost single-handedly for its passage. Public Law 92-195 entitled "Wild and Free Roaming Horses and Burros" passed in 1971, provided protection for burros on federal lands administered by the Bureau of Land Management and Forest Service. These legislative actions have been short-sighted in the impact they would have on public resources, because they contain essentially no control measures (Ball 1959, Cook 1975). The National Park Service was exempt from provisions of this Act, but burro control was curtailed in most parks until the late l970s. For a number of years, two commercial burro trappers removed burros, selectively, from Death Valley, through an arrangement with the monument. Burro trapping and direct reduction was terminated in Death Valley National Monument during the 1960s. Feral burros have created serious management problems in Bandelier National Monument, Death Valley National Monument, Grand Canyon National Park, Lake Mead National Recreation Area, and Virgin Islands National Park. Between 1983-1986, more than 6000 burros were removed from Death Valley; this was then the largest single concentration of burros in the United States. The Lake Mead National Recreation Area presently has the largest concentration of burros on National Park Service lands. Feral burros occur in several countries other than the United States, and are especially abundant in Australia (Woodward 1976). The burro herd in the Kimberley and Victoria River Districts was estimated at between 60,000 and 110,000 in 1981 (McCool et al. 1981).

Carothers et al. (1976) present an excellent history of the controversy surrounding burro problems in the southwestern United States, with special emphasis on the Grand Canyon. Part of the controversy surrounds the effects of feral burros on

the environment, and originated because of conflicting reports presented in earlier studies (for review see Carothers et al. 1976, Norment and Douglas 1977). McKnight (1958), in one of the first reports on burros, described intensive damage to vegetation and competition with wildlife. Conversely, Welles and Welles (1960a,1961a,b,1962) and Moehlman (1974) rejected the proposal that burros destroy vegetation or negatively impact co-existing small vertebrates, although Welles and Welles (1961) acknowledged that burros needed to be controlled to preserve the biota. However, neither Moehlman nor Welles and Welles assessed browsing intensity or impacts on small mammals or reptiles.

The time and location of observation are important variables affecting this controversy; burros had only colonized parts of Death Valley when Welles and Welles conducted studies there. Burros increased in numbers in Death Valley following cessation of direct removals. Environmental impacts escalated with increased densities. Burro reproductive rates, foal survival, and environmental damage have been shown to vary with herd density. Investigators familiar with only low density populations have sometimes regarded burros as innocuous. Recent studies have shown burros to be responsible for extensive habitat damage by overgrazing, selective species removal, trampling of plants, soil disturbance leading to erosion (Farrell 1973; Koehler 1974; Fletcher and Wauer 1976; Carothers et al. 1976; Woodward and Ohmart 1976; Norment and Douglas 1977), impact on small vertebrates (Yancey and Douglas 1983; Yancey 1984; Carothers et al. 1976), and competitive interactions with desert bighorn sheep (Seegmiller and Ohmart 1981; Ginnett and Douglas 1982; Dunn and Douglas 1982).

The kinds of evidence presented to substantiate claims of burro interactions with native plants and animals is another important consideration affecting this controversy. The oft cited paper by McKnight (1958) represents a compilation of survey information from land managers throughout the western states, but no scientific data. This was the first widely-read compilation of information about burros. The report provided a valuable service by creating more widespread recognition of the problems burros create.

Aging

Burros live 10-15 years in the wild and longer in captivity. Of 631 burros harvested at China Lake Naval Weapons Center, California, only 12 individuals were >10.5 years old; males lived longer than females. Maximum estimated ages were 15.5 and 20.5 years for females and males, respectively (Johnson et al. 1987). Ruffner and Carothers (1982) reported 78% of animals in the Bedrock Canyon population, Grand Canyon, were between one month and 4 years old, and the remaining 22% were 5 years old. In the Lower Canyon herd 49% were between one month and 4 years; the remaining 51% were from 5-15 years old. In southwestern burro populations 50% of the individuals usually are $\geq$4 old (Moehlman 1974, Norment and Douglas 1977). However, in the Bedrock Canyon population and in a herd from the Chemehuevi Mountains of southern California, only 22 and 36% of the individuals

were >4 years of age (Woodward 1976). In a harvested sample of 197 burros from Australia, the mean age was 4 years (S.D. ±3.25, McCool et al. 1981), which was ascribed to continuing harvesting. Both males and females >10 years of age were present.

Reproduction and Group Behavior

Burros have conservative life strategies. Sexes are segregated for most of the year into male, female, and mixed groups. The only long-term association between any two individuals is that between a female and her foal. Moehlman (1974) discusses group composition seen in Wildrose Canyon, Death Valley. Mixed groups are more common during the breeding season and when animals are dependent upon water (Moehlman 1974). In Death Valley, males began congregating near water sources with females and young in about April (Norment and Douglas 1977), remaining in mixed groups through the summer, and segregating again in autumn as cooler temperatures allow dispersal from water. Breeding occurs in spring and summer in the desert when burros are congregated near water. Although females are polyoestrus and can breed throughout the year, most breeding is confined to spring and summer. Some individuals breed and give birth out of synchrony with the majority of the herd; a few young animals are seen throughout the year in Death Valley. Natality in Death Valley appeared to peak in late spring and early summer; the majority of births occur between April and July (Moehlman 1974, Norment and Douglas 1977). A seasonal concentration of natality also is seen in African deserts, where breeding occurs following summer rains and "greenup" of the vegetation (Klingel 1974, 1977, 1979).

Male burros did not maintain harems in Death Valley. Territorial males were observed herding females within their territory, but alliances were ephemeral. Harems have been reported to occur in insular populations (McCort 1979; Kuprikova 1990a,b). Territorial males had sole access to estrous females within their territories in Death Valley, but did not restrict their mating to them (Moehlman 1974). Relatively few adult males (5-6) in the Wildrose area of Death Valley exhibited territorial behavior; conversely, a large number of males in Butte Valley maintained territories. The differences in territoriality between the two areas was thought to be related to population density. The Wildrose area had a much lower density (0.41 burros/km^2) than Butte Valley (3.8 - 4.9 burros/km^2). Moehlman (1974) suggested that the Wildrose herd may be developing into a territorial-based breeding population. An alternative hypothesis might be that there were proportionately as many territorial males as non-territorial males in each area. Woodward (1979) discusses loose social organization as being well adapted to the low carrying capacity of deserts, and considers territorial behavior to be similarly adaptive when precipitation is periodic.

Studies of burros in Death Valley by Douglas and his students (Dunn 1982; Ginnett 1982; Yancey 1984; Norment and Douglas 1977; White 1980) did not specifically address territorial aspects of behavior. It was noted that both males and females may feed, or traverse territories without challenge. Territorial males remained

close to the female they were courting, challenging other males that approached too closely. Klingel (1974, 1977) considers the wild ass and Grevy's zebra to be the only territorial equids. In Africa, territories are established by *E. africanus* only in grazing areas used during the rainy season (Klingel 1977). In the desert southwest, territories are established in burro concentration areas having permanent water sources. In both regions, the territory serves to decrease harassment of females by non-territorial males.

Group integrity is ephemeral in burros except for the group comprised of the female and her foal, or her foal and yearling. Klingel (1974, 1977, 1979) reports that there are no permanent bonds between any two adult animals. Individuals may be solitary, or occur in a variety of associations. These groups are variable and their composition may change within hours (Moehlman, 1974). Sexual segregation during the non-breeding season is not a rigid system. Females were seen with males throughout the year in Death Valley (Norment and Douglas 1977). In Australia, the common herd size was in the dozens; groups of 150-200 burros were not uncommon in areas of high density (McKnight 1967).

The female, her foal of the year, and frequently a yearling from the previous year's birth formed the most common group. Young females appeared to remain with their mother for 2-3 years, until after they had foaled (Moehlman 1974, White 1980). Little is understood about how long mother-foal associations last, or how the home range of a young female relates to the home range area of her mother. Kuprikova (1990b) reported that on Ogurchinsky Island females and young burros in a harem use the territory of their male.

Male foals remain with their mother for most of the first year, then join male groups. Little is understood about how male home ranges and territories relate to their mother's home range or to that of the male group they associated with. About 24 young males were marked with wide, conspicuous collars in the Butte Valley area of Death Valley; all of these animals moved completely out of the study area - probably in response to population density. Some of these marked individuals were captured at China Lake Naval Weapons Center, about 50-80 air km to the west. The remainder were never relocated, although extensive ground and aerial searches were conducted (C. Douglas, personal observation).

Burros have one foal per year in years having adequate precipitation. The gestation period is 12 months (Asdell 1964). In Death Valley, some animals breed as yearlings, but most breed at 2 years and foal at 3 years. Reproduction in Death Valley was confined largely to spring and summer. Woodward (1976), however reported breeding year-around along the lower Colorado River; jennies in that area reached sexual maturity at one year of age. The difference in breeding strategies between the areas undoubtedly is related to differences in elevation and climate. Desert bighorn sheep also have a more attenuated reproductive season along the lower Colorado River than they do at more northerly latitudes (Monson and Sumner 1980). Johnson et al. (1987) found female burro reproductive activity on the Naval Weapons Center, California (NWC) began at age 1.5 with a 14% pregnancy rate. The

pregnancy rate increased to 79% in age class 3.5, and varied from 58-78% for females through age class 10.5. Feral burros remain fertile into old age; two females in age class 15.5 were pregnant. The percentage of pregnant and/or lactating females of reproductive age (76%) was similar between the NWC and two burro populations in the Grand Canyon (Ruffner and Carothers 1982). Sixty percent of lactating females on the NWC also were pregnant, indicating that burros can give birth in consecutive years (Johnson et al. 1987). Moehlman (1974), however, reported that in Wildrose Canyon, inter-foaling intervals were typically two years. This observation might have been related to herd density, which was high at the time of Moehlman's study. Wolfe et al. (1989) used blood serum concentrations of reproductive hormones and rectal palpitation in horses and burros to determine pregnancy status. Mean apparent incidence of pregnancy was 25% in yearling burros, and 72% in burros >2 years old. Data from these studies indicate high levels of pregnancy in burros >2 years of age.

Survival of young burros is generally high in western desert areas; only a few dead foals were seen in 3 different study areas of Death Valley (C. Douglas, personal observation). White (1980) reported a first year survival rate of 66% in Butte Valley, Death Valley National Monument. Moehlman's data (1974) yielded estimates of 72 and 79% first year survival. Ohmart et al. (1975), Morgart (l978), and Seegmiller and Ohmart (1981) found no evidence of foal mortality. Conversely, Ruffner and Carothers (1982) reported 76-89% pregnancy rates in two herds in the Grand Canyon, but recruitment rates of only 11 and 17%, respectively. Choquenot (1991) reported >70% of mature females were pregnant in two burro populations in Australia that had experienced earlier herd reductions. Juvenile mortality was 3 times as great at high herd density as at low density, and was associated with poorer juvenile body condition and slower growth. In a harvested sample of 197 burros from Australia 64% of the females were pregnant, and 17% of these were lactating (McCool et al. 1981). Five pregnant females appeared to have conceived on the foal heat (postpartum oestrus), based on the accompanying foal and foetal age.

Population Dynamics

Different approaches have been taken to examine factors that drive population change. Two conceptual approaches to population regulation have been termed top-down (predation) versus bottom-up (resources) regulation. Each approach has its advocates, and the ecological literature is replete with examples (see article by Matson and Hunter, and review in Ecology, 1992 Vol. 73 No.3). Predation and density have long been recognized as important factors regulating population growth and survival in wildlife species. A number of wildlife researchers have studied density's relation to predation as regulating mechanisms. Feral burros are not known to be preyed upon by predators, with the possible exception of mountain lions. However, reports from Australia indicate that burros are strongly protective of foals when dingoes threaten. Corbett (in McCool et al. 1981) observed that when jennies segregate from family groups to give birth, the neonatal foal is particularly vulnerable to attack by dingoes, and almost always succumbs to attack.

In desert areas having erratic weather patterns, availability of nutritious forage can be a major regulating mechanism for populations. Years having small amounts of precipitation during months critical for plant growth usually have poor survival of young ungulates, especially desert bighorn sheep. Density was found to be secondary to precipitation in regulating bighorn lambs in the Lake Mead area of southern Nevada (Douglas and Leslie 1986). Choquenot (1988, 1991) provided evidence that maximum densities of feral burros in northern Australia were imposed through food availability. An inverse relationship between density and percentage of females successfully foaling was suggested for Death Valley burros (Norment and Douglas 1977). An estimated 24 foals were born into the Wildrose Canyon herd during a 12 month period of high population density; approximately 57% of the adult females foaled. The following year, 90% of the marked females foaled during a 12 month period of lower population density caused by trapping removals (Norment and Douglas 1977). Researchers are beginning to agree that both top-down and bottom-up factors operate on all populations and communities simultaneously. The discussion is now about what controls the strength and relative importance of these factors under varying conditions (See Ecology 1992 Vol.73 No.3).

Since relatively few foals die in herds in the western United States, population increases of 20% and more per year have been reported for Death Valley and other western areas (Morgart 1978, Norment & Douglas 1977). At that rate of increase, the population could double in size every 4 years. Woodward (1976) reported a recruitment rate of about 20% every 18 months in the Chemehuevi Mountains, California population. Adult survival apparently is high; Norment and Douglas (1977) found a 5% loss in adults per year in Death Valley, while Rudman (1990) found only a 3% mortality rate on St. John, U.S. Virgin Islands. Annual rates of increase for feral burro populations in North America range from l.2-29% (White 1980; Morgart 1978), whereas a finite rate of increase of 23-28% per year was estimated for populations in northern Australia (Choquenot 1990) following herd reduction of about 40%.

Conley (1979) questioned the seemingly high rates of annual increase being reported for burro populations in the United States, and regarded population increases of 20% as being unlikely to occur. Perryman and Muchlinski (1987) used existing data from autopsies and live removals at the NWC to model population dynamics of feral burros. They calculated relatively high mortality rates, and recruitment rates of 20%, 22% and 12% for 1980, 1982, and 1983 respectively. They concluded that the only condition resulting in an increase approaching 20% is one in which the pregnancy rate is 100%. Conley (1980) also concluded that a 20% rate of increase could be obtained only if 1) survival rates are high, 2) 80% or more of the animals in all age classes breed, 3) the age at first parturition is 3 years, and 4) the breeding extends beyond 8 to 10 years of age. All of these conditions have been met by burro herds. Several unusual assumptions made by Perryman and Muchlinski seriously biased the data used in Leslie Matrix modeling: l) age class data were smoothed in such a way that age class 7-9 was the oldest group, despite the author's acknowledgement that burros lived longer, 2) ages and pregnancy rate for live captures (representing 4003/4635 or 86% of the sample) were estimated visually by unknown persons, 3) assuming a survival rate of age class 7-9 to be 0.00, while acknowledging it as a statistical artifact

of smoothing, 4) assuming a fecundity rate for age class I (0-2 yrs) of 0.00, while acknowledging that two-year-old animals can produce foals, 5) assuming a fecundity rate of one-half that of the pregnancy rate in autopsied burros, and 6) assuming that because 60% of the females sacrificed on the NWC in 1981 were pregnant while in poor condition, that this indicated burros do not show a marked decrease in reproductive effort when they are in poor physical condition. Jenkins (1989) also commented on the inappropriateness of this population model. Eberhardt (1982) reported observed rates of increase for two feral horse herds in Oregon to be about 20% per year. A theoretical modeling of population dynamics suggested adult survival to be the critical parameter in determining rates of increase. His results help support the validity of wide-spread observations by field researchers that some populations of burros had rates of increase $\geq$20% per year.

Using 0.57 foals/female/year, Butt et al. (1979) modelled several control methods and determined that a 20% cropping of immature burros each year for 5 years reduced the population by 20%; other similar methods produced greater reductions, but this method was recommended because it does not radically alter the population structure and is easy to implement.

Movements

Feral burros in Death Valley have wide ranging movements in the fall and winter when they are not water dependent. In summer, 60% of the Wildrose population was restricted to within 2 km radius of water, and about 98% were restricted to within 4 km of water; in winter 80% were seen at $\geq$6km from water. Distances of 5-10 km were covered daily by burros moving to water in Australia. Interactions between burros and native wildlife are most likely in summer when wildlife has a similar water dependency (Norment & Douglas 1977). Movements in spring to different elevations coincide with "greenup" of the vegetation (Dunn & Douglas 1982; Dunn 1984; Norment & Douglas 1977; White 1980). The areas used by burros in the spring also are important foraging areas for bighorn sheep; annuals and new shrub growth first appear at lower elevations, and on selected slopes. Burros can traverse mountainous terrain expediently. A burro immobilized and fitted with a numbered collar in Wildrose Canyon was located 2 hours later in the Skidoo area, 8 air kilometers distant. Daily movements of 5-10 km to water were reported for burros in central Australia (Hoffman 1983). McCool et al. (1981) found that burros used very hilly sandstone country, and were capable of traversing steep terrain.

Burros are remarkably faithful to their home range areas. Herds in 5 different areas of Death Valley differed in distribution of transferrin alleles (Blake 1977; Blake, Douglas & Thompson 1981). Herds in adjacent drainages only 8 air km apart had significantly different distributions of alleles, indicating insignificant amounts of mixing between herds during the breeding season. These differences in allelic distributions were attributed to the founder effect and to animals returning each summer to the same water sources and breeding within the resident group. Since gestation in burros is about one year in length, females apparently foal, breed and reproduce year after

year with members of the group utilizing one congregation area. Since the peak of reproduction occurs during spring and summer, most females have already bred when cooler weather permits dispersal from congregation areas. Casual observations of females with foals outside the normal reproductive season suggests that females breeding out of synchrony with most of the herd were young animals having their first birth (C.L. Douglas, personal observation).

Home ranges of burros averaged 32 km^2 along the lower Colorado River (Woodward 1979) but only 3 km^2 at Bandelier National Monument (Morgart 1978). The unusually small sizes of home ranges at Bandelier were attributed to availability of permanent water and comparatively good forage conditions in contrast to desert ecosystems. In Death Valley, animals marked and equipped with radiocollars in Wildrose Canyon ranged over an area of 425 km^2 (105,000 acres). Mean home range size for 24 animals was 68 km^2 (16,800 acres), with no significant differences between the sexes. Fall-winter ranges had a mean area of 34 km^2 and extremes of 1.0-104 km^2, while spring-summer ranges averaged 12 km^2 (Norment and Douglas 1977). The larger home ranges recorded by Norment and Douglas probably reflect reduced competition for space due to removal of 139 animals by trapping, directly after Moehlman's study. Moehlman (1974) estimated a mean home range size of 10 km^2 in Wildrose Canyon (range 1.3-40.6 km^2), when the population was large, but did not use marked animals or telemetry to derive her estimates. She also thought Wildrose burros did not use Nemo Canyon, the Skidoo area, and Emigrant Canyon. Based on marked and telemetered animals, Norment and Douglas (1977) demonstrated that those movements occurred on a regular basis. Moehlman likely underestimated the winter component of burro home ranges when animals moved farther from water. Moehlman (1974), Woodward (1976), Seegmiller and Ohmart (1976), Norment and Douglas (1977), and Morgart (1978) reported no significant difference in home range size between the sexes.

Table 1 summarizes home range data from various studies; these are the only reports known to us that recorded burro home ranges in the western United States. The habitat types represented in Table I are quite diversified. Topography and the quantity and quality of habitat unquestionably affect home range size. High population density has been shown to be related to a decreased size of burro home ranges. Elevation and forage attributes of the habitat have buffering effects, allowing denser packing of animals when forage is abundant. The relatively high density of animals in Bandelier and the resulting size of home ranges compared to those in Butte Valley and Tin Mountain (Table 1) help illustrate this phenomenon. The highest densities recorded were in Butte Valley and the Tin Mountain area of Death Valley. These areas have abundant, permanent sources of water, and ample forage. Small home ranges recorded in Bandelier National Monument also were thought to be related to abundant forage and linear orientation due to topography.

Table 1. Comparison of home range data from various burro studies. Data are means ± S.E. with n in parentheses.

STUDY	LOCATION	Mean Home Range Size (km^2)	Mean Male Home Range (km^2)	Mean Female Home Range (km^2)	Maximum Density (km^2)
Dunn 1984	Tin Mountain, Death Death Valley N.M. CA	7.4 ± 1.2 (10)	5.3 ± 1.3 (5)	9.6 ± 1.7 (5)	4.32
White 1980	Butte Valley Death Valley N.M. CA	9.9 ± 2.2 (11)	8.8 ± 2.4 (6)	11.4 ± 4.2 (5)	3.8 - 4.9
Moehlman 1974	Wildrose Canyon Death Valley N.M. CA	10.0 ± 1.2 (48)	12.3 ± 2.3 (23)	8.7 ± 1.0 (25)	0.77
Norment & Douglas 1977	Wildrose Canyon Death Valley N.M. CA	68.1 ± 5.7 (24)	72.1 ± 7.6 (14)	62.5 ± 8.6 (10)	0.54
Seegmiller & Ohmart 1981	Bill Williams Mtns. Arizona	19.2 ± 3.7 (14)	15.2 ± 2.4 (8)	24.3 ± 7.9 (6)	3.30
Woodward 1976	Lower Colorado River Arizona	30.1 ± 6.1 (15)	28.7 ± 4.6 (9)	30.5 ± 14.3 (6)	0.41
Morgart 1978	Bandelier Natl. Mon. New Mexico	2.9 ± 0.4 (21)	2.6 ± 0.7 (6)	2.7 ± 0.4 (15)	2.55

Food Habits

By being larger than native desert ungulates, the burro requires more food and water. Much of the success of burros in arid regions stems from their ability to survive on poor quality forage - an ability that is related to their monogastric digestive system and generalized food habits. Burros have large faces and mouths, and a simple, non-ruminant, digestive system. Their dentition is adapted for grazing, but they function as food generalists. Burros prefer grasses and forbs when available, but readily browse on perennial shrubs. Various reports classify burros as browsers or grazers, depending in large part upon the time of year stomach or fecal samples were collected. In the relatively few studies having data throughout the year, burros are shown to be opportunistic, eating grasses and forbs when available, and switching to shrubs when necessary (Browning 1960, Hansen and Martin 1973, Woodward 1976, Ginnett 1982, Ginnett and Douglas 1982, Douglas and Hiatt 1987). Results of burro food habit studies differ due to differences in elevation, differences in communities from which samples were collected, and condition of the plant community.

Burros in Wildrose Canyon, Death Valley functioned almost exclusively as browsers (Moehlman 1974, Norment and Douglas 1977), and inflicted extensive damage on the shrub community. Most perennial grasses had been removed from the area by burro overgrazing. Conversely, White (1980) found limited browsing on shrubs in Butte Valley, where a major part of burro diets consisted of red brome (*Bromus rubens*), an abundant exotic grass. Burros used 40 species of plants in Butte Valley, 11 species of which were important throughout the year. The average burro diet, determined by microhistological fecal analysis, consisted of 48% grasses, 25.0%

shrubs, 19% perennial and annual forbs, and 7% unknown dicots (Douglas and Hiatt 1987). Browning (1960) analyzed 19 stomach samples of burros from the Cottonwood Mountains, Death Valley, and found the annual diet to consist of 10% grasses, 39% forbs, and 51% browse. McMichael (1964b) analyzed 9 stomach contents from the Black Mountains, Arizona (February, April, May, and July 1963) and determined species content. McMichael also observed burros and determined feeding and watering patterns; during summer both sheep and burros watered at the same springs and ate the same plants. Ginnett (1982) identified 48 taxa eaten by burros in the Cottonwood Mountains of Death Valley; monthly diets contained from 19-31 taxa, depending upon availability of annual forbs. Burros were primarily browsers during winter months, then switched to a diet consisting predominantly of perennial grasses during April. The annual diet in his study area consisted of 48% browse, 41% grasses, 3% forbs and 8% unknowns.

In the Bill Williams Mountains of Arizona, Seegmiller and Ohmart (1981) found an annual diet of 40% browse, 22% grasses, and 33% forbs. Woodward and Ohmart (1976) analyzed 89 fecal samples from the Chemehuevi Mountains of California, and found the annual diet consisted of 61% browse, 4% grasses, 30% forbs, and 5% unknown. Hansen and Martin (1973) found the annual burro diet in the lower Grand Canyon, Arizona consisted of 68% grasses, 9% forbs, and 23% browse. Ruffner et al. (1977) identified 23 species of plants in July diets of burros inhabiting the Bedrock Canyon area of the Grand Canyon. Eight species comprised 77% of the diet, with grasses being the most important component, followed by browse and forbs. Burros in the Bedrock Canyon area foraged on a wide variety of plant species, but were highly selective when preferred foods were available (Jordan et al. 1979). Douglas and Hiatt (1987) summarized information from several diet studies conducted in Death Valley; a total of 119 species were eaten by burros, which reflects their generalized diets. Location, time of year samples were collected, the kinds of samples, and weather all affect results of diet studies. Although burros may prefer grasses and forbs to browse (Woodward and Ohmart 1976), the species of plants in an area will often force them to be predominantly browsers.

A few studies have attempted to relate nutrient quality of forage species to burro diets (Brady and Hanley 1975, Norment and Douglas 1977, Ginnett 1982). Norment and Douglas (1977) also related burro movements to productivity of various species throughout their study area, and projected carrying capacity for burros based on forage biomass. Although their computations suggested more burros could be maintained on the study area, excessive habitat damage had occurred with the existing population. Watkins (1976) determined chemical composition and in vitro digestibility of the 9 major forage species used by burros in the lower Sonoran Desert; the samples, collected in September, were generally high in fiber, low in crude protein (4-20%), and had low in vitro digestibilities (35-70%).

Physiology

Animal physiologists have long been interested in adaptations of animals to heat stress. The burro has served as a research subject in stress physiology and related areas such as water relationships. The burro is exceptionally tolerant of dehydration, being able to withstand a water loss of 30% of the body weight (Maloiy 1970). The burro eliminates relatively large amounts of feces because food is not as well digested as it is in ruminants. Fecal water content is relatively high, resulting in fecal water loss about 3 times that in the camel (Schmidt-Nielsen 1964). Dr. Bruce Dill became interested in heat stress in animals because of problems construction workers experienced while building Hoover Dam. Dill and his collaborators studied various aspects of stress physiology in man and burros, including sweat gland function and properties of sweat (Robertshaw and Taylor 1969, Dill et al. 1979); hunger and thirst in the burro (Dill et al.1980); and regulation of sweating and responses to dehydration and rehydration (Bullard et al. 1970). At ambient temperatures of 5 and 50 °C, Maloiy (1971) measured a body temperature range of 35 to 39 °C; Tomkiewicz (1979) measured a similar annual range of body temperatures of 35-42 °C.

The burro's capacity for dehydration is rivaled by few mammals. Burros have moderate amounts of body hair, and poor behavioral adaptations for avoiding water loss. Burros are able to maintain a relatively constant blood volume when dehydrated, which permits salivation and digestion of forage even under extreme conditions (Yousef et al. 1970). Maloiy (1970, 1973) found that burros experimentally exposed to dehydration and simulated desert temperatures had depressed food intake and depressed digestibility of dry matter; however, an intermittent heat load as found in the desert had no effect on either parameter. Feces and evaporation were the main routes of water loss in burros. After suffering a water loss of 30% of body weight, the burro can drink enough water in 2-5 minutes (24-30 l) to restore its deficit (Maloiy 1970). Maloiy and Boarer (1971) studied response of hematological changes in the Somali donkey exposed to dehydration; Yousef and Dill (1971) studied cellular and plasma volumes in the burro under desert and mountain conditions.

The energetics of burros walking on grades of 0-17% were compared with that of man under the same conditions. The burro was found to require half of the energy expended by man to walk on a horizontal surface. The lower cost of walking in the burro is of major importance to its survival in the desert (Yousef et al. 1972).

In donkeys, arterial blood entering the cranium through the internal maxillary artery flows in a countercurrent manner beside cooled venous blood from the nasal passages, in the rete of the cavernous sinus, before going to the brain. This serves to reduce the effects of rising body temperatures by protecting the brain, which is the most critical internal organ (Yousef et al. 1972).

Impact on Habitat

Because desert plant communities have low productivity, any large grazing animal can have a profound impact on individual plants and community composition. Burros are one of the largest grazing/browsing ungulates in the southwestern states. An average burro requires approximately 10 pounds of dry forage per day, as determined from weight of stomach contents, and theoretical estimates. A grazing animal requires approximately its own weight in forage each month; in Death Valley, the average adult burro weighed about 350 pounds (C.Douglas, unpublished data). Burros modify plant communities they forage in. The popular and scientific literature contains numerous accounts of burro damage to ecosystems throughout the western states (McKnight 1957, 1958; Weaver 1959; Weaver et al. 1969; Weaver and Mensch 1969, 1970a,b; Weaver and Hall 1971; Weaver 1972a,b,c; Hansen 1973; Farrell 1973; Weaver 1973, 1974; Sanchez 1974; Fletcher and Wauer 1976; Reddick 1981). Seegmiller and Ohmart (1981) reported destructive foraging on Ocotillo (*Fouquieria splendens*), Smoke trees (*Dalea spinosa*), and Little-leaf palo verde trees (*Cercidium microphyllum*) along the Colorado River. Seegmiller and Ohmart (1981) and Woodward (1976) found burrobush plants (*Ambrosia dumosa*) heavily modified by browsing, and occasionally browsed to the ground. Farrell (1973) reported that palo verde trees suffered the greatest damage; burros commonly broke off branches 1/2 to 2 1/2 inches in diameter, chewed the basal portion, then discarded the rest. He reported that palo verde twigs and branches have high concentrations of protein, total digestible nutrients, and phosphorous. McMichael (1964) reported palo verde and mesquite trees in the Black Mountains of northwestern Arizona were hedged to approximately 5 feet, and most branches less than 1\4 inch had been removed.

Fisher (1975) measured shrubs inside and immediately outside a burro exclosure established in 1972 in Wildrose Canyon, Death Valley. He resampled two years later and reported substantially lower numbers of annual plants outside the exclosure, except for the annual buckwheat (*Eriogonum* spp.); some shrubs outside the exclosure had lower volumes than those inside, but others were more voluminous outside. Ten years later Yancey (1984) found no significant difference between total plant volume inside and outside the exclosure. She found that the Wildrose exclosure had lower species diversity than other sites in Wildrose Canyon, and concluded that the exclosure was not representative of the area.

Vegetation recovery was studied following burro removal from Wildrose Canyon and Butte Valley, Death Valley (Longshore and Douglas 1988). Both areas had burro exclosures established in 1972. Longshore and Douglas found significant differences in species diversity, but no differences in mean volumes of perennial shrubs inside and outside the Butte Valley exclosure in 1986 and 1987. Over a period of 3 years there was a general trend in mean shrub volumes toward equality inside and outside the exclosure, suggesting rapid recovery from relatively minor browsing by burros. Perennial grasses had been extensively grazed in Butte Valley, where grasses (largely exotics) comprised 48% of burro diets. Perennial grasses were present inside but not outside the exclosure in Butte Valley in 1985 and 1987. In Wildrose Canyon significant differences were found in species diversity, but no difference in mean

volumes of perennial shrubs inside and outside the exclosure in 1986 and 1987 (transects established in 1986).

Norment and Douglas (1977) assessed browse impact on plants in Wildrose Canyon, Nemo Canyon, Skidoo, and Emigrant Canyon of Death Valley. They found 46% of shrubs in Wildrose Canyon showed evidence of browsing. Thirty percent of plants were heavily browsed, indicating burros were affecting the structure of the plant community. About 11% of the shrubs appeared to be in danger of being removed from the area. An assessment of browse impact by Yancey (1984) in the same part of Wildrose Canyon, using the same method Norment and Douglas had in 1977, showed that species reported as being the most heavily browsed in 1977 comprised a smaller percentage of the plant community in l984 - indicating that burros were changing composition of the vegetation by selectively removing preferred species. During his study of flora and vegetation in the Cottonwood Mountains of Death Valley, Peterson (1984) identified an aberrant shrub community unlike any other in the range; this 1400 ha *Ericameria cooperi - Ephedra nevadensis* association appeared to have originated from one or two other shrub communities by plant removal. Peterson attributed plant removal and modification of the parent community to burro overgrazing and overbrowsing. Burro overgrazing was responsible for change in community composition along the lower Colorado River in western Arizona; the greatest overgrazing occurred near the river but decreased to light or moderate use at distances >2.5km from water (Hanley 1976). Hanley (1976) found overgrazing resulted in a decrease in canopy cover of *Ambrosia dumosa* from about 2.3 to 0.04% and a decrease in canopy cover for all species from 8.6 to 2.8%.

In Bandelier National Monument, New Mexico, burro damage was most pronounced in pinyon-juniper associations (Koehler 1974). Use of annual production was estimated to exceed 80%, and forage species were almost eliminated in the burros' preferred habitat. In some areas the bark on large cholla plants had been chewed off from ground level to about 3 feet above ground; yuccas also were destroyed by burros (Koehler 1974).

Bennett et al. (1981) studied effects of burro foraging on 4 vegetation types from the canyon rim to the river in Grand Canyon National Park. Species diversity and mean importance values were highest at the rim, and lowest in communities near the river. Simple communities with fewer than 15 species were severely impacted, whereas more diverse systems showed less impact. Carothers et al. (1976) investigated burro impacts to riparian areas in the Grand Canyon; they found 28 species of vascular plants on the control plot compared to 19 on the impact plot. Total vegetation cover on the control plot was 80%, compared to 20% on the impact plot. The mean area occupied by individual shrubs was reduced on the impact plot. The average absolute density of small mammals was 52/hectare on the control plot, and 13/hectare on the impact plot. Relative densities of small mammals were studied in a burro free and in a burro impacted area of Death Valley (Norment and Douglas 1977); absolute density of shrubs was greater on the control plot, and relative density of small mammals was 260% greater than on the impact plot.

Impact on Soils

Soil compaction is an aspect of environmental degradation caused by burros that has received minimal study. Farrell (1973) examined soil compaction by burros in western Arizona, and found only slight variation in bulk density between disturbed and undisturbed areas. However, plant growth was inhibited and erosion accelerated in areas trampled by excessive burro concentrations (Farrell 1973). Douglas and Fenn (unpublished data) studied soil compaction in Death Valley by using bulk density sampling and soil penetrometer readings. They found treads of burro trails in Butte Valley were as heavily compacted as treads of relatively heavily used jeep roads in the same area and soil type. Compaction extended 6-10 inches below the soil surface. The severity of soil compaction was surprising because soils in Butte Valley are granitic, and thus are relatively coarse and have poor compressibility. Heavily used burro trails on steep slopes in Death Valley and Grand Canyon have contributed to major soil movement and erosion. Carothers (1976) discusses and illustrates burro damage in Grand Canyon along the Colorado River. Compacted trails are almost impervious to penetration by water; precipitation tends to run off compacted soils, leading to erosion. Compacted soils also are resistant to plant colonization. Hundreds of miles of such trails are present in Death Valley and Lake Mead National Recreation Area.

Interaction with Desert Bighorn Sheep

Much has been written about the effects of feral burros on desert bighorn sheep. Many reports have been speculative and unsubstantiated by empirical data. Some concepts in early reports are simply erroneous, and have been disproved by later studies. For example, McKnight (1958), in a paper often quoted by subsequent workers, writes that, "In general, burros are wasteful foragers, frequently pulling entire plants up by the roots, eating only one or two mouthfuls, and dropping the remains on the ground." He states that, "There seems to be agreement among competent observers that rutting occurs in the fall and foaling in the spring", and that, "...a jack will seek to gather a harem of jennies, will fight the other jacks, etc., much in the manner of wild horses. There seems to be a tendency to breed every year, even if range conditions are poor." None of these statements has been supported by subsequent research. The latter two have been demonstrated to be incorrect (Moehlman 1974, Klingel 1974). Burros were wasteful of plant materials along the lower Colorado River where branches broken from paloverde trees were not completely divested of leaves (Woodward and Ohmart 1976), and on occasions such as was observed (by C.L. Douglas) in Death Valley, when burros were feeding on annual plantain (*Plantago insularis*). In some years, plantain covers the surface in localized areas. Burros are skillful in grazing on plantain as soon as the basal rosette of leaves has formed, and pull them from the ground with their lips and teeth. Burros dropped some of these tiny plants while chewing. It was our experience that burros in Death Valley were not especially wasteful foragers, but this probably varies between areas and depends upon the kinds and availability of plants being eaten.

Because burros eat a wide range of plant species, overlap in food selection with that of native desert ungulates would be expected. In the Cottonwood Mountains, burros and bighorn sheep exhibited little, if any, intraspecific resource partitioning in terms of diet composition. A total of 55 taxa was identified in annual diets of bighorn and burros, collectively; of these, 67% were used in common (Ginnett 1982). In both species, individual dietary niche breadth was responsible for 79% of the population niche breadth, suggesting that individual variation in diets is of little importance in determining dietary niche breadth in these species (Ginnett 1982). Both species operate as facultative generalists, selecting a narrower range of species in spring, a period of relative abundance, and a broader range of species in the winter. Bighorn, however, because of their ruminant digestion and slower gut clearance, must be more selective of what parts of plants they eat.

Walters and Hansen (1978) reported a range from 20% to 61% similarity between annual bighorn and burro diets from various areas in the Grand Canyon. Potter and Hansen (1979) reported 44% similarity for the Grand Canyon area. Seegmiller and Ohmart (1981) studied burro and bighorn diets in western Arizona; similarity values calculated from their data yielded dietary overlaps of 40% during spring to 50% during summer (Ginnett 1982). Similarity indices indicate trends between studies, but indices cannot be compared directly unless the same index was used. Similarities of diets between burros and bighorn does not justify a conclusion that the two species are competing for forage, although that situation might exist in some areas. For competition to be substantiated between two species the following must be established: 1) present or past niche overlap, 2) limited resources, and 3) depression in reproductive potential of one or both populations. The desert bighorn and burros live in areas having environmental uncertainty. It seems reasonable to assume desert bighorn are resource limited. Burros may also be resource limited, but because of their generalized food habits, they are less limited by forage resources than bighorn. In deserts of the western states, habitats of both species have continually fluctuating carrying capacities, being highest in spring and lowest in winter. Primary productivity of desert habitats is low, and dependent upon the amount and timing of precipitation. Availability of nutritious forage is thought to be the most limiting resource of these species (Norment and Douglas 1977). Foraging strategies of bighorn sheep have evolved in synchrony with their habitats, whereas feral burros have not evolved with the same resource set.

Feral burros have an advantage over bighorn sheep by being monogastric and food generalists. Burros are able to survive on forage having lower nutrient content than ruminants can subsist on. This is accomplished by increasing the rate of gut clearance and processing more volume of forage. Ruminants are restricted in their ability to increase the rate of gut clearance because of the structure of their digestive system. While they presumably can extract more nutrients from a given amount of forage than burros, bighorn also require forage having a higher nutrient content. Ruminants have been known to die, in winter, with stomachs full of undigested forage because the protein content was too low to keep rumen microorganisms alive and reproducing.

Body size is known to influence dominance among species of the same trophic level (Berger 1985); Berger suggests that establishment of exotics in an area must lead to either monopolizing of resources used by smaller species, or to causing smaller species to shift niches. Bighorn ewes in the Cottonwood Mountains of Death Valley used Quartz Spring, which was fenced to exclude burros, significantly more than other unfenced springs in that range (Dunn and Douglas 1982; Dunn 1984). Dunn (1984) also found through observation and time-lapse camera records, that bighorn would not come to drink at springs when $\geq$3 burros were present. Rams were more tolerant of burro presence than ewes. Limiting use of the range by ewe groups may place limitations on nutrient intake.

Ninety adult burros in Death Valley weighed between 147 and 159 kg (C.L. Douglas, unpublished data); the largest adults weighed about 180 kg. Some of the heaviest individuals were 2-3 year old males; however, most individuals in those age classes had not attained maximum body weight. Adult desert bighorn rams in the Lake Mead area weigh about 41-68 kg and ewes weigh about 34-52 kg; if 45 kg is used as an average weight, one burro equals the same relative weight as 3-4 bighorn. A desert ecosystem has a biomass limitation for grazing and browsing organisms, which include ungulates, lagomorphs, rodents, and insect herbivores. Because precipitation patterns are highly variable in desert areas, so too is production of plant biomass. Both quantity and quality of forage resources are important. A food generalist such as a burro can adapt to low quality forage by eating more of it, thereby acquiring at least maintenance levels of nutrition. Bighorn sheep must remain selective and eat the most nutritious parts of plants. Since sheep cannot vary the rate of gut clearance as much as burros, and cannot be as general in their food selection, they are at a competitive disadvantage under poor range conditions. Although adults may be able to survive on body stores and maintenance or sub-maintenance level nutrition, reproduction and postpartum survival of the young will be affected. The presence of an exotic herbivore exacerbates any natural shortage of food resources for native herbivores when there is a high degree of overlap in their diets. Woodward makes an interesting analogy between the effects of an overpopulation of burros and the effects drought have on plant resources. Burro overgrazing leads to less plant biomass available for native ungulates, and thus a lowered carrying capacity of the habitat (Woodward 1976).

Competition with Desert Bighorn Sheep for Water

Burros and bighorn may use the same water sources (Welles and Welles 1961a; Dunn 1984) at the same time. In Dunn's study, a bighorn ram and single burro were recorded, by time-lapse camera, drinking from opposite sides of a water puddle about 1 m in diameter. Welles and Welles (1961a) recorded sheep and burros drinking together at Lost Spring in Death Valley. At this spring, water forms pools at the top and bottom of a step in the drainage, such that animals drinking at the top source are separated physically from those drinking at the lower source. Dunn and Douglas (1982) found bighorn rams were less intimidated by burros than ewes. Nevertheless, some rams waited for hours until burros left a spring before going to

drink. Ewes generally would not drink if 3 or more burros were present at the spring. Rams drank at the springs burros utilized, but a spring not used by burros received much heavier use by ewes than springs used by burros. Burros have the tendency to lounge in groups at water sources, often remaining there for hours, or even entire days. Dunn (1984) regarded this interaction as interference competition. No active aggression was recorded between the species.

Adult bighorn consume about one gallon of water when visiting a water source. If necessary, they can go for several days without water. Desert bighorn are adapted to desert conditions by having concentrated urine, relatively dry feces, and the ability to rehydrate relatively quickly after drinking (Turner 1973). Survival of the burro in deserts is enhanced by its ability to withstand high degrees of dehydration and heat (Dill et al.1980). Yousef et al. (1970) studied the effects of dehydration on body fluids of two female adult burros. They reported a decrease of 32% in ICFV, 17% in ECFV, and only 7% decrease in plasma volume. Upon dehydration, burros decrease intracellular fluid volume more than the volume of other water partitions. The small decrease in blood plasma volume suggests that burros maintain a relatively stable blood volume under dehydration. This is thought to help explain their ability to generate saliva and feed on dry forage even when dehydrated. Burros have a greater need for free water than bighorn because: they are much larger animals; the amount of feces produced by burros is greater than that of desert bighorn and contains more water; and the urine of burros is much less concentrated than that of bighorn. Davis et al. (1978) found an average water turnover rate of 66 ml/kg/day (SE 20.9) in 4 juvenile and 2 adult burros. Two burros 3 years of age had water turnover rates of 123 and 140 ml/kg/day. These values represent moisture lost from the body to the environment, and thus represent daily water requirements. Using these figures, a 159 kg pound burro would require about 22 liters of water per day (assuming the individual is in a state of water balance). Water is a limiting resource in the desert; the potential for burros to usurp water that would otherwise be used by wildlife, and to interfere with bighorn obtaining water is a serious management problem.

Burro presence at springs could influence the amount of water bighorn can consume because of apprehension in approaching a spring and remaining there long enough to drink adequately. This potential decrease in water intake could result in decreased milk production during lactation, which could lead to lower lamb survival. Additionally, limiting use of the range by ewe groups may place limitations on nutrient intake. Nutritional quality of vegetation is strongly correlated to reproductive success (Caughley 1970).

Annotated Bibliography

The following annotated bibliography was compiled to assist in preparation of a burro management plan and environmental impact statement for the Lake Mead National Recreation Area. We initially intented to compile information from only North American scientific literature; this proved to be impractical, because some government and agency reports contain information warranting inclusion. Additionally, literature from Australia and elsewhere contains important and relevant information. Reports cited in the literature review are mostly results of research, i.e. primary sources of information, as opposed to secondary sources or expressions of opinion. If the report contained a comprehensive abstract, it is presented in the bibliography in its entirety, in quotations. Some abstracts are directly from Zarn's bibliography, and are so noted. Those abstracts without quotations and not from Zarn were abstracted by the authors. For a variety of reasons, some of the reports in the bibliography are not referenced in the literature review; we initially planned to delete these from the bibliography, but have included them for the sake of completeness, both historic and otherwise. Despite repeated efforts, we were unable to obtain several reports published in foreign journals.

Asdell, S. A. 1964. Patterns of mammalian reproduction (2nd edition). pages 530-532. Cornell University Press.

ABSTRACT: A summary of the reproductive physiology of burros. The gestation period in the ass is about 365 days, with considerable variation being induced by seasonal or nutritional factors.

Asdell, S. A., Robert M. Chew, and C. Kayser. 1965. *in* Mayer, William, and Van Gelder, Richard, editors. Mammalian reactions to stressful environments. Academic Press.

ABSTRACT: Brief references to experimental data pertaining to the water metabolism of burros (pages 99, 106, 108, 110, 128, 134-6, 139-41).

Ball, Walter S. 1959. Wild burro legislative problems in California. Desert Bighorn Council Transactions 3:11-13.

ABSTRACT: A general discussion of the results and problems associated with the burro removal provisions of the 1957 California "burro sanctuary" bill. Between 1957 and 1959, 248 "pet or beast-of-burden" removal permits were issued for 681 burros; of this total number, 22 permits for 337 burros were for pack teams. Applications to capture large numbers of burros for use in races, old miner's days, and similar events were not approved. An additional permit is required from the National Park Service to capture burros within Death Valley

National Monument. Enforcement is difficult because of problems identifying burros as feral or transfers. Section 4187 of the California Fish and Game Code allows killing burros on private property when they damage such; 1 request (for 25 burros) was received and it was granted.

Barnes, W. C. 1930. Wild burros. American Forests and Forest Life 36:640-642.

ABSTRACT: The article discusses burros in the west, their uses and how they were rounded up. Of interest is mention of the slaughter of 1,000 burros in the Grand Canyon. The author mentions that very little publicity was given because park officials feared public reaction and pressures that might be imposed. This fear came from previous experiences with horse slaughters. (from Zarn et al., 1977).

Behan, R. W. 1978. Political dynamics of wildlife management: the Grand Canyon burros. Transactions of the North American Wildlife and Natural Resource Conference 43:424-433.

ABSTRACT: A generalized discussion, using the Grand Canyon burros as a case history, of how scientific problems are affected by politics and emotions; included are suggestions on how all parties involved may more effectively reach a consensus on such issues.

Bennett, Debra K. 1980. Stripes do not a zebra make, part I: a cladistic analysis of *Equus*. Systematic Zoology 29(3):272-287.

ABSTRACT: "Living and extinct species in *Equus* have not been reviewed for nearly a century. More than 20 morphological, mostly cranial characters of *Equus* and *Dinohippus* are here explained; synapomorphies uniting *Equus* and *Dinohippus* and autapomorphies within *Equus* are discussed. Significant outgroups compared are *Dinohippus Quinn*, *Astrohippus Stirton*, and *Neohipparion Gidley*.

Cladistic analysis indicates that *Equus* is a monophyletic taxon closely related to *Dinohippus*, and that *Equus* can reasonably be divided into 2 (and only 2) subgenera, *Equus (Equus)* and *Equus (Asinus)*, each of which is characterized by a suite of autapomorphic features. The North American fossil record contains close relatives of every living species of equid except *E. quagga*. An examination of the zoogeographic implications of the cladistic hypothesis here presented indicates a complex pattern of migration from North America to Eurasia during Blancan through late Pleistocene time, and a strong zoogeographic relationship between Africa and North America demonstrated by the equids."

Bennett, Peter S., Arthur M. Phillips, George A. Ruffner, Steven W. Carothers, and Roy R. Johnson. 1981. Effects of burro foraging on 4 types of Grand Canyon vegetation. *in* Proceedings of the 2nd Conference on Scientific Research in the National Parks. U.S. Department of the Interior, National Park Service.

ABSTRACT: "Burros, introduced into the Grand Canyon region 100 years ago, are well adapted to [their] desert environment. Without known native predators the burros are increasing their numbers by 10 to 20% per year. Population control is largely through environmental resistance. They have prospered to the detriment of the natural ecosystems, changing the ecological composition of the National Park.

Research to evaluate this change was undertaken in 4 vegetation types situated between the canyon rim and the Colorado River. Relative densities, frequencies and cover were determined and the importance value derived. The mean importance value decreased from 0.213 to 0.154 with an F-probability for this difference of 0.036. Data was analyzed to provide the species diversity index and the evenness index. The mean species diversity index declined from 0.117 to 0.074 with an F-probability of 0.999. The degree of decrease varies according to the kind of statistic used, the plant species involved and the complexity of the communities.

Simple communities with fewer than 15 species are severely impacted. More diverse ecosystems show less effect. The type and degree of effect varies according to the type and complexity of the communities involved. Overall, foraging by feral burros has a demonstrable effect on Grand Canyon ecosystems."

Berger, Joel. 1985. Interspecific interactions and dominance among wild Great Basin ungulates. Journal of Mammalogy 66(3):571-573.

ABSTRACT: "Interspecific behavioral hierarchies are a possible way by which species partition resources (Morse,1974). Because body size influences dominance among species of the same trophic level (Fisler, 1977), one must suspect that in areas where exotic species have become established they have either monopolized resources directly from smaller native species or caused smaller species to shift niches. The Great Basin Desert of North America is an area where concern has been amplified over such a scenario because feral equids such as horses (*Equus caballus*) and burros (*E. asinus*) coexist with numerous native species of ungulates [i.e. bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), elk (*Cervis canadensis*), and bison (*Bison*)]... In this note, I present information on interactions among sympatric bighorn, pronghorn, mule deer, and feral horses and evaluate the extent to which behavioral dominance influences resource use.

From 1976 to 1983 over 9000 hours were spent observing Great Basin ungulates in several locations... Associations among [them] were not common preferences... a total of 28 interspecific social interactions (ISI) were rec ISI is

defined as one in which an individual or group of a given species retreats by running from a member or members of a different species... Of the 28 ISI, 13 involved groups displacing groups; the remainder were of solitary individuals either supplanting groups (10 of 15 ISI) or being supplanted by groups (5 of 15 ISI).

Horses, the largest species, were involved in 20 ISI and were dominant in 19... Among native ungulates, no species was clearly dominant over the other... In all 8 ISI among native species, only groups of animals displaced groups of another species... Solitary native ungulates never caused either groups or solitary individuals of a native species to leave an area...

Interactions may be more frequent in areas where population densities of various species are greater than those found in the Great Basin, or perhaps when resources are limited or localized.

In summary, individuals of species of larger size accrue spatial advantages because they are rarely displaced by smaller species, but whether the net gains are turned into reproductive profits is doubtful. Evidence to support the idea that behavioral competition results in niche segregation among pronghorn, bighorn, mule deer, and feral horses in the Great Basin Desert is lacking."

Berger, Joel. 1983. Predation, sex ratios, and male competition in equids. Journal of Zoology (London) 201(2):205-216.

ABSTRACT: "Existing data indicate that a greater preponderance of adult females rather than adult males occurs in most species of mammals. The hypothesis that such differences arise as a result of inter-male reproductive competition for females (and not predation) was examined in the *Equidae* by comparing populations of horses (*Equus caballus*), asses (*E. asinus*), and 2 species of zebras (*E. zebra* and *E. burchelli*) in predator-free, predator-rich and insular ecosystems.

Evidence is presented that: 1) sex differences in adult mortality occur, 2) they relate to the type and intensity of natural predation, and 3) asymmetries in sex ratios are most often explicable in terms of intermale reproductive competition... The sole exception to this occurred in an extreme climate where greater female mortality was presumed due to increased gestational and lactational costs... Additional data are necessary to help clarify the proximate variables that alter adult sex ratios and to determine whether patterns observed in North American feral forms and native African species apply to Asian Equids and other ungulates."

Berger, Joel. 1986. Wild horses of the Great Basin: social competition and population size. University of Chicago Press. 326 pp.

ABSTRACT: Very brief references to feral burros as they compare to feral horses in terms of sex ratios (pages 90-93, 175), group patterns (page 129), and interspecific dominance relations (pages 254-255); also a short section on

exotics in the Great Basin. All references cited on these pages are abstracted in this bibliography.

Blake, John G. 1977. Serum protein polymorphisms of the feral ass (*Equus asinus*) in Death Valley National Monument. Contribution number CPSU/UNLV 011/01. Technical Report # 23. (also M.S. thesis, University of Nevada-Las Vegas). National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 82 pp.

ABSTRACT: "Ten transferrin phenotypes, controlled by 4 codominant alleles were observed among the burros examined from the Panamint Mountains, Death Valley National Monument, California. Nine transferrin phenotypes were recorded from samples taken from the Butte Valley herd, 6 from the Hanaupah Canyon herd, 5 from the Wildrose Canyon herd, and 4 from the Johnson Canyon herd.

Two albumin phenotypes, controlled by 2 codominant alleles were recorded from the samples analyzed. A common phenotype was recorded from the samples analyzed. A common phenotype was recorded from all 4 herds; a rarer type was recorded from the Wildrose Canyon herd and from the Hanaupah Canyon herd. Statistical analyses of the distribution of alleles revealed significant differences between the various herds. The overall level of heterogeneity among the herds of the Panamint Mountains burro population was extremely significant. The data indicate that the herds are operating as relatively independent demes with, at best, a very reduced rate of gene flow between herds.

Conclusions based on the genetic data are supported by observed behavioral data. Patterns of movement in relation to altitude and distance from water, together with the timing of reproductive activity, are important in maintaining the genetic unity of the herds.

The causes for the establishment of the observed differences are not known. It is speculated that a burro reduction program carried on between 1939 and 1969 depleted the herds to such low levels that the distribution of alleles was skewed. Lack of migration between herds would account for propagation of the skewed distribution.

Three transferrin alleles display clinal patterns of variation between the 4 herds. All 4 alleles display changes in frequency significantly correlated with distance. It is suggested that a very low rate of gene flow, rather than an environmental variable, is responsible for the observed patterns of variation."

Blake, John G., and Charles L. Douglas. 1978. Albumin polymorphism in the feral ass of Death Valley National Monument, California. Animal Blood Groups and Biochemical Genetics 9(1):9-12.

ABSTRACT: "Evidence is presented for the occurrence of a 2nd allele in the albumin system of the donkey. Samples were collected from 127 feral donkeys

in 4 locations within the Panamint Mountains of Death Valley National Monument, California. A common phenotype, electrophoretically characterized by a single band, was recorded from all locations. A rare, double-band phenotype was recorded from 2 locations."

Blake, John G., Charles L. Douglas, and Linda F. Thompson. 1981. Spatial variation in transferrin alleles frequencies among herds of feral donkeys in Death Valley National Monument, California. Journal of Mammalogy 62(1):58-63.

ABSTRACT: "Serum proteins were studied to clarify interrelationships of seemingly disjunct herds of feral donkeys in the mountains of Death Valley National Monument, California. Sera of 162 donkeys from 5 localities in the Panamint Mountains were examined by starch-gel electrophoresis to asses polymorphic variation in transferrins. Four homozygous and 6 heterozygous transferrin phenotypes controlled by 4 codominant, autosomal alleles were identified with ^{59}Fe autoradiography. Significant interlocality heterogeneity in genotype distribution and allele frequency distribution among herds was demonstrated. The maximum distance between adjacent herds was 52 km and the minimum distance was 14 km. There are no major physical barriers to movements between herds; furthermore, donkeys are highly mobile animals capable of extensive travel. Behavioral isolation of adjacent herds occurs from May through July, during the peak of reproduction. This isolation is reinforced by fidelity of individuals to their respective home ranges, and to physiological dependence on permanent sources of water. Adjacent herds may overlap during winter when breeding and dependence on water sources are reduced."

Brady, Ward, and Thomas Hanley. 1975. Forage production of feral burro habitat in the Havasu resource area, Colorado River Valley, California-Arizona. Report submitted to the Bureau of Land Management, Havasu Resource Area. 25pp.

Brigham, W. R. 1974. Report of the feral burro committee. Desert Bighorn Council Transactions 18:62-63.

Brookshier, Frank. 1974. The burro. University of Oklahoma Press. 370 pp.

Brown, Daniel G., and Fannie H. Cross. 1969. Hematologic values of burros from birth to maturity: cellular elements of peripheral blood. American Journal of Veterinary Research 30(11):1921-1927.

ABSTRACT: "Hematologic values of male and female burros at different age periods from birth through 2 years were determined. The data were obtained from 105 burros, 51 males and 54 females, during a period of 9 years. Most of

the values for 1-year-old burros were similar to those for adult burros, and all values for 1.5-year-old burros were within the normal limits for mature burros."

Brown, Daniel G., D. F. Johnson, and Fannie H. Cross. 1965. Late effects observed in burros surviving external whole-body gamma irradiation. Radiation Research 25(3):574-585.

ABSTRACT: "The status of female burros surviving single and multiple exposures of gamma radiation for periods of 10 and 13 years has been described. Mortality ranged from 10% in the 320-R group to 50% in the 545-R group; there have been no deaths in the controls.

The majority of deaths have been associated with physiologic and pathologic changes comparable to early irradiation injury observed in burros. The principal lesion has been thrombocytopenia with a corresponding decrease in megakaryocytes in the bone marrow.

Fertility does not appear to be affected, and no adverse effects have been observed in the offspring from irradiated survivors."

Brown, Daniel G., William G. Magrane, Fannie H. Cross, and R. A. Reynolds. 1972. Clinical observations of eyes of cattle, swine, and burros surviving exposure to gamma and mixed neutron-gamma radiation. American Journal of Veterinary Research 33(2):309-315.

ABSTRACT: "Clinical observations of the eyes of cattle, swine, and burros which survived radiation exposures to gamma and mixed neutron-gamma radiation for several years were described. Significant irradiation effects were not found in the eyes of burros and swine, but 6.7% of irradiated cattle were affected with opacities characteristic of radiation-induced lesions."

Browning, Bruce. 1960. Preliminary report of the food habits of the wild burro in the Death Valley National Monument. Desert Bighorn Council Transactions 4:88-90.

ABSTRACT: Twenty "burro stomachs were collected by the National Park Service in Cottonwood Canyon in the Cottonwood Mountains of the Panamint Range which lies on the west side of Death Valley." Five were collected in April 1959, 10 in November 1959, and 5 in March 1960.

"The food items [found in the stomachs] reveal... that the burro exhibits superior adaptability to its environment. Almost every common browse in the collection area was utilized by the burro except creosote bush [*Larrea tridentata*], and even this resinous shrub has been recorded as used for food by the burro. The preponderance of bursage [*Ambrosia dumosa*], especially in the fall diet, may show some preference, but also might reflect the abundance of this plant. Bursage is probably the most prevalent ground cover in the mixed

[creosote bush scrub and shadscale scrub] association... the desert bighorn sheep shows little or no preference for this shrub.

There is a significant shift in the diet of the burro between the spring and the fall. Forbs [generally unidentified species] comprised almost 65% of the spring foods and several stomachs were completely filled with green forbs. Apparently the burro is able to seek them out wherever they are available. In the fall, of course, the forbs are dried up and the burro falls back on browse plants for food. Browse [primarily bursage] made up over 75% of the food found in the fall diet and the few forbs present were unidentified stem fragments.

Grass occurred in over half of the stomachs examined and made up 10% of both the spring and fall diets. *Galleta*, the common bunch grass in the area, probably contributes to this percentage, being utilized when green in the spring and also when dried up in the fall. It seems reasonable to say that the burro is an opportunist and... will eat those food plants most available." A table of the 32 plant species found in the 20 burro stomachs in terms of volume % and frequency for both spring and fall is included.

Bullard, R. W., D. Bruce Dill, and Mohamed K. Yousef. 1970. Responses of the burro to desert heat stress. Journal of Applied Physiology 29(2):159-167.

ABSTRACT: "Two female burros were studied with regard to regulation of sweating and responses to dehydration and rehydration under the natural desert conditions of Boulder City, Nevada, in July. Sweat in the donkey appeared to be expelled in cycles of 2 or less per minute which occur synchronously all over the body surface. The sweating rate was determined by both central and skin temperatures. Cooling the major portion of the skin area during sweating appeared to reduce the magnitude of cycles, but not the overall sweating rate until general body cooling had occurred. However, heat applied locally to the skin or sweat glands had a marked stimulating effect suggesting that the local temperature of the gland is important in its function and that reflex regulation of sweating, acting by way of peripheral thermal detectors, is less important. The most potent stimulating agent upon intradermal injection was epinephrine. Other autonomic agents were almost completely ineffective upon the rate of sweating. Moderate dehydration, amounting to 14% and 9% of body weight during desert exposures, did not greatly alter blood concentrations, performance, or temperature regulation. Rehydration was rapid and precise after this degree of dehydration."

Bureau of Land Management. 1977. Rules proposed for helicopter use in management of wild horses and burros.

ABSTRACT: The proposed regulations would implement provisions of the Federal Land Policy and Management Act of 1976 which modify earlier laws prohibiting the use of mechanized equipment in gathering horses and burros.

Bureau of Land Management. 1982. Wild horse and burro report. U.S. Government Printing Office.

Bureau of Land Management. 1988. Wild horse and burros. *in* Boundary adjustments: Death Valley and Joshua Tree National Monuments.

Bureau of Land Management, California State Office. 1968. Feral animals: burro. *in* The California desert.

Bureau of Land Management, Ridgecrest Resource Area, California Desert District. 1980. Wild horse and burro herd management area plan for the Saline Valley and Lee Flat herd management area. U.S. Forest Service, Inyo National Forest.

ABSTRACT: "This management plan addresses management of feral burros in the Saline Valley and Lee Flat Herd Management Area. This area is administered by the Ridgecrest Resource Area, California Desert District of the Bureau of Land Management and the Inyo National Forest, U.S. Forest Service.

This plan will replace both the Bakersfield District Interim Burro Management Plan (1976) and the Evaluation and Management Plan for Wild Free-roaming Burros of Saline Valley (1976). A number of factors, including capture program results, monitoring results, and implementation of the California Desert Plan, all dictate that a new plan is necessary. The general objective of the management plan is to manage wild and free-roaming burros in the Saline Valley and Lee Flat areas in an ecological balance with the natural values of the area.

This management plan, a joint document of the Bureau of Land Management and U.S. Forest Service, is written in accordance with the Wild Free-roaming Horse and Burro Act of 1971 (as amended), the California Desert Plan (1980) and current policy."

Bureau of Land Management, Susanville District. 1973. Wild horses and burros.

ABSTRACT: A report which evaluates the present horse and burro situations in the Susanville District of California. Based on research on the present populations, including the range condition and competition with other animals, the report recommends the implementation of certain management practices. Populations were determined by use of aerial survey counting techniques. (from Zarn et al., 1977).

Bureau of Land Management, Susanville District. 1974. Wild horses and burros: environmental analysis. 52 pp.

ABSTRACT: This summary of an 18-month study of the wild horses and burros in the Susanville District indicates definite over-grazing and competition problems there. Population counts reported were partially determined by aerial surveys. Eight alternative recommendations are made. (from Zarn et al., 1977).

Butt, Mark T., Alan R. Tipton, and Patrick F. Scanlon. 1979. Population dynamics and control strategies for free-ranging burros: a modelling approach (abstract only). Virginia Journal of Science 30(2):46.

ABSTRACT: "A literature search was used to generate data on reproductive success and longevity of feral burros. Using a modified Leslie matrix 7 possible population age structures were generated. Of these, the simulation using 0.57 foals/female/year and a standard mortality produced results comparable to published material on domestic burro reproduction and observations on feral animals. From a stable age structure with 1413 females, 5 control methods were evaluated: 1) reduction of natality by exogenous drugs, 2) % cropping of adults, 3) % cropping of young, 4) predetermined cropping of all ages, and 5) % cropping of all ages. A 20% cropping of immature burros for 5 years reduced the population from 1413 to 1130, a 20% decrease. Although other methods produced greater reductions, this method is considered the most useful approach for managing burros for the following reasons: 1) population structure is not radically altered, 2) a significant reduction of animals is imposed, 3) young animals are more vulnerable, and 4) the control could be carried out with limited funds and knowledge of the population to be controlled."

California Department of Fish and Game. 1961. Status of feral burros in California. 5pp.

California Department of Fish and Game. 1972. Status of feral burros in California. 8pp.

ABSTRACT: A review of state and federal burro legislation. The department states that: "Though specific and often extensive areas are known in which burros are devastating the range, it should not be assumed that these conditions necessarily prevail on all burro ranges. However, it should be clearly understood that burros present serious problems when left unmanaged. The new federal legislation makes it clear that the intent is to preserve the wild, free-roaming burros and horses. It must be realized that in so doing they must be managed and kept in balance with the other resources." (from Zarn et al., 1977).

Carothers, Steven W. 1976. Feral asses on public lands: an analysis of biotic impact. in An ecological survey of the riparian zone of the Colorado River between the Grand Wash Cliffs, Arizona. Report on file at NPS/DVNM. 12 pp.

Carothers, Steven W., Merle E. Stitt, and Roy R. Johnson. 1976. Feral asses on public lands: an analysis of biotic impact, legal considerations and management alternatives. pages 396-406. *in* Transactions of the 41st North American Wildlife and Natural Resources Conference. Wildlife Management Institute.

ABSTRACT: "The results of this investigation demonstrate conclusively that the feral ass has a negative effect on the natural ecosystem of the lower reaches of the Grand Canyon. The principal impact of the feral ass is habitat destruction through grazing and trampling.

On the study area where feral asses occurred the vegetation cover and rodent populations were significantly reduced when compared to the study area where feral asses were absent. On the control plot, 28 species of vascular plants were found compared to 19 on the impact plot. The total vegetation cover on the control plot was 80%, compared to 20% on the impact plot. The mean area (m^2) occupied by each individual acacia or mesquite shrub was 27.9 m^2 on the control plot and 20.7 m^2 on the impact plot.

The mammal species diversity was higher on the control plot (0.79) than it was on the impact plot (0.70) In addition, the average absolute density of small mammals from March 1974 to January 1975 on the control plot was 52 mammals/ha, approximately 4 times the 13 mammals/ha found on the impact plot. 0Thus, differences between the 2 areas in mammalian species composition and diversity were attributed to the depauperate flora, particularly the forbs and grasses, on the 209 mile canyon impact area."

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51(1):53-71.

ABSTRACT: "An eruptive fluctuation is defined operationally as an increase in numbers over at least 2 generations, followed by a marked decline. Reported eruptions in ungulates suggest that the upswing is initiated by a change in food or habitat and is terminated by overgrazing. An apparent exception--the Kaibab eruption--probably also fits this pattern. The interpretation causally linking reduction of predators on the plateau with increase of deer is an overstatement of evidence. Eruption of established populations is essentially the same process as the buildup of populations initiated by liberation, with the difference that in the 2nd case a zone of high density migrates radially from the point of liberation.

Eruption of thar (a goat-like bovid) after liberation in New Zealand was studied by sampling populations at different distances from the point of liberation. The aim was to determine trends of demographic statistics across an eruptive fluctuation that spans 50 years. Although fecundity varied across

this eruption, the major influence on rate of increase was traced to variation in death rate. The major component of this variation was the rate of mortality over the 1st year of life. Trend in death rate, and hence in rate of increase, was associated with trends in other population statistics that are easier to measure. The most useful correlative of rate of increase is probably the level of fat reserves.

While we do not know whether trends in population statistics of thar reflect those of other ungulates during an eruptive fluctuation, the generality of the reported trends may usefully serve as a testable hypothesis."

Choquenot, David. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology 72(3):805-813.

ABSTRACT: "The food hypothesis of population regulation was tested using 2 predation-free populations of feral donkeys in tropical northern Australia. Growth, body condition, and age-specific rates of fecundity and mortality were compared between the 2 populations. One of the populations was roughly 1/2 the density of the other, following an experimental reduction 3-4 yr previously. Fecundity was high and independent of density, with >70% of mature females pregnant in both populations. Age at maturity and juvenile mortality displayed some density dependence. Populations conformed to predictions of the food hypothesis, abundance being ultimately regulated by food-related juvenile mortality. At high density, juvenile mortality was 3 times as great as at low density, and was associated with poorer juvenile body condition and slower growth. Differences in rates of juvenile mortality are associated with nutritional status of lactating females, which is in turn determined by density-dependent competition for quality forage. The effects of competition for forage upon juvenile mortality synchronize lactation with an annual flush of quality forage at the onset of the monsoonal wet season."

Choquenot, David. 1990. Rate of increase for populations of feral donkeys in northern Australia. Journal of Mammalogy 71(2):151-155.

ABSTRACT: "Rate of increase was measured for 2 populations of feral donkeys in northern Australia following substantial (≥ 40%) reductions in density. Rates of increase were measured directly as the average annual exponential rate of population increase (r). Estimated rates of increase for the populations were r = 0.21 and 0.25, corresponding to finite rates of 23% and 28% per annum. Because populations were below ≥ 40% initial densities, food availability was not limiting; hence, estimated rates of increase probably were the maximum potential rate of increase for the species in northern Australia."

Choquenot, David. 1988. Feral donkeys in northern Australia: population dynamics and the cost of control. M.S. thesis, Canberra College of Advanced Education, Canberra, Australian Capital Territory.

Cleary, Edward. 1973. Selective exclusion fencing in wild burro and bighorn sheep management. Desert Bighorn Council Transactions 17:106-109.

ABSTRACT: "Interspecific competition for water by wild burro and bighorn sheep in the Wood's Mountains was eliminated by use of a steel-pipe fence. The fence enclosed Wood's Spring, the only permanent water source in the area, in such a manner as to deny water to the burro without denying water to the bighorn sheep... [The] uprights were set 8 to 10 feet apart. Two runners were strung between each upright, the 1st about 18 inches and the 2nd about 36 inches above the ground... A single strand of barbed wire then was strung above the top runner." Observations were made during May, July, September, and March; the signs indicated that the sheep were using a narrow rock ledge leading into the spring above the fence and in several places were jumping the fence. Burro and burro sign were always outside the fence where they drank the spring overflow.. "Without water, the burro were forced to seek both water and food outside of the Wood's Mountains. Thus, fencing indirectly eliminated competition for food and directly eliminated competition for water between these 2 species." Some reinvasion of burros occurred, but this was in an exceptionally wet period which reduced the limiting effect of water supply.

Clutton-Brock, Juliet. 1981. Asses, mules, and hinnies. pages 91-101. *in* Domesticated animals from early times. University of Texas Press. 208 pp.

ABSTRACT: A history of the origins of burros and their domestication by man.

Committee on Wild and Free-Roaming Horses and Burros, Board of Agriculture and Renewable Resources, National Research Council. 1982. Wild and free-roaming horses and burros: final report. National Academy Press, Washington, D.C. 80 pp.

ABSTRACT: This report was the 3rd and last phase of a research study assigned to the National Academy of Sciences Committee on Wild and Free-Roaming Horses and Burros by the Public Rangelands Improvement Act of 1978 and agreed to by a contract with the BLM. The end-product of Phase I was large report (cited separately in this bibliography) which reviewed existing (c1980) knowledge on wild horses and burros and proposed a research plan. Phase II was an evaluation of 5 horse and burro research projects proposed in Phase I and contracted by the BLM; this was a small fraction of the total research program recommended in Phase I. This final summary report

recommending management programs for wild horses and burros concluded Phase III.

From the Executive Summary: "...Ecological niches to which Pleistocene equids related do not exist today, and no other animals in the contemporary North American fauna would have the same niche relationships as the modern-day equids, with or without the latter's presence...

...Statements have been made that horse and burro populations typically increase at rates ranging from 16 to 22% per year. However, the Phase I report explored several biases in the [data] and concluded annual rates of increase of 10% or less... More data are needed...

Although there is some evidence of density-dependent processes in feral equid populations, they do not appear effective enough to self-limit populations below levels at which they significantly impact the vegetation. Starvation has been... reported for some burro populations...

According to some investigators, the desert bighorn... have been affected by cattle, domestic sheep, and goats; several [researchers] have implicated competition with wild horses. A 40-year publication history chronicles a wide range of research and investigators, some of whom conclude that wild burros compete with desert bighorns for water, vegetation, and/or space and have been one factor in sheep decline...

Wild horse and burro census methodology will continue to rely on some form of aerial technique, but the present method misses animals, the percentage depending on the nature of the terrain and vegetation. Fixed-wing aircraft census in gentle topography with low vegetation in the Phase II research located about 93% of the horses present, but in a wooded mountainous area it counted only 40%. Helicopter census in the same area counted 48%. If accurate census is desired in such areas, and for burros, some form of capture-recapture or removal method will be necessary... Annual census do not appear necessary [from a scientific perspective]. It should be possible to manage herds adequately with 1 census every 2 or 3 years."

Fertility control via the removal of the most fecund mares, chemosterilization of dominant band stallions, and injecting or implanting steroids into mares is discussed.

Committee on Wild and Free-Roaming Horses and Burros, Board of Agriculture and Renewable Resources, National Research Council. 1980. Wild and free-roaming horses and burros: current knowledge and recommended research, phase 1: final report. National Academy Press, Washington, D.C. 382 pp.

ABSTRACT: This report is the end-product of Phase I of a 3-phase research study assigned to the National Academy of Sciences Committee on Wild and Free-Roaming Horses and Burros by the Public Rangelands Improvement Act of 1978 and agreed to in a contract with the BLM. It reviewed existing [c1980] knowledge on wild horses and burros and designed a research plan. Phase II evaluated 5 discrete horse and burro research projects proposed in Phase I

and contracted by the BLM. Phase III was a final summary report (cited separately in this bibliography) recommending management programs for feral horses and burros.

Conley, Walt. 1979. The potential for increase in horse and ass populations: a theoretical analysis. pages 221-229. *in* Denniston, R. H., editor. Symposium on the ecology and behavior of wild and feral equids. University of Wyoming. 236 pp.

ABSTRACT: A simple computer model is developed and the results analyzed. "The analytical and conceptual difficulties associated with rates of increase in animal populations [using] examples that reflect the sort of life history patterns seen in horse and ass populations [are presented]. [A] series of theoretical boundaries for rates of increase in such populations [are established]; boundaries they are not expected to exceed... [A] series of graphs... represent various combinations of the primary population parameters of survival and reproduction [and] clarify the interactions that result in various observed rates of increase.

The sensitivity of rates of increase to changes in various population attributes and life history patterns is a subject of considerable importance to attempts to establish such rates from wild populations... The rate of increase is particularly sensitive to: 1) the shape of the survival function, 2) the proportion of the adult female population that actually produces young, and 3) the age at first breeding. In contrast, the rate of increase is relatively insensitive to: 1) maximum age attained by the breeding females, and 2) the presence of post-reproductive animals. [Eight hypothetical survival schedules are presented. Schedule 1 represents a theoretical maximum, with no deaths prior to maximum age 14; Schedules 2 through 8 represent successive decreases in survival rates].

...Assuming that female survival schedules in wild populations are approximately [as shown in Schedule 4], and that the proportion breeding is on the order of 50% or 60%, finite rates of increase of about 1.05 are to be expected. Additionally, if survival schedules in the males are lower than those of females, then the results presented here are higher than would be obtained in wild populations [and, again, are conservative].

Finite rates of increase higher than 1.20 can only be obtained if the real survival schedules are similar to Schedules 1, 2, or 3 AND if the proportion breeding is 0.8 or greater across all age classes, AND if age at first breeding is 3 years, AND if breeding span beginning at age 3 extends beyond about age 8 to 10... Empirical values for the various population attributes considered here are simply too low to conclude that rates of increase in wild populations approach 20%, much less exceed that level."

Cook, C. Wayne. 1975. Wild horses and burros: a new management problem. Rangeman's Journal 2(1):19-21.

ABSTRACT: "The Wild Horse and Burro Act was short-sighted in the impact it would eventually have on the public land resources and therefore had deficiencies. If the inadequacies of this bill were not evident at the time the act was passed, they very definitely are now and the proponents of the bill should now try energetically to amend the bill so that it can be properly administered toward a workable solution. The bill essentially has no control measures, and as a result numbers of wild horses and burros will continue to increase at a rate that is incompatible with the ability of the land resources to sustain them. The bill needs to be amended to allow aircraft to be used by the agencies to manage these animals in moving them, counting them, and in corralling them for removing numbers. The bill needs to be amended to allow transfers of title either by gift or sale to individuals in order to control numbers. Serious consideration should be given to amending the bill to allow for complete removal of horses and burros from some areas and the establishment of horse and burro ranges, where they can be managed appropriately."

Davis, Thomas P. 1975. Physiological studies on the feral burro, *Equus asinus*. Contribution number CPSU/UNLV 006/06. (also M.S. thesis, University of Nevada-Las Vegas). National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 91 pp.

ABSTRACT: "A study of body fluids and body composition of the immature feral burro was undertaken. In addition, blood constituents and respiratory metabolism were studied. Blood hematology was measured on 41 burros from Death Valley, California.

Diurnal rhythm was observed in Hb and Hct, which are positively correlated to each other. However, Ps showed no significant diurnal rhythm. There were no significant differences in mean Hct, Hb, RBC, Ps, or differential counts between burros in the field and burros in the laboratory. Normal values for blood biochemistry and hematology of immature burros were obtained. Variation among ungulate species and other parameters such as growth affect blood constituents but few data, especially blood biochemistry were available on the adult burro for comparison. Normal values for blood volume, plasma volume, extracellular fluid volume, intracellular fluid volume, and total body water of immature burros were obtained. Blood volume, plasma volume, and red blood cell volume were higher than in the adult burro. Extracellular and intracellular fluid volumes varied little from adult burro and other ungulates. Body water loss per day and turnover rates were determined and compared to other wild and domestic ungulates. Differences were dependent on ambient temperature and aridity.

Body composition of the immature burro is very similar to the adult burro. Comparisons to other ungulates were presented and differences were noted in body fat as the immature burro had more body fat than the adult burro and Angora goat, but less than adult domestic cattle and wether sheep.

There is a significant difference and relationship between respiratory metabolism of the juvenile and adult burro. This relationship demonstrates that

as age increases, oxygen consumption decreases as expected with cessation of growth and changes in volume surface ratio. Diurnal rhythm occurs in respiratory activity of immature burros with periods of quiescence accompanied by decreased VO_2 at night.

This study provides basic physiological data on the juvenile burro which should stimulate further research on this unique but little studied feral ungulate."

Davis, Thomas P., Mohamed K. Yousef, and H. D. Johnson. 1978. Partition of body fluids in the burro. Journal of Wildlife Management 42(4):923-925.

ABSTRACT: "This study was undertaken to determine water turnover rate, to partition the various body fluid compartments in burros ranging in age from 1 to 72 months old, and to relate the various body fluid compartments of young and adult burros to body weight.

Daily water turnover rate in burros ranging in age from 1.6 to 2.4 months was approximately 28% less than that of the 4-month-old. However, water turnover rate in the 4-month-old was similar to that obtained on the 6-year-old burros. Since water turnover rate is a measure of the total daily water exchanged between the animal and its environment, it is then considered an adequate measurement of the daily water need of the animal (assuming that the animal is in a state of water balance). This measurement is of extreme interest since burros in the USA are concentrated in the deserts of the southwest where free surface water is at a premium." Burro management requires "an estimate of their water needs... By knowing the yearly available free water in a desert area and the daily water requirement for each burro, a better policy for the management of wild herds can be instituted."

Desert Bighorn Council, Committee on Burro-Bighorn. 1957. Burro-bighorn competition and control. Desert Bighorn Council Transactions 1:70-76.

ABSTRACT: Transcripts of a brief group discussion concerning burro use of water, burro-proof fence design, and burro population and status in Death Valley National Monument, Grand Canyon National Park, and Lake Mead National Recreation Area. To summarize the consensus "A definite control of some type is apparently necessary, and it has been used in many instances where it is legal."

Dill, D. Bruce, Lars F. Soholt, Janene Miller, H. Randolph, and Terry S. Goudy. 1979. Properties of sweat, burro and man. Comparative Biochemistry Physiology A 62A(2):317-320.

ABSTRACT: "Sweat of 2 burros (*Equus asinus*) was collected after 2 desert walks, one at 38 °C, one at 41 °C. Sweat from 1 burro was about twice as concentrated as from the other. In that respect and in respect to concentrations

of chloride, sodium and potassium, their sweat was like that of man. Low concentrations of bicarbonate were present in burros' sweat; [this] contrasted with little if any in man's. Urea nitrogen plus ammonia nitrogen were found in higher concentrations in burros' sweat than in man's sweat."

Dill, D. Bruce, Mohamed K. Yousef, Craig R. Cox, and Robert G. Barton. 1980. Hunger versus thirst in the burro. Physiology and Behavior 24(5):975-978.

ABSTRACT: "The burro (*Equus asinus*) can withstand deprivation of both food and water for up to 48 hours even in summer heat. This ability depends in part on his capacious cecum and colon where food is stored and is digested by bacterial action for hours after his last meal. In 8 such periods of deprivation maximum temperatures ranged from 35 to 45 °C and estimated increases in osmotic pressure in 2 burros ranged up to 17%. Given free choice of hay and water at the end of deprivation they chose hay always when estimated increase in osmotic pressure was less than 10%. In one case the second 24-hour period included an 8-hour walk. In this case the estimated increase in osmotic pressure was 17% in both and both chose water first. Their ability to eat dry hay after long periods of dehydration is essential to their survival in hot deserts where they can graze for 24 hours before returning to a water source."

Douglas, Charles L., and Hermi D. Hiatt. 1987. Food habits of feral burros in Death Valley, California. Contribution number CPSU/UNLV 006/46. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 25 pp.

ABSTRACT: "The purpose of our study was to document seasonal food habits of feral burros in Butte Valley, an area of high burro density in Death Valley, California, and to synthesize available information about plant species eaten by burros in Death Valley. A total of 119 plants have been eaten by burros in Death Valley. In Butte Valley, burros ate 40 plants: 15 shrubs, 7 grasses, and 18 forbs. Eleven species were important throughout the year; 29 others were eaten infrequently. The average burro diet in Butte Valley consisted of 48% grasses, 25% shrubs, 19% forbs, and 7% unknown dicots. Burros have been considered to be browsers or grazers by various authors. Selection of forage classes is related to availability of grasses, which are preferred when available. Diets in Butte Valley were deficient in phosphorus for lactating females, although foals were born and nursed without incident. Regression of phosphorus and protein for forage species in Butte Valley and the Cottonwood Mountains indicates a strong linear relationship (r=0.73) between these nutrients."

Douglas, Charles L., and David M. Leslie, Jr. 1986. Influence of weather and density on lamb survival of desert mountain sheep. J. Wildlife Mgmt. 50:153-156.

ABSTRACT: "This report concerns the effect of weather on lamb survival in desert mountain sheep (*Ovis canadensis nelsoni*) to 6-8 months of age in the River Mountains, Nevada, and how it integrates with density to limit the population. Regression analyses were used to examine relationships between lamb survival and weather variables from 1970 to 1982. Autumn precipitation (Sep-Dec) of the preceding year (during gestation) had a significant ($P < 0.05$), positive effect on lamb survival. Herd density was significantly ($P < 0.05$) and inversely related to lamb survival. Spring winds had a positive and significant ($P < 0.05$) effect on lamb survival. Multiple regression revealed that 87% of the variability in lamb survival was accounted for by autumn precipitation during gestation (52%) and sheep density (35%)."

Douglas, Charles L., and Christopher Norment. 1979. Ecological studies of feral burros in Death Valley. pages 373-383. Proceedings of the 1st Conference on Scientific Research in the National Parks. U.S. Department of the Interior, National Park Service.

ABSTRACT: A synopsis of earlier research by Douglas and Norment which is abstracted in this document.

Douglas, Charles L., and Christopher Norment. 1977. Habitat damage by feral burros in Death Valley. Desert Bighorn Council Transactions 21:23-25.

ABSTRACT: "This report presents results of an analysis of browse impact upon vegetation in 4 contiguous areas in the northern Panamint Mountains, Death Valley National Monument, California. Browse impact was evaluated by the Vesey-Fitzgerald method. The analyses demonstrate that browsing by burros is altering composition of the vegetational community in Wildrose Canyon. Of all shrubs in Wildrose Canyon, 45.7% exhibit some evidence of having been browsed, while the survival of 12.2% is threatened by severe browsing. *Acamptopappus shockleyi* and *Ambrosia dumosa* were the species most affected by browsing. Burros inhabit Wildrose Canyon and vicinity for about 6 months each year. Vegetation in the 3 other locations (Nemo Canyon, Wood Canyon, and Skidoo) is utilized only sporadically by burros and is less damaged."

A review of other investigations on burro impact on vegetational communities shows that "burros are versatile foragers having relatively unspecialized food habits... although burros may prefer grasses and forbs to browse, the species of plants in an area will force them to be predominantly browsers."

Douglas, Charles L., and Christopher Norment. 1976. Movements of burros in Death Valley: the Wildrose-Emigrant area. Contribution number CPSU/UNLV 006/07. National Park Service, Cooperative Park Service Resources Studies Unit, University of Nevada-Las Vegas. 38 pp.

ABSTRACT: "Population figures obtained during the initial phase of the investigation indicate a downward trend in the burro population of Wildrose Canyon and vicinity since Moehlman's censuses in 1972.

Male/female ratios observed by Moehlman were almost balanced (0.505/0.495); our data indicate an average ratio of 0.646/0.354. Selective trapping and removal is thought to account for this change. Female/foal ratios averaged 58% for all observations.

Movements of burros in Wildrose Canyon and vicinity are discussed. Data are presented on numbers of animals using various parts of the range, by month. Movements of burros to various elevations were analyzed through time. Our data are similar to those of Moehlman, but differed in that we found... up to 27% of the burros at elevations below 3500 feet during autumn and early winter. Moehlman does not mention movements of burros to lower elevations.

Our data and those of Moehlman agree on seasonal distribution of burros in miles from the nearest water source, with the percentage of animals observed at distances greater than 2 miles from water increasing with the progression from summer to winter. Large movements away from water occurred from September through December.

Our preliminary data indicate generally larger home ranges for both males and females than those reported by Moehlman. Home ranges of females varied from 2.37 to 31.74 miles^2; males occupied areas of 7.91 to 35.37 miles^2. Methods of calculating home ranges are discussed.

A hypothesis is proposed that animals move into and out of areas in response to the quality and quantity of available browse. The ability of burros to respond to vegetational changes is moderated by their varying seasonal dependence upon water. Vegetational changes observed in Death Valley are discussed in relation to observed movements of burros.

The quantity and quality of important browse species are being studied by several methods. Vegetational transects and quadrats are being utilized to determine annual biomass production and utilization. Energy content and nutrient content of browse species also are being determined.

The impact of burros on small mammal populations is being investigated by means of 2 large trapping grids in which mammals are trapped, marked, and released. One grid is in Wildrose Canyon; the other is in the Daylight Pass area, in similar habitat. These studies will be reported upon at a later time."

Dunn, William C. 1984. Ecological relationships between desert bighorn and feral burros in Death Valley National Monument, California. Contribution number CPSU/UNLV 006/32. (also M.S. thesis, University of Nevada-Las Vegas). National Park Service, Cooperative Park Resources Studies Unit, University of Nevada-Las Vegas. 144 pp.

ABSTRACT: "Distribution, habitat partitioning and population status of desert bighorn and feral burros in the Cottonwood Mountains of Death Valley were studied from 1980-1982. Ewe groups were found mostly on the precipitous western escarpment of the study area, whereas rams were found throughout most of the study area. During winter, most observations of bighorns were at lower elevations.

Burros were found in rolling terrain of the southern part or in a flat basin on the eastern part of the study area. During winter, movement to lower valleys occurred following rainfall.

Bighorn were observed most frequently in the shadscale vegetation zone, on westerly aspects, at elevations between 5200 and 6500 feet, and on steep slopes (>38%). Burros were observed most frequently in the shadscale vegetation zone, on southerly and easterly aspects, at elevations of 7100-7500 feet, and on gentle slopes (<31%).

Ewe groups used Quartz Spring, a spring that was inaccessible to burros, significantly ($p<0.001$) more than springs used by burros. Fifty-five percent of spring use by rams occurred at Yashiro Spring, which also was heavily used by burros.

Reproduction appears to be adequate to maintain a stable bighorn population of 60-70 animals. However, the population may be in danger of decline because there are too few breeding adults to limit inbreeding to acceptable levels (<1% per generation). The burro population has increased by 16% per year and is believed to be near, or at, carrying capacity.

The presence of burros at certain springs during summer apparently has limited use of springs and surrounding habitat by ewe groups. Continued increase in the burro population may serve to further restrict range use by ewes and contribute to a decline in the bighorn population."

Dunn, William C., and Charles L. Douglas. 1982. Interactions between desert bighorn sheep and feral burros at spring areas in Death Valley. Desert Bighorn Council Transactions 26:87-96.

ABSTRACT: "Use of springs by desert bighorn sheep and feral burros was examined as part of a study on resource partitioning between these species. Spring use by ewe groups was almost entirely restricted to a spring not used by burros while ram group use was not affected by the presence of burros. The number of burros present affected sheep use of springs, although the impact varied with different intensities of burro use. Evidence also suggests that temporal shifts in drinking times of bighorn may occur at springs used by burros. The potential adverse impact of limiting use of springs by ewe groups are discussed."

Eberhardt, L. L., A.K. Majorowicz, and J.A. Wilcox. 1982. Apparent rates of increase for two feral horse herds. J. Wildlife Management 46(2):367-374.

ABSTRACT: "Rates of increase for 2 Oregon feral horse (*Equus caballus*) herds were estimated from direct aerial counts to be about 20% per year. These rates can be achieved only if survival rates are high, and reproduction exceeds that normally expected from horses. A population dynamics model suggests adult survival to be the key parameter in determining rates of increase, and there is some direct evidence of high adult survival rates. Management implications are discussed."

Elliot, Nelson. 1959. Effects of wild burros on range conditions. Desert Bighorn Council Transactions 3:9-10.

ABSTRACT: General anecdotal discussion of the burro's effect on water, soil and vegetation.

Engel, R. E., S. Cartwright, and F. A. Spurell. 1964. Classification of circulating leukocytes in the normal Mexican burro. American Journal of Veterinary Research 27:1478-1484.

Farrell, Joel E. 1973. Behavioral patterns of feral burros as influenced by seasonal changes in western Arizona. M.S. thesis, Arizona State University. 34 pp.

ABSTRACT: "This study of utilization of waterholes and effects on desert environments by feral burros was conducted in the west-central regions of Arizona. Investigations began in April of 1972 and were concluded in March of 1973. A total of 4 waterholes, 2 man-made, the others natural, were used for investigative purposes. Bulk densities of soil, forage analysis of browse plants, and surveys of vegetational damage provided information on the impact of burros on desert environments. Daily observations at waterholes provided information on numbers, time, and seasonal utilization.

The pattern of daily use of waterholes by burros in this study varied with season... [In general] heaviest use was from just after sunset until about midnight. From midnight until 1 hour before dawn few burros visited the waterholes. During the last hours of darkness, use dropped to zero and remained there until dusk. During the hot dry period preceding summer rains the burros arrived [earlier and stayed later; during the winter the opposite occurred.]

Damage to [soils and] surface terrain near waterholes and along trails was minimal. Although there was only slight variation in bulk densities between disturbed and undisturbed sites... excessive burro concentrations inhibited plant growth and accelerated erosion in certain areas. Compaction and crusting of [the sandy loam soils near waterholes] were apparent [and inhibited emergence of some annual seedlings such as *Plantago*, *Amsinckia*, and *Erodium*]. Contour-trailing was evident but was not a serious problem at the waterholes.

Some of the browse plants used by the burros were damaged from over-utilization along trails and near trails where animals tended to concentrate. [*Encelia*, *Ephedra*, graythorn, *Tamarix*, and squaw-bush were damaged, while *Ambrosia*, cholla, *Larrea*, *Prosopis*, and *Cereus giganteus* (saguaro) were not]. Palo verde suffered the greatest damage. It was common practice [for burros] browsing [palo verde to] break off branches 0.5 to 2.5 inches in diameter... After chewing on the [basal portion] of the branch for a short period they would drop the remaining portion and disregard it. Forage analysis did show that palo verde twigs and bark have a relatively high percentage of digestible protein and total digestible nutrients [and also high concentrations of phosphorus. The percentage of protein and digestible protein in squaw-bush was also relatively high compared to *Ephedra*, graythorn, *Fouquieria* (ocotillo), and *Tamarix* which were also analyzed].

Contamination of waterholes was not evident at any of the waterholes in this study. Holes dug by burros in the sand at waterholes provided water for other wildlife [deer, coyotes, and birds] as well as burros.

It is possible that burro watering and feeding activities during the evening hours may prohibit wildlife and livestock from using these areas. Mule deer in this region normally go to water from dusk until mid-morning [yet in this study come to water from dawn to mid-morning.] Apparently the deer have altered their normal watering patterns to avoid peak periods of [burro] activity [at the springs]."

Ferris, Roscoe E. 1972. 1971 wild horse and burro act (Public Law 92-195). Desert Bighorn Council Transactions 16:9-13.

ABSTRACT: "A new Federal law was passed on 15 December 1971 which provides for protection, management and control of wild free-roaming horses and burros on public lands administered by the Bureau of Land Management and the Forest Service. Implementation of the act will have an impact upon the desert bighorn sheep. The direction and the extent of this impact will be dependent upon the regulations, policies, and guidelines developed to implement the act and the final interpretation of its provisions through administrative and court decisions."

Ferry, P. 1955. Burro or bighorn?. Pacific Discovery 8(6):18-21.

ABSTRACT: "Park rangers say that whenever the burro and the bighorn have overlapped in their range, the bighorn has invariably been crowded out. The bighorn is a super-sensitive creature that must have a completely balanced range; it has neither the burro's stamina nor that animal's ability to adapt itself to a shrinking range and a diminishing water supply. In any contest between the 2, the bighorn must inevitably yield. The burros thrive best from 5,000 to 7,000 feet above the valley floor, the bighorn thrives best from 5,000 feet upward. The

controversy must be resolved soon before the burro and bighorns have a detrimental effect upon the range."

Findley, James S., Arthur H. Harris, Don E. Wilson, and Clyde Jones. Mammals of New Mexico. page 338. University of New Mexico Press. 360 pp.

ABSTRACT: "At one time the wild burro was common in some parts of New Mexico. Some older residents of Corrales, Sandoval County, recall hunting them in the local Rio Grande Valley. A small wild herd still exists in the canyons running from the Jemez into White Rock Canyon of the Rio Grande."

Fish and Wildlife Service. 1989. Feral hoofstock: burro (*Equus asinus*). *in* Wildlife Restraint Handbook. U.S. Fish and Wildlife Service.

ABSTRACT: "Our experience includes both trapped and free-ranging feral burros. We have tried several drugs and drug combinations, but have settled on the combination of 3 mg of M-99 and 200 mg of xylazine as the drugs of choice. The dose will be satisfactory for adult burros (300-350 pound females; 350-400+ pound males).

Drugged burros will frequently not become recumbent; therefore, it is essential to have a rope and enough help so that the animals can be cast. Approach and casting of an ambulatory drugged burro is relatively easy, as the animal's judgment and reaction times are greatly reduced by the drug. Because many of the animals will be ataxic and staggering, the threat of the terrain to the animal's safety should be considered.

Our recommended dose rate for M-99 on burros is higher than that of the manufacturer. American Cyanamid recommends 0.4 mg/45 kg (100 pounds). We prefer the higher rate.

Because M-99 impairs the drugged animal's thermoregulatory system, the body temperature must be carefully monitored. The temperature must not rise more than 10° above normal or in all probability you will be confronted with the problem of how to dispose of a carcass. One other note of caution is that the projectile syringes tend to become embedded in equines. To minimize this risk, use the lowest charge that will propel the dart to the animal."

Fisher, Jack. 1975. Impact of feral asses on community structure in the *Acamptopappus-Grayia* plant community, Panamint Mountains, Death Valley National Monument. Report on file at NPS/DVNM. 20 pp.

ABSTRACT: "In February 1972 the National Park Service set up a [609 m^2] burro exclosure at 1454 m elevation in central Wildrose Canyon, on the west side of the Panamint range. [It] is 2 miles east of Wildrose Spring and is in the upper elevational end of the *Acamptopappus-Grayia* plant community...

In 1972 there was a population of 220 identified asses [using] Wildrose Canyon... All of the perennial species found in the exclosure transect are listed as preferred browse species by feral asses (Moehlman, 1974)...

The most significant differences between 1973 and 1974 average [plant] volumes occurred in *Acamptopappus shockleyi*, *Ambrosia dumosa*, and the perennial grasses *Oryzopsis hymenoides* and *Stipa speciosa*. With *Acamptopappus shockleyi*, the total density outside the exclosure dropped from 263 plants in 1973 to 107 plants in 1974 [i.e. 47% of total to 20%], while the dead shrub density increases from 110 to 250 [plants, i.e. 36% of total to 46%]... *Lycium andersonii* increased from 17% of the total plant volume outside the exclosure in 1973 to 30% in 1974... Outside the exclosure, browsing asses removed the material produced by the most palatable species...

[At 2 miles from Wildrose Spring] we have demonstrated a significant difference within 2 years in shrub volumes of *Acamptopappus shockleyi*, *Coleogne ramosissima*, *Dalea fremontii*, *Grayia spinosa*, and *Ambrosia dumosa*. Moehlman's data (1974) [showing no change on transects from 1 to 10 miles from Wildrose Spring], combined with the data presented here, suggests that there is some considerable and uniform impact by feral asses in this plant community that is not restricted by distance from water.

...[N]either of the perennial grasses [*Oryzopsis* and *Stipa*] are... found outside the exclosure. All annual plants are found in substantially lower numbers outside the exclosure, except for *Eriogonum* spp.

...[In the 1320-1660 m elevation zone of the Panamint Mountains] *Acamptopappus* is 1 of the dominant plants, comprising 24% of the total plant volume and 50% of the total number of perennial plants inside the exclosure. Heavy browsing activity by feral burros is here demonstrated to have an effect on the community structure. As [*Acamptopappus*] is being selectively removed [outside the exclosure], the resources are tied up in community members not preferred as browse by feral asses."

Fletcher, Milford R., and Roland H. Wauer. 1976. Feral burro management at Bandelier National Monument, New Mexico. Desert Bighorn Council Transactions 20:54-55.

ABSTRACT: "Recently completed studies have shown that Bandelier National Monument in north-central New Mexico is showing severe erosion and vegetative changes. Vegetative trend measurements show that more than 50% of the range is in a downward trend. In February 1975, the National Park Service placed a team of marksmen on the monument to reduce the population of feral burros by approximately 1/3. Fifty-two burros were killed. Recent surveys indicated that the population will have resumed its February 1975 level by summer 1976."

Fowler de Neira, Lynn E., and Mark K. Johnson. 1985. Diets of giant tortoises and feral burros on Volcan Alcedo, Galapagos. Journal of Wildlife Management 49(1):165-169.

ABSTRACT: Diets of feral burros, *Equus asinus*, and giant tortoises, *Geochelone elephantopus vanderburghi*, were compared during 1980 on Volcan Alcedo, Isabela Island, Galapagos Archipelago. Feral burros consumed many of the foods used by tortoises. During the wet season [February-April] dietary similarity was 45.4%, but during the dry season [November] dietary similarity increased to 78.4%. These findings were primarily due to common use of grasses and *Sida rhombifolia*. Grasses and *Sida* spp. were important tortoise foods all year. Burros fed primarily on grasses during the warm rainy season, but during the cool dry season they shared *Sida* spp. with tortoises as a primary staple. Both herbivores congregated in watering areas during the dry season. "We can only speculate as to whether or not feral burros are depleting food resources needed for tortoise survival on Volcan Alcedo. During the dry season burros appeared to prefer *Phoradendron henslovii* [a shrubby parasite growing in trees]. The small proportions of this food in fecal samples and the obvious browse line suggest that burros have the capacity to deplete favorite food. Perhaps *Sida* spp., which appear important for tortoise survival, will be depleted in the future. Because both species use many of the same foods and share *Sida* spp. as a staple, the presence of feral burros may jeopardize the continued survival of tortoise populations if the forage supply is depleted."

"Food competition is only 1 possible impact that feral burros exert on Alcedo tortoises. Fowler and Roe (1984) also found that burros trampled 18% of tortoise nests on Alcedo. Burro mortality is higher than has been reported elsewhere, and Fowler (1983) suggested it was caused by lack of free drinking water during the prolonged dry season. In a variety of reports reviewed by Fowler (1983), mortality of adult burros ranged from 1 to 5%, and most adult mortality was caused by humans. Burro populations on Alcedo are not subjected to predators or humans, adult mortality was from 5 to 7%, and 97% of all observed mortality occurred during the latter part of the dry season (Fowler, 1983). A succession of abnormally wet years could reduce burro mortality and allow populations to increase. This might ultimately result in a higher frequency of nest trampling as well as competition for forage. A conservative management strategy might be to remove or significantly reduce feral burro populations on Volcan Alcedo to provide insurance against shortages of forage and increases in the burro population in the future."

Fowler de Neira, Lynn E., and J. H. Roe. 1984. The emergence success of tortoise nests and the effect of feral burros on nest success on Volcan Alcedo, Galapagos. Copeia 1984(3):702-707.

ABSTRACT: "Volcan Alcedo on Isabela Island has a giant tortoise population of 3000-5000 and a feral burro population of 500-700 animals. To investigate the possible impact of burros on nest success, we monitored tortoise nests.

The natural emergence success of *Geochelone elephantopus Vanderburghi* during the 1979/80 nesting season was approximately 65%. Clutch sizes averaged between 11 and 14.5 eggs per nest, incubation periods varied from 90 to 150 days, and 75% of all nests contained 1 or more undeveloped eggs.

Feral burros frequented the 2 main tortoise nesting zones and caused damage to incubating eggs by trampling. Of the 28 nests studied on the south caldera floor, 32.1% were broken into by burros. In the north caldera floor nesting area, 60 nests were monitored; 11.7% were disturbed by burros."

Fowler de Neira, Lynn E. 1983. The population and feeding ecology of tortoises and feral burros in Volcan Alcedo, Galapagos Islands. Ph.D. dissertation, University of Florida, Gainesville. 150 pp.

Freeland, W. J., and David Choquenot. 1990. Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. Ecology 71(2):589-597.

ABSTRACT: "Populations of feral donkeys in northern Australia are limited by density-dependent mortality during the first 6 months of individual's lives. A female's ability to raise her offspring successfully increases with age and is dependent on her maintaining high levels of stored mineral nutrients (calcium, phosphorus, and sodium). A low proportion of offspring was successfully raised in a population at carrying capacity where females had low levels of stored mineral nutrients. Females in a growing population that had been reduced to 45% of carrying capacity had high levels of stored minerals and successfully raised a higher proportion of offspring. Females in the population at carrying capacity ingested a species-poor diet (predominantly a grass, *Sehima nervosa*) containing low levels of nitrogen and mineral nutrients, and high levels of crude fibre. Females in the growing population ingested a more species-rich diet with higher levels of nitrogen and minerals, and less crude fibre. Levels of calcium, phosphorus, and potassium in the faeces of females in the population at carrying capacity were higher than those in the food ingested. The reverse was true for females in the growing population. At the time of sampling (early dry season), 17% of females in the population at carrying capacity and 0% of females in the growing population were eating or had recently eaten clay. Increased salivary secretion and gastrointestinal irritation caused by high-fibre diets (even when lubricated by clay) may be responsible for mineral depletion of females at carrying capacity, and hence population limitation through the inability of females to raise offspring."

Fulwider, D. S. 1965. Bakersfield's boom in burros. Our Public Lands 14(4):14-15.

ABSTRACT: The article concerns the 3000 burros in the Bakersfield district and their impact on the environment: the ever decreasing amount of forage in

the vicinity of waterholes, competition between the burro and bighorn sheep, and competition with domestic livestock. California legislation prohibits killing burros and has established some 2 million acres of public domain land in Saline, Eureka, Panamint, and Armagosa Valleys as a burro sanctuary. Cooperation is needed to properly manage the burro and studies are needed to know how to correctly manage them. (from Zarn et al., 1977).

Gadi, I. K., and O. A. Ryder. 1983. Molecular Cytogenetics of the *Equidae*. Cytogenetics and Cell Genetics 35(1):124-130.

ABSTRACT: "A (G+C)-rich satellite DNA component (p=1.716 g/ml) has been fractionated from the total DNA of the Iranian subspecies of the Asiatic wild ass, *Equus hemionus onager*, by successive dactinomycin-CsCl and netropsin sulfate-CsCL isopycnic gradients. Complementary H3-RNA (CRNA) transcribed from the satellite DNA hybridized predominantly to the centromeric and telomeric constitutive heterochromatic regions of onager chromosomes. These studies have suggested that satellite DNAs with similar sequences are present in the centromeric, as well as telomeric, heterochromatic regions of some onager chromosomes. The centromeric region of the fusion metacentric t(23;24) of the onager is deficient in sequences homologous to the onager 1.716 g/ml satellite DNA, indicating a loss of satellite DNA during fusion or an amplification of the satellite DNA in the centromeric regions of the acrocentric chromosomes 23 and 24 subsequent to fission. Sequences complementary to onager 1.716 g/ml satellite DNA show extensive hybridization to the constitutive heterochromatin of the feral donkey karyotype, consistent with a view of conservation and amplification of similar or identical sequences in the 2 species."

Ginnett, Tim F. 1982. Comparative feeding ecology of feral burros and desert bighorn sheep in Death Valley National Monument. M.S. Thesis, University of Nevada, Las Vegas, NV. 86pp. (see citation below)

Ginnett, Tim F. 1982. Comparative feeding ecology of feral burros and desert bighorn sheep in Death Valley National Monument. Contribution number CPSU/UNLV 006/26. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 86 pp.

ABSTRACT: "Feeding habits of sympatric feral burros and desert bighorn sheep were examined monthly during 1980 in the Cottonwood Mountains of Death Valley National Monument. Analysis of feces indicates that burros and bighorn sheep utilize many of the same forage taxa, resulting in a moderate degree of dietary overlap. Bighorn sheep maintained constant proportions of browse, grasses, and forbs in their diets year-round. Proportions of individual forage species in the diet, however, were subject to wide seasonal variation.

Burros, contrastingly, were found to switch from a predominantly browse diet in winter to a diet consisting mainly of grasses during summer. Forb use remained at a constant low level year-round. Seasonal variations in individual forage species utilization followed the same general trends as the variations in browse, grass, and forb categories. Seasonal food niche breadths were calculated for both species by comparing usage to availability. Burros were found to be relatively generalized feeders during winter, becoming highly selective in spring with the onset of plant growth. Desert bighorn sheep exhibited a similar temporal shift in niche breadth but were less generalistic during winter and less selective feeders during summer. Overall, burros were more generalized foragers than were bighorn sheep. It is postulated that potential for forage competition exists, and that due to their more highly opportunistic pattern of feeding, burros should be expected to outcompete desert bighorn sheep if a competitive situation were to exist."

Ginnett, Tim F. and Charles L. Douglas. 1982. Food habits of feral burros and desert bighorn sheep in Death Valley National Monument. Desert Bighorn Council Transactions 26:81-87.

ABSTRACT: (summary version of CPSU/UNLV Contribution number 006/26 by same author)

Godfrey, E. B. 1979. The economic role of wild and free roaming horses and burros in rangelands in the western United States. Final report submitted to Intermountain Forest and Range Experimental Station. 39 pp.

Golden, F. H., and Robert D. Ohmart. 1976. Summer observations on desert bighorn sheep in the Bill Williams Mountains, Arizona. Desert Bighorn Council Transactions 20:42-45.

ABSTRACT: "Observations were made on summer movements, daily activities, and early breeding season behavior of desert bighorn sheep in the Bill Williams Mountains, Arizona. Bighorns were seen principally on steep slopes of ridges, peaks and mesas, and heavily dissected foothills, but were seen in washes or open flatland on a few occasions. Foraging activities and watering were intermittent as the day progressed. Breeding activity began in early July, exemplified by a fight between 2 rams and a few successful copulations. Interspecific interactions were not observed between bighorn sheep and cattle or sheep and burros, although bighorns were seen in close proximity to both species."

Haley, Thomas J., Frank D. Cartwright, and Daniel G. Brown. 1966. Plasma minerals in normal and neutron irradiated burros. Nature 212(5064):820-821.

ABSTRACT: "Fourteen burros were exposed to neutron irradiation of either the whole body or the torso at various doses from 100 to 440 rads. In animals of which only the torsos were irradiated, significant changes in plasma concentrations occurred in phosphorus, iron and copper. Whole body fast neutron irradiation with doses of 100-440 rads resulted in a significant elevation of the plasma concentrations of magnesium, phosphorus, iron and copper, but not of any of the other elements."

Haley, Thomas J., N. Komesu, and Daniel G. Brown. 1966. Plasma corticosterone levels after fast neutron exposure in burros. Radiation Research 27(4):566-569.

ABSTRACT: "Fast neutron irradiation with dose varying from 100 to 440 rads caused a marked increase in plasma corticosterone levels at 1 hour postirradiation. Whole-body irradiated animals returned to control levels in 24 hours, whereas the body-only irradiated animals showed a secondary significant rise at 48 hours."

Halloran, A. F. 1949. Desert bighorn management. North American Wildlife Conference Transactions 14:527-537.

ABSTRACT: In this report on the Kofa Game Range in Arizona it is mentioned that during the height of the dry season burros were using the best feed and some of the last water on the Range.

Hanley, Thomas A. 1976. Carrying capacity relationships of feral burro habitat in a Sonoran Desert ecosystem. M.S. thesis, Arizona State University. 156 pp.

ABSTRACT: "A study was initiated in February, 1974, in the Lower Colorado Valley to investigate forage production, utilization, and carrying capacity of feral burro habitat. Production of major browse species was measured in exclosures and paired plots by the twig length increment technique. Annual herbaceous vegetation was harvested. Nutritional quality of *Ambrosia dumosa*, *Cercidium microphyllum*, *Lycium andersonii*, and *Plantago insularis* was analyzed in terms of gross energy, crude protein, phosphorus, and beta-carotene content. Browse utilization transects were used to determine seasonal patterns of range utilization. Production, utilization, and nutritional quality measurements were determined quarterly to investigate seasonal variation. Precipitation, temperature, and soil moisture were monitored throughout the year. Perennial vegetation communities were classified and mapped.

Soils in the study area were entisols and aridisols, ranging in texture from sand to sandy loam. Precipitation in 1975 totaled 70 mm. Winter precipitation of 31 mm resulted in *Plantago insularis* production of 62 kg/ha (dry weight) in 1975. High variances complicated analysis of shrub production measurements.

Nutritional quality generally paralleled changes in plant phenology. [Beta-carotene appears to be useful as an indicator of general nutritional quality. Although nutrient content is probably not a limiting factor for feral burro populations, it does have a bearing on the amount of forage that necessarily will be consumed.] Browse utilization transects demonstrated a utilization gradient ranging from heavy to light with increasing distance from the Colorado River. Overgrazing [of the Cercidium-Larrea community] occurred near the Colorado River but decreased to light or moderate use [in the Cercidium-Ambrosia community which occurs] at distances greater than 2.5 km from water. [The vegetation community map suggests that the utilization pressure gradient was responsible for the change in community composition with distance from the river.] Overgrazing resulted in a decrease in canopy cover of *Ambrosia dumosa* from about 2.26 to 0.04% and a decrease in total canopy cover for all species from 8.64 to 2.80%. No plant species appear to act as increasers or invaders under heavy burro utilization pressure in the study area. A simulation model [representing the interrelationships between various measurements of shrub, browse tree, and nonpalatable species (represented by *Ambrosia dumosa*, *Cercidium microphyllum* and *Larrea tridentata*, respectively), precipitation, and burro density] is presented to aid in understanding feral burro impact on similar ranges. Importance of [the temporal and spatial variance of] precipitation patterns to carrying capacity relationships is emphasized.

[Because it is difficult to accurately measure net primary production of hot desert shrub species yet relatively easy to quantify burro impact on vegetation, it may be more practical to assess carrying capacity on the basis of the latter.] It is suggested that future investigations concentrate on identifying patterns and stages of feral burro impact, and that management considerations be based on acceptable levels of impact."

Hanley, Thomas A., and Ward W. Brady. 1977. Feral burro impact on a Sonoran Desert range. Journal of Range Management 30(5):374-377.

ABSTRACT: "Impact of feral burros on native desert vegetation was studied in the Havasu Resource Area, Lower Colorado River Valley, California-Arizona. Browse utilization ranged from heavy to light with increasing distance from the Colorado River. Over-grazing occurred near the Colorado River but decreased to light or moderate use at distances greater than 2.5 km from water. Over-grazing decreased the canopy cover of *Ambrosia dumosa* from about 2.26% to 0.04%, and decreased total canopy cover for all species from 8.64% to 2.80%. No plant species appear to act as increasers or invaders under grazing pressure by burros on the study area."

Hanley, Thomas A., and Ward W. Brady. 1977. Seasonal fluctuations in nutrient content of feral burro forages, lower Colorado River valley, Arizona. Journal of Range Management 30(5):370-373.

ABSTRACT: "Nutrient contents of wooly Indianwheat [*Plantago* spp.], white bursage [*Ambrosia dumosa*], desert-thorn [*Lycium* spp.], and foothills palo verde were determined seasonally during 1974 and 1975 in the Havasu Resource Area, California-Arizona. Gross energy content showed the least seasonal variation. Crude protein, phosphorus, and β-carotene contents increased during the pulse of growth produced by winter precipitation, then slowly declined. Although the forage species analyzed appeared to be deficient in phosphorus, feral burros in the study area appear to be in excellent health."

Hansen, Charles G. 1973. Evaluation of burro activity in Death Valley National Monument. Report on file at NPS/DVNM. National Park Service, Death Valley National Monument. 43 pp.

Hansen, Charles G. 1971. Burro use of the Wildrose-Nemo area of Death Valley National Monument, California. Report on file at NPS/DVNM dated 1 December 1971. 10 pp.

Hansen, Charles G. 1969. Report on burro numbers in Death Valley National Monument. Report on file at NPS/DVNM dated 4 April 1969. 8 pp.

Hansen, Charles G. 1968. Burro damage to the ecosystem in Death Valley National Monument. Report on file at NPS/DVNM dated 5 December 1968. 3 pp.

Hansen, R. M., and P. S. Martin. 1973. Ungulate diets in the lower Grand Canyon. Journal of Range Management 26(5):380-381.

ABSTRACT: "Plant fragments were identified and quantified by a microscopic examination of the dung of the burro, cattle, and bighorn in the west end of the Grand Canyon, Arizona. Genera of plants common to the diets of all 3 ungulates were: *Sphaeralcea*, *Bromus*, *Tridens*, *Muhlenbergia*, *Acacia*, *Ephedra*, *Opuntia*, and *Tidestromia*. Wherever free ranging large herbivores occur, as in the Lake Mead National Recreation Area, it is possible to study their diets by analysis of their dung... as the percentage of relative density of plant fragments discerned... is considered to be similar to the percentage of dry weights for the ingested plants...

Burros and bighorns occurred on opposite sides of the Colorado River where we obtained the samples; but since most of the principal plants in both ungulates' diets were eaten by both, intense food competition could possibly develop wherever they were forced to live together...

[The March burro diet consisted of 44% *Bromus rubens*, 15% *Muhlenbergia porteri*, 11% *Agropyron* spp., 5% *Plantago insularis*, 5% *Tridens* spp., 4% *Aristida wrightii*, 4% *Oenothera* (?), and smaller amounts of numerous other species. It] reflects, in part, the availability of green, growing plants. *Bromus*,

Muhlenbergia, and *Agropyron* were in green growth stages at the time that the sample was obtained, and as soon as these plants reach maturity we would expect them to become of minor importance in the diet of the burro..."

The annual burro diet consisted of 25% *Muhlenbergia porteri*, 15% *Aristida wrightii*, 14% *Tridens* spp., 9% *Tamarisk pentandra*, 8% *Phragmites communis*, 7% *Bromus rubens*, 5% *Opuntia* spp., 5% *Nolina* (?), and smaller amounts of numerous other species. Overall, the annual burro diet contained 68% grasses, 9% forbs, and 23% browse.

Hoffman, R. 1983. Social organization of several feral horse and feral ass populations in central Australia. Zeitschrift fur Saugetierkunde 48:124-126.

ABSTRACT: "The studied animals were descendants of livestock which had become feral at least 40-60 years ago, and had not been hunted for the last 20 years. The adjacent, but not overlapping homeranges of the different populations centered around artificial waterholes or stretched along dry "river" beds with several tiny waterholes. The distance which the animals covered on their daily migration to waterholes varied between 5 and 10 km...

The total population size of the asses was N=60, their sex ratio was 1:1. In general, the asses showed a "loose" social organization similar to other feral ass populations. Mare and foal units were the smallest group types, sometimes accompanied by other mares, yearlings and stallions. Stallions were not territorial. Mares in heat avoided other mare groups and were followed by all adult and subadult stallions of the population, which frequently fought over breeding access to the mare..."

Jacot, Francis Jake. 1973. Burro management and the National Park Service. Desert Bighorn Council Transactions 17:98-100.

ABSTRACT: "The basic policy of the National Park System is that "Non-native species of plants and animals will be eliminated where it is possible to do so by approved methods which will preserve wilderness qualities" in natural and historic parks. "...control of exotic species will be undertaken only when they are undesirable in terms of public health, recreational uses and enjoyment, or when their presence threatens significant scientific features or the existence of important native species." Thus, policy requires the elimination of free-roaming burros and horses from natural and historical parks, and possible control of these animals in recreational parks."

Jenkins, Stephen H. 1989. Comments on an inappropriate population model for feral burros. Journal of Mammalogy 70(3):667-670.

ABSTRACT: "The general lesson of this reanalysis of Perryman and Mulchlinski's (1987) data is that relatively little can be learned about potential

population-growth rates from age-distribution data alone, or even age distribution data combined with a fecundity schedule for a population... It is unfortunate that such [age distribution] data are so limited because they are relatively easy to obtain, particularly by wildlife-management agencies in the process of monitoring harvests or controlling pest species. If a single survivorship probability is known, however, together with a standing-age distribution that can be assumed to be stable, then equation (1) can be used to estimate population growth rate."

Johnson, Robert A., Steven W. Carothers, and Thomas J. McGill. 1987. Demography of feral burros, *Equus asinus*, in the Mohave Desert. Journal of Wildlife Management 51(4):916-920.

ABSTRACT: "Age, sex, and body and reproductive condition of 631 burros, and sex of 79 burro fetuses were determined from the Mohave Desert, California. The age distribution was skewed to young age classes in both sexes. Twelve individuals lived >10.5 years, and males lived longer than females. The postnatal sex ratio (61 Male:100 Female) was skewed, whereas the prenatal sex ratio (68.1 Male:100 Female) did not differ significantly (P>0.05) from parity. Males had better body condition than females. Poor female body condition was associated with costs of pregnancy and/or lactation. Females of reproductive age (>1.5 years) had a 61.9% pregnancy rate and a 35.2% lactation rate. Sixty percent of lactating females were also pregnant, which indicated that burros can give birth in consecutive years."

Jones, Fred L. 1980. Competition: burros. pages 202-207. *in* Monson, Gale, and Sumner, Lowell, editors. The desert bighorn: its life history, ecology & management. University of Arizona Press. 370 pp.

ABSTRACT: A brief review of his own and others research on and anecdotal observations of the interaction between desert bighorns and feral burros in terms of food, water, and social interactions.

In the Panamint Mountains in 1955 "Burros have taken all of this over and are ruining the range. The use of *Larrea* at the lower elevations and the naturally poor quality of feed below 6500 feet means there is a naturally poor range that has been severely overbrowsed... *Franseria* is nearly a remnant plant--being eaten out. Some noticeable use of *Larrea*, the first I have seen. Some very dry *Ephedra*... Plant growth extremely scant... just like the floor of Panamint Valley... at the higher elevations burros have nearly killed out grasses and such forbs as *Phlox* and are using bush lupine heavily--uprooting much of it. The vegetation is being changed to practically pure sagebrush and *Haplopappus* with some gray horsebrush and bush lupine."

"Where burro and bighorn use the same water holes, direct competition obviously exists. It may be detrimental to the bighorn when the supply is limited. Burros tend to congregate at or near water, particularly [from dusk to

dawn; bighorns are basically diurnal water users]. Being large, burros use more water than bighorn and are more dependent on it."

Concerning the fouling of springs, the author tells of an instance when, upon observing a spring, his research associate determined it to be polluted by burros and not used by bighorn. The surrounding area, however, had extensive bighorn sign that had simply been blotted out near the water by the burros.

"In summary, although burro and bighorn are often compatible, especially in some places like Death Valley and in some seasons of plenty of food and water, the consensus nevertheless is that bighorn-burro competition can on occasion be severe, generally to the detriment of the bighorn."

Jordan, James W., George A. Ruffner, Steven W. Carothers, and Arthur M. Phillips III. 1979. Summer diets of feral burros (*Equus asinus*) in Grand Canyon National Park, Arizona. pages 15-22. *in* Denniston, R. H., editor. Symposium on the ecology and behavior of wild and feral equids. University of Wyoming. 236 pp.

ABSTRACT: "Summer diets of 63 burros (*Equus asinus*) from 2 study areas in Grand Canyon were analyzed with respect to the availability of forage resources. Bush muhly (*Muhlenbergia porteri*), big galleta (*Hilaria rigida*), and three-awn (*Aristida* spp.) comprised 43.9% of the diet of burros inhabiting the Bedrock Canyon study area, while mesquite (*Prosopis juliflora*), six-weeks fescue (*Festuca octoflora*), and catclaw (*Acacia greggii*) made up 52.0% of the diet of burros occupying the Lower Canyon study area. Several heavily utilized plant species, particularly perennial grasses, were relatively rare within the study areas. Burros are able to forage on a wide variety of plant species, but are highly selective when preferred foods are available."

Kingsley, Kenneth J. 1981. Mammals of the Grapevine Mountains, Death Valley National Monument. M.S. Thesis, University of Nevada, Las Vegas, NV. 190pp. (see following reference)

Kingsley, Kenneth J. 1981. Mammals of the Grapevine Mountains, Death Valley National Monument. Contribution number CPSU/UNLV 018/05. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 190 pp.

ABSTRACT: "The Grapevine Mountains form the northeastern boundary of Death Valley and range in elevation from below sea level to 8738 feet. They include 6 major biotic communities in approximately 400 mi^2. Mammal distribution was determined by various methods including small mammal trapping, bat netting, ground and aerial survey for large mammals, time-lapse movie filming at water sources, and examination of records of other observers.

Forty-one species were recorded. More that 400 specimens of small mammals were collected. Detailed species accounts were prepared for each species.

The mammalian fauna of the Grapevine Mountains is typical of mountain ranges in the southern Great Basin. No unexpected species were encountered. Species distribution was as expected, based on previous studies. Populations of most rodent species were low during the period of study, probably as a result of low rainfall during several preceding years."

Klingel, Hans. 1979. A comparison of the social organization of the equids. pages 23-30. *in* Denniston, R. H., editor. Symposium on the ecology and behavior of wild and feral equids. University of Wyoming. 236 pp.

ABSTRACT: "The 6 species of extant equids are remarkably uniform with respect to size, morphology, physiology, general life habits, and behavior. One of the most striking differences concerns social organization, and 2 distinct types of mating systems have evolved.

Plains zebra, mountain zebra, and horse live in family groups consisting of 1 stallion, 1 to several mares and their young. These groups are stable with respect to the adult members who are not closely related to each other. Adolescent mares are abducted by other stallions who thereby start a family or increase the number of their mares. Young age classes live in bachelor groups which are to some extent stable.

The social units live in large overlapping home ranges whose sizes depend on ecological factors. There is no competition whatsoever for space, i.e., these species are non-territorial. Mating rights are established by the stallions through their presence with the mares, and their position is respected by other stallions. This system breaks down when adolescent mares display the estrous stance, which attracts stallions from the vicinity of the group.

In Grevy's zebra, African wild ass, and Asiatic wild ass, some of the adult stallions are territorial and inside their territories dominant over, and at the same time, tolerant towards all their conspecifics. Mares, foals, and non-territorial stallions live in unstable groups of varying size and composition, and the only permanently stable units are those of mares and their young. In Grevy's zebra territories are kept, by the same stallions and in the same places, for years, even though they may be abandoned for some time during the height of a dry season.

With the exception of a few small populations, equids live in areas of seasonal or irregular rainfall patterns and they are accordingly forced to migrate. The non-territorial species move always as complete reproductive units, and they therefore seem to be sociologically well adapted to regular as well as irregular changes of the environment. In contrast to this, the territorial species should be better suited to constant or regularly changing conditions, especially since the strong attachment of the stallions to their territories (as in Grevy's zebra) leads to a segregation of the sexes.

The actual distribution of the various species (with 1 exception: mountain zebra) is not in accordance with the sociological features, and other adaptations

are considered to be decisive for the performance under extreme conditions. Both types of social organization have evolved from the certainly more primitive system of Eohippus. The various types of social organization of bovids may serve as a model."

Klingel, Hans. 1977. Observations on social organization and behaviour of African and Asiatic wild asses (*Equus africanus* and *E. hemionus*). Zeitschrift fur Tierpsychologie 44:323-331.

ABSTRACT: African and Asiatic Wild Asses (*Equus africanus* and *E. hemionus*) were observed, respectively, in the Danakil Desert of Ethiopia and the Karakum Desert of Turkmenistan. "Members of both species were found solitarily and in smaller or larger groups or herds. Solitary animals were almost exclusively adult stallions. The groups consisted of stallions and/or mares, with or without foals.

The smaller groups were stallion or mare groups or groups of 1 stallion with a few mares, whereas the larger ones usually contained more than 1 stallion. The largest stallion groups consisted of 10 in *E. africanus* and 11 in *E. hemionus*. The largest *E. africanus* herds numbered 43 and 49 head and contained [11 stallions each]; those of *E. hemionus* numbered 60, 107, and 135 head, respectively, of which the one of 107 consisted of 1 male, 77 females, and 36 foals, whereas the other 2 contained a higher proportion of adult stallions...

No permanent associations of any 2 or more adults seem to exist in either species... Individuals or small groups were recorded joining others and/or separating from them in an irregular pattern. Young and subadults up to the age of 2-3 years were regularly seen in company of an adult mare who could be considered to be the mother, and such associations are obviously the only lasting ones.

In *E. africanus*, the 2 large herds [formed in the mornings] in a limited area of good grazing... In the evenings the herds broke up.

In both species a proportion of the adult males were found solitarily, and some *E. africanus* males could be recorded as resident in a particular area for several weeks. These stallions are considered territorial... In all encounters it was quite obvious that [the territorial stallions were] the dominant individuals in the area and that [their] status was not challenged by the trespassers, who were, however, tolerated within the territory.

The sizes of the territories could only be assessed from the distances between territorial stallions... Distances between [*E. africanus*] stallions ranged from 4 to 7 km, mean 5.5 km (n=7). Territory sizes are calculated accordingly from 12 to 40 km^2, mean 23 km^2. [For *E. hemionus*] only 3 distances of about 5, 7 and 10 km were taken, which can only be used for a very rough estimate of the territory sizes which are in the same order as, or even larger than those of *E. africanus*.

The territories are advertised through the presence and behaviour of the territorial individual... The dung piles which are found in an irregular pattern

inside the territories have no apparent effect on trespassers. They seem, however, to serve an important function for the orientation of the territorial individual, at least in *E. africanus*.

The territorial stallions are dominant over all of their conspecifics, and they demonstrate their dominance by their behaviour. There was no indication of the existence of a dominance order among the adults; they all seemed to be of equal rank, but dominant with respect to the young. No indication of a regular leadership was observed, and any adult, male or female, could initiate a migration and be the leader for some time. No antagonism was observed when another individual took the lead.

The social organization of *E. africanus* and *E. hemionus* is... characterized by the very large territories and the conditional defense by the territorial individual... no biological explanation can be given for [the large territories]. Since the territories function as mating areas preventing disturbance from other stallions, it can be speculated that larger territories are safer than smaller ones as this reduces the chance that the stallion, during precopulatory driving, chases the mare out of his territory. However, the safety factor seems to be excessive, and only a small portion of the territory is actually used for the purpose.

[Of the 6 species of extant equids, *E. africanus*, *E. hemionus*, and *E. grevyi* are territorial, while *E. quagga*, *E. zebra*, and *E. przewalskii* are non-territorial]. In comparison with the bovids, it is difficult to see the adaptiveness of territoriality in the desert and semi-desert habitats, especially as there seems to be a strong attachment of the stallions to their territories in at least 2 of the 3 [territorial species] (*E. grevyi* and *E. africanus*). The non-territoriality of *E. quagga*, *E. zebra*, and *E. przewalskii* would seem to be far better adapted to extreme environments. In fact only *E. zebra*, of this sociotype, does (or did) succeed in desert habitats. On the other hand, those species that seem sociologically adapted to either constant or regularly changing habits, i.e. the territorial ones, are obviously not able to compete successfully with their cogenerics, and possibly other ungulates, but are restricted to habitats which are or were only marginal to *E. quagga* and *E. przewalskii*."

Klingel, Hans. 1974. A comparison of the social behaviour of the *Equidae*. pages 124-132. *in* Geist, V., Walther, F., editors. The behaviour of ungulates and its relation to management. International Union for Conservation of Nature and Natural Resources. 941 pp.

ABSTRACT: "In the *Equidae* 2 types of social organization have evolved. The plains zebra (*Equus quagga*), mountain zebra (*E. zebra*), horse (*E. przewalskii*) and possibly also the Asiatic wild ass (*E. hemionus*) live in coherent family groups, consisting of 1 stallion, 1 to several mares and their young. Surplus stallions are found in stallion groups. The young leave their original families in a set pattern. No territories are established in these species.

In the Grevy zebra (*E. grevyi*) and the wild ass (*E. africanus*) the stallions keep large territories which they, however, only defend under certain conditions, i.e. when an oestrous mare is near the boundary.

Apart from the mare-foal relationships there are no personal bonds between any 2 or more individuals.

Most of the equine populations live in areas with marked seasons. In the non-territorial species the reproductive groups migrate as units. In the territorial species the sexes segregate for part of the year, a feature which will certainly influence the reproductive rate, especially in areas with irregular rainfall."

Knapka, J. J., K. M. Barth, and Daniel G. Brown. 1968. Late effects of whole-body irradiation on nutrient digestibility by the burro. Journal of Animal Science 27(3):656-659.

ABSTRACT: "Four digestion trials were conducted with 21 nonirradiated and 11 irradiated mature burros. The 1st trial was designed to determine the effect of age on nutrient digestion and results indicated that 3-year difference in age did not significantly affect digestion of organic matter, crude protein, ether extract, crude fiber or nitrogen-free extract.

The results of the 3 trials that compared digestion of irradiated and nonirradiated burros indicated that there were no significant differences in the digestion of proximate nutrients as a result of irradiation. However, irradiated burros consistently digested less crude fiber than nonirradiated burros."

Knapka, J. J., Daniel G. Brown, and K. M. Barth. 1968. Food intake and growth of burro foals after 250 roentgens of cobalt-60 whole-body gamma irradiation. Radiation Research 36(1):158-165.

ABSTRACT: "Possible late effects of sublethal levels of whole-body gamma irradiation on growth of burro foals were studied. Two trials included 31 nonirradiated foals and 32 foals that were exposed to 250 R of ^{60}Co gamma radiation during their fourth month of life. The foals were weaned 90 days postirradiation and allotted into treatment groups based on radiation treatment, weight, sex, and size. Each group was then randomly selected to be fed a ration containing either 9%, or 14%, or 18% crude protein in the first trial and either 9% or 18% in the second trial. The length of these trials was 364 days. Criteria studied to evaluate the treatments included feed consumption, body weight gains, feed efficiency, increase in height, and increase in heart girth. Least-squares analysis of these data indicated that radiation had no significant effect on any of the traits tested. There was a consistent though nonsignificant trend for irradiated foals to be less efficient in feed utilization than their nonirradiated counterparts."

Koehler, David A. 1974. The ecological impact of feral burros on Bandelier National Monument. M.S. thesis, University of New Mexico. 78 pp.

ABSTRACT: "During the period June, 1973 to May, 1974, studies were undertaken to determine the impact of a feral burro herd upon vegetation, soils, wildlife, and archeological sites within the Bandelier National Monument near Los Alamos, New Mexico.

Vegetation types within the project area were defined and delineated on aerial photos for developing a vegetational map of the Monument. Concurrently, paced transects and ocular estimates were used to establish range and soil conditions and trend for each circumscribed type. Acreages of each type were tabulated as categorized by condition and trend. The sensitivity of plant species to grazing pressure was determined by establishing the order of disappearance of these species within their normal plant association.

Censusing techniques revealed a resident burro population of 107-120 animals. This estimate was obtained by a track count and sighting method. Observations of burro behavioral characteristics were conducted to facilitate future control or management programs. Ranges of the herd within the Monument were established for both the summer and winter seasons.

Within the study area, no excellent range conditions were found. About 4,397 acres were found to be in good range condition, 6,282 acres in fair condition, 5,486 acres in poor condition, and 4,184 acres in very poor condition. Significantly, all of the 9,671 acres found to be in poor or very poor condition were south and west of the rim of Frijoles canyon, which apparently provides an effective barrier to burro migration. Trend measurements indicated the same contrast. Above the south rim of Frijoles, 4,152 acres exhibited... improving condition, 69 acres were in stable condition, and no sites showed a downward trend. Of the area below Frijoles canyon, 8,353 acres showed a deteriorating trend, 1,850 acres were stable, and 5,968 acres was in upward trend.

Damage [due to foraging by burros] was most pronounced in the pinyon-juniper and juniper plant associations which comprise the burros' preferred habitat. Forage species have been almost eliminated... [and] grasses persist only under the physical protection afforded by opuntia or dense brush. Damage by burros was found to be compounded by trespass cattle - as many as 30 cattle were illicitly utilizing the Monument in summer months with the apparent knowledge of their owners. The impacted area exhibits drastically reduced productivity, substantial soil loss, and widespread invasion of undesirable species. [In their present condition, the annual forage production of the preferred plant associations is about 50 pounds/acre.] Burros individually consume 11 pounds of forage each day or 4,015 pounds annually. The annual forage requirement for 110 burros is over 440,000 pounds. Add to this the forage consumption of variable numbers of trespass cattle, each cow consuming 30 pounds per day. Common range management practices dictate that less than 45% of annual production be utilized in order to obtain improved or stable forage production. In the juniper and pinyon-juniper associations and in certain types of ponderosa pine

As forage plants disappear from the vegetative community, an invasion by annual and perennial weeds has occurred. In many instances, soil loss following the removal of forage cover has prevented even the establishment of weedy species. The more desirable browse plants such as *Cercocarpus montanus* are often severely hedged... In certain locales, even the bark on the base of large cholla plants had been chewed off from ground level to approximately 3 feet above ground. Yuccas have... been destroyed by browsing burros... Along trails [in good condition range areas] frequently travelled by burros there are corridors of overgrazing... 50 to 100 feet wide.

Soil conditions were found to be well correlated with vegetative conditions... [Those] within the pinyon-juniper and juniper associations are the most severely damaged. Forage cover is usually sparse and in some cases virtually non-existent. Grass plants are often so badly pedestalled that they could easily be uprooted by grazing. Small shrubs are found growing on hummocks 8-10 inches above current ground level... Burro trails on slightly sloping ground have become gullies several feet deep... On level areas in the Monument's southern half, trampling and compaction resulting from an intricate network of burro trails has eliminated a substantial proportion of ground from productivity.

During the summer... small groups comprising 2-6 animals were observed frequently during daylight hours... Two jennies, each with the previous years foal, were the most common aggregation. Dominant males were found to be solitary... [At] the periphery of the burro range, small groups of 4-6 animals consistently comprised of the same individuals were observed over a period of several months. Toward the interior of the range, where numbers were more concentrated, day-to-day aggregations appeared to be random... Shortly after sundown, burros began coming down into the major canyons for water. Large congregations of animals [20-30] frequently remained together for several hours around watering locations.

The winter foraging preferences of mule deer and burros are basically the same, [and they] were seen to be competing directly with burros for diminishing amounts of forage.

It was concluded that the feral burro herd had effectively destroyed the capacity of their preferred habitat to support their current numbers. A program to reduce and control this herd is considered to have urgent priority in order of prevent further resource devastation."

Koehler, J. W. 1960. The California undomesticated burro. Bulletin of the California State Department of Agriculture XLIX(1):1-6.

ABSTRACT: The California burro, *Equus asinus*, originated from the Somali wild ass, *Equus asinus somalicus*. They live from 25 to 40 years and were imported to America in the 16th century. A discussion and map outline the burro populations in California. The author mentions problems of competition between the burro and other animals including domestic livestock for food and water. A history of California legislation concerning the burro is outlined. In 1939 a law was passed prohibiting the capture of an undomesticated burro for

the purpose of using the carcass for animal food. In 1953 an amendment to the 1939 bill was passed which made it unlawful to kill undomesticated burros for any purpose. In 1957 the burro became State property and possession could be had by citizens only for the purpose of domesticating and using them for pets or beasts of burden. A sanctuary was established along with a permit system for those wanting to capture burros. Problems with implementing the legislation are discussed.

Kovach, Steven D. 1987. Feral burro report, 1987. Desert Bighorn Council Transactions 31:35.

ABSTRACT: "[A] review of feral burro management by the U.S. Bureau of Land Management, National Park Service, and the U.S. Navy..."

Kovach, Steven D. 1986. Feral burro report, 1986. Desert Bighorn Council Transactions 30:23.

ABSTRACT: "Management of feral burros by the U.S. Bureau of Land Management, National Park Service, and the U.S. Navy is reviewed."

Kovach, Steven D. 1984. Burro committee report. Desert Bighorn Council Transactions 28:57.

ABSTRACT: "Management of feral burros and horses by the Bureau of Land Management, National Park Service, and the U.S. Navy is reviewed."

Kovach, Steven D. 1982. Report of the feral burro committee. Desert Bighorn Council Transactions 26:101-102.

ABSTRACT: "Activities concerning feral burros by such agencies as the Bureau of Land Management, National Park Service, U.S. Navy, and U.S. Fish and Wildlife Service are reviewed."

Kuhn, U. S. G. III, Roy E. Kyner Jr., and Daniel G. Brown. 1964. Response of burros to mixed neutron and gamma radiation. Radiation Research 23(1):78-93.

ABSTRACT: "Eighty-eight burros (*Equus asinus*) were exposed to prompt neutron and gamma radiations from a nuclear detonation. The median lethal dose was determined to be 374 rads with 95% confidence limits of 336 to 410 rads. Because of the mixed nature of the radiation and the possible significance of dose rate, estimation of an RBE for neutrons is not justified on the basis of the findings. The mid-line dose of gamma rays in an especially

prepared burro cadaver was found to be 70% of the free field dose. A high incidence of remarkable central nervous system symptoms and early mortality was observed. Otherwise, clinical reactions and postmortem findings were similar to those observed in studies with external total-body gamma irradiation (^{60}Co, ^{182}Ta, Zr-^{95}Nb) of the species."

Kuhn, U. S. G. III, and Daniel G. Brown. 1962. Head irradiation of the burro with cobalt-60. Journal of the American Medical Association 180:671-675.

ABSTRACT: "The response of burros to gamma irradiation of the head from ^{60}Co was characterized by the rapid onset of symptoms suggestive of brain damage, hyperglycemia, and early mortality. Death followed respiratory paralysis. Pathological changes in the brain included subarachnoid hemorrhage, perivascular cuffing, extravasation of plasmatic fluid, neuronophagia, and early satellitosis. The relationship of survival time to dose rate is discussed."

Kuprikova, Y. A. 1990. The island population dynamics of feral *Equus asinus*: 1. population structure. Zoologicheskii Zhurnal 69(9):126-137. [in Russian with English summary].

ABSTRACT: "The social organization of the population of individually recognized animals was studied for 5 years. By 1985 there were 83 specimens [on] Ogurchinsky Island with the male to female proportion being 1.2:1. Most stable is a family unit consisting of a female with young of different age which can temporarily expand due to the addition of a younger specimen. Among adult females alliances of a varying permanence may appear. Family units and individual females are united by an adult male to harem groups. One of several adult females mating with the same male for several years constitute a core of the group. Some females leave one harem for another. Some males are united to bachelor groups of a transient composition. Some males prefer a solitary way of life."

Kuprikova, Y. A. 1990. The island population dynamics of feral *Equus asinus*: 2. spatial distribution. Zoologicheskii Zhurnal 69(12):125-131. [in Russian with English summary].

ABSTRACT: "The spatial distribution of the feral *Equus asinus* population which was studied for years on Ogurchinsky Island [is described]. The animals are divided into 4 categories: harem males, single males, bachelors, and females with young. The harem males stay in their own territories. Bachelors move freely around the major part of the island interacting with single and harem males. Females and the young animals in the harem use the territory of their male. The females are indifferent to each other and avoid the bachelor

groupings. The spatial-ethological structure of the feral asses is rather plastic resembling such of the wild African asses."

Leadabrand, Russ. 1957. Burro Sanctuary on the Mojave. Desert Magazine 20(12):5-7.

ABSTRACT: The passage of California State Senate Bills 31 and 32 provides a large burro sanctuary (6,000 mi^2) in Inyo County and extends current protective legislation for the burro. The sanctuary includes almost all of Death Valley National Monument and the State legislation does not affect operation of the feral burro management program within the monument. The protective law makes California the owner of all feral burros in that state. It prohibits killing, wounding, capturing or possession of any undomesticated burro. Those wishing to capture an undomesticated burro for a pet or pack animal can do so by obtaining a permit for the California State Department of Agriculture; 12 permits per year are authorized. The law also allows owners and tenants of land being damaged or destroyed by burros to apply for a permit to kill them. (from Zarn et al., 1977).

Leadabrand, Russ. 1956. Long-eared Problem Child of the Desert. Desert Magazine 19(6):10-12.

ABSTRACT: The article outlines and discusses 2 opposing attitudes concerning burros. One side says that the burro helped make the west what it is today and is entitled to respect and protection. Others hold the view that the burro is reverting to the wild, is taking the forage that properly belongs to the native wildlife of the region. Legislation protecting the burro in California is outlined and a history of how the wild burro became established is given. (from Zarn et al., 1977).

Lee, D. H. K. 1972. Large mammals in the desert. page 123. Yousef, Mohamed K., Horvath, Steven M., and Bullard Robert W., editors. Physiological adaptations: desert and mountain. Academic Press. 258 pp.

ABSTRACT: "The significance of a rising body temperature [in the burro] is somewhat reduced if the most susceptible or most critical internal organs can be spared. A remarkable provision for sparing the brain has been described for the donkey... In these animals, arterial blood brought to the cranium through the internal maxillary artery flows in countercurrent fashion beside cooled venous blood from the extensive nasal passages, in the rete of the cavernous sinus, before it goes to the brain. Evaporative cooling from nasal inspiration is thus directed largely to the benefit of the brain."

Longshore, Kathleen M., and Charles L. Douglas. 1988. Vegetational recovery following burro removal in Death Valley National Monument. Contribution number CPSU/UNLV 035/04. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 36 pp.

ABSTRACT: "The recovery of vegetation has been studied for 3 years in the Panamint Mountains of Death Valley National Monument following removal of more than 6000 feral burros. The purposes of the study were: 1) to establish baseline data on vegetation in Butte Valley and Wildrose Canyon, areas that formerly had heavy and moderate burro densities, 2) to compare plant composition, volume, and density in permanent transects inside and outside exclosures established in Wildrose Canyon (1972) and Butte Valley (1973), and 3) to establish procedures for long-term monitoring of vegetational recovery in Death Valley National Monument.

Eight belt transects, each 50 m x 2 m, were established in Butte Valley in 3 vegetational communities and inside an exclosure. Four transects were established in Wildrose Canyon, 2 within an exclosure and 2 outside it. Data were gathered in late April-early May from 1985 through 1987 to establish the baseline data set.

Earlier studies of burro food habits and browsing impact on the vegetation revealed that burros browsed extensively on shrubs in the Wildrose area, but relied much less on shrubs in Butte Valley. Shrubs comprised an average of 25% of burro diets in Butte Valley. Most of their diet consisted of grasses and forbs, and as a consequence, evidence of browsing on shrubs was greatly reduced from that in Wildrose Canyon.

In Butte Valley, all species of perennial shrub in the transects are known to have been eaten by burros. During all 3 years of data collection, the densities of shrub species were higher outside than inside the exclosure. This is contrary to expectations, and probably reflects micro-habitat differences rather than browsing impact. Over-browsing would be expected to change the composition and diversity, but that was not apparent in this situation. In 1985, the mean volumes of *Ephedra nevadensis*, *Haplopappas cooperi*, and *Hymenoclea salsola* were greater ($P<.05$) inside the exclosure. In 1986, only *Haplopappas cooperi* had a significantly greater volume inside the exclosure. These yearly variations are difficult to assess. Over the 3 years of this study there was a general trend in mean volumes toward equality inside and outside the exclosure. This suggests that burro browsing in the mixed shrub community of Butte Valley had a low level of impact on shrubs and they are recovering rather rapidly. Mean volumes of shrubs were not significantly different inside or outside the exclosure, although individual species varied in volume inside and outside the exclosure.

Perennial grasses in Butte Valley have been grazed extensively. Perennial grasses were present inside but not outside the exclosure in 1985 and 1987. Some grass plants were present in outside transects in 1986, perhaps as a result of increased precipitation. Some burros were still present in Butte Valley in 1986, and may have damaged grasses by grazing or trampling. Grasses comprised, on average, 48% of burro diets in Butte Valley; the exotic red brome

(*Bromus rubens*) was the major species involved. Burros trampling of the soil crust creates favorable sites for establishment of red brome.

Baseline data were established for the creosote bush [*Larrea*] and blackbrush [*Coleogyne*] communities, but there were no exclosures in these communities permitting comparison of vegetation inside and outside.

In Wildrose Canyon burros were reported by earlier investigators to function mainly as browsers. Earlier studies have demonstrated significant impact by burros on forage species, and on small vertebrates. Fisher (1974) [cited in this bibliography] reported lower densities of plants outside the exclosure, and evidence of heavy browsing.

Ten years later, Yancey (1984) [cited in this bibliography] compared total plant volume inside and outside the exclosure and found no significant difference between the 2. She found that the Wildrose exclosure had lower species diversity than other sites in Wildrose Canyon and concluded that the exclosure was not representative of the area.

We found significant differences in species diversity, but no difference in mean volumes of perennial shrubs inside and outside the exclosure in 1986 and 1987 (transects were established in 1986). In both years *Acamptopappas shockleyi* and *Ambrosia dumosa* had greater densities outside the exclosure, whereas *Lycium* had higher densities inside in 1987. Perennial grasses had lower densities outside the exclosure, but there was no difference in mean volumes inside and outside the exclosure. Earlier studies demonstrated heavy grazing impact on perennial grasses in Wildrose Canyon.

Additional transects will be established in Wildrose Canyon in 1988 to sample more representative sites and sites that have had more extensive impact by burros. After establishment of a database for those transects, a long-term monitoring strategy can be developed."

Maloiy, G. M. O. 1973. The effect of dehydration and heat stress on intake and digestion of food in the Somali donkey. Environmental Physiology and Biochemistry 3(1):36-39.

ABSTRACT: "The changes in intestinal digestion of the Somali donkey due to both a simulated desert environment (exposure for 12 hours at 22 °C (dry bulb) and 18 °C (wet bulb), followed by a further 12 hour period of exposure to an ambient temperature of 40 °C (dry bulb) and 24 °C (wet bulb), referred to here as 22-40 °C condition, and to a stress condition consisting of a water restriction up to a 15% level of dehydration (with and without heat load) were investigated. Dehydration at both environmental temperatures (22 °C and 22-40 °C), separately, depressed food intake and increased apparent digestibility of dry matter, but an intermittent heat load as found in the desert environment per se had no effect on either parameter."

Maloiy, G. M. O. 1971. Temperature regulation in the Somali donkey. Comparative Biochemistry and Physiology A 39A(3):403-412.

ABSTRACT: "In controlled laboratory experiments the metabolic rate, body temperature, respiratory, sweat and heart rates were measured in adult donkeys weighing between 125 and 180 kg. At high ambient temperatures (40-50 °C) the sweating rate rose to 145 g H_2O/m^2 per hour and the respiratory rate to approximately 130/minute. In cool conditions (10 °C) the metabolic rate rose to approximately 5 ml oxygen/kg per minute from a value in thermal neutrality (22-32 °C) of 4 ml/kg per minute. Between ambient temperatures of 5 and 50 °C the rectal temperature ranged from 35 to 39 °C."

Maloiy, G. M. O. 1970. Water economy of the Somali donkey. American Journal of Physiology 219(5):1522-1527.

ABSTRACT: "Water balance, food intake, volume, and concentration of urine and changes in body weight were examined in the Somali donkey subjected to heat stress and dehydration. The effects of an ambient temperature of 22 °C or changes between 22 and 40 °C at 12-hour intervals and a level of dehydration causing 15% loss of body weight at each of these temperatures on food intake and digestion were investigated. Dehydration at each environmental temperature depressed food intake and increased apparent digestibility of dry matter, but a periodic heat load without dehydration had no effect on either parameter. The animal's appetite failed altogether when 20-22% of its initial body weight had been lost. Fecal and evaporative routes were the main avenues of water loss in all experimental conditions. Evaporative water loss was reduced by 65 and 52%, respectively, when animals were dehydrated at 22 °C and 22-40 °C. The donkey can survive a loss of water corresponding to 30% of its original body weight even at an ambient temperature of 40 °C, and can drink in 2-5 minutes enough water (24-30 l) to restore its deficit. Even when water was freely available, urine volume was low (0.7-1.2 l/day). The donkey's kidney was not able to excrete a highly concentrated urine. When the donkey was offered various concentrations of NaCl solution as its sole source of drinking water, the maximum level accepted by the animal was 0.75-1.00% NaCl."

Maloiy, G. M. O., and D. H. Boarer. 1971. Response of the Somali donkey to dehydration: hematological changes. American Journal of Physiology 221(1):37-41.

ABSTRACT: "The donkey can tolerate the same degree of water loss from the body (30%) as sheep and camels. A dehydrated donkey can drink, within 2-5 minutes, 20-30 l of water to repair such a deficit. A study was made of the effects of dehydration and rehydration on various blood parameters in 5 donkeys and 3 Zebu steers. Increases in plasma osmolality, Na, Cl, Hb, packed cell volume, red blood cells, and plasma proteins were observed in dehydrated animals. Neither dehydration or rehydration had any observable effect on mean cell Hb. This remained at 22 pg (10-12 g) and 16 pg for the donkey and the Zebu steer, respectively, under all experimental conditions. In the donkey, decreases in mean cell volume and in intracellular and extracellular water were observed. Plasma volume was also reduced from a mean control value of 9.6 to 6.2 l. Most of the blood parameters were restored to their normal values within 24 hours after the animals were rehydrated."

McCool, C. J., C. C. Pollitt, G. R. Fallon, and A. F. Tirmer. 1981. Studies of feral donkeys in the Victoria River-Kimberleys area: observations on behaviour, reproduction, and habitat and some possible control strategies. Australian Veterinary Journal 57:444-449.

ABSTRACT: "A total of 197 [feral] donkeys were shot in the spring when pasture conditions were poor... Males comprised 97, and females the balance. The mean age was 3.99 (± 3.2 s.d.) years with that for males and females being 3.67 years and 4.31 years, respectively... Of the foals which were sexed, 28 were male and 27 female... The proportions of males to females in each age category, that is, foetuses, foals and adults, did not vary significantly from unity...

All except 8 animals were found in very hilly sandstone country where the predominant fodder was spinifex [grass]. The bulk of the spinifex was "hard" (*Triodia roscida* and *T. inutilis*) with small interspersed patches of "soft" spinifex (*Plectrachne pugnens*)... [The donkeys] watered from water holes and occasional springs in the sandstone country.

Donkeys traversed the study area along well-defined pads. These usually radiated out from waterholes with occasional cross-pads connecting radial pads. When animals fled from the shooting party they usually went along these pads. No erosion was seen in association with these pads. The majority of jennies were found in groups of up to 15 accompanied by their foals and a mature jack. Every jenny group was accompanied by a mature jack... Most jacks were found in "bachelor groups" of up to 10 but a few were solitary. The bachelor groups consisted mainly of juveniles and the extremely old jacks. Most mature jacks whether in family groups or bachelor groups showed evidence of fighting... All [damage] appeared to be consequences of donkey bites. (The jack appears to maintain his family group throughout the year, and not just during the breeding season. The family groups in the sample were still intact even though the majority of jennies were pregnant at the time of sampling.)

The leadership role of the family group jack became apparent when shooting commenced. If jennies were shot first, the jack would bray in the direction of the shooters, then either lead or shepherd the remnants of the group away, sometimes braying as he went. When the jack was shot first, the rest of the family group appeared confused and milled around aimlessly within firing range. (This is in contrast with observations by Berger on feral horses in the Grand Canyon, where flight from alarm situations was usually random.) When portions of family groups managed to evade the shooters they were usually found within 2 to 3 km on subsequent days...

Sixty-four percent of the jennies were pregnant and 17% were lactating... Some [jennies] were cycling at approximately 9 months of age, and a few had foaled by 2 years of age, and all females 2 years or older were either pregnant, lactating or cycling. Five pregnant females appeared, on the basis of foal-at-foot age and foetal age, to have conceived on the foal heat. [There was] a marked seasonality in the breeding pattern which was not correlated with the rainfall pattern. Over 50% of conceptions had occurred before the onset of the Wet Season [i.e. summer]... (This is not surprising in view of the ability of the donkey to maintain good body condition in times of poor nutrition... [and] is probably a reflection of the seasonally polyestrous reproductive pattern of *Equidae*.)

...[T]he sample appeared uniformly well-conditioned with sleek coats, moderate subcutaneous fat cover and extensive omental, perirenal and pelvic channel fat. Feral cattle in the survey area were so poor in condition that some were shot on humane grounds, and domestic cattle in adjacent areas were so poor in condition that mustering had to be canceled.

The flat facial conformation and extensive sinus structure of the donkey skull made penetration of the donkey skulls by frontal shots difficult. The frontal shot was most commonly presented to the donkey shooter. Body shots were not always immediately effective... The most effective strategy in this study was to immobilise the group with anterior thoracic shots either into the front of the chest..., or behind the shoulder followed by immediate dispatch with brain shots at close range. (An average of 3 shots is required, even by professional shooters, to kill a donkey over the normal range at which they are seen in the field.)

...Donkeys were in abundance in the area, and...[t]he major effect of casual shooting [by pastoralists] has been to reduce the average age of the population rather than reduce overall numbers.

The reproductive performance of the sample is remarkable. There exists a large surplus of fertile jacks, and it appears that annual breeding of the jennies is commonplace with some conceptions occurring on foal heat... This parallels the observations collated by McKnight (1958) in relation to the American feral burro, but not with those of Moehlman (1974) who observed [that] foaling was usually biennial. The breeding pattern in the sample was highly seasonal, whereas McKnight (1958) believes that seasonality of breeding is apparent but not marked in the American situation...

...[T]he economics of harvesting donkeys for pet-food [are] very tenuous. Most are found in rugged country which causes extensive vehicle damage and limits access to freezer facilities. Meat yield is low (40 kg) compared to available feral horses and cattle in the area (90 kg). [In addition, there is a] known tendency of pet-meaters to select only the larger older animals. The jacks are the larger, and they exist in numbers greatly in excess of that required for breeding.

Letts et al. (1979) recommended that Northern Territory pastoralists be granted a subsidy on ammunition used in the control of feral animals. The authors support this approach... Optimal impact would be achieved by having organised "donkey drives" over large areas. Helicopters have proved useful in

harding large numbers of donkeys for on-the-spot slaughter for pet-meat. Inquiries of graziers in the area indicate that donkeys are more difficult to muster with helicopters than cattle... Water-traps will also be useful in less-favoured areas."

McCort, William D. 1980. The behavior and social organization of feral asses (Equus asinus) on Ossabaw Island, Georgia. Ph.D. dissertation, Pennsylvania State University. 219 pp.

ABSTRACT: "The objective of this study was to describe and analyze the behavior and social organization of the feral asses on Ossabaw Island, Georgia. The Ossabaw feral asses arranged themselves into 9 to 13 relatively stable groups which varied from 4 to 22 individuals. Three basic types of groups were present: 1) Type I groups with 1 adult male, 1 to several adult females and their offspring, 2) Type II groups with a dominant adult male, 1 to several subordinate adult males, and several adult females with foals, and 3) Type III bachelor groups composed of adult males. The 3 types of groups suggest male and female strategies of the asses to maximize their individual reproductive success (RS). Males strive for exclusive access to group females but because of intrasexual selection, many males attain type II and III positions instead. Female asses do not show apparent intrasexual selection but do exhibit a considerable amount of intersexual selection. Each of the groups of feral asses remained in separate, well-defined areas. Type I and Type II group areas were exclusive, defended territories that varied from 0.7 to 5.1 km^2 (mean 2.7 km^2, n=7). The 2 Type II group areas were undefended home ranges and were 2.2 and 18.8 km^2. The costs to Type I and II males to maintain their territories were offset by variable territory sizes and increased RS. The asses spent most of their daylight hours feeding on *Spartina alterniflora* and were also active during the night. Dominance relationships were linear and stable among adult males. Dominant Type II males clearly had higher RS compared to subordinate males. Adult females seldom expressed their dominance relationships. Adult males sniffed, defecated, and/or urinated on the excreta of other asses. Female urine spots, particularly those of estrous females, incited adult males to sniff and urinate. The first male to detect an estrous female by responding to her excreta may be able to mate more successfully and conceal information concerning sexual receptivity by excreting on top of the female's feces pile or urine spot. The male asses had either 3 different reproductive strategies or only 1 reproductive strategy with 3 different states or decisions of the same strategy. Type I males exclusively mated their harem females. Type II dominant males mated the majority of times with their group females, but not exclusively. Type III bachelor males seldom had access to females, but when they did manage to abduct a female from a Type I or Type II group, mating was competitive and chaotic as the bachelors mated in a gang rape fashion. Male RS was maximized via polygyny and was highly variable. Female asses invested far more in their offspring than males. Parent-offspring conflicts were

very strong between mothers and their foals as each attempted to maximize their inclusive fitness."

McCort, William D. 1979. The feral asses (*Equus asinus*) of Ossabaw Island, Georgia: mating system and the effects of vasectomies as a population control procedure. pages 71-83. *in* Denniston, R. H., editor. Symposium on the ecology and behavior of wild and feral equids. University of Wyoming. 236 pp.

ABSTRACT: "The objective of this study was to analyze the social organization, and in particular the mating system of the feral asses on Ossabaw Island, Georgia. The 80 feral asses assorted themselves into 8 to 11 relatively stable groups which varied from 4 to 22 individuals. There were 3 distinct types of groups: I) Groups with 1 adult male and 1 to several adult females with offspring, II) Groups with 1 dominant adult male, 1 to several subordinate males, and several adult females with offspring, and III) Bachelor groups composed of adult males. The reproductive strategy of each male varied with the type of group he was in. In all 3 group types, male reproductive success (RS) was much more variable than female RS. Vasectomies performed as a population control procedure did not alter the overall social organization of the feral asses. However, the vasectomies did result in female asses maintaining abnormally long attachments to their last born young, and eventually the unusual mating of the young males within their family groups."

McKnight, Tom L. 1976. Friendly vermin: a survey of feral livestock in Australia. University of California Publications in Geography, Volume 21. University of California Press. 104 pp.

ABSTRACT: The chapter "Feral Donkeys" traces the origin and spread of feral burros throughout Australia, their distribution, and methods of population control. Excerpts from the text follow:

"[It was reported that] in the McArthur River area of the Northern Territory... a team of 40 donkeys was turned loose in 1936, and within 3 decades had bred up to number about 1500 individuals... The Kimberley district [of Western Australia] has been home of the greatest concentration of donkeys, both domesticated and feral, to be found on the continent. The reason for this unusual situation is simply that horses could not be used reliably in the district, due to [their susceptibility to Walkabout disease, an extremely fatal, non-infectious disease caused by the ingestion of certain shrubs], and donkeys were pressed into service to fill the void... Sporadic observations of feral donkeys were reported from just after the turn of the century, but it was not until the 1930's that the word "pest" began to be used in describing the feral mobs... [By the mid-1950's] donkeys were officially proscribed as vermin [and] the powerful Agriculture Protection Board of Western Australia began inventorying the feral populations and organizing destruction techniques. [The following]

give an indication of the magnitude of the situation: 1957, an estimated 30,000 donkeys on a six-station area. October 1957, 1000 donkeys seen within 10 miles of one waterhole in the East Kimberleys... Shooting, trapping, and poisoning were all tried and it was concluded that systematic shooting drives were the most efficient means of rapid and inexpensive destruction... Tremendous numbers of donkeys have been killed:... February 1959, some 30,000 donkeys destroyed in 3 years on Ord River, Mistake Creek, and Spring Creek Stations... During the first half of [the 1960's] it was estimated that some 40,000 donkeys were killed in the Kimberleys, and the feral population in 1965 was less than half as large as it had been 10 years earlier... Shooting teams are still employed by various stations and groups of stations, with most of the shooting taking place around watering points, in some cases with a spotlight at night. The carcasses are normally left to rot where they fall. With this type of operation, destruction costs about 40 cents per donkey... The Victoria River district in the Northern Territory... is another region where Walkabout disease has severely restricted the use of horses, and donkeys have been unusually common for many decades...

Based on responses to the questionnaire/interview survey, the total [number of feral donkeys is between 66,000 and 125,000], with the largest numbers by far found in Western Australia and the Northern Territory.

Although the behavior patterns of feral donkeys and feral horses are generally similar, there are... important differences in their natural histories... [Donkeys] seem to prosper more than any other ungulate except the camel in the heat and aridity of the Outback... they eat almost any plant that grows. They are adept at digging for soakage water in dry stream beds and will drink saltier water than either horses or cattle. They can negotiate very rough country, which enables them to range widely in search of feed and water if necessary... The herding habits of feral donkeys are distinctly gregarious. Although individuals, pairs, and small groups are sometimes reported, most informants emphasized the large size of typical mobs [i.e. herds]... Mobs often include several dozens of animals, and groupings up to 150 or 200 individuals are not uncommon in areas where donkeys are numerous... In order to avoid persecution from their only predator, man, donkeys often retreat to broken, rocky, hill country.

The principal objection to [the donkeys] existence lies in the amount of feed and water which they consume; pastoralists prefer that their domesticated stock have no such competition. In some parts of the Kimberley and Victoria River districts, it is alleged that donkeys are in such concentrations as to cause pasture deterioration through overgrazing... In common with other large feral ungulates, donkeys are hard on fences... [They] occasionally disturb cattle by stampeding them and have been known to attack cattle with hooves and teeth... If a donkey is killed, its meat, hide, and hair are all marketable... however the profit is usually small, and the salvage sale of these products is normally not attempted. They are small and lightly-framed animals so that only a limited amount of meat can be cut for the pet food market.

The only approach to management of feral donkeys has been in terms of elimination. Poisoning is occasionally resorted to, either by spreading poison

grain or by poisoning a water hole... most donkey control, however, is accomplished by shooting... A continued reduction in numbers is indicated, with remnant populations (in some areas rather large remnant populations) existing indefinitely."

McKnight, Tom L. 1958. The feral burro in the United States: distribution and problems. Journal of Wildlife Management 22(2):163-179.

ABSTRACT: "Brought to North America during the early years of colonization, domesticated asses were soon found to be well suited for use as pack animals in the dry Southwest. However, with the advent of improved means of transportation, burros were frequently turned out on the range to shift for themselves. Being hardy and adaptable, they took readily to a feral existence.

Utilizing an extensive mail-questionnaire survey, plus field interviews and observations, the writer was able to determine the approximate distribution and numbers of feral burros in the United States. These now total between 5,500 and 13,000. The greatest numbers are in California, Arizona, and Nevada, with smaller populations in 7 other states. For the most part, the burros inhabit steep-side canyons and other rugged terrain.

A great variety of plants are included in the burro diet, including some with very low nutritional value. [The burro's range of food plants is broader than the bighorn's; also the burro can be destructive by pulling entire plants out by the roots and then only eating 1 or 2 mouthfuls.] Availability of water is the key to existence in the desert, but burros spoil the water holes for other animals by trampling the area and fouling the water. Although details are obscure, it seems that burros tend to breed in late spring or early summer, foaling some 11 or 12 months later. There are few predators remaining in the Southwest that are capable of acting as a check on the burro population; hence, depletion of the range by overuse and deliberate control by man are the principal factors limiting the growth of the burro population.

The chief problem associated with the presence of feral asses is the competition they offer for food and water with other animals, and their proclivity for denuding the vegetation and accelerating erosion in areas of concentration. As the burros are introduced animals, it is a case of native species suffering while an exotic prospers.

Particularly handicapped are desert bighorn sheep. Wherever the range of the bighorn has been invaded by considerable numbers of burros, the bighorn has yielded. Domestic livestock also feel the press of burro competition in some areas.

The number of burros present today is considerably less than it was a few decades ago, mainly as a result of persistent shooting and trapping by stockmen and government range and wildlife managers. Partially as a result of an abortive attempt to encourage "no-closed-season" hunting of burros in California, that state now has a law that provides almost complete protection for feral burros. No other state recognizes burros in their game laws.

Various plans have been advanced for the management of the burros: 1) extermination, 2) complete protection, 3) classification as a game animal, 4) establishment of a burro sanctuary. None of these is satisfactory in itself; some sort of compromise is necessary."

McKnight, Tom L. 1957. Feral Burros in the American Southwest. Journal of Geography 56(7):315-322.

ABSTRACT: "Although the existence of wild burros in various parts of the West has been a long-recognized fact, there has never been a comprehensive study to determine their distribution or to analyze the inter-relations between burros and the native fauna and domestic livestock. It is the purpose of this article to outline the present pattern of burro distribution, as well as to describe the basic land-use conflicts that exist in areas of burro concentration.

Results of a detailed mail-questionnaire, supplemented by field interviews and observations, indicate that there are between 5500 and 13,000 feral burros existent today in the western United States. They are found in parts of 10 states, with principal concentrations in southeastern California, western Arizona, and Southern Nevada. The burros usually inhabit rugged terrain, can subsist on almost any vegetation, and are subject to very little predation. Thus, depletion of the range by overuse and deliberate control by man are the principal factors limiting the growth of the burro population. Frequently the presence of feral burros is detrimental to the range, water holes, and other herbivorous animals. The major problem is competition for food and water with desert bighorn and with livestock."

McMichael, Thomas J. 1964. Relationship between desert bighorn and feral burros in the Black Mountains of Mojave County, Arizona. Desert Bighorn Council Transactions 8:29-36.

ABSTRACT: A total of 125 feeding-minutes for bighorn and 380 feeding-minutes for burros were recorded using Buecher's technique. Bighorn fed mostly on *Fouquieria* (ocotillo) and *Acacia* whereas burros fed mostly on forbs; both animals fed on *Encelia*. Both burro and bighorn like to stand in the shade of rocks and ledges, especially during the summer. Vegetation near these areas and around spring showed overuse. Burros were found to occasionally use all but the most rugged areas. The area of highest combined burro-bighorn use was in the upper foothills. Bighorn would travel 2.4 km across rugged mountain terrain to a seep in the mountains instead of traveling 0.8 km across an open flat to a spring. There is sufficient overlap of food habits and summer range of the 2 animals to keep bighorn from reaching their maximum population density in the Black Mountains.

McMichael, Thomas J. 1964. Studies of the relationship between desert bighorn and feral burro in the Black Mountains of northwestern Arizona. M.S. thesis, University of Arizona. 38 pp.

ABSTRACT: "This study of the relationships between desert bighorn sheep and feral burros was conducted in Warm Springs Canyon of the Black Mountains, Mohave County, Arizona from July 1962 to September 1963.

Sheep and burros were located and observed to determine their feeding and watering patterns, their daily movements, and their seasonal distribution. [Table 1 summarizes the percent of feeding time spent by sheep and burros on various plants during each of the 4 seasons.] Samples of the contents of 8 sheep stomachs were collected during the 1962 and 1963 [December] sheep hunts through the cooperation of the hunters and the Arizona Game and Fish Department. [Permits] for collecting 9 burros for stomach contents samples [were issued in February, April, May, and July 1963]. These samples were analyzed for comparative occurrence of food items. [The frequency of plants in stomach contents samples show all animals eating forbs, sheep only eating perennial grasses, and primarily burros eating annual grasses; note that burro and sheep samples were collected during different seasons. Burro stomachs were found to commonly contain *Encelia*, *Fouquieria* (ocotillo), and *Ephedra*, while sheep stomachs commonly contained *Ephedra*, *Eriogonum*, *Acacia*, *Bebbia*, *Boerhaavia*, *Cercidium*, and *Peucephyllum*; in all cases only presence was determined, not relative quantities. During the summer] both species feed on the same plants on a daily basis, but the burros have already removed much of the annual growth from the [area]. The vegetation near the springs and summer resting places showed damage by burro browsing. The palo verde [*Cercidium*] and mesquite [*Prosopis*] trees were hedged to approximately 5 feet, and most branches less than 0.25 inch in diameter had been removed... [*Acacia*] and [*Ephedra*] also showed hedging. [Overall, burro diets were composed of 1.0% grasses, 88% forbs, and 11% browse species.]

Sheep and burros were frequently found near the springs during the summer months. Here they fed on the same plant species, drank at the same time of day, and used the same shade to avoid the heat.

Sheep were seen going 1.5 miles across rugged mountain terrain to a seep in the mountains rather than crossing a 0.5 mile flat to a spring in the open.

Although no direct harm to the sheep could be attributed to the burros, it is felt that under limiting conditions they could have a negative effect."

McQuivey, Robert P. 1978. Competition with wild horses and burros. pages 58-59. in Nevada Department of Fish and Game, Biological bulletin no. 6: the desert bighorn sheep of Nevada. Nevada Department of Fish and Game.

ABSTRACT: "Burro and bighorn competition has been documented in many different areas of California and Arizona. Weaver (1959, 1972, and 1973) found competition occurred between the 2 species for food, space, and water in 7 of 14 bighorn study areas. Mensch (1970) indicated that burro competition in

parts of Imperial County may have been responsible for a 60% decline in sheep numbers. Burro competition was considered severe enough in parts of California that management plans for habitat improvement included some burro reduction. Sumner (1959) recognized competition for both forage and water between burros and bighorn in Death Valley, California. St. John (1965) concluded that the most important problem facing desert sheep in Death Valley is forage competition with burros. McMichael (1964) found a considerable overlap in the food habits and summer use areas of bighorn and burros in Arizona. He concluded that high density burro numbers were significant in suppressing sheep populations. Seegmiller and Ohmart (1975) found that diets of bighorn and burros along the Lower Colorado River overlapped markedly during all seasons of the year.

A complete inventory of wild burros has not been conducted in Nevada. Current emphasis is on wild horses; consequently, population estimates and distribution of wild burros is not yet completed. Limited census data from the Bureau of Land Management and the Department of Fish and Game aerial surveys show that the following areas, within the distribution limits of bighorn, harbor burros: Lone Mountain-Weepah Hills, Mormon Mountains, Meadow Valley Range, Bird Spring Range, Spring Mountains, Black Hills, Black Mountains, Muddy Mountains, McCullough Range, Eldorado Range, Arrow Canyon Range, and La Madre Range. Most burro populations occupy the valleys and benches which are on the fringes of bighorn sheep habitat. Populations are small and have traditionally been controlled by local residents. Competition with bighorn in most areas is presently not a problem. The real threat to bighorn is the potential for increased burro numbers and an expansion of their distribution which could results in serious competition." All citations in the abstract are cited in this bibliography.

Mensch, J. L. 1970. Survey of bighorn sheep in California. Desert Bighorn Council Transactions 14:125-126.

ABSTRACT: "In October 1968 a comprehensive study of bighorn sheep was undertaken in California. At the present, 5 of a total 14 sheep range surveys have been completed...

In [Imperial county] water is available mainly as stored runoff in natural tanks or tinajas. The large amounts of water required by feral burros rapidly deplete these sources, limiting the range available to bighorn. Competition with burros and with the desert mule deer appears to be the factor limiting sheep populations in this portion of the desert.

In portions of [northeastern San Bernardino county] competition between bighorn and feral burros is also severe. A decline of 60% has occurred after the recent entry of burros into the area. This competition appears to be mainly for food and living space."

Mills, Stephen. 1982. The Burros in Death Valley. Oryx 16(5):411-414.
We were unable to obtain this report on interlibrary loan.

Moehlman, Patricia Des Roses. 1974. Behavior and ecology of feral asses (*Equus asinus*). Ph.D. dissertation, University of Wisconsin. 251 pp.

ABSTRACT: "The behavior and ecology of feral populations of *Equus asinus* were studied in the Northern Panamint Range of Death Valley National Monument for 20 months during 1970-73.

Seasonal population size and distribution were determined by individual identification and road, aerial, and watering source censuses. Female home ranges varied from 0.5-7.2 mi^2, and male home ranges varied from 0.9-15.7 mi^2. The peak density in the Wildrose study area occurred in the spring-summer months. In the fall and winter approximately 60% of the population moved out of the study area. The high density within 2 miles of Wildrose Spring during summer months was probably related to water needs.

Feral asses were primarily browsers in the Wildrose study area. Individuals drank approximately once every 24 hours during the hot-dry summer. Females with young foals (less than 1.5 months old) drank several times a day. The peak periods of drinking for the population were between 1900 and 2100 hours during the summer months. Diurnal activity in summer was distributed between feeding (51%), resting (17.2%), standing (18.9%), walking (8.9%), and other (4%). A sample 24-hour watch on 1 territorial male showed activity both day and night...

Behavior patterns used in social interactions are described and quantified by sex and age class. Communication signals are classified in 4 categories: auditory, visual, tactile, and olfactory. Five types of vocalizations were distinguished: brays, grunts, growls, snorts, and whuffles. Prominent among 16 recognized displays were frontal threats, rear threats, facial expressions, estrous postures, alert postures, and yawning. Two types of tactile communication were used in greeting and mutual grooming contexts. In the olfactory category the most conspicuous display, flehmen, was used extensively by adult males in a reproduction context.

Social groups consisted of stable (longer than 1 week) associations of female with offspring, and temporary (2 hours to 1 week) associations of various composition including 1) several males, 2) 1 female with offspring, 3) 2 or more females with offspring, 4) mixed male(s) and female(s), and 5) yearlings. Sixty percent of the temporary groups observed contained 4 or less individuals.

Interindividual spacing within social groups was recorded at 5 minute intervals. Females and young foals were the only animals that spent most of their time within 1 yard of each other. The majority of adult-adult interindividual spacing distances were greater than 10 yards. Genetically related adult females, however, spent 69.2% of their time within 1-4 yards of each other. Female-male spacing decreased when the female was in estrus. Then the

most dominant male would generally stay within 1-4 yards from the female while the subordinate males were at distances of 15+ yards from the female.

Territorial behavior was exhibited by 5 males. Territories were occupied from March through August and ranged from 0.31 to 0.80 mi^2 in size. Three of these males were observed on the same territories 4 years in succession. Overt defense and marking of boundaries were infrequently observed. Both male and female conspecifics were tolerated on territories. Territorial males had sole access to estrous females within their territories, but did not restrict their mating behavior to them. Non-territorial copulations occurred frequently. Outside the territory dominance was reflected in relative distance from the estrous female.

Reproduction was year round with peaks in natality in May, June, and July. Gestation was approximately 12 months. Inter-foaling intervals were typically 2 years. Copulatory behavior was described and quantified. Frequency of copulations per male per hour was higher on non-territorial areas. This mating system which combines territoriality and a loose non-territorial dominance structure may reflect the effects of hundreds of generations of domestication. This population may be in the process of selecting for a territorial system."

Moehlman, Patricia des Roses. 1972. Getting to know the wild burros of Death Valley. National Geographic 141(4):502-517.

ABSTRACT: Popularized, illustrated summary of Moehlman's 1974 Ph.D. dissertation. She "favors a management plan that would retain the burros at a level the area would comfortably support."

Morgart, John R. 1978. Burro behavior and population dynamics, Bandelier National Monument, New Mexico. M.S. thesis, Arizona State University. 94 pp.

ABSTRACT: "A study on the biology of feral burros (*Equus asinus*) was conducted on Bandelier National Monument, New Mexico from 20 May 1975 to 21 May 1976. Primary considerations were the investigation of population parameters, behavior, distributions and movements.

An estimated 140 burros inhabited the southern 2/3 (72.8 km^2) of the monument. Approximately 90-100 used the study area (39.1 km^2). Age ratio of the herd was 57% adults, 21% yearlings, and 22% colts. Sex ratio was 43% males and 57% females. Black and brown burros made up 95% of the population with the remaining 5% being gray.

Jennies are polyestrous and capable of breeding throughout the year; however, a definite breeding and foaling season was observed on Bandelier corresponding to the summer months (June through October). Twenty-three colts were born on the study area in 1975 and accounted for a 29% recruitment to the herd.

No notable seasonal migration of burros was observed. Annual home ranges (n=21) averaged 2.86 km^2 (range 1.30 to 5.96 km^2). No significant

differences in size between age and sex groups were found. The majority of burro sightings (mean = 61%, n=2603 individuals) were on mesa tops. Use of canyon walls and canyon bottoms averaged 28% and 11% respectively.

In all seasons, burros primarily fed upon grasses with blue gramma (*Bouteloua gracilis*) being highly preferred. Animals rarely browsed; however, this behavior was more evident in winter when availability of grasses and forbs was lower.

Two native ungulates occurred on Bandelier: the elk (*Cervus elaphus*) and the mule deer (*Odocoileus hemionus*). Competition with elk was minor due to marginally overlapping areas of distribution. Deer, on the other hand, occupied the burro's range year-round. Competition for browse with burros in the winter months could be significant in limiting deer numbers.

A general lack of predation or other types of population controls preclude the possibility of burro numbers becoming stable. If the present decline in resource quality is to be checked, an extensive and intensive management program should be initiated to control feral burros on Bandelier National Monument."

National Advisory Board for Wild Free-Roaming Horses and Burros. 1976. Proceedings. John Day, Oregon.

National Advisory Board for Wild Free-Roaming Horses and Burros. 1975. Proceedings. China Lake, California. 136 pp.

ABSTRACT: These proceedings of the 8th meeting of the Board primarily contain suggestions and recommendations made by various groups representing conservation, wildlife, and wild horse and burro organizations with regard to the management and control of burros.

National Advisory Board for Wild Free-Roaming Horses and Burros. 1975. Proceedings. Rock Springs, Wyoming.

National Advisory Board for Wild Free-Roaming Horses and Burros. 1974. Proceedings. Reno, Nevada.

National Advisory Board for Wild Free-Roaming Horses and Burros. 1973. Proceedings. Billings, Montana. 34 pp.

ABSTRACT: These proceedings contain then-current information on pending legislation and lawsuits, recommendations of the Board, feral horse and burro population data, and government agency management reports.

National Advisory Board for Wild Free-Roaming Horses and Burros. 1973. Proceedings. Lake Havasu City, Arizona.

National Advisory Board for Wild Free-Roaming Horses and Burros. 1973. Proceedings. Salt Lake City, Utah.

National Park Service, Death Valley National Monument. 1984. Cooperative burro removal to alleviate overgrazing and restore natural ecosystems. *in* Natural and cultural resources management program and final environmental impact statement, Death Valley National Monument, California-Nevada.

ABSTRACT: The most serious exotic pest present in the Death Valley ecosystem is the feral burro. The feral burro, numbering over 5,000 at the beginning of FY 1984, is implicated in the destruction of native plants, compaction of soil, accelerated erosion on destabilized hillsides and the decline of native desert bighorn sheep through competition for water and food. Intensive feral burro removal measures were begun in October, 1984. During fiscal 1984, 2,093 burros were removed from the monument. It is estimated that between 2,500 and 3,000 burros remain in the monument. Removal of the remaining burros is scheduled for completion at the end of FY 1986.

National Park Service, Bandelier National Monument. 1976. Feral burro management, Bandelier National Monument, New Mexico. 85 pp.

National Park Service, Bandelier National Monument. 1974. Burro management program assessment for Bandelier National Monument. 57 pp.

National Park Service, Death Valley National Monument. 1982. Impacts on exotic species: feral burros. *in* Proposed natural and cultural resources management plan and final environmental impact statement.

National Park Service, Death Valley National Monument. 1976. Management Options for Natural and Cultural Resources: Death Valley National Monument, California and Nevada.

National Park Service, Death Valley National Monument. Proposed feral burro management plan for Death Valley National Monument, California-Nevada. 33pp.

National Park Service, Death Valley National Monument. 1973. Regulation of excess wildlife population. *in* Wilderness study: Death Valley National Monument, California and Nevada.

National Park Service, Death Valley National Monument. 1972. Report on the annual census of burros.

National Park Service, Denver Service Center. 1974. Proposed Wilderness Area: Death Valley National Monument, California and Nevada.

National Park Service, Grand Canyon National Park. 1979. Burro population and distribution in Grand Canyon National Park.

ABSTRACT: A report on a 1977 helicopter mark-recapture population and distribution survey of burros in Grand Canyon National Park. Lincoln Index calculations show 266 burros in the 3 herd areas contained entirely within the park, and a transient population of 12 burros in the Grand Wash Cliffs Herd.

National Park Service, Grand Canyon National Park. 1976. Feral burro management plan and environmental assessment.

National Park Service, Grand Canyon National Park. 1980. Feral burro management and ecosystem restoration plan and final environmental impact statement. 65pp.

National Park Service, Grand Canyon National Park. 1979. Immobilization and herding feasibility studies in Grand Canyon National Park.

ABSTRACT: Experiments were conducted to test the feasibility of live removal of burros from within Grand Canyon. Phase I used an immobilization drug and helicopter transport, while Phase II used professional wranglers to capture and herd burros out of the canyon; the planning, execution, costs, and results of both are described.

Phase I proved feasible, but difficult and expensive. The average cost per burro was about $900 plus $200-350 in helicopter transport costs. Problems were encountered with actually darting the burros (as they tended to retreat out of range) and with burro death. The latter was caused both by overdoses and by injuries received from falls after becoming immobilized on the steep terrain.

The herding method, while effective in moderate terrain, is not effective in rugged terrain not suited to horse use. In addition, the lack of potable water in many areas restricts or complicates this method of burro control. Under

acceptable terrain and water conditions, the average cost per removed burro was about $450.

National Park Service, Grand Canyon National Park. 1977. Proposed Colorado River management plan: final environmental statement.

National Park Service, Grand Canyon National Park. 1979. Summary of estimated costs of various management alternatives of Grand Canyon burro management.

ABSTRACT: "Estimated cost to government / option:
$0 / No action
$15,000 / Manage herds: 20% removal by shooting by NPS
$35,000 / Manage herds: 50% removal by shooting by NPS
$50,000 / Live removal by public; shooting remainder and fencing by NPS
$70,000 / Manage herds: 90% reduction by shooting by NPS
$70,000 / Manage herds: 20% reduction by live removal by NPS
$83,000 / Total removal by shooting and fencing by NPS
$85,000 / Euthanasia with drugs and fencing by NPS
$175,000 / Manage herds: 50% reduction by live removal by NPS
$275,000 / Trapping and herding by NPS
$300,000 / Manage herds: 90% reduction by live removal by NPS
$360,000 / Live removal and fencing by NPS
no estimates available / sterilization
no estimates available / restoration of predators"

National Park Service, Lake Mead National Recreational Area. 1975. Natural resources management plan and environmental assessment.

Nellis, D. W., Rebecca Rudman, and A. B. Swanbeck. 1987. The behavior and ecology of feral burros on St. John, U.S. Virgin Islands. final report submitted to U.S. Fish and Wildlife Service.

ABSTRACT: See Rudman's dissertation (1990) for detailed results of this 18-month study on the behavior and ecology of feral burros on St. John.

Niece, R. L., and D. W. Kracht. 1967. Genetics of transferrins in burros (*Equus asinus*). Genetics 57(4):837-841.

ABSTRACT: "The transferrins of 136 female and 86 male burros were typed by starch gel electrophoresis. Autoradiography was required to clearly identify 10 different phenotypes. Jenny-foal family data were consistent with the

hypothesis that transferrins are controlled by 4 codominant autosomal alleles each determining 2 bands."

Norment, Christopher, and Charles L. Douglas. 1977. Ecological studies of feral burros in Death Valley. Contribution number CPSU/UNLV 006/09. Special Report # 9. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas.

ABSTRACT: "An ecological study of a population of feral burros was carried out in a 600 km^2 area in the Panamint Mountains, Death Valley National Monument, California, in 1975-1976. Home range movements, population size, secondary productivity, metabolic energy requirements, changes in the nutritional content of major browse species, primary productivity of major forage species, and effects of burros upon the vegetational communities in the area were investigated.

Population size as observed during road censuses ranged from a low of 44 to a high of 102, with a mean of 78; mean density was 0.41 burros/km^2.

The mean sex ratio observed was 2.1 males:1 female. Observed age distribution was 86.3% adults, 4.1% yearlings, and 9.6% foals. The discrepancy between the sex ratio and age distribution of (this population) is due mainly to the effects of the trapping program operated by the National Park Service, which has resulted in the preferential removal of females and young animals.

It appears that there may be an inverse relationship between population density and percentage of females successfully foaling, indicating that some density dependent factor could be operating...

Animals marked in wildrose Canyon ranged over an area of 425 km^2. Mean home range area for 24 burros was 68 km^2, with no significant differences between home range sizes of males and females. Fall-winter ranges had a mean area of 34 km^2, while spring-summer ranges averaged 12 km^2.

Almost all burros spent the summer in Wildrose Canyon, Emigrant Canyon, or Arcane Meadows, with the majority being observed within the 1210 to 1525 m elevational range and 2 km of water... Most burros were observed at higher elevations and at greater distances from water than during summer months... During the fall, winter, and early spring months, there was contact between groups of burros that appear to be isolated during the summer, and the Wildrose Canyon herd exchanged several members with herds in Emigrant Canyon and Tuber Canyon...

Movements of burros were also correlated with forage quality. Home range sizes vary inversely with density.

Feral burros, which are primarily browsers in the Panamint Mountains, had a noticeable effect upon the vegetation in the study area, with the greatest impact in Wildrose Canyon... Of all shrubs in Wildrose Canyon, 45.7% exhibited some evidence of having been browsed, while the survival of 12.2% was threatened by severe browsing. *Acamptopappus shockleyi* and *Ambrosia dumosa* were most affected...

Burros may have a negative effect upon small mammal densities in the study area, although our data remain inconclusive. Relative density in Wildrose Canyon was 15 individuals per 2.2 ha and 39 individuals per 2.2 ha in an area free of burros...

Analyses of changes in nutrient and energy composition of major browse species show that they parallel changes in phenology... burros are able to tolerate forage of lower quality than are ruminants... (and) may simply compensate for low nutritional levels by ingesting increased amounts of forage.

Primary productivity of major browse species and herbaceous vegetation in the shadscale community in Wildrose Canyon was conservatively estimated to be 232.4 kg/ha... Analyses of energy requirements of the feral burro indicate that the theoretical carrying capacity in the area has not been reached. However, concentration of animals near permanent water during the late spring and summer causes certain areas to be severely affected by browsing and trampling activities, with some shrubby species being threatened with eradication from areas near water in Wildrose Canyon. Thus, the present density of burros in the Wildrose-Emigrant portion of the Panamint Mountains is too great for the area to support without adverse environmental impact."

O'Farrell, Michael J. 1978. An assessment of impact of feral burros on natural ecosystems of the Lake Mead National Recreation Area, Arizona-Nevada. Contribution number CPSU/UNLV 013/05. Lake Mead Technical Report # 4. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 37 pp.

ABSTRACT: "Feral burros are widespread throughout the Lake Mead National Recreation Area although major concentrations occur along the east side of Lake Mohave, Willow Beach, Fortification Hill, Echo Bay and the section extending from Temple Bay along the east side of the Overton Arm of Lake Mead. Burro movements appear to extend beyond Park boundaries and onto adjacent Bureau of Land Management lands. Winter and summer represent times of greatest use of habitat within park confines, although in summer, movements are restricted to the vicinity of water. Burro densities were determined by aerial survey for the 2 areas of greatest burro concentration (Granite Wash - 0.93/mi^2; Temple Bay - 0.62/mi^2).

Vegetative composition was examined for a high burro use area (Granite Wash) and for a control site (near Bullhead City). The 2 areas were similar vegetatively; however, differences were observed between the areas in either abundance or occurrence of key annual species known to be used as burro food. Transects were also examined for browse impact; browse impact was conspicuously absent near water. Within 0.25 mile of a spring, only 20% of the vegetation showed severe browse impact and the number of converging trails contributed to compaction and denuding of soil within this area.

Small mammal populations were monitored throughout the study both at Granite Wash and the Bullhead control site. The magnitude of rodent densities indicate that plant productivity has been superior and that burros were having

no competitive effect on rodents. Weather records for most of this decade support the conclusion that conditions have been optimal for plant production. I suggest that such conditions have minimized burro impact. However, the potential for significant deleterious impact is present and would be expected with suboptimal climatic conditions."

Ohmart, Robert D. 1977. Final report on the burros of the Chemeheuvi and Bill Williams Mountains: Havasu Resource Area. Report submitted to Bureau of Land Management, Havasu Resource Area. 14 pp.

ABSTRACT: A summary 18 months of burro research in the Chemehuevi Mountains; the 3 semi-annual reports (all authored by Ohmart, Woodward, and Seegmiller) which were the basis of this final report present more complete data and are abstracted below.

Ohmart, Robert D. 1974. Burro research in the Havasu Resource Area, Arizona-California. Desert Bighorn Council Transactions 18:61.

ABSTRACT: "Preliminary results concerning feral burro ecology in the Havasu Resource Area are presented. Methods and drug dosages for capturing feral burros also are described.

The morphine-like compound M-99 has been used successfully to capture and mark more than 60 wild burros. A relationship exists between body size and dosage, but the burro's wide tolerance for M-99 has allowed the successful capture of 2 to 3-week old young to adults with a 2.25 mg dosage. A tranquilizing agent, Azaperone (30 mg) has been used in conjunction with M-99. No drug fatalities have been experienced... 6 animals, however, [required] a 2nd dart. Three-cc syringes with 1-1/8-inch barbed needles proved most satisfactory. Animals generally show "prancing" signs within 4 to 5 minutes after darting and are immobile after 15 minutes. Drugged animals show a depressed respiratory rate (10.6/minute, range 2-17) and an increased heart rate (90 beats/minute, range 48-228)... In cool weather, adult burros have been immobilized as long as 2 hours... Some individuals have been captured 3 times during a year without showing signs of developing a tolerance... The antagonist, M50-50, is injected intramuscularly (IM) or intravenously (IV). IM injections of 4.5 mg revive a burro in 10 to 17 minutes. IV injected animals are revived within 1 to 1.5 minutes.

Burros in the study area are dependent on the Colorado River as a water source during the summer months, and they drink about every 24 hours. Movements are generally within 2 miles of the river. In winter, burros are less dependent upon water and may drink only every 2 to 3 days. During this period they range from 2 to 8 miles from the river.

The primary food item for burros in the study area is an annual forb, wooley Indianwheat (*Plantago* spp.). This is supplemented with ripened mesquite beans during the summer, and by greening shrubs during the spring. Wooley Indianwheat is a cool season forb and lack of sufficient winter rainfall will result

in its absence. Thus, burros probably become more dependent upon shrubs in years of low annual plant production."

Ohmart, Robert D., James E. Walters, R. Roy Johnson, and Edward J. Bicknell. 1978. On estimating burro numbers: a more reliable method. Desert Bighorn Council Transactions 22:45-46.

ABSTRACT: "The technique of marking [with paint pellets] and recounting feral burros was used in 3 localities in Arizona to gain reliable estimates on burro densities. Data indicate that direct air counts, at best, only reveal 30 to 35 percent of the total burro population because of the difficulty in spotting burros due to the rugged terrain they occupy. Information on time, manpower, and other costs is included for a 15,360 ha area in the Black Mountains, Mohave County, Arizona."

Ohmart, Robert D., Susan L. Woodward, and Richard F. Seegmiller. 1975. Feral burros on the Havasu Resource Area, Colorado River Valley, California-Arizona: semi-annual report (contract period 1 January 1975 to 30 June 1975). Report submitted to the Bureau of Land Management, Havasu Resource Area. 31 pp.

ABSTRACT: The 3rd and last semi-annual report in a broad study to gather data on burros and their interactions with native wildlife. Note that all observations of behavior were made during winter and spring (1 January through 31 June 1975). To some extent earlier work is summarized here.

Home range sizes for 15 marked burros in the Chemeheuvi Mountains varied from 0.5 to 38 mi^2, with a mean of 11.6 mi^2. Female home ranges varied from 0.5 to 38 mi^2; the largest home range belonged to a 10 year old female. Male home ranges varied from 4.5 to 21 mi^2. "[I]n most instances the longest axis of a home range is oriented perpendicular and not parallel to the course of the Colorado River. [It is] likely that the sparser vegetation of the Chemeheuvi mountains necessitates broader movements [than burros in Death Valley exhibit]. No distinct pattern of home range use was discernible other than seasonal movements toward or away from the river. All the ranges overlapped, and some are entirely contained within others. The loose social structure and the instability of most social groups reflects this non-exclusive pattern of home ranges.

In January through March, burros were foraging almost exclusively on the interfluves. The major washes were used to access the Colorado River, and the riparian zone was entered only when passing to the river for water. Very little feeding took place in either the washes or the riparian habitat. By mid-June burros were rarely seen on the interfluves during daylight hours. By that time ambient temperatures surpassed 120 °F in the afternoons, and burros sought shade under palo verdes, mesquites and salt cedars. The mesquite bean crop attracted the burros into the riparian zone in July and August. Probably due to the depletion of cured annuals (particularly *Plantago insularis*)

resulting from heavy grazing and 2 years of drought, the burros spent less time on the bajadas in the winter of 1974-1975 than in the previous year.

Thirty-nine plant species were identified in the burro diet for 1974. Desert wheat grass (*Plantago insularis*) and palo verde (*Cercidium floridum*) were by far the most salient components. Together with arrowweed (*Pluchea sericea*) and mesquite (*Prosopis* spp.) they formed over 50% of the annual diet. However, predominance in the diet varied seasonally among these 4 species... The 1974 annual diet... consisted of 3.2% grasses, 29.1% forbs and 61.4% browse... [The variations in diet between other study areas and the Chemeheuvi Mountains] no doubt reflect differences in the species composition of the plant communities in the different study areas, and also indicate the great versatility of the burro and the unspecialized nature of its food requirements... The species diversity in their diet is correlated with the diversity of plants sprouting... in response to sporadic precipitation. Highest diversities occurred in February, April and December. Each of these months was preceded by a month in which some rain fell. Also, each was a relatively cool month in which burros could cover a wide area and visit springs and tinajas near which forbs and grasses are likely to be found. The lowest species diversity in the diet occurred in July and August when burros were essentially confined to the river's edge... [Palo verde and] cured burroweed (*Hymenoclea salsola*) also seems to be preferred over the green material. Burros were observed eating the skeletons of dead cholla (*Opuntia acanthocarpa*) as well as the live joints...

Mortality in the Chemheuvi herd will be practically nonexistent for the next few years since 0 to 5 year old individuals presently comprise 95% of the population. We have not observed any colt mortality, and life expectancy for jennies appears to be 12-14 years and 13-15 years for the jacks... [I]t seems reasonable to estimate that the 20 to 25% recruitment seen in feral burro populations takes place not annually, but somewhat closer to every 18 months...

Shoulder height appears to be a good indicator of age in the feral burro. Full growth is not achieved until sometime after 2 years of age... Sexual maturity is reached before full growth...

Burro sightings were much more sporadic in the winter and spring of 1975 than during the same seasons the previous year. Burros appeared to be moving around much more and to be using areas farther from the river (3 to 8 miles). No large (>10) burro groups were encountered. These conditions are attributed to the depletion of the range and the absence of... rains during the winter... In mid-June, after a week of daily maximum temperatures in excess of 110° F, burros began congregating in the major washes within 1.5 miles of the Colorado River."

Ohmart, Robert D., Susan L. Woodward, and Richard F. Seegmiller. 1974. Daily and seasonal movements of feral burros (*Equus asinus*) in the Havasu Resource Area, Colorado River Valley, California-Arizona: semi-annual report (contract period 1 January 1974 to 30 June 1974). Report submitted to the Bureau of Land Management, Havasu Resource Area. 33 pp.

ABSTRACT: The 1st semi-annual report in a broad study to gather data on burros and their interactions with native wildlife. Note that all observations of behavior were made during the winter and spring (1 January through 30 June 1974). At this time 38 burros had been immobilized, measured and radio-collared.

"The distance covered by a burro in a single day is often less than a mile. This is especially true in cool weather or after rains when the burros do not have to travel to the Colorado River for water... Burros spend most of their time on the interfluves. Major washes, at least in the cool seasons, appear to be the main avenues for travel to the Colorado River. If water is available in springs, tenajas, or arroyo channel sands, burros do not go to the river to drink..." Typically less than 10 minutes is spent in the mesquite-tamarisk riparian vegetation on the river bank. With regard to distribution "[a] shift toward the river with prolonged drought and the onset of hot weather is indicated in both the aerial surveys and ground observations."

Fecal analysis of over 70 samples was underway, but no results were available. "Field observations show a reliance on cured annuals (especially *Plantago insularis*) throughout the winter and spring months... greening shrubs and flowering forbs [supplemented this in the spring]. They have been seen to take the following perennials: *Fouquieria splendens*, *Lycium andersonii*, *Ambrosia dumosa*, and *Krameria grayi*. *Cercidium floridum* is a minor element in their diet [in the winter and spring]... Considerable damage is done to ocotillo, which has its stems broken and bark (including thorns) stripped; but no plants seem to have been killed by concentrated browsing... In many instances *Ambrosia* is closely cropped and stunted, if not destroyed. However, only the new growth and flowers of *Lycium* and *Krameria* are removed. With annuals, the whole plant, including roots, is consumed. *Lupinus* spp. is avoided and possible *Cryptantha* spp. also. *Encelia* is a species which is definitely ignored, if not avoided." Table 4 lists 63 plants found in the Trampas Wash area and notes which ones the burros have been observed eating.

"Attention has been paid to any type of social behavior among burros which might influence their distribution or density. So far no definite sign of territoriality or dominance on the part of a jack has been observed... In general, males travel singly or in small groups of 2-5 animals. This breaks down when a female is in estrus and as many as 20 males may attend and copulate with her. Jennies remain alone with their colts or in a jenny group composed of 2, seldom 3, jennies and their colts. During the month of May... this general pattern has changed and larger jenny groups and mixed groups have been seen. This may be due to a restriction of movements and hence increase in population density to within 1-2 miles of the Colorado river, presently their only water supply."

"Analysis of body measurements from immobilized adults indicates there are no significant differences between sexes... Figure 1 gives means and ranges [male and female] for these various body measurements." The approximate adult means (in cm) are: total length (235), tail (35), hind foot (50), shoulder height (115), ear (25), neck (65), heart girth (130), orbital width (20), and lower jaw (40).

Ohmart, Robert D., Susan L. Woodward, and Richard F. Seegmiller. 1974. Feral burros of the Havasu Resource Area, Colorado River Valley, California-Nevada: semi-annual report (contract period 1 July 1974 to 31 December 1974). Report submitted to Bureau of Land Management, Havasu Resource Area. 13 pp.

ABSTRACT: The 2nd semi-annual report in a broad study to gather data on burros and their interactions with native wildlife. Note that all observations of behavior were made during the summer and fall (1 July through 31 December 1974). To some extent earlier work is summarized here.

"The past 6 months work has yielded a population estimate for the Havasu Resource Area, a record of summer and fall movements and concentrations of burros, the verified existence of male territories, the probable age of sexual maturity in females, and further insights into the social behavior of feral burros..."

Ground estimates show 70-90 burros in the Chemehuevi Mountains, 60-80 in the Bill Williams Mountains, and 500 in the Havasu Resource Area. Fixed-wing aircraft estimates are very similar, though adult-young ratios are slightly under field estimates. "Recruitment is approximately 25%".

"By mid-June [in the Chemeheuvi Mountains] burros were rarely seen on the interfluves. Instead they frequented the washes and the riparian zone along the Colorado River. At this time ambient temperatures were reaching 125◦ F in the afternoon, and the mesquite bean crop was ripe and forming a major part of the burro diet. At the same time an annual forb, *Plantago insularis*, the winter staple, was being depleted on the hillsides within a mile or so of the river. The typical diurnal pattern of movement for late June and all of July was for burros to move into the washes early in the morning and to reach the riparian zones at the mouths of the washes by 0900 or 1000 hours. They spent all day hidden in the pockets of mesquite and tamarisk which edge the Colorado River. At about 1730 hours the burros moved back into the washes and worked their way upstream after dark. At dawn they could be found grazing on the interfluves about 1 mile from the river. Social groups were much more stable than at other times of the year, probably because movement was minimized."

In June and July one 4-year old collared jack established a 0.25 mile^2 territory at the mouth of a wash. Five jennies and their colts were frequently seen on the territory, but solitary males were generally expelled. "On several occasions [he] was seen patrolling the borders of his territory, and in the evening he seemed to round up the jennies and colts feeding therein. These jennies usually went directly to [him] when he approached them, while they ran from any non-territorial jack... August saw the decline of [his] attachment to his territory [and] by September he had abandoned it."

"In the early part of the day in August, burros were seen less and less often at the river. Ambient temperatures remained high, but the bean crop had been exhausted. Activities were concentrated in the desert washes, where shade and preferred browse were available. Burros trekked to the river in mid- to late afternoon and moved upstream again early in the morning...

Burro sightings in October and November were very sporadic... No longer requiring water every day, it appears that burros were wandering extensively and opportunistically taking whatever forage was available in the hills. Most sightings were made 2 or more miles from the river, and most frequently burros were grazing on the interfluves...

It appears that young jennies leave their mothers just before the birth of a sibling. Yearling females wander with the small jack groups, which are usually composed of 1 to 3 year old males...

Summer burro observations [in the Bill Williams Mountains] indicated their movements to be largely nocturnal... Generally, during the daylight hours, the burros were... 0.25 to 3 miles from the edge of the riparian vegetation of the Bill Williams River. In the late evening or nightfall the burros began a trek into the riparian communities where they remained until the early morning hours, before moving laterally up the washes or along the ridges... On no occasion was a burro seen watering in daylight hours...

Herd instability among burros was evidenced since the exact same composition of individuals in any herd was never seen on 2 successive days.

Foraging observations of burros and bighorn indicated that the cured herbaceous layer, especially *Plantago insularis*, to be predominate in their summer diets... both used palo verde (*Cercidium microphyllum*) heavily. Burros, rather than selecting a portion of the annual new growth at the branch tips, generally chew and break off branches ranging from 6 inches to 6 feet in length and 0.25 to 1.5 inches in diameter. They then shred and consume a small section of the broken end of the branch and leave the remainder.

A sample of 48 burros in the Chemehuevi Mountain population contained 21 adult males, 15 adult females and 12 colts (4 males, 5 females, 3 of unknown sex). If this proportion of colts to adults holds true every year, if most females foal at 2 years of age, and if jennies typically have a colt every year, we can expect a population explosion from 500 to 1900 burros in the Havasu Resource Area by 1980 and potentially to 4600 by 1985."

Perryman, Pamela, and Alan Muchlinski. 1987. Population dynamics of feral burros at the Naval Weapons Center, China Lake, California. Journal of Mammalogy 68(2):435-438.

ABSTRACT: In 3 years between 1980 and 1983, 4661 burros were removed from the China Lake Naval Weapons Center, most by direct round up procedures during winter or trapping at watering holes in summer. All were aged and sexed; sampling bias is considered negligible as 95% of the total population was removed. A life table was generated, survival, mortality and recruitment rates calculated, and population growth rates modeled.

The survival rates for groups aged 0-2, 1-3, 2-4, 3-5, 4-6, 5-7, 6-8, and 7-9 years were 0.88, 0.96, 0.86, 0.82, 0.70, 0.52, 0.65, and 0.00 respectively. Average mortality rates for 1980, 1982, and 1983 were 0.207, 0.240, and 0.205, respectively. "A rough estimate of the annual recruitment rate was calculated for each sample by dividing the percentage of foals by the percentage of yearlings plus adults. The values were 20%, 22%, and 12% for 1980, 1982, and 1983 respectively."

"If the survival rates calculated in this study are realistic, and pregnancy rates high (60-80% age-specific, 70-80% constant)... populations increase at rates of, or approaching, 10%. With these survival rates, the only condition resulting in a rate of increase approaching 20% [as other researchers have stated] is one in which the pregnancy rate is 100%... A population of burros with a large proportion of young, high survival rates, and a pregnancy rate of 70% or greater is capable of doubling in size in 10 years or less."

Peterson, Paul M. 1984. Flora and physiognamy of the Cottonwood Mountains, Death Valley National Monument, California. Contribution number CPSU/UNLV 022/06. (also M.S. thesis, University of Nevada-Las Vegas). National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 241 pp.

ABSTRACT: A detailed flora of the Cottonwood Mountains. The floristic composition of 1400 ha in the Mixed Shrub Zone near Cottonwood Springs appears to have been altered by burros to create an *Ericameria cooperi-Ephedra nevadensis* Association: "Historically, the area above Cottonwood Springs supported a ranch operation and may have been subject to heavy grazing from site to site, over time. Presently, a large population of feral burros ranges within a few miles of this spring. Yoder et al. (1983) found that grazing appeared to stimulate *Ericameria cooperi* 6-13 fold, *Ephedra nevadensis* 6-10 fold, and *Hymenoclea salsola* 2-3 fold in the Alabama Hills, Inyo County. These are 3 of the 4 most dominant shrubs found in this [aberrant Mixed Shrub] Association. It is my hypothesis that the community structure of this association is controlled, in part, by the presence of introduced grazers [i.e. burros] and that this association represents a shift in species composition from the *Coleogyne ramosissima- Ephedra nevadensis* or the *Grayia spinosa-Lycium andersonii* Associations."

Potter, Loren D., and Scott Berger. 1977. Deer-burro utilization and competition study, Bandelier National Monument. Final report to National Park Service, Bandelier National Monument. 44 pp.

ABSTRACT: Clip plots and collections of deer and burro fecal material, all spanning several seasons and vegetation communities, were analyzed to assess competition between deer and burros in terms of forage use and food habits.

"Four [vegetation] sampling locations were chosen... to represent variations in vegetational type and in areas used by both deer and burros... 3 are in range conditions classified as poor or very poor and are in a trend of deterioration." Tables detail the species and total weight of living material, total standing dead material, and total standing biomass for exclosure and free use areas in each of the 4 sites during both spring and fall. In the Lower Lummis site "there is severe use of blue grama (*Bouteloua eriopoda*), squirreltail (*Sitanion hystrix*),

sand dropseed (*Sporobolus* spp.), and six-weeks fescue (*Festuca octoflora*). The use of unpalatable low shrubs, such as snakeweed (*Gutierrezia sarothrae*), indicates the severity of grazing pressure. The utilization of living material was 61 and 50% [over the winter and summer, respectively. The Upper Lummis site also shows heavy grazing on blue grama and snakeweed.] Here the utilization of living material was 68 and 31% [over the winter and summer, respectively. In the Capulin area heavy over winter use occurred on blue gramma, the dominant grass; [this was] somewhat reduced over summer. [The use of living material was 52 and 48% over the winter and summer, respectively.] In the Lower Frijoles area black grama was the dominant grass cover and was [used heavily. The use of living material was 32 and 51%, respectively.]

[As] utilization studies do not provide information on the users of the plant species... the [determination of seasonal feeding habits and] relative use of the plant cover by deer and burros was based on the microscopic examination of fecal samples from both animals and at several times of the year; [25 taxa were identified]. Several general relationships are apparent. Grasses make up a minor part of deer forage, varying from no detection in November in the juniper type to a maximum of 5.6% in March in the same type. The use of forbs by deer appears also to be low, even in the spring and summer months. Low percentages of forbs were likewise detected in the burro material. Most outstanding are the high percentages of shrubs and trees in the deer pellets from all sites and at all seasons, ranging from 94 to 99%. Conversely, the diet of burros does not include an equivalent percentage of grasses. The percentages of the latter range from 64 to 95%. The decreased use of grass by burros appears to occur in winter and very early spring. This is the time when the previous heavy use of this forage would have reduced its availability as well as its accessibility in many areas because of snow-cover. During this period the use of shrubs and trees as a substitute increased to as much as 35%. The period of November to March is the usual critical period for both browsers and grazers. Even without the impact of overgrazing, and there is no doubt that Bandelier National Monument is overgrazed. Low growing herbaceous vegetation, often deciduous or dried, is less available in the winter months. [Consequently] all large animals, and even small mammals, turn to evergreen and semi-evergreen shrubs and trees and to the buds and twigs of these woody plants. The burro use of shrubs and trees in winter and spring appears to be least in the higher vegetational types of ponderosa pine and pinyon-juniper, and greatest in the lower types of juniper and along the river flats. These latter areas are those which exhibit the greatest visual impact of pruning on shrubs, destruction of grass cover, and the most severe soil erosion... Because of the low use of grasses by deer, there does not appear to be any serious competition for these taxa, nor among the forbs. Among the shrubs and trees, however, there are indications of competitive, or at least common, use of several species. Of principal importance would be the common use of 4-wing saltbush (*Atriplex canescens*) and mountain-mahogany (*Cercocarpus montanus*) in the pinyon-juniper type, but more especially in the juniper type. In the early spring, species of juniper furnished an important part

of deer diet and at that time also burro use was relatively high. In the two January samples the percentage use of oak (*Quercus* spp.) was greater for burros than for deer. A small amount of burro use of cholla (*Opuntia imbricata*) was common but only in one sample for deer and never in large amounts for either."

The results of overgrazing... have extended beyond the primary effects on the vegetation itself and are often severely evidenced [by] sheet erosion. [Areas adjacent to burro trails in] pinyon-juniper stands, dominated by blue grama grass, become severely overgrazed. If the trail is downslope [gully development occurs]. On the Plateau area between Frijoles and Lummis [yellow Indiangrass (*Sorghastrum nutans*) has been overgrazed and a stand of flannel mullein (*Verbascum thapsus*) has developed... The latter] species was one of the common forbs detected in the fecal material of burros. [Mountain mahogany (*Cercocarpus* spp.) is] severely browsed by deer throughout the year... Burros have been observed to browse it and the analysis of fecal material show it to be an important part of the winter diet of burros at a time when deer and burros share the same wintering areas and forage is at a premium. One of the unusual browsing habits of burros is tearing up [yucca] rosettes [and chewing on the bases of the leaves.

In July 1974 the skeleton of [1 burro was found and was believed to be the result of mountain lion kill]."

Potter, Robert L., and Richard M. Hansen. 1979. Feral burro food habits and habitat relations, Grand Canyon National Park, Arizona. pages 143-153. *in* Denniston, R. H., editor. Symposium on the ecology and behavior of wild and feral equids. University of Wyoming. 236 pp.

ABSTRACT: "The feral burro (*Equus asinus*) population in Grand Canyon has been periodically reduced by burro hunts between the 1920's and 1969. Experienced land managers seem to agree that heavy use by burros over many years has resulted in damage to vegetation in places. Presently (1968 to 1969), there are at least 300 burros in 116,000 acres of Park Service land at Grand Canyon. In August of 1977, food habits of burros were estimated by fecal analysis from 10 study areas from about mile 80 to mile 110 of the Colorado River. Vegetation data from these 10 study areas were collected the following spring. Diet composition for native herbivores was determined when their feces were present on an area. About 20% of burro and desert sheep (*Ovis canadensis*) diets, as well as about 30% of the relative herbaceous plant cover, consisted of 1 species of plant, foxtail chess (*Bromus rubens*), a common annual exotic grass of the desert Southwest. [Without regard to local or seasonal variations, overall] diet overlap was estimated to be about 12% between burros and mule deer (*Odocoileus hemionus*), 44% between burros and desert bighorn sheep, and 40% between desert bighorn sheep and mule deer. Feral burros inhabiting the desertscrub community in Grand Canyon National Park consume primarily grasses (66%), second, forbs (16%), and last shrubs (11%). Vegetation data when related to diet information indicates feral

burros select plants most readily from habitat types also apparently important to desert bighorn sheep. In order to document alleged habitat destruction by feral burros in Grand Canyon National Park, we feel the Park Service should construct grazing exclosures."

Reavley, W. 1974. Wild Horse Board suggests sweeping changes. Conservation News 39(22):12-14.

ABSTRACT: The decisions of the National Wild Horse and Burro Advisory Board made at the Reno, Nevada 1974 meeting are discussed. To deal with the increasing populations, the Board's plan was as follows: "A series of intensive management units (or wild horse refuges) would be established throughout representative ranges in the West, with the exact number yet unknown but possibly varying between 10 and 20. The remainder of the wild horse and burro populations not in the designated management areas would then be removed from the balance of the public domain." Vehicles such as helicopters would have to be used to round up the left-over horses and burros and those not claimed would be sold to defray the cost of rounding them up. This plan is in conflict with existing legislation. (from Zarn et al., 1977)

Reddick, Phillips B. 1981. Feral burro management program, Naval Weapons Center, China Lake, California. *in* Department of the Navy final environmental impact statement for the Naval Weapons Center, China Lake, California, technical appendix I. 74 pp.

ABSTRACT: "Feral burro activities on the Naval Weapons Center (NWC) are promoting alterations in the structure of the vegetation and small mammal community, particularly in the vicinity of riparian areas. Grazing and trampling by the burro are, in combination, resulting in pronounced decreases in vegetation cover and species richness as disturbance increases with proximity to NWC water sources. Habitat disturbance by the burro is favoring the proliferation of exotic, unpalatable species of plants at the expense of native species which serve as valuable forage to the resident faunal community.

Decreases in vegetation cover are reflected in general by decreases in densities of small mammals. Small mammal densities in the immediate vicinity of NWC springs would be reduced markedly below numbers presently extant were it not for the presence typically of stands of riparian "oasis" vegetation which serve as impenetrable barriers to burro ingress. Such reduction in small mammal densities can be expected to ensue eventually even in these areas as burros continue to damage and reduce riparian "oasis" vegetation through trampling, soil compaction, and digging for water.

Habitat disturbance, as manifested by alterations in vegetation composition is reflected in the structure of the small mammal community, with the diversity and density of specialist species decreasing as disturbance increases. Of serious concern, in fact, is the indication that burro disturbance may have

already resulted in the local extinction of some specialist species from certain riparian areas of the NWC. Should this be the case, recovery of these areas to their original species complement, even with cessation of disturbance, could require a long period of time due to the considerable distances by which they are separated and thus comparatively isolated with respect to small mammal dispersal.

In summary, the presence of a large population of feral burros upon the NWC is resulting in the alteration of native habitat to a condition wherein vegetation cover is on the decline, overall species diversity within the vegetation and small mammal community is diminishing, and the survival of species tolerant of disturbance is favored."

Robertshaw, D., and C. R. Taylor. 1969. Sweat gland function of the donkey (*Equus asinus*). Journal of Physiology 205(1):79-89.

ABSTRACT: The results of this study are: "1) Donkeys sweat on exposure to heat and in response to intravenous adrenaline infusion, 2) Thermal sweating was abolished by the adrenergic-neurone blocking agent bethanidine but not by atropine, 3) Sympathetic decentralization (by preganglionic sympathectomy) abolished thermal sweating but adreno-medullary denervation had no effect, 4) Exercise resulted in sweating from both sympathetically innervated and decentralized skin and from the innervated skin of animals which had previously undergone adreno-medullary denervation, 5) Insulin-induced hypoglycaemia resulted in sweating from pympathetically decentralized skin and from innervated skin in 2 out of 4 animals. Adreno-medullary denervation abolished the sweat gland response to insulin administration, 6) Cold exposure inhibited the response of innervated sweat glands but not that of decentralized glands to adrenaline infusion, and 7) It was concluded that heat-induced sweating of the donkey is controlled by adrenergic nerves; adreno-medullary secretion may contribute to sweating during exercise, and that cutaneous blood flow is important in the response of the glands to humoral stimulation."

Rothfuss, Edwin L., Tim Coonan, Shirley Harding, and Naomi L. Hunt. 1990. An administrative history of the removal of feral burros from Death Valley National Monument. National Park Service, Death Valley National Monument. 56 pp.

ABSTRACT: "Beginning in 1983, Bureau of Land Management [BLM] wranglers, under contract to the National Park Service [NPS], removed 6,000 burros from Death Valley National Monument. Helicopter and horseback roundups proved efficient and humane. Animal protection groups had 1 year to remove stragglers before direct reduction began. The animal protection groups agreed to take all burros captured out for adoption, but took only 60%. Remaining animals were sold at public auction, through sealed bids, or by telephone bid, or "adopted out" using BLM corrals.

Interagency cooperation was essential because on adjacent federal lands in southern California, BLM and the U.S. Navy simultaneously removed an additional 5,400 feral burros and horses. Removal operations required close coordination between managers, scientists, and resources management specialists, animal protection groups, and concerned citizens monitored the program closely. Also, information specialists and park naturalists played a key role in public relations--news releases, exhibits, and hundreds of interpretive talks to literally thousands of visitors. Agreement and coordination between NPS, BLM and animal protection groups required weekly, sometimes daily, coordination and communication at both top management and field levels.

Some factors contributing to the successful conclusion of the 3-year program for the live removal of 6,000 burros from Death Valley included: 1) complete and thorough research and documentation before project implementation, 2) once, having an approved plan, following it, with firm adherence to NEPA processes, 3) establishing and continuing open, frank and honest communication between all participating individuals/groups, and 4) developing and maintaining an excellent interpretive/public relations program.

In Summary, the 1983-1986 burro removal program-- despite some difficult times-- was highly successful. It could not have been successful without the cooperation and help from the animal protection groups, especially the Fund for Animals; the cooperation of the Bureau of Land Management, and the support of the American public, which was gained through years of effort by park interpreters."

Rudman, Rebecca. 1990. Behavior and ecology of feral burros on St. John, U.S. Virgin Islands. Ph.D. dissertation, Cornell University. 184 pp.

ABSTRACT: "An 18-month study on the behavior and ecology of feral burros (*Equus asinus*) was conducted on St. John, one of the U.S. Virgin Islands. Social organization and diurnal activity patterns were observed. Feeding habits were determined by fecal analysis and direct observation. [Population size, age structure, and sex ratios were determined and an annual rate of increase estimated].

The grouping patterns of feral burros... were recorded from June 1984 through September 1985. Nineteen different grouping patterns (social units) were observed for adult burros. When the frequency distributions of these units were determined separately for male and female adults, a significant difference in social organization between the sexes was found. The most common adult female social grouping was composed of one or more adult females and their offspring. Solitary adult females were seen relatively infrequently. In contrast, solitary adult males were the most commonly observed social unit for adult males, followed by multiple adult male groups. The feral burros tend to form loose temporary associations rather than stable long-term groups; all social units except that of an adult female and her most recent offspring were unstable, as individuals often changed associations over a period of days to

weeks. A mating strategy of conditional but non-seasonal territoriality was employed by dominant male burros.

The social organization of the St. John burros is more similar to that of the feral burros in the Death Valley region of California than to the stable harem bands seen for the burros on Ossabaw Island off the coast of Georgia, but there are significant differences in social organization between St. John and Death Valley burros. The social systems of all 3 populations are variations of the system seen for their ancestral species, the true wild ass of northern Africa. Habitat differences in terms of climate, resource distribution, topography, and size are a major influence on the social organization of both wild and feral ass populations. Social organization is also directly influenced by mating systems, and environment plays a key role in shaping mating strategies as well. The ability of E. asinus to adopt very different types of social organizations and mating strategies in response to differences in environmental circumstances helps to explain why this species is so successful at establishing thriving populations almost anywhere that it is introduced.

The diurnal activity patterns of feral burros on St. John... were observed between June and October 1984. The burros spent the greatest percentage of their time feeding (54%), followed by resting (27%), and then standing (6.6%), walking (6.2%), and engaging in other activities (6.0%). Adult male burros tended to feed less and rest more often than adult females and juveniles. Resting was more frequent at midday than during the morning or evening hours, when feeding frequency increased; [such patterns are caused by high midday temperatures]. The burros also rested more during dry months compared to wet months. Similar results for general activity patterns were found for... feral burro populations in [Death Valley and on Ossabaw Island]. Differences between activity patterns of these populations and St. John burros are probably the result of environmental differences, as are the differences between the time budgets of St. John burros and captive burros. A comparison of activity patterns of other equid species with those of burros suggests that, for all equid species, feeding and standing/resting behaviors are much more frequent than any other activities under many types of environmental conditions.

The feeding habits of feral burros... were studied using both a fecal analysis method and direct observations in an effort to determine if these burros were affection the vegetation of the island. A total of 130 plant species in 47 families were consumed by the burros. Grasses were most abundant in their diet (41%), followed by browse plants (23%), legumes (20%), and forb plants (10%). The grass *Panicum maximum* and the leguminous tree species *Acacia macracantha*, *A. farnesiana*, and *A. tortuosa* were the most frequently eaten plant species, together comprising over 20% of the diet. Types of plant species consumed differed very little between wet and dry months or wet and dry locations, but frequency of consumption did differ greatly for some plant species. Evidence from exclosures suggests that the St. John feral burros do affect plant species composition of some areas on the island. In addition, these burros are probably spreading the distribution of the Acacia species, while their preference for the black mangrove (*Avicennia germinans*) could endanger the mangrove swamps on St. John; [leaves of the latter are consumed even though

exuded salt coats the leaf surfaces]... No problem with salt and water balance was apparent.

The age structure of the population, based on all known animals, was 79% adults, 11% yearlings, and 10% foals. A sex ratio of 53 males:47 females was found. Population size was estimated to be 240 individuals, with an annual rate of increase of 7% based on a 3% mortality rate and a 10% recruitment rate of juveniles into the adult population. While not as high as the rates of increase found for other feral burro populations, the present increase rate of 7% will cause the feral burro population on St. John to double by 1996...

At this time the feral burro population does not seem to be having a serious effect on the tropical forest ecosystem of St. John. However, if the population continues to grow, irreversible damage could be inflicted upon the vegetation via overgrazing and trampling. Soil erosion may be accelerated as well."

Ruffner, George A., and Steven W. Carothers. 1982. Age structure, condition and reproduction of two *Equus asinus* (*Equidae*) populations from Grand Canyon National Park, Arizona. Southwestern Naturalist 27(4):403-411.

ABSTRACT: "Sixty-three animals from 2 isolated burro herds in Grand Canyon National Park were autopsied. Significant differences in age structure and body condition were found when the 2 populations were compared. Differences in female reproductive rates were not significant. However, the younger herd which was in better condition had a higher recruitment rate (17% versus 11%). Earliest female reproductive activity was observed at 1-2 years, and parturition took place in spring and early summer. We suggest that demographic differences between the 2 populations result from differing habitat quality and previous burro reduction programs of the National Park Service."

Ruffner, George A., Steven W. Carothers, James W. Jordan, and Arthur M. Phillips III. 1977. Diets of feral burros (*Equus asinus*) from the Bedrock Canyon area, Grand Canyon National Park, Arizona. Final research report to National Park Service, Grand Canyon National Park. 14 pp.

ABSTRACT: "Twenty-three species of plants were identified in the July diets of feral burros inhabiting the Bedrock Canyon study area. Eight species comprised almost 77% of the diet. Grasses were the most important component of July burro diets, followed by browse and forbs.

Thirteen species of plants, not encountered on vegetation transects, constituted 50.9% of the July diet of feral burros in the study area, indicating the highly selective nature of burro foraging. These findings suggest that feral burros did not utilize forage resources in relation to their availability. Feral burros may locally extirpate preferred plant species as a result of their selective foraging habits and the fragile nature of the plant communities in the arid habitats they occupy.

Our data and that from previous studies indicate that diets of feral burros are influenced by the composition of vegetation within an area. Although burro diets are somewhat selective within a given habitat type, these animals exhibit a wide tolerance for a variety of forage and habitats."

Russo, J. P. 1973. Burro food habits and competition. Prepared for the National Advisory Board on Wild and Free-roaming Horses and Burros. Arizona Department of Game and Fish. 8 pp.

ABSTRACT: The author uses the results of 10 studies in different geographical areas to give evidence that direct competition exists between feral burros and desert bighorn sheep and the desert deer. These 3 [species] utilize many of the same forage plants, many of the same water places and inhabit much of the same habitat. The author recommends control of feral burros to insure proper conservation of the range. (from Zarn et al., 1977).

Russo, J. P. 1956. The desert bighorn sheep in Arizona. Arizona Department of Game and Fish. 153 pp.

ABSTRACT: "Bighorn sheep range is approximately 1/3 of Arizona... Early accounts of bighorn sheep in Arizona are few and are mentioned only briefly in historical literature... Animals competing with bighorns were investigated to determine the degree of range deterioration for which each species was responsible and the economic importance of each animal." A discussion of management recommendations is included.

Saint John Jr., Kenneth P. 1965. Competition between desert bighorn and feral burros for forage in Death Valley National Monument. Desert Bighorn Council Transactions 9:89-92.

ABSTRACT: A brief, generalized review paper on burro and bighorn ecology and competition between them. Most information is from Browning (1960), McKnight (1958), and Welles and Welles (1961) which are all cited in this bibliography.

Sanchez, Peter G. 1974. Impact of feral burros on the Death Valley ecosystem. California-Nevada Wildlife Transactions :21-34.

ABSTRACT: The author discusses feral burros in Death Valley National Monument. His paper covers topography and vegetation, wildlife, burro impacts, competition with native animals, vegetation changes, springs, burro control activities, and management considerations. He concludes: "Damage by feral burros is 1 of a number of man-caused problems affecting the integrity of

a natural ecosystem in Death Valley. To be effective, other habitat management projects such as restoration of former wildlife habitat, rehabilitation of old mining scars, relief of human impact by recreational activity and others, cannot be successful if destructive influences remain. For example, it is of no benefit to bighorn to rehabilitate a spring formerly used by them if burros will move in. It is impractical to revegetate an abandoned mining road if burro impact negates management's efforts. For restorative actions to be assured reasonable success, such actions must be delayed until a primary destructive force is rendered inoperative. If burro control is unacceptable, the public must accept the ecological fact of life that is reached and native populations will continue to decline significantly. In the long term, this disappearance of some native species can be expected." (from Zarn et al., 1977).

Schmidt-Nielsen, Knut. 1964. Desert animals: physiological problems of heat and water. pages 81-93. Oxford University Press.

ABSTRACT: "The donkey has not been much used as an experimental animal and the generalizations given below are tentative because they are mostly based on observations of a single animal. The donkey has, when no water is used for heat regulation, a rate of water expenditure of about 2.5 times that in the camel. In summer, when water is used for heat regulation, the rate is 3 to 4 times as high as in the camel. The main reasons for the higher rate of water loss in the donkey are a) the fluctuations in body temperature are smaller than in the camel, b) the fur coat is thinner, and c) the behavioral adaptations which reduce heat gain are not as extreme. The donkey, like the camel, has an exceptional tolerance to dehydration of the body, being able to withstand a water loss of 30% of the body weight. The donkey eliminates rather large amounts of feces because the food is not as well digested as in ruminants. The water content of the feces is also relatively high, resulting in a fecal water loss some 3 times that in the camel. The available information indicates that plasma volume is relatively well maintained as dehydration progresses. This may be 1 of the explanations for the high tolerance to water depletion. The drinking capacity of the donkey is impressive, it can ingest in a few minutes more that 25% of its body weight in water. The drinking seems adjusted to a restoration of the water content to the normal level, and over-hydration has not been observed."

Seegmiller, Richard F., and Robert D. Ohmart. 1981. Ecological relationships of feral burros and desert bighorn sheep. Wildlife Monographs 78:1-58.

ABSTRACT: "The ecological relationships of feral burros and desert bighorn sheep in the Bill Williams Mountains, Arizona, were studied from May 1974 through June 1975 to assess possible competitive interaction.

Burro population estimates... were from approximately 60 to 90 individuals. Natural mortality in burros appeared low, while annual natality was estimated to

be from 20 to 23%. From a cumulative count, at least 17 bighorn sheep occupied the study area.

The movements and distributions of burros and bighorn sheep were restricted to close proximity of permanent water and growing riparian and cultivated vegetation from May through October... Both species moved farther from the river from November through April.

Annual home ranges of burros averaged 19.2 km^2 (range: 8.8-50.1 km^2). Burro winter-spring home ranges were significantly larger than those in summer...

Burros occupied a large proportion of bighorn sheep range during June through October 1974 (65%), November 1974 through March 1975 (100%), and April 1975 through June 1975 (85%). The foothill habitat type was the most widespread type near the river and was used predominantly by burros during all seasons.

Fecal analysis revealed that the annual burro diet consisted of 22% grasses and sedges, 33% forbs, 40% browse, and 5% unknowns, while the annual bighorn diet consisted of 8% grasses, 31% forbs, 54% browse, and 7% unknowns. The number of plant species used in common, proportional to the total number of plants eaten by both burros and bighorn sheep, averaged (weighted on an annual basis by season) 47%. Indexes of dietary and habitat overlap... averaged 47 and 51%, respectively. In areas of sympatry, burros were estimated to consume roughly from 1.5 to 2.0 times as much of shared forages as the bighorn sheep population. Six of the 10 major plants consumed by burros and bighorn sheep were shared and comprised 59 and 46% of burro and bighorn sheep diets, respectively. The annual forb, Indianwheat [*Plantago* spp.], was preferred by both...

Burro-bighorn sheep interference competition for access to either food or water was not observed. Both were seen foraging in close proximity (10 m) and seemingly showed no concern for the other's presence.

The monthly mean group sizes of burros varied little from the annual average of 4.7 individuals. Burros were seen most frequently in unstable dominant jack herds.

The high degree of dietary and habitat overlap documented in this study could not be interpreted as demonstrating burro-bighorn sheep competition for food in the strictest sense, because it was not known what factors in the environment were most limiting to the burro and bighorn sheep populations. However, we conclude from both empirical data and theory that burros and desert bighorn sheep are limited by the fraction of the total vegetative biomass that is of sufficient nutritive value and digestibility for growth and reproduction. From that, the obvious depletion by burros of several forages shared with bighorn sheep suggested that exploitation competition between the 2 species either was occurring or was imminent. The burro's larger population size, more rapid rate of increase, and cecal digestive system, the latter of which allows subsistence on a larger segment of the vegetation biomass (i.e., lower quality, more fibrous forage), indicate that the burro would be the superior competitor. Thus we predict that, following competitive equilibrium, the bighorn sheep population would be relegated mainly to surviving in the most rugged habitats

that could not be exploited as efficiently by burros and, during the summer, at the edges of the cultivated fields that provide an abundant supply of green forage adjacent to rugged escape terrain and permanent water.

Uncontrolled growth of the burro population in the Bill Williams Mountains is predicted to reach equilibrium only after they further deplete the vegetational cover over the landscape and reduce the population of desert bighorn sheep, and possibly other native fauna."

Seegmiller, Richard F., and Robert D. Ohmart. 1976. Feral burro-desert bighorn sheep relations, Bill Williams Mountains, Arizona. Transactions of the 2nd North American Wild Sheep Conference 1:35-37.

ABSTRACT: "Eight months, spanning 1 year, were spent observing and photographing feral burros and desert bighorn sheep in the Bill Williams Mountains, Arizona. Movements of both burros and bighorns during the cooler months extended farther from the Bill Williams River and generally encompassed a larger area than during the warmer months. Greatest interspecific overlap in habitat use occurred during January through March on long steep slopes extending from high mesas, peaks and ridges and during April through June in Foothill habitat. Forage observations and fecal composition analysis showed considerable interspecific overlap. Burro-bighorn interactions at watering sites in summer and during the bighorn lambing season were not observed, although both were seen in close association shortly after lambing, with young lambs present. Estimates of burro population numbers and annual reproduction rates exceeded those of bighorn sheep."

Seegmiller, Richard F., and Robert D. Ohmart. 1975. Feral burros within desert bighorn habitat. Desert Bighorn Council Transactions 19:45.

ABSTRACT: "Burro movements varied seasonally. In summer they were within 3 to 4 miles of the river, and in winter they ranged as far as 8 miles from the river. No burro-bighorn interactions were seen during the summer at water or during the lambing season, although both species were seen in close association. Based on field observations, diets of burros and bighorn overlapped markedly in all seasons. Both species relied principally upon the annual herbaceous layer, especially Plantago insularis."

Short, C. E., and P. R. Welch. 1965. Observations on the effects of a fertility management program on the fertility of the burro. Veterinary Medicine 60:634-636.

ABSTRACT: "A 3 year study to evaluate the effects of a fertility management program in a herd of 125 female burros indicated that the low fertility level and irregular estrous cycle of the burro contribute to breeding problems. Treatment

of infected burros with Mixed Equine Bacterin (Norden), Furacin solution (Eaton), and Valsyn gel (Eaton) increased the probability of conception and decreased the mortality rate of newborn foals."

Slade, Larry M., and E. Bruce Godfrey. 1982. Wild horses: *Equus caballus* and allies. pages 1089-1098. *in* Wild animals of North America: biology, management, economics. Johns Hopkins University Press.

ABSTRACT: While the chapter deals primarily with wild horses, the following excerpts pertain to burros:

"Few Issues associated with wild horses at the present time are more widely disputed by various interest groups than estimates of population size. The Wild Horse and Burro Act of 1971 (PL-92-195) was passed basically to save a species of animal that was near extirpation. Yet less than 5 years later, other interest groups were complaining that populations were expanding at alarming rates. While these divergent opinions were expected, they were commonly not based on scientifically defensible estimates of population. As a result, considerable controversy still exists today. This controversy represents 1 of the major reasons for establishment of the research program suggested in the Rangeland Improvement Act of 1978 (PL 95-514)....

[Table 55.1 - Bureau of Land Management wild horse and burro inventory estimates of population]...

The grazing preference of horses and their year-round use of most ranges suggest that forage competition with other species can become severe when forage supplies are scarce. Perhaps the prime area of agreement concerns the ability of wild burros to dominate scarce water supplies in the U.S. Southwest. This factor is generally accepted as being detrimental to populations of desert bighorn sheep...

The BLM oversees...nearly 22 times as many burros as the Forest Service....The Wild Horse and Burro Act of 1971 (PL-92-195) changed the status of wild horse and burro populations."

Sleznick Jr, Jim. 1963. The bighorn sheep of Lake Mead National Recreation Area. Desert Bighorn Council Transactions 7:58-60.

ABSTRACT: Forage competition between burros and bighorn may occur in washes at times, but generally the bighorn utilize the less accessible canyon walls and rimrock, while the burros use the flatter land farther from the lake.

Smith, A. E. 1968. An approach to burro management in California. Desert Bighorn Council Transactions 12:59-62.

ABSTRACT: "An interagency effort has started in California to develop a management plan for the feral burro. Involved are both State and Federal

agencies. The background and approach toward this work is presented. The goal is better resource management on the public lands that will improve conditions for the burro, wildlife, livestock and the range."

Smith, A. E. 1969. Burro problems in the Southwest. Desert Bighorn Council Transactions 13:91-97.

ABSTRACT: "A survey was made of current burro problems in the southwestern United States, of the steps that are being taken to correct them, and of the studies which are being conducted." The survey was in the form of a standard questionnaire sent to the National Park Service, Forest Service, Bureau of Sport Fisheries and Wildlife, 23 wildlife refuges, 6 state offices of the Division of Wildlife Services, 6 state wildlife agencies, the Bureau of Land Management, and 41 colleges, institutes, museums, and experiment stations; brief summaries of the responses are included. With the exception of the National Park Service and a few National Wildlife Refuges, "there is an apparent lack of specific information on burros and related problems. Basic knowledge of the species has increased very little in the past ten years. Detailed inventories, studies, and management plans are needed."

Stromberg, M. W., R. L. Kitchell, E. A. Usenik, and J. M. Lagerwerff. 1962. Electrocorticographic patterns in normal pigs and burros. American Journal of Veterinary Research 23:737-743.

ABSTRACT: "A series of electrocorticograms recorded from both mature and immature pigs, and mature burros, appeared to be generally similar to electrical activity recordable from the cortex of other mammals. Groups of waves of 3- to 6-per-second frequency in the ECG patterns of the relaxed burro appeared to be unique. Activity in the alpha frequency range such as may be recordable from man was observed in the pig but not in the burro. Sleep patterns in both the big and burro were characterized by marked slowing and increased amplitude. Electrical activity similar to sleep spindles was recorded from the burro. Photo flicker response (cortical driving) was usually easy to demonstrate in the burro but less so in the pig."

Sumner, Lowell. 1959. Effects of wild burros on bighorn in Death Valley National Monument. Desert Bighorn Council Transactions 3:4-8.

ABSTRACT: General information on burro sightings at water sources in the Cottonwood and Panamint mountains. It is mentioned that *Atriplex canescens* is a burro food that is lightly used by bighorn.

Sumner, Lowell. 1953. Special report on the status of wild burros and bighorn, Death Valley National Monument. Report on file at NPS/DVNM dated 27 May 1953. 4 pp.

Thomas, Heather Smith. 1979. The feral burro. pages 176-189. *in* The wild horse controversy.

ABSTRACT: A general narrative about burros on public lands and the damage that they cause. Non-technical in nature and generally not well referenced.

Thoms, Ralph E., and Daniel G. Brown. 1961. Response of burros to neutron-gamma radiation. Health Physics 6(1/2):19-26.

ABSTRACT: "The response of burros to neutron-gamma radiation was studied. Seven animals received 180 rads (145 rads n, 35 rads gamma) at a rate of 6 rads per min. The death of 2 burros at this dose level was unexpected. The clinical symptoms of these animals resembled those of central nervous system damage, heretofore seen with larger doses and much higher dose rates. The 5 survivors exhibited symptoms of neurological derangement but to a much lesser degree. The interval between exposure and maximum depression of leukocytes was 1 week, a shorter period than has been recorded in other burro studies. The initial rise in number of neutrophils and the depression of lymphocytes followed previously observed patterns. Epilation began as expected; however, the delayed epilation reported here is without recorded precedence in this species. There is an indication of a weight-response relationship to neutron-gamma irradiation in the burro. A comparison to the hematological response of man and burros to similar amounts of neutron-gamma radiation is presented."

Tomkiewicz Jr., S. M. 1979. Heterothermy and water turnover in feral burros (*Equus asinus*) of the desert southwest. M.S. thesis, Arizona State University.

ABSTRACT: "Body temperature (T_B) and subcutaneous temperature (T_S) of 5 free-ranging and 15 captive burros were monitored by temperature sensitive implants. T_B and T_S were related to environmental parameters and activity. Tritiated water turnover rates were monitored on 2 free-ranging and 12 captive burros. Relationships between season, age and body weight were examined.

Burros exhibited a pronounced heterothermy (35.0 - 41.6 °C). Mean T_B was lower in free-ranging burros than in captive burros. In both free-ranging and captive burros, T_B was dependent on time of day and air temperature (T_a). Males maintained consistently lower T_B (mean = 36.5 °C) than females (mean = 38.2 °C) in summer.

During summer, burros remained quiescent throughout most of the day and were active nocturnally. Males engaged in more strenuous activities during

periods of maximum summer heat load than did females. Fighting or copulation resulted in a rapid increase in T_B of males (0.1 °C/minute).

During winter, activities were not restricted during the daytime and burros were observed at greater distances from permanent water. A sexual difference in T_B did not exist in winter.

Water turnover rates were higher for burros in summer than in winter. Absolute water loss increased with age and body weight during summer and winter. Weight specific water loss increased with age and weight in summer; however, in winter, weight specific water loss was lower in colts than adults.

An [generalized conceptual] ecophysiological model [based on water availability and use] was developed to explain the breeding biology of feral burros in the desert southwest."

Turner Jr., Jack C. 1973. Water, energy and electrolyte balance in the desert bighorn sheep, *Ovis canadensis*. Ph.D. dissertation, University of California-Riverside. 138 pp.

ABSTRACT: A desert bighorn sheep study in the Santa Rosa Mountains of the Sonoran Desert in which corralled animals "were used to determine minimal water and energy requirements, seasonal changes in body fluid distribution and the effects of water deprivation on food consumption, body temperature, elimination and excretion, and the distribution of body fluids." Water metabolism, electrolyte metabolism, nutritive energy metabolism, and water deprivation effects data are compared with similar data on other desert species collected by other researchers.

"Controlled daytime hypothermia and its relation to the water economy of desert animals has proven significant to the camel, donkey, several East African ungulates, and some breeds of domestic sheep. The bighorn... also has a labile body temperature."

"The kidney has been shown to play not only an important role in water conservation but also in regulation of ions in most desert species [references]. Under conditions of water deprivation and environmental heat load, these mammals reduce the volume and increase the osmotic concentration of urine excreted. Except under conditions of diuresis, small amounts of urine... were lost from the bighorn... This is in contrast to domestic sheep, the camel, the burro, and many African bovids who produce copious quantities of urine except when stressed with dehydration... [T]he ability of the bighorn to excrete concentrated urine is exceeded only by a few desert rodents. Even the burro and camel fall short of the bighorn. The effects of dehydration on the urine concentration and total electrolyte budget of captive bighorn reflect trends found in many other large desert animals, but are generally more pronounced... Urinary concentrations of sodium are much lower in ruminants not experiencing water deprivation. This appears to be incidental to their herbivorous diet." The water content of feces in the burro ranges from 1.81 to 2.45 g H_2O/g (Yousef, Dill, and Mayes, 1970). Bighorn sheep feces ranges from 0.83 g H_2O/g for a dehydrated animal to 1.8 g H_2O/g for a hydrated animal. Urine flow for

dehydrated burros is 0.58 l/day at 1.4 osm./l concentration; a hydrated animal produces 1.35 l/day at 1.0 osm./l. Bighorn range from 0.08 l/day at 3.9 osm./l dehydrated to 1.09 l/day at 0.7 osm./l hydrated.

Ruminants, in general, show reduced digestive efficiency when maintained on diets high in crude fiber as compared to being fed a low percentage of crude fiber." The digestive efficiency of the bighorn is greater "than the donkey (41% apparent digestibility) but these differences relate more directly to ruminant vs. non-ruminant digestion (Maloiy, 1970). Food intake of dehydrated captive bighorn does not show an appreciable decrease as in the burro (Maloiy, 1970)... The rise in the bighorn's apparent digestibility when experiencing dehydration is also shared with the donkey (Maloiy, 1970) and the eland.

Tolerance to dehydration amounting to 20% loss of body weight is shared by many desert animals: the camel [references], the burro (Yousef et al., 1970), the guanaco and the bighorn... Reductions in blood volume have been regarded as the main cause of explosive heat rise and death in the desert... The burro and the camel, unlike the bighorn, maintain a relatively constant plasma volume under dehydration (Yousef et al., 1970). The greatest contribution of water from captive bighorn was from the ECFV. The ICFV was altered only slightly... This is a departure from that anticipated.

The burro, camel and other desert ruminants generally lose similar amounts of water from their respective ECFV and ICFV. Although the camel, bighorn, donkey, guanaco, and merino are capable of consuming large quantities of water at 1 time, rarely is rehydration complete after 1 drinking."

Turner, Monica G. 1984. Habitat utilization by burros in Virgin Island National Park. Journal of Wildlife Management 48(4):1461-1464.

ABSTRACT: Burro utilization of 5 habitats was sampled on St. John; these were 1) moist forest, 2) mangrove, 3) dry cactus/woodland, 4) beach, and 5) grassy flats. Habitat use was measured by counting the number of scat piles along each trail and the number of burro trails leading from either side of each trail; grass density was also measured. Burros preferentially utilized dry regions, a fact mostly explained by the abundance of grasses in these habitats relative to the moist regions. Superior shelter areas and ease of travel also seem to contribute to the preferential use of dry habitats.

U.S. Congress. 1973 (15 August). Federal Register 38:22002.

ABSTRACT: The objective of these regulations is to provide criteria and procedures for protecting, managing, and controlling wild free-roaming horses and burros as a recognized component of the public land environment.

U.S. Congress. 1977 (25 January). Proposed rules: wild free-roaming horse and burro management. Federal Register.

ABSTRACT: "This proposed rule amends 43 CFR Part 4700, "Wild Free-Roaming Horse and Burro Protection, Management, and Control", to implement Section 9 of the Wild Free-Roaming Horse and Burro Act (16 USC 1331-1340) as provided by Section 404 of the Federal Land Policy and Management Act of 1976 (43 USC 1701). This amendment to the Wild Free-Roaming Horse and Burro Act authorizes the use of helicopters or, for the purpose of transporting captured animals, motor vehicles in administering the provisions of the Wild Free-Roaming Horse and Burro Act, as amended. The provision also directs that the use of helicopters and motor vehicles be undertaken 1) in accordance with humane procedures prescribed by the Secretaries of the Interior and Agriculture, 2) under the direct supervision of the appropriate Secretary or a duly authorized officer or employee of their Departments, and 3) only after a public hearing."

U.S. Congress. 1959. Public Law 86-234. Statutes at Large 73:470.

ABSTRACT: An amendment to U.S. Code, Title 18, Chapter 3, which prohibits the use of aircraft or motor vehicles to hunt wild horses or burros on federal land.

U.S. Congress. 1971. Public Law 92-195. Statutes at Large 85:649-651.

ABSTRACT: A law requiring protection, management and control of wild free-roaming horses and burros on public lands. All such animals are placed under the jurisdiction of the Secretary of the Interior or the Secretary of Agriculture.

U.S. Congress. 1978 (16 February). Wild free-roaming horses and burros: uniform marking procedure. Federal Register.

ABSTRACT: This notice announces the use of the International Alpha Angle System for marking excess wild free-roaming horses and burros. There is a need to clearly identify excess animals acquired by private citizens under the Adopt-a-Horse program. This marking will protect and identify animals under the custody of private citizens and help prevent disposal in violation of the law.

U.S. Congress, House of Representatives, Committee on Interior and Insular Affairs. 1971. H.R. 795 and H.R. 5375, legislation to authorize the protection, management, and control of free-roaming horses and burros on public lands. Hearing before a subcommittee of the Committee on Interior and Insular Affairs, House of Representatives, on H.R. 795, H.R. 5375 and Related Bills, 92nd Congress, 1st session.

ABSTRACT: Testimony concerning legislation designed to authorize protection, management, and control of free-roaming horses and burros on public lands.

U.S. Congress, House of Representatives. 1971. Protection, management, and control of wild free-roaming horses and burros on public lands. House Report 681 to accompany S. 1116, 92nd Congress, 1st session.

ABSTRACT: The conference report concerning the disagreement between the House and the Senate regarding S. 1116, a bill to require the protection, management, and control of wild free-roaming horses and burros on public lands.

U.S. Congress, House of Representatives. 1971. Protection, management and control of wild free-roaming horses and burros on public lands. House Report 480 to accompany H.R. 9890, 92nd Congress, 1st session.

ABSTRACT: The House report concerning H.R. 9890, a bill to require the protection, management, and control of wild free-roaming horses and burros on public lands.

U.S. Congress, House of Representatives. 1959. Amendment of Title 18, United States Code, to prohibit the use of aircraft or motor vehicles to hunt certain wild horses or burros on land belonging to the United States. House Report 833 to accompany H.R. 2725, 86th Congress, 1st session.

ABSTRACT: The House report concerning H.R. 2725, a bill to prohibit the use of aircraft or motor vehicles to hunt feral horses or burros on lands belonging to the United States.

U.S. Court of Appeals, Ninth Circuit. 1988. Animal Protection Institute of America versus Hodel, Secretary of the U.S. Department of the Interior, et al.

ABSTRACT: The court affirmed an injunction holding that the Secretary of the Interior violated the Wild Free-Roaming Horses and Burros Act. The Wild Free-Roaming Horses and Burros Act was amended to require that the adopters participating in the Interior Department's "adopt-a-horse" program be a "qualified individual" who could "assure humane treatment and care" for the animals. The Animal Protection Institute of America (APIA) claimed that the Secretary transferred title to adopters knowing that they intended to use the animals for commercial purposes once they received title after caring for the animal for 1 year. The district court granted the APIA injunctive relief, holding that when the Secretary has knowledge of such an intent, he cannot transfer title to that adopter.

U.S. Congress, Senate. 1983. Amending the Wild Free-roaming Horses and Burros Act of 1971 (16 U.S.C. 1331-1340), as amended: report together with additional and minority views. Senate Report No. 98-339. 32 pp.

ABSTRACT: The full text of S. 457, the 1983 [3rd] amendment to Public Law 92-195. Some of the stated purposes of this bill are to "Recognize that wild horse and burro populations are thriving and not in danger of disappearing... Recognize that it is the intent of Congress to maintain... a population of wild horses and burros consistent with the principle of multiple use... [and] Authorize humane and supervised use of helicopters and motor vehicles to remove horses and burros from lands under the administration of other Federal agencies."

U.S. Congress, Senate. 1971. Protection, Management and Control of Wild Free-Roaming Horses and Burros on Public Lands. Senate Report 242 to accompany S. 1116, 92nd Congress, 1st session.

ABSTRACT: The Senate report concerning S. 1116, a bill to require the protection, management, and control of wild free-roaming horses and burros on public lands.

U.S. Congress, Senate Committee on Interior and Insular Affairs. 1974. Wild free-roaming horse and burros act of 1971: the administration of Public law 92-195--The Wild Free-Roaming Horse and Burros Protection Act of 1971. Hearing before the Committee on Interior and Insular Affairs, United States Senate, 93rd Congress, 2nd session. 140 pp.

ABSTRACT: The proceedings of a hearing "to receive testimony from administration witnesses regarding their actions and intentions under Public Law 92-195... The intent of the Congress in adopting this act is clear--these animals are to be protected--not managed to extinction. Concern has been expressed that the administration is, in fact, using the act to confine these horses and burros or to rid the range of them altogether... There is justifiable concern that congressional intent to preserve these animals... is not being fully followed by those charged with administration of the law. [from opening statement by Senator H.M. Jackson]" Included are full texts of the Public Law 92-192, Senate Report 92-242, House Reports 92-480 and 92-681, plus administration testimony, reprints of 6 newspaper articles, and 6 letters, all concerning the administration of Public Law 92-195. The Senate and House Reports discuss the bill and present a legislative history.

U.S. Congress, Senate Committee on Interior and Insular Affairs, Subcommittee on Public Lands. 1971. Protection of wild horses and burros on public lands: S. 862, S. 1116, S. 1090, and S. 1119 to authorize the Secretary of the Interior

and the Secretary of Agriculture to protect, manage, and control free-roaming horses and burros on public lands. Hearing before the Subcommittee on Public Lands of the Senate Committee on Interior and Insular Affairs, Senate, on S. 862, S. 1116, S. 1090, and S. 1119, 92nd Congress, 1st session. 193 pp.

ABSTRACT: The full texts of the 4 bills, Departmental reports explaining them, and 36 statements of testimony before the committee. Also, 39 representative letters and reprints of 12 newspaper articles, all concerning this legislation to authorize protection, management, and control of free-roaming horses and burros on public lands.

U.S. Congress, Senate. 1959. Wild Horses and Burros. Senate Report 802 to accompany H.R. 2725, 86th Congress, 1st session.

ABSTRACT: The Senate report concerning H.R. 2725, a bill to prohibit the use of aircraft or motor vehicles to hunt feral wild horses or burros on lands belonging to the United States.

U.S. Department of the Interior, and U.S. Department of Agriculture. 1988. Administration of the Wild Free-Roaming Horse and Burro Act: 7th report to Congress, 1988. 32 pp.

ABSTRACT: A statement of general policy, notes on the creation of the Wild Horse and Burro Advisory Board, reviews of wild horse and burro management, maintenance, research, and marketing contracts, removal and disposition of excess wild horses and burros, litigation, and funding and expenditures. Appendices include Board recommendations, Bureau of Land Management [BLM] and Forest Service [FS] population estimates, summaries of BLM and FS accomplishments during FY 1986-7, and a listing of wild horse and burro herd areas administered by the BLM.

U.S. Department of the Interior, and U.S. Department of Agriculture. 1974. A report to Congress by the Secretary of the Interior and the Secretary of Agriculture on administration of the Wild Free-roaming Horse and Burro Act, Public Law 92-195. 58 pp.

ABSTRACT: The report fulfills section 10 of Public Law 92-195, the Wild Free-Roaming Horse and Burro Act. The review presents the progress made and the problems encountered by these 2 agencies in their administration of wild horses and burros. It also contains considerations for legislative changes which will assist the agencies in meeting the intent of amendments to the 1971 act in a more effective, humane, and cost-conscious manner. Two amendments to the 1971 act are being considered. The 1st amendment would permit the use of aircraft or other motorized vehicles to be used for the

protection, management, and control of wild horses and burros. The use of such equipment would be in accordance with humane procedures prescribed by the 2 secretaries. The 2nd amendment would authorize the 2 secretaries to sell or donate excess animals to private individuals or organizations. Extensive appendices. (from Zarn et al., 1977).

Wagner, Frederic H. 1983. Status of wild horse and burro management on public rangelands. Transactions of the 48th North American Wildlife and Natural Resource Conference 48:116-133.

ABSTRACT: A brief review of wild horses and burros in North America including history, distribution, dietary preferences, forage consumption rates, habitat preferences, problems of census, and rates of herd increase. The balance of the paper deals with various management dilemmas and practices.

Walker, M.T. 1978. Ecological similarities between feral burros and desert bighorn sheep, Black Mountains, northwestern Arizona. M.S. Thesis, Arizona State University.

ABSTRACT: "The primary objective of this study ws to examine selected ecological relationships between feral burros (Equus asinus) and desert bighorn sheep (Ovis canadensis nelsoni) in the Black Mountains, Arizona; concomitantly data were gathered on cattle (Bos taurus) and desert mule deer (Odocoileus hemionus). A total of 15 months were spent collecting field data between June 1976 through September 1977. A population of 456 burros was estimated by the use of a ratio estimator. Direct counts of bighorn sheep from helicopter surveys indicated approximately 35 sheep in the study area. Burro and bighorn sheep annual recruitment rates of 23 and 47 percent, respectively, were estimated from obtained age ratio data.

Seasonal distributions of burros always exceeded those of sheep. Both sheep and burro distributions were greatest during the cooler months (October through May) and both species, in addition to deer, were most frequently observed at or very near (0.0-0.8 km) permanent water sources during the warmer months (June through September).

Burros predominantly used foothills during all seasons except winter (December through February), whereas sheep predominantly used butte slopes during all seasons except summer (June through August). In areas of sympatry, greatest overlap in habitat use occurred during the winter and spring (March through May) months on butte slopes. Division of the study area into specific habitat types revealed that burros used low, gentle terrain (below 671 m elevation and less than 40 percent slope), while sheep used high, steep terrain (above 671 m and greater than 40 percent slope). Deer were observed using washes most often (48 percent of total observations) during the summer months and mes tops most often (64 percent of total observations) during the winter months. Temperature, amount of precipitation and habitats proximal to

permanent water sources were factors determined to influence seasonal habitat use.

Of the 59 plant species utilized by burros, 45 (76 percent) were also used by sheep, 37 (63 percent) by cattle, and 14 (24 percent) by deer. Woolly plantain (Plantago insularis), globe mallow (Sphaeralcea sp.), and red brome (Bromus rubens) were the plant species most commonly taken by the four vertebrate species. Burro and cattle diets consisted primarily of forbs (47 and 53 percent, respectively) while those of sheep and deer consisted primarily of browse (49 and 96 percent, respectively).

Burro-bighorn-cattle-deer aggression at permanent watering sites was not observed during the period of study. Of the five permanent water sources studies, only in one instance was "water fouling" subjectively observed and burros were suspected of being a contributing factor.

Although the percent of saturation of dissolved oxygen was not measured as an indication of "foulness" it was however measured monthly to indicate differences in relative water quality for three permanent water sources. Water at two of these sources exhibited a decrease in dissolved oxygen content from May 1977 to August 1977. The factor most responsible for these decreases was the rate of water flow at the spring heads.

These data indicate substantial ecological overlap between burros and sheep in addition to moderate dietary overlap between cattle and burros, and cattle and sheep. This and other informmation procurred during this study could, when combined with carrying capacities, result in a proper range-wildlife management program for the Black Mountains, Arizona."

Walters, James E. 1981. Movements and home ranges of feral burros on the Tonto Plateau, Grand Canyon National Park. *in* Proceedings of the 2nd Annual Conference on Scientific Research in the National Parks. U.S. Department of the Interior.

ABSTRACT: "From September 1977 to May 1979, the movements of feral burros on the Tonto Plateau have been monitored through sightings of animals fitted with color-coded collars and radio transmitting equipment. Data from 6 radio collars and 32 color-coded nylon collars has been plotted resulting in a pattern of movements and home ranges for the Tonto Plateau burro herd. These data demonstrate the continual use of major side canyons as year round habitation sites for burros on the Tonto Plateau area. Except for the activity of immature males, there seems to be relatively little lateral movement on the Tonto Plateau by this herd. Sightings of collared animals in the Lower Canyon herd area (River Miles 198 to 235) also indicate continued occupancy of major side canyons by specific members of the burro herds."

Walters, James E., and Richard M. Hansen. 1978. Evidence of feral burro competition with desert bighorn sheep in Grand Canyon National Park. Desert Bighorn Council Transactions 22:10-16.

ABSTRACT: "This report presents information on burro surveys in Grand Canyon National Park, and the relationship of burro and bighorn distributions. Food habits of burros were determined for 10 localities from fecal samples. Samples were also collected for mule deer and desert bighorn sheep from 6 of these localities. Data from these collections indicated a 52% overlap between diets of burros and bighorns and an overlap of 6-12% between burros and deer." Range competition and the use by burros of "un-burro-like" steep, rugged terrain is also discussed; in this case such unnatural use is determined by the distribution of vegetation in the Canyon.

Watkins, Kathleen A. 1976. Chemical composition and *in vitro* digestibility of feral burro forage. M.S. thesis, Arizona State University. 32 pp.

ABSTRACT: "Nine major forage species used by the feral burro (*Equus asinus*) in Lower Sonoran Desert habitat were analyzed for chemical composition and *in vitro* digestibility. Samples of *Acacia gregii*, *Ambrosia dumosa*, *Cercidium microphyllum*, *Hymenoclea salsola*, *Krameria grayi*, *Lycium andersonii*, *Plantago insularis*, *Pluchea sericea*, and *Prosopis juliflora* were collected in September, 1975 near Lake Havasu, Mohave County, Arizona. An additional sample of *Plantago insularis* was collected in February, 1976. Van Soest's detergent analyses were used to determine cell-wall constituents, hemicellulose, cellulose, lignin, and silica. Crude protein was determined by the Kjeldahl nitrogen method. Inoculum from a Holstein cow was used for *in vitro* fermentation of forages. Results indicated that [excepting February *Plantago*, an annual forb just beginning its year's growth] these forages are high in all fibrous fractions. [Cell-wall constituents ranged from 23.94% (February *Plantago*) to 68.71% (*Ambrosia*), hemicellulose from 7.78% (February *Plantago*) to 19.57% (*Lycium*), cellulose from 11.38% (February *Plantago*) to 34.36% (*Ambrosia*), and lignin from 2.31% (February *Plantago*) to 16.46% (*Lycium*)]. Silica content of the forages was low except in *Plantago* [which was subject to soil contamination]. The forages were generally low in [crude] protein [ranging from 3.76% (September *Plantago*) to 19.55% (February *Plantago*)]. *In vitro* fermentation indicated that these forages were not highly digestible. The mean *in vitro* true digestibility was 56.26% [and the range (excepting February *Plantago*) was 35.29% (*Lycium*) to 69.52% (*Pluchea*)]. The one exception was February *Plantago* which had an *in vitro* true digestibility of 89.39%.

[As a] summative equation developed by Deinum and Van Soest (1969) to predict the [*in vitro* true] digestibility of a forage by its chemical composition was not accurate for these forages, an equation was derived from regression analysis which accurately predicted the digestibility of the forages analyzed. Further studies would help to determine if this equation is applicable to a wider range of desert forages.

It is stressed that these results were based on one collection period in September [with the exception of *Plantago*]. Most species were in a dormant state, and 1975 was a particularly dry year. The [*in vitro*] true digestibility values reported here could thus be considered as minimum values."

Wauer, Roland H. 1973. Feral burro control program, Bandelier National Monument. National Park Service, Bandelier National Monument. 34 pp.

Wauer, Roland H. 1974. Feral burro management program for Bandelier National Monument. National Park Service, Bandelier National Monument, Santa Fe, New Mexico. 56 pp.

ABSTRACT: A plan "to restore and preserve the natural and cultural environment within Bandelier National Monument. In order to accomplish this, a program to reduce and control the feral burro population will be implemented, along with continuing research for the development of a long-range management and vegetation restoration plan." The article thoroughly discusses burro impact on the monument. (from Zarn et al., 1977).

Wauer, Roland H. 1961. Sheep-burro relationships in south Anvil Spring Canyon: burro survey report part II. Report on file at NPS/DVNM dated 3 July 1961. 9pp.

Wauer, Roland H., and H. H. Bozarth. 1961. Notes on burro survey of Butte Valley and vicinity, June 20-22, 1961. Report on file at NPS/DVNM. 4 pp.

Wauer, Roland H., and John G. Dennis. 1980. Impacts of feral burros upon the breeding avifauna of a pinyon-juniper woodland in Bandelier National Monument, New Mexico. pages 338-357. *in* Proceedings of the 2nd Conference on Scientific Research in the National Parks.

ABSTRACT: Two breeding bird populations were used as a basis for determining impact of feral burros upon a pinyon-juniper woodland environment at Bandelier National Monument, New Mexico. Data were obtained by Emlen transects on 2 adjoining mesas separated by Frijoles Canyon, a natural barrier to burros. Elevations, slopes, and dominant vegetation are comparable. The non-burro area (Frijoles Mesa) supported a breeding avifauna of 440 individuals, and the burro-used Frijolitos Mesa supported a breeding avifauna of 303.5 individuals per 40 ha, a 31% difference. The Frijoles Mesa avifauna provided significantly higher species diversity value (3.303 versus 3.111), higher evenness value (0.953 versus 0.924), greater standing crop biomass (15,669 g versus 8056 g), and greater consuming biomass (4294 g versus 2192 g). These data illustrate that the Frijolitos Mesa impact area is significantly limited in its ability to support an avian population typical of non-impacted pinyon-juniper woodlands of northern New Mexico, and that limitation is the result of the deterioration of the environment caused by feral burros.

Weaver, Richard A. 1974. Feral burro and wildlife. *in* Proceedings of the Vertebrate Pest Conference.

ABSTRACT: "Feral burro have caused devastating damage to the vegetation and soil which has resulted in a deterioration of the entire biota. Wildlife numbers have declined where there is competition with burro for food, water or space. The Department of Fish and Game made a burro study in conjunction with bighorn investigations. There are an estimated 3,400 free-roaming wild burro in California. They are found in 7 of the 14 bighorn study areas and have caused problems in each of these areas."

Weaver, Richard A. 1973. Burro versus bighorn. Desert Bighorn Council Transactions 17:90-97.

ABSTRACT: "Seven of 14 bighorn study areas in California have feral burro populations. These have created a problem in each of these areas. Burros compete directly with bighorns for food, space and also water if it is in short supply. Burros have damaged the vegetation and soil and have had a detrimental effect on the entire biota. Based on knowledge gained during bighorn investigations, the 1968 burro inventory was revised. The present estimated burro population for California is 3400 animals." Burro abundance, distribution, and impact on the habitat and wildlife are documented for each of the 7 study areas.

Weaver, Richard A. 1972a. Big game investigations: feral burro survey. Final Report Project W-51-R-17. California Department of Fish and Game. 14 pp.

ABSTRACT: "Seven of the 14 bighorn study areas in California have free-roaming feral burro populations. Burros have created a problem in each of these areas. They compete directly with bighorn for food, space and also water if it is in short supply. Burros have caused devastating damage to the vegetation and soil which has had a detrimental effect on the entire biota. With the knowledge gained during the bighorn investigations the 1968 burro inventory was revised. The present burro population is estimated at approximately 3400 animals in [California]."

Citing a National Park Service study in Death Valley National Monument: "[Vegetation] transects were made on 2 routes reaching about 8 km from the water... Radiating out from the water tank the vegetation and soil show an abundance of use and disturbance. The plants are either eaten or trampled while the disturbed soil is subject to wind and water erosion. Feral burros in the Wildrose area [of the Monument] have virtually eliminated certain species of plants for 1.6+ km from the water, including 4 species of grasses. Eight km away from water grasses have been seriously reduced. The study concludes that burros are not only damaging the plant community, but they also affect the animal community dependent on the plants."

Weaver, Richard A. 1972b. Conclusion of the bighorn investigation in California. Desert Bighorn Council Transactions 16:56-65.

ABSTRACT: "Feral burros are competing with bighorn and other wildlife in many places. We have determined and mapped the extent of burro range. Burro have increased their range since 1951 when a law to give them total protection was enacted. Sheep have declined in numbers as burro encroached on previously burro-free range. A location called Sheep Spring in the Providence Mountains was free of burro in 1953, the first time I visited it. Waterhole counts were made there during our investigations. Twenty of more burros are using the spring and have eliminated all perennial grasses near the springs. Sheep numbers have declined by 30% in this period of approximately 15 years. The burro is the dominant animal and bighorn will wait for burro to leave, or bighorn will leave if burro come in while they are drinking. This has been observed at the spring described above. Therefore, if there is insufficient water, there is direct competition for water. If a tinaja is the only source of water, burro have been known to totally usurp the water and then leave, but sheep are reluctant to leave their preferred habitat of good escape terrain. This problem has long been recognized (Dixon 1939) but it is not just a case of burro or bighorn. Welles said it best (Welles and Welles 1961): "for the sake of the entire biota, the burros must be controlled.""

Weaver, Richard A. 1972c. Desert bighorn sheep in Death Valley National Monument and adjacent areas. California Department of Fish and Game. 20 pp.

ABSTRACT: Competition between desert bighorn sheep occurs in the Death Valley National Monument and adjacent areas. The author observed bighorns and burros at water at the same time but his experience shows that "The burro is the dominant animal and bighorn will wait for burro to leave or bighorn will leave if burro come while they are drinking." Burro populations have increased in the subject area. (from Zarn et al., 1977).

Weaver, Richard A. 1959. Effects of burro on desert water supplies. Desert Bighorn Council Transactions 3:1-3.

ABSTRACT: At developed, man-made watering sites burros paw at leaky pipes until they are broken at a coupling, and can break down cement, masonry, and metal pools. Detritus accumulates in canyon bottoms from heavy burro traffic, choking diversions built to protect water developments, resulting in storm water, silt, and debris burying the development.

Weaver, Richard A., and John Hall. 1971. Desert bighorn sheep in southeastern San Bernardino county. California Department of Fish and Game. 26 pp.

ABSTRACT: Competition between desert bighorn sheep and feral burros occurs in southeastern San Bernardino county, California. Direct competition for food, water and space was reported. In the area mentioned on 1 side of the Colorado River where there is a small burro population, the sheep used water from the river. On the other side where burro numbers were great, sheep were never observed using the river. The authors state that "Burros are dominant and bighorn sheep will not challenge them even for water." (from Zarn et al., 1977).

Burros in the Whipple and Chemehuevi mountains are spreading to new areas and have almost eliminated perennial grasses where they range and take the available water. Burros have caused the disappearance of bighorn from the Whipples and are severely competing with the remaining bighorn in the Chemehuevis.

Weaver, Richard A., and J. L. Mensch. 1970a. Bighorn sheep in northwestern San Bernardino and southwestern Inyo counties. California Department of Fish and Game. 16 pp.

ABSTRACT: "Competition between sheep and burros [in northwestern San Bernardino and southwestern Inyo counties] appears to be mainly for food and space. Perennial grasses which have been shown to be a prime food for bighorn are depleted in many areas through burro overuse with secondary food plants being heavily used by burros. In addition, food plants in the vicinity of springs which are very important to sheep are overused and trampled by burros."

Weaver, Richard A., and J. L. Mensch. 1970b. Desert bighorn sheep in northern Inyo and southern Mono counties. California Department of Fish and Game. 9 pp.

ABSTRACT: "Competition with feral burros may be severe in the Hunter Mountain areas and in the lower elevations of the Inyo, Last Chance, Saline, and Nelson ranges [of Inyo and Mono counties]. These areas are or have been critical as wintering sites particularly during severe winters. Although not fully utilized at the present by bighorn, competition probably was much greater in the past and may have contributed to low [bighorn] populations at the present."

Weaver, Richard A., and Mensch J.L. 1969. A report on desert bighorn sheep in eastern Imperial county. California Department of Fish and Game. 16 pp.

ABSTRACT: Competition between desert bighorn sheep and feral burros occurs in eastern Imperial county, California. Observations showed that there was definite competition for water and probable competition for food around watering holes. "A reduction in the burro population would allow for a sizeable increase in the sheep population and may allow permanent sheep populations

in areas which are now only seasonally used because of lack of water." (from Zarn et al., 1977).

Weaver, Richard A., J. L. Mensch, and R. D. Thomas. 1969. A report on desert bighorn sheep in northeastern San Bernardino county. California Department of Fish and Game. 26 pp.

ABSTRACT: "Competition between bighorn sheep and feral burros was very evident in many portions of the area surveyed [in northeastern San Bernardino county]. Severe competition for food and space was observed in the western portion of the Granite Mountains, in the Foshay Pass area of the Providence Mountains and throughout the Woods mountains. Competition in these areas is already very severe and if left unchecked will probably result in further serious declines in bighorn populations. Burros are continually increasing their range and both species cannot be maintained at the present level."

Welles, Ralph E. 1962. What makes a valid observation? Desert Bighorn Council Transactions 6:29-40.

ABSTRACT: "For many years, statements have been made without proof regarding burros and their exact effect on sheep in Death Valley National Monument to the present time. There is no question that the burro is bad for vegetation, watershed and wildlife in general, but I cannot find anywhere a yardstick to measure specifically and exactly any reduction yet in the Monument population of bighorn because of burros. People, yes; burros, no... This statement was based not only on our own observations at that time, but reflected the consensus of opinion of all the field men who had participated in the 1955 census."

Welles, Ralph E., and Florence B. Welles. 1967. The status of the feral burro and wildlife water sources in Death Valley National Monument. Report on file at NPS/DVNM files dated 6 June 1967. 65 pp.

Welles, Ralph E., and Florence B. Welles. 1961a. The bighorn of Death Valley. U.S. Government Printing Office. 242 pp.

ABSTRACT: This study summarizes and analyzes 1643 hours of fieldwork done between 18 December 1954 and 1 March 1961. Feral burros are mentioned briefly in several places, generally with reference to their interaction with desert bighorn at waterholes. "...[T]he incredible mass of misinformation about the wild burro that has been accumulated and disseminated through highly respected channels was initially the result of the misreading of sign at waterholes. The obvious abundance of burro sign and the apparent lack of

bighorn sign in the vicinity led to a quick and specious conclusion that there was no bighorn sign present, that therefore bighorn did not utilize the water source, and that this failure was due to the fact that burros had somehow rendered it unusable for bighorn, thereby forcing them to abandon the entire area... The drinking, mating, [and] fighting activity of a band of half a dozen burros can obliterate a 6-month collection of sheep sign in 1 visit to a spring. During our... 1955 survey of "burro-fouled springs"... we visited 45 springs which were in constant utilization by burros and found only 1 contaminated by defecation... We found sheep tracks coming down to within 25 feet of the water, then vanishing in the loose earth which had been churned up by much shuffling of burro hooves.

[The burros] threat to bighorn survival is indirect, and present control methods are reducing the threat to a minimum. While all ecological wisdom urges the complete elimination of all exotic species from the biota, it cannot be argued that the burro is eliminating the bighorn, since healthy herds of both species are thriving together on some ranges and have done so for at least 25 years."

Welles, Ralph E., and Florence B. Welles. 1961b. The feral burro in Death Valley: summary. Desert Bighorn Council Transactions 5:32-33.

ABSTRACT: Burros and bighorn were observed feeding in the same areas in Death Valley National Monument, but with significant topographical barriers of differing relative ruggedness separating their respective sections of the foraging areas.

Welles, Ralph E., and Florence B. Welles. 1960a. The feral burro in Death Valley. Report on file at NPS/DVNM. 52 pp.

ABSTRACT: "There are probably less than half the number of burros originally believed to inhabit the monument area. Of the estimated maximum population of 900, we observed 154... The feeding habits and behavior of the burro are not as directly competitive with other wildlife as has been believed. In its preferred habitat the burro is not in significant conflict with other species... Burros and bighorns have been observed feeding in the same area, but with significant topographical barriers of relative ruggedness separating their respective sections of foraging area... The burro does not always totally destroy the cover for other species in spring areas. The watering habits and behavior of the burro are not as directly competitive or destructive as has been believed... The nocturnal watering habit of the burro lessens the direct competition between it and the diurnal bighorn... Without controls the burro population would logically be expected to exceed the carrying capacity of the range within a very short time... There are 2 important large animals in Death Valley National Monument, the bighorn and the burro. The bighorn, if it had been left alone, would have

"managed" itself, but people and the burro have arrived..." (from Zarn et al., 1977).

Welles, Ralph E., and Florence B. Welles. 1960b. Progress report on current Death Valley burro survey. Desert Bighorn Council Transactions 4:85-87.

ABSTRACT: An area 0.4 km long in Cottonwood Canyon is browsed heavily by both burros and bighorn. The burros primarily eat *Ambrosia dumosa*, while the bighorn seemed to favor *Bebbia juncea*. This divergence of food preference may be another indication of the possibility of coexistence between burro and bighorn.

Springs reported by earlier writers to be fouled by burros to the exclusion of bighorn were found to be clear and clean, though burros were using them. Bighorn were using some, but not others, for unknown reasons.

Welles, Florence B. 1955. Bighorn-burro survey, Death Valley National Monument. Report on file at NPS/DVNM dated 7-12 February 1955. 9 pp.

White, Leslie D. 1980. A study of feral burros in Butte Valley, Death Valley National Monument. M.S. Thesis, University of Nevada, Las Vegas, NV. 124 pp. (see following citation)

White, Leslie D. 1980. A study of feral burros in Butte Valley, Death Valley National Monument. Contribution number CPSU/UNLV 006/16. National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 124 pp.

ABSTRACT: "The estimated size of the feral burro population in Butte Valley, Death Valley National Monument, ranged from 300 individuals in summer to 75 individuals in winter. Estimated summer density was 3.8 burros/km^2 and is the highest density reported for any herd in Death Valley. The mean summer home range of males was 2.2 km^2, that of females 6.8 km^2. There was a significant difference between home range sizes. The mean yearly home range of both sexes was 9.9 km^2 and did not vary statistically between sexes. The realized rate of increase, r, during 1976-1979 was 0.012/year, substantially less than 0.18-0.29/year reported for other herds in the southwest. The herd has caused moderate to severe impact on the vegetation within 0.8 km of the major water source in the valley. Impact on vegetation beyond 0.8 km of the spring has been minor. Preference of forage is not based on caloric content, either between herbaceous and woody species or among woody species. Herbaceous species were preferred when available."

Wilding, J. L., A. W. Kimball, M. W. Whitaker, B. F. Trum, and J. H. Rust. 1952. Some blood values of the southwestern burro. American Journal of Veterinary Research 13:509-513.

Willson, Roscoe D. 1957. Will it be life or death for Arizona nightingales? Arizona Days and Ways Magazine (3):38-39.

ABSTRACT: This article was prompted by a bill introduced into the Arizona State Senate to protect wild burros in that state. The author states that the burros has been cited by biologists for competition with desert bighorn sheep but the same biologists report that the number of bighorn is steadily increasing and occasional hunting of bighorn is allowed. The only problem caused by burros is that they "frequently congregate around desert water holes, and for a time, at least, prevent cattle, bighorn and other wildlife from watering." The author favors some sort of protection for burros. (from Zarn et al., 1977).

Wolfe, Michael L., Legrande C. Ellis, and Robert MacMullen. 1989. Reproductive rates of feral horses and burros. Journal of Wildlife Management 53(4):916-924.

ABSTRACT: "We used blood serum concentrations of reproductive hormones to estimate pregnancy rates in 553 feral horses (*Equus caballus*) from populations in Nevada, Oregon, and Wyoming and 173 burros (*E. asinus*) from California. We determined levels of progesterone, pregnant female's (mare's) serum gonadotropin, and estradiol-17β by radioimmunoassay procedures. Pregnancy determination based on all 3 hormone criteria correctly classified pregnancy status diagnosed by rectal palpation in 86.7% of 113 horses examined. Progesterone levels >2.00 ng/ml were the most reliable endocrine criterion for pregnancy diagnosis (accuracy rate= 81.8%) and correctly predicted ultimate reproductive performance in 89.4% of 38 radio-collared horses. Mean incidence of pregnancy among mares >2 years old in composite samples from Nevada, Oregon, and Wyoming was 57.0%, 61.0%, and 81.4%, respectively. Pregnancy rates did not differ significantly between lactating and non-lactating mares. Pregnancies among yearling mares were confirmed by rectal palpation and lactation rates of 22.2% and 11.9% among 2-year-old animals in Nevada and Wyoming, respectively. Agreement between pregnancy rates of 37 burros estimated by rectal palpation and progesterone levels (>2.00 ng/ml) was 73.0%. Mean apparent incidence of pregnancy in burros >2 years old was 72.3%; 25% of the yearlings were pregnant."

Wood, H. W. 1974. Death Valley: desert wilderness in danger. National Parks and Conservation Magazine 48(2):4-9.

ABSTRACT: The author laments the present situations at Death Valley National Monument. In addition to too many tourists and miners, he complains about too many burros. "Feral burros, offspring of the burros of the early miners trample and graze rare Death Valley grasses and flowers. The feral burros compete with bighorn sheep and other creatures for palatable, edible plants. Burros also muddy up the water holes and defecate in them. Such pollution does not seem to bother the burros, but, bighorn sheep require isolated watering places with clear, clean water. Every year there are more and more burros and fewer sheep." (from Zarn et al., 1977).

Woodward, Susan L. 1979. The social system of feral asses (*Equus asinus*). Zeitschrift fur Tierpsychologie 49(3):304-316.

ABSTRACT: "Marked feral asses were studied for over 2 years in the desert Chemehuevi Mountains, California. Young males were generally observed in unstable all-male groups of 2 to 5 individuals. Older males tended to be solitary when not accompanying estrous females. Females were most frequently seen alone with their foals or with other females and foals. The female-foal relationship is the most stable ass association, but yearling females may form bonds with young males lasting over 8 months.

Individual feral asses had a mean home range size of 32 km^2, with no significant difference between the sexes. All home ranges of marked animals overlapped. One 4-year old marked male occupied a territory of 0.5 km^2 from June through August 1974.

With 1 exception, extant wild equids of desert regions display a social organization similar to that of the feral ass, whereas equids of more humid grasslands possess a harem structure like that of the feral horse. The loosely structured territorial system of arid land equids is adapted to the low carrying capacity of deserts. The population remains dispersed for most of the year, and individuals may be opportunistic foragers. Breeding is restricted to the rainy season, when primary production is relatively high, permitting a concentration of adults and favoring the survival of young.

In North American deserts, the territorial system may be breaking down in some feral ass populations, because year round breeding can and does occur. In addition, aperiodic rainfall reduces and may even eliminate the possibility of maintaining several adult asses on a territory."

Woodward, Susan L. 1976. Feral burros of the Chemehuevi Mountains, California: the biogeography of a feral exotic. Ph.D. dissertation, University of California-Los Angeles. 178 pp.

ABSTRACT: "Feral burros have become naturalized members of local faunas in various parts of the western United States. One population was studied in the Chemehuevi Mountains, California, along the lower Colorado River to see how this exotic animal uses its adopted environment. Twenty-seven feral

burros were captured, aged and marked for future identification. The activities of these marked burros were monitored for over 18 months. Information was gathered on population size and structure, annual recruitment, possible dispersal from the distribution area, social interactions which might affect the dispersion of the population, daily and seasonal movements of individuals and the population as a whole, habitat preference, and diet.

The Chemehuevi population numbers about 80 burros. There is no defined breeding season, and the recruitment rate is approximately 20% every 18 months. Two year old jennies were foaling. With no known dispersal out of the distribution area and with negligible predation, this recruitment rate means a potential doubling of the population in 5 years.

Individual burros covered a mean 30 km^2 during the year. The greatest distance between any 2 sightings of a given marked animal was 24 km. There was no significant difference in home range sizes between jacks and jennies. All of the home ranges overlapped. This together with the instability of social groupings and the lack of antagonism among most burros gave the population the cohesiveness of a herd.

Burros spent the summer months within 3 km of the river. Greater wandering was possible during the cool months of the year and marked burros were found as far as 13 km from the river. Burros preferred to drink at springs, tinajas, and tanks when water was available in these ephemeral supplies rather than make the trek to the river.

While forbs were available in winter and spring, burros spent almost all their time on the interfluves. They utilized the desert washes more heavily during the warmer months, when they sought shade as well as forage. The Colorado riparian habitat was heavily used only during the hottest days of June, July, and August.

According to microscopic analysis of plant fragments in burro feces, the 1974 diet consisted of 4% grasses, 30% forbs, 61% shrubs, and 5% unknowns. The winter annual *Plantago insularis* was the most important item in the burro diet. When this was grazed out, burros turned to browse; palo verde (*Cercidium forlidum*) became the mainstay of the diet for the second half of 1974. Mesquite (*Prosopis* spp.) and arrow-weed (*Pluchea sericea*) were important during the summer when the burros were more or less confined to the riparian vegetation. In all 39 food items were identified by microscopic analysis of burro dung collected in the Chemehuevi Mountains study area during 1974."

Woodward, Susan L., and Robert D. Ohmart. 1976. Habitat use and fecal analysis of feral burros (*Equus asinus*), Chemeheuvi Mountains, California (1974). Journal of Range Management 29(6):482-485.

ABSTRACT: "Between January and March burros spent from 60 to 79% of their time on the interfluves. In April, habitat use was predominantly in washes with a high of 59% in July. During the summer months, when daily maximum

ambient temperature approached 48 °C, much of their time was spent in densely shaded pockets of vegetation along the Colorado River.

Thirty-nine plant species comprised the diet in 1974, desert Indianwheat (*Plantago insularis*) and palo verde (*Cercidium floridum*) being the most common. These 2 species, combined with mesquite (*Prosopis* spp.) and arrowweed (*Pluchea sericea*) formed over 50% of the annual diet. The 1974 diet consisted of 3.9% grasses, 30.1% forbs and 61.1% browse." Wooly Indianwheat grass was primarily used from January through May, mesquite and arrowweed during summer, foothills palo verde and desert-thorn [*Lycium*] during fall, and white bursage during winter.

"Population increases of 20-25% every 13-18 months and little predation bespeaks the need for unceasing management and possible control to prevent deterioration of the native flora and fauna."

Wright, G. M. 1935. Big game of our national parks. Scientific Monthly 41(2):141-147.

ABSTRACT: The article discusses endangered animals found in the national parks. Mention is made of the Rocky Mountain Bighorn: "Very little is known concerning the sheep of Grand Canyon. These faded-out desert bighorns, with their very massive, tightly curled horns, live in the canyon below the rim, and, in their practically impenetrable habitat, they are seldom seen. It may be assumed, however, that the recent removal of over 1000 feral burros may react favorably upon their food supply and consequently upon them." (from Zarn et al., 1977).

Yancey, Myrna J. 1984. A study of burro-small vertebrate interactions in Death Valley National Monument, California. Contribution number CPSU/UNLV 021/06. (also M.S. thesis, University of Nevada-Las Vegas). National Park Service, Cooperative National Park Resources Studies Unit, University of Nevada-Las Vegas. 90 pp.

ABSTRACT: "Two study sites were established in Death Valley canyons having histories of high and low *Equus asinus* populations. Temperature, precipitation, soil moisture, and soil particle size were equivalent between sites. There was a significant difference in number of burros observed in the 2 canyons. However, more were seen than expected in Nemo Canyon which had been considered a lightly used burro area. In Nemo Canyon, there has been a 4-fold increase in threatened shrubs since 1977 that has been paralleled by a 4-fold decrease of threatened plants in Wildrose Canyon. This supports current observations that more burros are using Nemo than in the past. Total browse impact was similar in both canyons, and the same plant species were selectively browsed in both sites. There was no difference in plant diversity between Nemo and Wildrose. Both sites had more plant species than a burro exclosure established in Wildrose Canyon in 1972. Wildrose also had a greater range in plant volumes

than the exclosure, while Nemo and Wildrose were statistically the same. The average shrub volume in Nemo was approximately twice that of Wildrose. However, total plant volume was greater in Wildrose Canyon than in Nemo. Both sites showed a positive correlation between species and site in affecting plant volume. There was a subtle difference in plant composition between the 2 study sites. Nemo had more plants that have been preferentially browsed by burros, whereas Wildrose had a larger proportion of nonpreferred shrubs.

The overall rodent density in Nemo was approximately twice that of Wildrose. Nemo had larger densities of *Ammospermophilus leucurus* and *Dipodomys microps*. Wildrose had a larger density of *Perognathus longimembris*. Total biomass was significantly greater in Nemo than Wildrose during 86% of the study period. Mean species weights were larger in Wildrose, but Nemo had proportionally more heavy species and recaptures. Both sites had a positive correlation between species and site in affecting rodent biomass during the late summer and early fall. Rodent reproduction and diversity were equivalent between the 2 sites.

There were no statistical differences in lizard density of numbers between Nemo and Wildrose, although more *Uta stansburiana* were seen and captured in Nemo during the study period. *Uta stansburiana* was the most common species, followed by *Cnemidophorus tigris* in both sites."

Yancey, Myrna J., and Charles L. Douglas. 1983. Burro-small vertebrate interactions in Death Valley National Monument, California. Desert Bighorn Council Transactions 23:17-24.

ABSTRACT: "Study sites were established in Death Valley in Wildrose and Nemo canyons, which have histories of high and low burro populations. Climate and soils were equivalent between sites. An increase in threatened shrubs in Nemo has been paralleled by a decrease in Wildrose, indicating that more burros are using Nemo than in the past. Plant diversity was similar in both canyons, but plant composition was subtly different. Nemo had more heavily browsed species, whereas Wildrose has experienced selective removal of preferred species. Total plant volume was greater in Wildrose than in Nemo. Rodent diversity and reproduction were equivalent between sites. Mean species weights were greater in Wildrose, but Nemo had more large species, more rodent mass, and more recaptures. There were no statistical differences in lizard diversity or numbers between Nemo and Wildrose."

Yousef, Mohamed K. 1984. Physiological adaptations of less well-known types of livestock in arid zones: donkeys. *in* Yousef, Mohamed K., editor. Stress physiology in livestock volume II: ungulates. CRC Press. 272 pp.

Yousef, Mohamed K., D. Bruce Dill, and D. V. Freeland. 1972. Energetic cost of grade-walking in man and burro *Equus asinus*: desert and mountain. Journal of Applied Physiology 33(3):337-340.

ABSTRACT: "In the desert at 800 m altitude, 695 mm Hg, men and burros walked on grades of from 0-17% without a load or with a load equal to 25% of the subject's body weight. Walks on the 17% grade were made also at high altitude, 3800 m, 485 mm Hg. The energetic cost of walking determined by measuring O_2 consumption (VO_2) for each set of conditions was higher in man than burro. The net VO_2/kg was the same for load or no load in man and burro on all grades. The advantage of the burro over man walking upgrade was even greater than walking downgrade. The energetic cost of climbing a vertical meter was only 9 and 14% higher in man than burro; however, the cost of walking a horizontal meter required twice as much energy for man than for the burro. The superior economy of the burro in the desert was evident at 3800 m altitude. In the burro as in man the cost of walking was unchanged at altitude. The economy of the burro was due to its anatomy and mechanics of walking. The lower cost of walking in the burro was of major importance to his survival in hot deserts."

Yousef, Mohamed K., and D. Bruce Dill. 1969. Energy expenditure in desert walks: man and burro *Equus asinus*. Journal of Applied Physiology 27(5):681-683.

ABSTRACT: "The economy of energy expenditure of man has been compared with that of burro in grade walking. Two high school students and 2 female burros were subjects. Student and burro walked side by side with and without loads down and up a 2% grade on a hard-packed desert road. The net oxygen consumption, VO_2, in terms of body weight and unit distance is significantly higher in man than in burro walking under similar conditions. A load on the back amounting to 33 or 50% of body weight is carried by the burro nearly as economically as live weight. For man walking downgrade carrying 33% of his body weight costs significantly more per kg and per unit distance than his own weight. No significant difference in net VO_2 per kg and per unit distance was observed in man walking upgrade with and without a load. The energy cost of walking up a 2% grade is about 50% greater than walking downgrade in man and twice as great in burro. The lower cost of walking, the associated economy in food requirement, and tolerance of dehydration explain in part the superiority of the burro for desert transport."

Yousef, Mohamed K., and D. Bruce Dill. 1971. Red blood cell and plasma volumes in the burro, *Equus asinus*: desert and mountain. Journal of Applied Physiology 31(2):253-256.

ABSTRACT: "Observations were made on red blood cell volume (RBCV) and plasma volume (PV) of 2 female burros, in the desert, during 3 weeks at the

Barcroft Laboratory of the White Mountain Research Station, 3800 m, barometric pressure 485 mm Hg, and for 40 days postaltitude. During 3 weeks at altitude PV decreased rapidly in both animals and did not return to the control level until after 1 month postaltitude. The decrease in PV was accompanied by increases in hemoglobin concentration and hematocrit. In 1 animal RBCV did not change, whereas in the other there appeared to be an increase at altitude beginning the 7th day; it was significantly higher throughout the 40 days postaltitude. In the burro the ratio of body hematocrit to venous hematocrit prealtitude was 0.98 contrasted to 0.93 in man. At altitude there was a significant drop in the ratio of 0.92; postaltitude it was 0.99. It appears that in the burro as in man decreased plasma volume and dependent hemoconcentration generally occur during the 1st week at high altitude. Also RBCV eventually increases but in man and burro this does not become significant within 2 weeks and may not occur within 3 weeks."

Yousef, Mohamed K., and D. Bruce Dill. 1969. Resting energy metabolism and cardiorespiratory activity in the burro *Equus asinus*. Journal of Applied Physiology 27(2):229-232.

ABSTRACT: "The resting oxygen consumption (VO_2, in ml/min kg) and cardiorespiratory functions as influenced by fasting, feeding, and diurnal rhythm were studied in 2 burros. Values for VO_2 were similar in the 2 burros, agreeing with figures reported for man, horse, and mule. Respiratory minute volume (V_{stpd}, in l/min kg) in the burro is similar to that of the horse and mule, but much higher than in man. The work capacity index, VO_2/heart rate (HR), in the burro is much higher than that of sedentary man. Fasting 24 hours or more decreased VO_2, respiratory rate (RR), and HR. The effect of feeding on VO_2 persists for 2 hours. Diurnal fluctuations in ambient temperature are associated with changes in rectal temperature, VO_2, RR, and HR."

Yousef, Mohamed K., D. Bruce Dill, and M. G. Mayes. 1970. Shifts in body fluids during dehydration in the burro *Equus asinus*. Journal of Applied Physiology 29(3):345-349.

ABSTRACT: "The mechanism underlying the exceptional tolerance to dehydration in the burro are not fully understood. A study was conducted using 2 burros to partition body fluid compartments before and after dehydration. Dehydration for 48 hours including a 1 hour walk reduced body weight about 18%. Intracellular fluid volume decreased from 77.9 to 52.9 l, extracellular fluid volume from 53.2 to 45.8 l, and plasma volume only from 9.0 to 8.4 l. The ability of the burro to conserve blood volume and presumably to maintain circulatory adequacy gives a likely explanation of its well-being even after 20% dehydration. Man and burro walking at the same rate in the desert sweat approximately at the same rate in relation to surface area. The difference in water loss between 2 dehydrated nonexercising burros is found to be behavioral

and partly related to the time spent in the sun. Rehydration was rapid and overhydration did not occur. Water content of feces of dehydrated burros was similar to that of desert antelopes but greater than values reported on the camel's feces."

Zarn, Mark, Thomas Heller, and Kay Collins. 1977. Wild, free-roaming burros: an annotated bibliography. Technical Note 297. Bureau of Land Management/U.S. Forest Service. 29 pp.

ABSTRACT: Approximately 100 annotated references broken down into 4 categories: 1) Equine Science, 2) General, 3) Legislation, and 4) Populations, Habitat, and Competition. (Pertinent entries are cited individually in this document).

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Conservation Biology

Contributed Paper

Changes in Avian and Plant Communities of Aspen Woodlands over 12 Years after Livestock Removal in the Northwestern Great Basin

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Abstract: *Riparian and quaking aspen* (Populus tremuloides) *woodlands are centers of avian abundance and diversity in the western United States, but they have been affected adversely by land use practices, particularly livestock grazing. In 1990, cattle were removed from a 112,500-ha national wildlife refuge in southeastern Oregon. Thereafter, we monitored changes in vegetation and bird abundance in years 1–3 (phase 1) and 10–12 (phase 2) in 17 riparian and 9 snow-pocket aspen plots. On each 1.5-ha plot, we sampled vegetation in 6 transects. Three times during each breeding season, observers recorded all birds 50 m to each side of the plot's 150-m centerline for 25 minutes. We analyzed data with multivariate analysis of variance and paired t tests with p values adjusted for multiple comparisons. In both periods, riparian and snow-pocket aspen produced extensive regeneration of new shoots ($\bar{x}$ = 2646 stems/ha and 7079 stems/ha, respectively). By phase 2, a 64% increase in medium-diameter trees in riparian stands indicated successful recruitment into the overstory, but this pattern was not seen in snow-pocket stands, where the density of trees was over 2 times greater. By phase 2 in riparian and snow-pocket stands, native forb cover had increased by 68% and 57%, respectively, mesic shrub cover had increased by 29% and 58%, and sagebrush cover had decreased by 24% and 31%. Total avian abundance increased by 33% and 39% in riparian and snow-pocket aspen, respectively, ground or understory nesters increased by 133% and 67% and overstory nesters increased by 34% and 33%. Similarly, ground or understory foragers increased by 25% and 32%, aerial foragers by 55% and 57%, and overstory foragers by 66% and 43%. We interpreted the substantial regeneration of aspen shoots, increased densities of riparian forbs and shrubs, and increased avian abundances as a multitrophic-level response to the total removal of livestock and as substantial movement toward recovery of biological integrity.*

Keywords: aspen, avian abundance, Great Basin, habitat recovery, livestock grazing, riparian woodland, snow-pocket aspen

Cambios en las Comunidades de Aves y Plantas en Bosques de Álamo a lo Largo de 12 Años Después de la Remoción de Ganado en la Gran Cuenca Noroccidental

Resumen: *Los bosque ribereños y de Populus tremuloides son centros de abundancia y diversidad de aves en el occidente de Estados Unidos, pero han sido afectados adversamente por prácticas de uso de suelo, particularmente pastoreo de ganado. En 1990 se removió el ganado de un refugio nacional de vida silvestre de 112,500 ha en el sureste de Oregon. Desde entonces, monitoreamos cambios en la vegetación y la abundancia de aves en los años 1–3 (fase 1) y 10–12 (fase 2) en 17 parcelas ribereñas y 9 de álamo. En cada parcela de 1.5 ha muestreamos la vegetación en 6 transectos. Tres veces durante cada época reproductiva,*

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Paper submitted August 8, 2011; revised manuscript accepted January 20, 2012.

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DOI: 10.1111/j.1523-1739.2012.01903.x

observadores registraron durante 25 minutos a todas las aves 50 m a cada lado de la línea central de cada parcela. Analizamos los datos con análisis multivariado de varianza y pruebas pareadas de t con valores de p ajustados para comparaciones múltiples. En ambos períodos, los bosques ribereños y de álamo produjeron una regeneración extensiva de rebrotes nuevos ($\bar{x}$ = 2646 tallos/ha y 7079 tallos/ha, respectivamente). En la fase 2, un incremento de 64% en el diámetro promedio de árboles en los bosques ribereños indicó un reclutamiento exitoso en el dosel, pero este patrón no se observó en los bosques de álamo, donde la densidad de árboles fue más de 2 veces mayor. En la fase 2 en bosques ribereños, la cobertura herbácea nativa había incrementado en 68% y 57%, respectivamente, la cobertura arbustiva mésica había incrementado en 29% y 58%, y la cobertura de artemisa había decrecido en 24% y 31%. La abundancia aviar total incrementó en 33% y 39% en bosques ribereños y de álamo, respectivamente, las especies que anidan en el suelo o en el sotobosque incrementaron en 133% y 67% y las especies que anidan en el dosel incrementaron en 34% y 33%. Similarmente, las aves forrajeras de suelo o sotobosque incrementaron en 25% y 32%, los forrajeadores aéreos en 55% y 57% y los forrajeadores de dosel en 66% y 43%. Interpretamos la regeneración sustancial de rebrotes de álamos, el incremento de las densidades de hierbas y arbustos ribereños y el incremento en las abundancias de aves como una respuesta a nivel multitrófico de la remoción total de ganado y como un avance sustancial hacia la recuperación de la integridad biológica.

Palabras Clave: abundancia de aves, álamo, bosque ribereño, Gran Cuenca, pastoreo de ganado, *Populus tremuloides*, recuperación de hábitat

Introduction

Riparian woodlands composed of deciduous trees and shrubs occupy <1% of the western United States, but they support higher diversity and abundance of birds than other cover types (Dobkin & Wilcox 1986; Knopf et al. 1988; Skagen et al. 1998). Similarly, in the 11 western U.S. states (hereafter the West), aspen (*Populus tremuloides*) woodlands harbor greater avian diversity and abundance than surrounding vegetation (Turchi et al. 1995; Griffis-Kyle & Beier 2003; Hollenbeck & Ripple 2007).

Both aspen and riparian woodlands are greatly affected by land-use practices, and aspen are declining in much of the West because of altered fire regimes, succession to conifers, ungulate herbivory, drought, disease, and insect outbreaks (Romme et al. 1995; Kay & Bartos 2000; Worrall et al. 2008). Livestock grazing, primarily by cattle, has a pervasive influence on riparian areas in the West (Fleischner 1994; Belsky et al. 1999), including approximately 90% of the region's extensive federal lands (Fleischner 2010). Besides direct consumption of vegetation, trampling by cattle can cause soil compaction, reduced bank stability, channel widening, increased groundwater depth, and decreased abundance of stream macroinvertebrates (Belsky et al. 1999; Fleischner 1994, 2010). Through direct and indirect effects, cattle and wild ungulates (especially elk [*Cervus elaphus*]) can dramatically impair aspen's ability to regenerate (Fitzgerald & Bailey 1984; Kay & Bartos 2000; Kaye et al. 2005) in riparian and nonriparian settings.

Avian abundance in aspen and other deciduous riparian habitats in the West is reduced in the presence of cattle (Saab et al. 1995; Tewksbury et al. 2002; Earnst et al. 2005). Ground- and shrub-nesting birds tend to be most affected by cattle, as expected from the greater effect that cattle have on low-growing vegetation (Saab et al. 1995), but effects throughout the avian community have been documented in cases where cattle have highly altered vegetation (Tewksbury et al. 2002; Krueper et al. 2003).

In the high-desert riparian areas of Hart Mountain National Antelope Refuge (HMNAR) in southeastern Oregon (U.S.A.), cattle were contributing to the poor condition of riparian areas and were removed from the refuge after >120 years of grazing (USFWS 1994). The removal of cattle from this relatively large landscape (112,500 ha) in 1990 and subsequent monitoring of vegetation and avian abundance in years 1–3 and 10–12 after cattle removal, provide a unique opportunity to investigate long-term consequences of cattle removal at a landscape scale (Earnst et al. 2005). During the first 3 years after cattle removal, herbaceous cover and avian abundance, especially that of ground and understory specialists began to increase (Dobkin et al. 1998; Tewksbury et al. 2002). We compared vegetation structure and abundance of breeding birds in riparian and snow-pocket aspen 1–3 (phase 1) and 10–12 (phase 2) years after livestock removal.

Methods

Study Area

HMNAR is in the northwestern Great Basin in southeastern Oregon (42°25'N, 119°40'W) and is predominantly sagebrush (*Artemisia* spp.) shrubsteppe. Hart Mountain is a fault block that rises gradually from the east to 2438 m and drops as a steep escarpment to the west. Riparian woodlands and snow-pocket aspen stands provide the only trees except for a few stands of mountain mahogany (*Cercocarpus ledifolius*) and western juniper (*Juniper occidentalis*) (USFWS 1994). Of the 134 linear km of riparian habitat and snow-pocket aspen on

HMNAR, 29% is aspen along perennial streams, 10% aspen in snow pockets (small, relatively high-elevation depressions where snow collects), 11% willow (*Salix* spp.), 12% mixed deciduous, 29% sedge or grass meadow, and 9% sagebrush shrubsteppe (Earnst et al. 2005). Annual precipitation, primarily snow, is generally 20–30 cm on the tableland and 30–46 cm on the mountain (USFWS 1994).

Study Plots

The 4324-ha study area encompassed most aspen stands on the east side of the escarpment. We excluded 1 drainage with aspen from the study area due to difficult access and 1 drainage in which a prescribed burn was planned. Within the study area, the 17 riparian and 9 snow-pocket plots were well distributed throughout areas with aspen, and 3–10 plots were in each of the 5 drainages ($\bar{x} = 5.2$). Most riparian-aspen plots were in mature stands ($n = 13$). Two were in stands with little regeneration and a large proportion of dead trees, and 2 were in a young, dense, even-aged stand that had burned in a 1972 wildfire. Average elevation of riparian and snow-pocket plots was 1951 m (range 1873–2121 m) and 2145 m (2042–2212 m), respectively.

Plots were 1.5 ha (150 × 100 m) and separated by at least 125 m. The width of the aspen stand was often <100 m, and the remainder of the plot consisted of shrubsteppe vegetation. The center line of the plot, which was marked at 50-m increments with permanent steel fence posts, ran near and parallel to the stream.

Vegetation Measurements

On each of the 26 plots, 6 100-m vegetation transects were placed perpendicular to and bisected by the 150-m center line. Vegetation transects were 25 m apart, and location of the first was chosen at random within the first 12.5 m of the center line. The same vegetation transect locations were used in each phase. At 10-m intervals along vegetation transects, we measured canopy cover with a spherical densitometer and estimated percent ground covered by herbaceous vegetation, litter, and bare ground within a 0.125-m^2 sampling frame. We measured shrub cover (identified to species) as the percentage of the vegetation-transect line that was intercepted by live shrubs below 2 m (gaps <10 cm were ignored). We pooled riparian shrub species for analyses. We estimated tree density by counting all woody stems within 2 m of each vegetation transect line and recorded species, height, and diameter at breast height (dbh). We classified aspen stems as shoots if they were ≤1.5 m in height and as small- (0.1–6.0 cm dbh), medium- (6.1–18.0 cm dbh), or large- (>18.0 cm dbh) diameter trees if they were >1.5 m in height.

Within each set of vegetation measurements (ground cover, shrub cover, and aspen stem density), we tested for an overall difference between phases with a repeated-measures multivariate analyses (MANOVA). In each MANOVA, we tested for differences between phases within categories (such as shrub cover) with paired *t* tests, and we adjusted for multiple comparisons as in Benjamini and Hochberg (1995). Because plots were fairly evenly distributed throughout aspen on the east slope and plots were placed in aspen vegetation irrespective of drainage, we analyzed the data as a simple one-stage sample. We used only vegetation measurements taken within the wooded zone of each plot. Each 10-m section of the vegetation transect was defined as being within the wooded zone if it contained any tree stems or canopy cover. Both avian and plant data are given as means per wooded hectare.

For descriptive purposes, we report percent change between phases ([phase 2–phase 1]/phase 1 × 100%) in the text and phase 1 and phase 2 means in the figures. We used mean differences (the mean across plots of each plot's phase 2 minus phase 1 difference) and the standard error of the difference in statistical comparisons (Supporting Information).

We obtained precipitation data from a weather station at HMNAR headquarters. We pooled these data for October through June (when 86% of annual precipitation falls) annually (1941–2002) and used them as an index of moisture available to plants in a growing season (Dobkin et al. 1998).

Avian Surveys

We conducted modified fixed-width transect surveys during which observers walked slowly through the center of each plot for 25 minutes and recorded all birds detected by sight or sound within 50 m of the transect (Dobkin & Rich 1998). Surveys were conducted between 0.5 and 3.5 h after sunrise. In phase 1, each plot was surveyed 6 times, once on each of 2 consecutive days in each of 3 survey rounds. In phase 2, each plot was surveyed once in each of 3 survey rounds. Surveys were conducted during phenologically similar periods each year, 7 May–9 July in phase 1 (87% prior to 27 June) and 8 May–27 June in phase 2. In each year, a plot was surveyed by 2 or 3 different observers, and each was responsible for approximately the same total number of surveys and plots. The order in which plots were surveyed within a day alternated between consecutive visits.

For each of the 26 plots, we averaged mean number of individuals detected per visit within a year and among years within each phase (i.e., 1991–1993 and 2000–2002). We then calculated the mean difference in individuals per visit between phases for each plot and each species and conducted a paired *t* test (with plot as the sampling unit) to determine whether the difference

for each species was significantly different from zero. As a means of restricting analyses to those species with a sample size sufficient to provide a reasonable power to detect a difference, we used only species that occurred on at least 5 plots and had an average of ≥0.013 individuals/ha in either phase (32 species in riparian aspen, 23 in snow-pocket aspen). In addition, we analyzed only passerines, doves, and woodpeckers that nest or forage primarily in woody-riparian and snow-pocket areas on HMNAR. Avian nomenclature follows the most recent revision to the American Ornithologists' Union checklist (Chesser et al. 2011).

We assigned species to nesting guilds (ground and understory cup nesters, overstory cup nesters, and cavity nesters) and foraging guilds (ground and understory, overstory, aerial, and bark foragers) (Ehrlich et al. 1988) (Supporting Information). Change in number of individuals in each nesting and foraging guild per hectare (i.e., phase 2–phase 1) was calculated by pooling individuals for all species within each guild and treating the plot as the primary sampling unit. We used repeated measures multivariate tests (SAS Institute 2004) to test for an overall difference between phases (first among guilds and then species). If the difference was significant, we used a paired t test to test for a difference between phases for each guild and each species. We adjusted resulting p values for multiple comparisons with Benjamini and Hochberg's (1995) false discover rate to ensure that ≤5% of rejected hypotheses were rejected falsely. We made this adjustment because it is more powerful than holding the family-wise error rate at $p = 0.05$ and because the error rate is acceptable when an overall significant difference has been established and when one seeks to describe which species comprise the difference (Westfall et al. 1999).

Results

Riparian and snow-pocket aspen differed in stand structure, but both exhibited substantial regeneration (i.e., production of new shoots) ($\bar{x} = 2646$ stems/ha for riparian and 7079 stems/ha for snow-pocket aspen, phase 1 and 2 average) (Supporting Information). In both phases, aspen in snow-pocket plots were considerably denser than in riparian plots, primarily because they had 3.5 times more shoots and 2.3 times as many small-diameter trees per ha than riparian aspen (Supporting Information). Tree size was strongly skewed toward small trees in snow-pocket aspen, with shoots (<1.5 m in height) and small stems (<6 cm dbh) comprising 93% of all stems in snow-pocket plots and 77% of all stems in riparian plots. Snow-pocket plots tended to have more forb cover and less grass and sedge cover, but similar cover of riparian shrubs, sagebrush, and aspen canopy relative to riparian plots (Supporting Information). In both stand types, herbaceous and shrub communities were composed of native species.

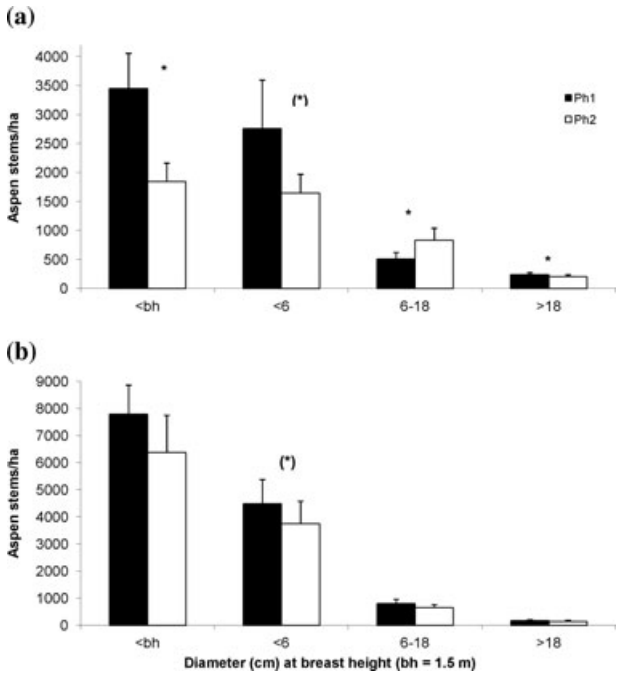


*Figure 1. Density of live aspen stems in 4 size classes (<bh, 1.5 m in height; other classes are >1.5 m in height and unit of measure is diameter at breast height in centimeters) in (a) riparian aspen plots (*n = 17; $F_{48,3} = 6.1$, p = 0.001*) and (b) snow-pocket aspen plots (*n = 9; $F_{24,3} = 1.1$, p = 0.36*) in years 1–3 (Ph1) and years 10–12 (Ph2) after cattle removal (multivariate repeated measures analysis and paired* t *tests with adjustment for multiple comparisons: (*)p < 0.10; *p < 0.05; **p < 0.01; ***p < 0.001).*

Riparian plots had more than twice as many total individual birds per hectare as snow-pocket plots (27.2 [SE 2.0] versus 13.0 [1.6], respectively; $t = 5.5$, $p < 0.0001$, 33 species pooled), and the difference was evident across all nesting and foraging guilds. Most species (27 of 32) were more common in riparian than snow-pocket aspen plots (on the basis of phase 2 means) (Supporting Information). The identity of 8 of the 10 most abundant species was the same in riparian and snow-pocket plots.

Change in Vegetation Structure and Composition

Riparian stands exhibited substantial changes in stand structure between phase 1 and phase 2, including decreases in the density of shoots (47% change from phase 1 to phase 2, $p = 0.02$), small diameter trees (40%, $p = 0.06$), and large diameter trees (16%, $p = 0.02$), and a 64% increase in medium diameter trees ($p = 0.02$) (Fig. 1a). The density of snags >18 cm in diameter (33.3 versus 33.8 stems/ha, phases 1 and 2, respectively; $t = 0.04$,

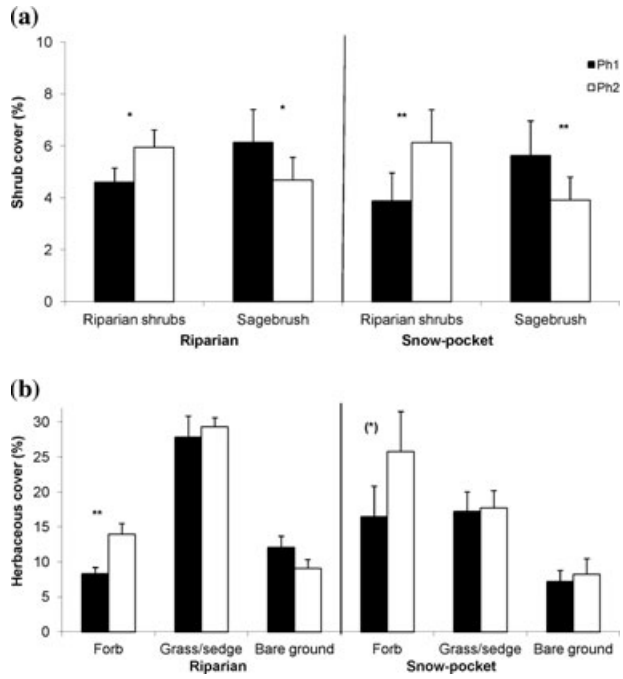


*Figure 2. Percent cover of (a) shrubs in riparian (*n = *17,* $F_{16,1}$ = *24.2,* p = *0.0002) and snow-pocket aspen plots (*n = *9,* $F_{8,1}$ = *25.5,* p = *0.001) and (b) herbaceous vegetation in riparian (*$F_{32,2}$ = *4.1,* p = *0.03) and snow-pocket aspen plots (*$F_{16,2}$ = *2.3,* p = *0.01) in years 1–3 (Ph1) and years 10–12 (Ph2) after cattle removal (multivariate repeated measures analysis and paired* t *tests with adjustment for multiple comparisons: (**)p < *0.10;* *p < *0.05;* **p < *0.01;* ***p < *0.001).*

$p = 0.97$) and canopy cover (54% versus 53%, $t = 0.71$, $p = 0.49$) did not change.

In snow-pocket stands the relative distribution of trees among size classes was unchanged from phase 1 to phase 2; however, there were consistent but nonsignificant decreases in the density of live stems in all classes (shoots, 18% decrease, $p = 0.25$; small diameter, 17%, $p = 0.24$; medium diameter, 19%, $p = 0.24$; large diameter, 14%, $p = 0.25$) (Fig. 1b). The density of snags >18 cm in diameter increased significantly (11.1 versus 29.7 stems/ha, $t = 3.79$, $p = 0.004$), and canopy cover declined significantly (55% versus 49%, $t = 2.71$, $p = 0.02$).

In riparian and snow-pocket plots, riparian shrub cover increased significantly (29% [$p = 0.03$] and 58% [$p = 0.008$], respectively) and sagebrush cover decreased significantly (24% [$p = 0.03$] and 31% [$p = 0.009$] respectively) (Fig. 2a). Cover of forbs increased substantially in riparian and snow-pocket plots (68% [$p = 0.006$] and 57% [$p = 0.08$], respectively) (Fig. 2b), and bare ground decreased nonsignificantly in riparian aspen (25% [$p = 0.12$]) (Fig. 2b). The combined category of grasses and sedges provided substantial cover in riparian and snow-pocket aspen plots (29% and 18%, respectively) and did not change significantly between phases (5% [$p = 0.62$] and 3% [$p = 0.89$], respectively).

Change in Bird Abundance

By 10–12 years after cattle removal, pooled avian abundance had increased by 33% in riparian aspen (from 20.4 to 27.2 individuals/ha, $p = 0.001$) and by 39% in snow-pocket aspen (from 9.3 to 13.0 individuals/ha, $p = 0.004$). Most species in both riparian aspen (69%, 22/32) and snow-pocket aspen (70%, 16/23) increased (Table 1). In riparian aspen, abundances of 10 species increased significantly and 2 decreased significantly after adjusting for multiple comparisons. In snow-pocket aspen, abundances of 4 species appeared to increase significantly and 1 to decrease significantly, but no differences remained significant after adjusting for multiple comparisons (Table 1).

Among nesting guilds, significant increases in avian abundance occurred in both riparian and snow-pocket aspen. Ground and understory nesters increased by 133% and 67%, and overstory nesters increased by 34% and 33% in riparian and snow-pocket aspen, respectively (Fig. 3a). Abundance in most foraging guilds also increased significantly: ground and understory foragers increased by 25% and 32%, aerial foragers by 55% and 57%, and overstory foragers by 66% and 43% in riparian and snow-pocket aspen, respectively (Fig. 3b). Neither the bark-gleaning foraging guild nor the cavity-nesting guild increased significantly in either plot type.

Most species that increased significantly in abundance between phases became more abundant in plots where they had been present in phase 1 (9 of 10 species) and were present on more plots than in phase 1 (5 of 10 species; Table 1). Likewise, the 2 species that decreased significantly in abundance between phases decreased in abundance in plots where they had been present in phase 1 and were present on fewer plots than in phase 1 (Table 1). Cavity-nesting species also were present in fewer plots in phase 2 than in phase 1 (5 of 8 cavity nesters in riparian aspen and 5 of 7 in snow-pocket aspen).

Total precipitation (1 October through 30 June) was greater, but not significantly, in phase 1 than in phase 2 (32.25 cm [SE 6.17] versus 19.48 cm [2.31], $t = 1.94$, $p = 0.12$). The tendency for higher rainfall in phase 1 was the opposite of that expected if the increase in bird abundance were related to increased precipitation. The total number of individuals per hectare (species pooled, averaged across plots) did not increase as precipitation increased, either within or between phases (Fig. 4a). Total precipitation increased nonsignificantly from 1941 to 2002 ($p = 0.08$, Fig. 4b).

For most species, increases in avian abundance at HMNAR did not reflect regional Breeding Bird Survey (BBS) trends in the Great Basin Bird Conservation Region

Table 1. Mean change in avian abundance from years 1–3 to years 10–12 after cattle removal on riparian and snow-pocket aspen plots ($n = 17$ and 9, respectively).

Abundance status[a] *and common name*	Scientific name	*Riparian aspen*		*Snow-pocket aspen*	
		change in individuals/ha[b]	*change in presence*[c]	*change in individuals/ha*[b]	*change in presence*[c]
Increasing					
Yellow Warbler	*Setophaga petechia*	1.64***	1	0.45[***]	2
White-crowned Sparrow	*Zonotrichia leucophrys*	1.37**	1	0.37	0
Warbling Vireo	*Vireo gilvus*	0.80***	3	0.35	0
Tree Swallow	*Tachycineta bicolor*	0.79	2	0.28[*]	2
Dusky Flycatcher	*Empidonax oberholseri*	0.70**	0	0.76	0
Empidonax spp.[d]	*Empidonax spp.*	0.31***	7	0.24[*]	1
Yellow-rumped Warbler	*Setophaga coronata*	0.28[*]	2	0.01	−2
Song Sparrow[e]	*Melospiza melodia*	0.27*	5		
Western Tanager	*Piranga ludoviciana*	0.26*	1	0.09	4
Cassin's Finch	*Carpodacus cassinii*	0.24	1	−0.04	−2
Mourning Dove[e]	*Zenaida macroura*	0.24*	4		
Spotted Towhee[e]	*Pipilo maculatus*	0.23*	8		
House Finch[e]	*Carpodacus mexicanus*	0.20*	7		
Dark-eyed Junco	*Junco hyemalis*	0.19[*]	6	0.37[**]	3
American Robin	*Turdus migratorius*	0.17	0	0.10	0
MacGillivray's Warbler[e]	*Geothlypis tolmiei*	0.16[*]	5		
Black-headed Grosbeak	*Pheucticus melanocephalus*	0.12	−1	0.05	−3
Lazuli Bunting[e]	*Passerina amoena*	0.12	2		
Western Wood-Pewee	*Contopus sordidulus*	0.09	−1	0.05	0
Orange-crowned Warbler	*Oreothlypis celata*	0.08	−1	0.11	0
Hairy Woodpecker	*Picoides villosus*	0.07	−4	−0.01	−4
Fox Sparrow	*Passerella iliaca*	0.02	−2	−0.05	−1
Decreasing					
European Starling[e]	*Sturnus vulgaris*	−0.70*	−1		
Bullock's Oriole	*Icterus bullockii*	−0.35**	−9	−0.06[*]	−6
House Wren	*Troglodytes aedon*	−0.28	−1	0.18	−1
Northern Flicker	*Colaptes auratus*	−0.10	0	0.10	−1
Swainson's Thrush[e]	*Catharus ustulatus*	−0.07	−5		
Hummingbird spp.[e,f]	*Selasphorus/Stellula*	−0.03	−1		
Mountain Bluebird	*Sialia currucoides*	−0.03	2	0.19	0
Brown-headed Cowbird	*Molothrus ater*	−0.01	0	−0.04	−2
Downy Woodpecker	*Picoides pubescens*	−0.01	−4	−0.04	−3
Sapsuckers[g]	*Sphyrapicus nuchalis, S. ruber*	−0.001	−1	−0.03	−4

[a] *For ease of presentation, increasing or decreasing status assigned on basis of riparian plots.*
[b] *Significance on the basis of paired t tests with adjustment for multiple comparisons:* * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; *[], differences significant before adjustment but not after.*
[c] *Change in presence is the change in number of plots in which the species was present.*
[d] *Species include Hammond's* (E. hammondii), *Cordilleran* (E. occidentalis), *Pacific-slope* (E. difficilis), *Willow Flycatchers* (E. traillii), *and unidentified* Empidonax *flycatchers. Dusky Flycatchers were analyzed separately.*
[e] *Species was too rare for meaningful analyses in snow-pocket stands. Criteria for inclusion were an average of ≥0.013 individuals/ha and occurring on ≥5 plots in either period.*
[f] *Hummingbird species includes Broad-tailed* (Selasphorus platycercus), *Rufous* (S. rufus), *and Calliope Hummingbirds* (Stellula calliope), *and unidentified hummingbirds.*
[g] *Sapsucker species includes Red-naped Sapsucker* (Sphyrapicus nuchalis), *Red-breasted Sapsucker* (S. ruber), *hybrids, and those recorded as unidentified.*

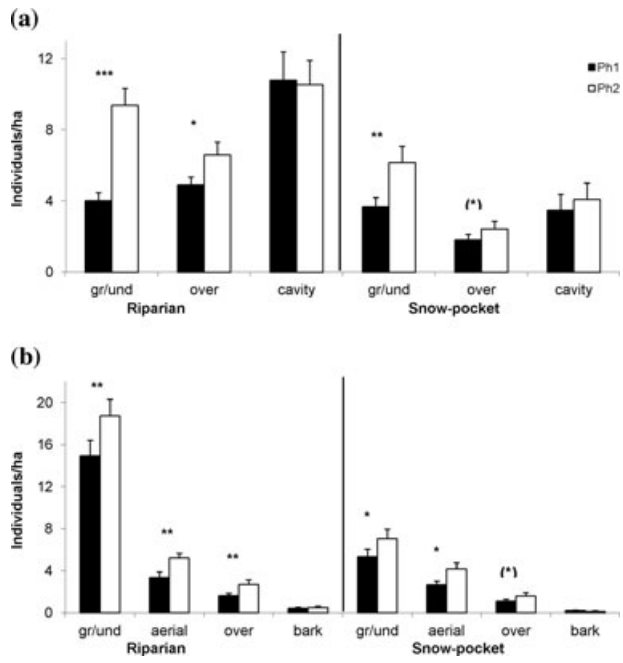


Figure 3. Avian abundance in years 1–3 (Ph1) and years 10–12 (Ph2) after cattle removal for (a) nesting guilds in riparian ($n = 17$, $F_{32,2} = 15.9$, $p < 0.0001$*) and snow-pocket aspen (*$n = 9$, $F_{16,2} = 6.2$, $p = 0.01$*) plots and (b) foraging guilds in riparian (*$F_{48,3} = 10.7$, $p < 0.0001$*) and snow-pocket aspen (*$F_{24,3} = 9.0$, $p = 0.0004$*) plots (multivariate repeated measures analysis and paired* t *tests with adjustment for multiple comparisons: (*)*$p < 0.10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).*

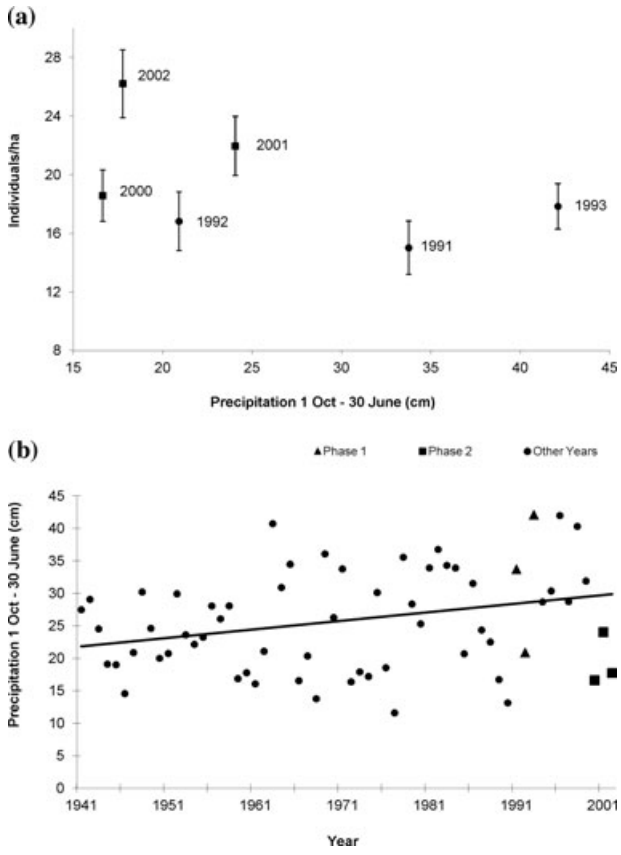


Figure 4. Total precipitation relative to (a) mean (SE) avian abundance (all species pooled) per plot visit each year and for (b) the 62 years preceding and during this study (1941–2002) (phase 1, 1–3 years after cattle removal; phase 2, 10–12 year after cattle removal). Mean total precipitation was 25.5 cm, and the slope of the long-term trend was 0.10 (SE 0.05) ($t = 1.8$, $p = 0.08$*).*

for 1991–2002 (Sauer et al. 2008). Of the 10 species with abundances that increased significantly in riparian plots, 3 increased significantly in the Great Basin (Mourning Dove [*Zenaida macroura*], Song Sparrow [*Melospiza melodia*], and Warbling Vireo [*Vireo gilvus*]), and 2 decreased significantly (Dusky Flycatcher [*Empidonax oberholseri*] and other *Empidonax*) (Supporting Information).

Discussion

Ours is the first study to quantify the response of avian and plant communities in aspen woodlands to the removal of livestock across ecologically informative spatial and temporal scales in the semi-arid Intermountain West and to illustrate the response at multiple, interrelated organizational levels. The increase in avian abundance across the 12 years following cessation of >100 years of livestock grazing was large and widespread throughout foraging and nesting guilds.

Increases in forb and shrub cover from phase 1 to phase 2 and the high density of aspen shoots and small trees in both phases created a structurally robust understory of native species. The recovering understory vegetation is the most parsimonious explanation for the strong increases that we documented in guilds of species that nest or forage in the understory (Saab et al. 1995; Tewksbury et al. 2002). Understory vegetation is adversely affected by livestock grazing (Belsky & Blumenthal 1997) and is an often overlooked component of habitat structural diversity that contributes substantially to avian diversity and abundance in aspen and riparian woodlands (Hobson & Bayne 2000; Scott et al. 2003; Dickson et al. 2009).

Overstory nesters and overstory and aerial foragers also increased significantly in our study. Other studies have documented effects of grazing throughout the avian community, especially when vegetation was altered extensively (Tewksbury et al. 2002; Krueper et al. 2003). Such widespread changes in avian communities may be expected if invertebrate abundance is affected by altered vegetation (Pettersson et al. 1995; McIver &

McInnis 2007) and if insectivorous avian communities mirror changes in their prey (Croonquist & Brooks 1991; Seagle & Sturtevant 2005).

Exceptions to the trend of increasing abundance were bark gleaners and cavity nesters, neither group increased significantly in either plot type. This result is consistent with the loss of 14%–16% of large-diameter trees in riparian (significant) and snow-pocket (nonsignificant) plots. Cavity nesters prefer aspen rather than other trees for nesting in boreal woodlands (Martin et al. 2004), and at HMNAR they preferentially nested in the largest aspen, both living and dead (Dobkin et al. 1995). Among cavity nesters in our study, only the European Starling (*Sturnus vulgaris*) decreased significantly. In addition, 6 of 8 cavity nesters in riparian aspen exhibited nonsignificant declines, including sapsuckers and the Northern Flicker (*Colaptes auratus*), which are the 2 primary excavators and keystone species in this cavity-nesting community (Dobkin et al. 1995; Martin & Eadie 1999).

Most aspen stands on HMNAR before livestock exclusion had either 1- or 2-layered aspen canopies (USFWS 1994), which reflected the episodic nature of successful recruitment of shoots into the canopy over many previous decades. This structural pattern is not uncommon in aspen woodlands in the West (Mueggler 1989; Suzuki et al. 1999; Wall et al. 2001) and is often attributed to extensive herbivory, either by wild ungulates or livestock (Kay & Bartos 2000; Ripple & Larsen 2000; Kaye et al. 2005), although insects, disease, or drought may also contribute to this episodic pattern (Kurzel et al. 2007).

We interpret the very high density of aspen shoot regeneration on most plots during phase 1 as an immediate response to release from grazing, but we discuss alternate explanations below. Similar large pulses in shoot density are well documented after other types of disturbance such as cutting or burning (Bartos & Mueggler 1981; Crouch 1983; Prévost & Pothier 2003). We documented a large decrease in shoot density from phase 1 to phase 2, which is consistent with density-dependent mortality expected among shoots at high density during recovery from a major disturbance (Bartos & Mueggler 1981; Crouch 1983), including ungulate browsing (Baker et al. 1997).

The canopies of riparian aspen stands became more layered during the 12 years following cattle removal, as evidenced by the 64% increase in medium-sized trees. The relatively low number of medium-sized trees in phase 1 indicates that conditions were not conducive to shoot regeneration and survival of stems to >6 cm diameter for several decades before phase 1. Likewise, the net loss of large-diameter trees indicates recruitment of medium- into large-diameter trees was inadequate to compensate for natural mortality in the latter, further indicating a paucity of medium-sized trees in prior decades. Elsewhere, the lack of a multilayered aspen canopy and gradual loss of large-diameter trees has been attributed to prolonged herbivory that limited the growth and survival of suckers in previous decades (Kay & Bartos 2000; Martin 2007; Hollenbeck & Ripple 2008).

Unlike riparian aspen stands, snow-pocket stands exhibited a slight thinning of all size classes rather than a change in relative stem size composition. Snow-pocket stands, relative to riparian stands, exhibited less self-thinning of shoots and small trees and did not exhibit an increase in medium-sized trees. The latter result suggests slower growth of small stems or lower survival of small stems into medium stems. Snow-pocket stands, which are denser, often on hillsides, and usually do not contain surface water, may have been used less by cattle (e.g., Roath & Krueger 1982) or may have a different optimal, or ecologically stable, stand structure and thus a different recovery trajectory (Laycock 1991; Strand et al. 2009). The statistically nonsignificant loss of large-diameter stems in snow-pocket stands was proportionately similar to that in riparian stands and appears characteristic of natural senescence after decades of limited regeneration (e.g., Martin 2007).

Browsing by wild ungulates, especially by elk in winter, negatively affects aspen regeneration and stand structure (Baker et al. 1997; Suzuki et al. 1999; Kaye et al. 2005). However, elk occurred only incidentally on HMNAR, and neither elk nor the relatively small mule deer (*Odocoileus hemionus*) population (800–1000 individuals) remain in the area during winter (Oregon Department of Fish and Wildlife, unpublished data), when most ungulate browsing of aspen occurs (e.g., Suzuki et al. 1999). Furthermore, mule deer abundance was fairly stable preceeding and during phase 1 (1985–1994) and declined somewhat between phases, and thus does not appear to explain changes in the density of aspen shoots, which was high in phase 1 and decreased between phases.

Little evidence links annual variation in precipitation and aspen regeneration (Ripple & Larson 2000; Hessl & Graumlich 2002; Martin 2007). Although phase 1 had higher precipitation and regeneration, the lack of multilayered aspen canopies in phase 1 stands does not appear consistent with multiple precipitation-induced peaks in regeneration that would be expected from long-term precipitation patterns (Fig. 4b) (Baker et al. 1997). Extreme and prolonged drought can contribute to stem mortality of larger size classes, especially as seen in sudden aspen dieback (Hogg et al. 2008; Worrall et al. 2008). However, our stands did not exhibit visual signs of insect or disease outbreaks or drought stress (S.L.E. and D.S.D., personal observation) or rapid crown dieback and cohort loss, which are characteristic of sudden aspen dieback (Worrall et al. 2008). Self-thinning is characteristic of some self-sustaining stands and need not indicate stress (Smith & Smith 2005). Furthermore, conditions during phase 2 were not those of an extreme or prolonged drought; precipitation increased over the long term and was above average before phase 2. Cattle removal remains the most

likely primary driver of the changes we documented, although aspen stand dynamics result from a complex interaction of processes (Romme et al. 1995) and interpretation will benefit from further dendrochronological and longitudinal studies.

Across the 12 years of livestock exclusion, aspen woodlands on HMNAR showed substantial movement toward recovery of biological integrity (as defined by Angermeier & Karr 1994). Relative to elsewhere in the Intermountain West of the United States, most of our stands exhibited high densities of regeneration in both phases (Mueggler 1989; Strand et al. 2009) and substantial recruitment of stems into the overstory (Suzuki et al. 1999; Wall et al. 2001; Rogers et al. 2010). The increased native forb and riparian shrub cover, with a concomitant decrease in sagebrush cover, indicate increased groundwater availability and improved riparian condition (Dobkin et al. 1998; Wright & Chambers 2002). The increased avian abundance and relatively high nesting success (Heltzel & Earnst 2006) illustrate a positive multitrophic-level response to livestock removal. Our study area serves as a landscape-level livestock exclosure (Bock et al. 1993) and can potentially provide comparison to ecologically similar sites in the vast semiarid, grazed ecosystems of western North America.

Federal land-management agencies operate under a mandate to manage for ecological values on lands grazed by livestock (e.g., BLM 2001), but these agencies are faced with the dilemma that livestock exclusion is generally the most effective means of improving degraded riparian areas (Elmore & Kauffman 1994). Nonetheless, given that livestock are present on ~90% (Fleischner 2010) of the 1.5 million km^2 of federally owned land in the West, reducing the negative effects of livestock on federal lands could potentially help restore large expanses of western ecosystems. Similarly, there is growing evidence that the presence of large predators, especially wolves (*Canis lupus*), affect wild ungulate abundance and behavior and initiate a trophic cascade that improves regeneration, health, and persistence of aspen and other deciduous vegetation (Ripple & Larsen 2000), an effect that could be spatially and temporally extensive in the West (Beschta & Ripple 2009). In addition to immediate benefits, diminishing the effects of domestic and wild ungulate populations is likely to improve the resilience of aspen and other woody riparian ecosystems as climate-mediated stressors such as wildfires and drought-induced mortality change in frequency.

Acknowledgments

We thank the U.S. Fish & Wildlife Service, Region 1, Office of Migratory Birds, for financial support of fieldwork, particularly M. Green and T. Zimmerman. Additional support was provided by the Great Basin Bird Observatory (J.A.B.), High Desert Ecological Research Institute (D.S.D), and U.S. Geological Survey Forest and Rangeland Ecosystem Science Center (S.L.E.). The Sheldon-Hart Mountain National Wildlife Refuge Complex provided logistical support. We thank W. Pyle and B. Reiswig for facilitating initiation of the project and D. Alonso, C. Dippel, and M. Nunn. The study benefited from suggestions by J. Barnett, J. Bart, M. Bray, J. Heltzel, W. Pyle, and A. Rich. Special thanks to our many field crew members. Reviews by D. Shinneman, S. Skagen, and 2 anonymous reviewers improved the manuscript. Any use of trade, product, or firm names is for descriptive purpose only and does not imply endorsement by the U.S. government.

Supporting Information

Data on avian abundance in phases and the difference in abundance between phases (Appendix S1) and cover and aspen stem density in phases and difference between phases (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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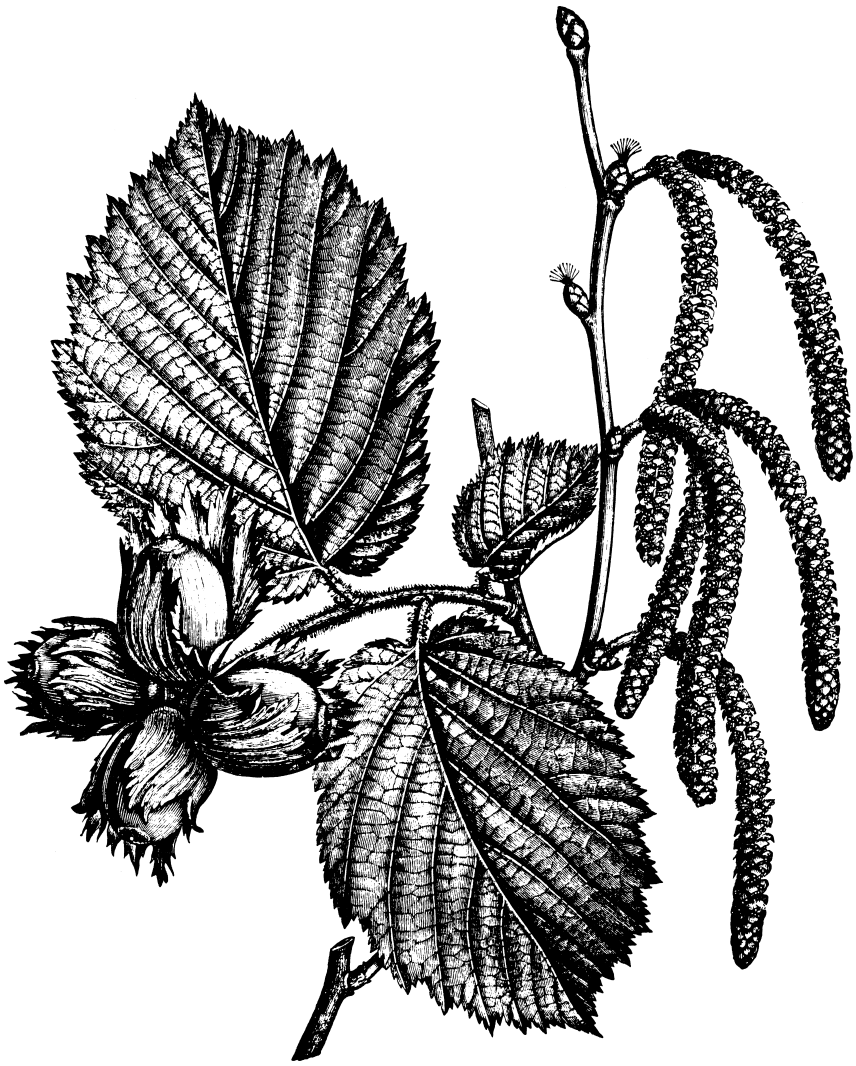
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Riparian Songbird Abundance a Decade After Cattle Removal on Hart Mountain and Sheldon National Wildlife Refuges[1]

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Abstract

Cattle were removed from the high desert riparian habitats of Hart Mountain and Sheldon National Wildlife Refuges in 1990. This study compares songbird abundance in 2000-2001 to that in 1991-1993 on 69 permanent plots. Of the 51 species for which detections were sufficient to calculate changes in abundance, 71 percent (36/51) exhibited a positive trend and 76 percent (16/21) of species exhibiting a significant change (either positive or negative) increased. The average increase among the 51 species was equivalent to 3.0 detections/km^2. Increasing species included species of concern in the Columbia Plateau: Yellow Warbler (*Dendroica petechia*), White-crowned Sparrow (*Zonotrichia leucophrys*), Song Sparrow (*Melospiza melodia*), Dusky Flycatcher (*Empidonax oberholseri*), Warbling Vireo (*Vireo gilvus*), Mourning Dove (*Zenaida macroura*), MacGillivray's Warbler (*Oporornis tolmiei*), and Orange-crowned Warbler (*Vermivora celata*). Aspen and willow associates, but not meadow associates, exhibited a significant increase in detections/km^2. Detections of ground/low cup and high cup nesting species, but not cavity nesting species, increased significantly. Ground/understory foraging species, aerial, and overstory foraging species increased significantly in detections/km^2, but bark gleaning species did not. For the 16 significantly increasing species in this study, patterns of change on Breeding Bird Survey routes during 1980-1999 suggest that the changes documented here are not merely a reflection of regional patterns.

Key words: aspen, cattle, grazing, Great Basin, riparian songbirds.

Introduction

During the last 15 years, much scientific and conservation attention has focused on the health of breeding songbird populations throughout the U.S. (e.g., Robbins et al. 1989, Martin and Finch 1995). In the semi-arid west, riparian habitats are of particular concern because they comprise only 1 percent of the landscape but support a higher diversity of breeding songbirds than any other habitat (Knopf et al. 1988a), and they have been severely affected by agriculture, recreation, timber harvest, water diversion, and, particularly, livestock grazing (Thomas et al. 1979, Chaney et al. 1990). Cattle deplete and sometimes eliminate riparian vegetation by grazing on the herbaceous layer and browsing on shrubs and young trees (Sedgwick and Knopf 1991), and they also cause soil compaction, channel widening, and lowering of the water table (Platts 1991).

Effects of cattle grazing on avian abundance have been demonstrated in several studies (see reviews in Saab et al. 1995, Tewksbury et al. 2002). In Saab et al.'s (1995) review of nine studies comparing species abundance in grazed and ungrazed systems, species most affected by grazing were primarily ground or near-ground nesting species and shrub nesting species, as expected from the greater effect that cattle have on the lower vegetation strata. Habitat generalists, canopy nesters, and cavity nesters tended to be less affected by grazing. However, effects throughout the avian community have been documented in cases where grazing has had a severe impact on vegetation (Krueper et al. 2003, Tewksbury et al. 2002).

The high desert riparian habitats of Hart Mountain and Sheldon National Wildlife Refuges (hereafter Hart and Sheldon), in southcentral Oregon and northwestern Nevada, respectively, are among those western landscapes affected by livestock grazing. On Hart, cattle were removed in the autumn of 1990, and a 15-year policy of no grazing was officially adopted in 1994 (USFWS 1994). Soon after cattle were removed, most riparian areas were classified as being in poor (50 percent) or moderate condition (25 percent) (USFWS 1994). Similarly, on Sheldon, season-long cattle grazing was recognized as one of the forces responsible for the poor health of riparian areas (USFWS 1981). Most cattle were removed in the autumn of 1990, although a few remained in one area until 1994, and an increasing feral horse population continued to impact some riparian areas throughout this study.

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[1]A version of this paper was presented at the **Third International Partners in Flight Conference, March 20-24, 2002, Asilomar Conference Grounds, California.**

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In 1991, the year following cattle removal on the refuges, a 3-year study of riparian songbird abundance and riparian vegetation condition was initiated. Dobkin (1994) found that cover of herbaceous vegetation had increased by the third year after cattle removal, consistent with both livestock removal and increased rainfall in the third year. The change in herbaceous vegetation was accompanied by a small increase in avian abundance, especially of ground and understory specialists (Dobkin 1994). There was little change in aspen or willow recruitment during the 3 years, consistent with the slow recovery of woody riparian vegetation. Dobkin et al. (1998) also compared riparian meadow plots inside a long-term livestock exclosure on Hart to adjacent plots recently grazed by cattle (1 to 3 years previously). They found that exclosure plots had higher avian species richness and abundance and were dominated by wetland and riparian birds rather than the upland species of recently grazed plots.

In this paper, we compare the abundance of riparian birds on a set of 69 plots surveyed 1 to 3 years and 11 to 12 years after livestock removal on Hart Mountain and Sheldon National Wildlife Refuges. Future analyses will include the final year of data collection (2002), and detailed vegetation measurements from each plot.

Study Area and Plots

Hart encompasses approximately 112,550 ha and includes Hart Mountain, a fault block that rises to 2,438-m elevation. Upland vegetation is primarily low sagebrush (*Artemisia arbuscula*), big sagebrush (*A. tridentata*) and silver sagebrush (*A. cana*) with some rabbitbrush (*Chrysothamnus* sp.). Riparian habitat provides the only trees except for scattered stands of mountain mahogany (*Cercocarpus ledifolius*), western juniper (*Juniper occidentalis*), a single stand of Ponderosa Pine (*Pinus ponderosa*), and white fir (*Abies concolor*) at higher elevations (USFWS 1994). Riparian habitats extend from 1,433 to 2,317 m in elevation, most are along narrow streams (<8 m width) varying from high to low gradient, and most zones of riparian vegetation are less than 50 m in width. Riparian habitat is classified into six cover types for the purpose of this study. Of the 134 linear km of riparian habitat on Hart, 29 percent is quaking aspen (*Populus tremuloides*) along perennial streams, 10 percent is quaking aspen in snow pockets (small, relatively high elevation depressions where snow collects), 11 percent willow (*Salix* sp.), 29 percent meadow (various species of grasses, sedges, and rushes), and 12 percent mixed deciduous shrub (including aspen, willow, black cottonwood, *Populus balsamifera,* mountain alder, *Alnus incana*, red-osier dogwood, *Cornus sericea*, waterbirch, *Betula occidentalis*, and chokecherry, *Prunus virginiana*). An additional 9 percent of streamside zones are dominated by non-riparian shrubs either because the valley and riparian zone were naturally narrow or because upland shrubs, primarily big sagebrush, have encroached to the streamside.

Sheldon encompasses 232,800 ha of high desert, and although only 32 km south of Hart, the climate is hotter and drier. Average precipitation is 15 cm at lower elevations (1,280 m) and 33 cm at higher elevations (2,225 m) at Sheldon (USFWS 1981), compared to 25.0 to 37.5 cm at Hart. The expansive uplands are broken by narrow canyons, rolling valleys, and broad rimrock tables. Upland vegetation is dominated by big sagebrush, low sagebrush, rabbitbrush, bitterbrush (*Purshia tridentata*), and greasewood (*Sarcobatus vermiculatus*). A few mountain mahogany, western juniper, and quaking aspen stands occur at higher elevations. Of the 83 linear km of riparian habitat on Sheldon, which occur primarily along Hell, Virgin, Thousand, Fish, and Badger Creeks, 52 percent is dominated by meadow, 12 percent by willow, and 7 percent by mixed deciduous shrubs. As much as 29 percent of riparian areas, however, are classified as nonriparian shrub (*table 1*). The amount of aspen and snow pocket aspen is negligible.

Table 1— *Distribution of avian plots relative to cover type availability (in km) on Hart Mountain and Sheldon National Wildlife Refuges. Riparian aspen includes some aspen in valleys but not along perennial stream segments. Proportion of length (km) is the proportion of the total perennial stream lengths on a refuge made up by each cover type.*

	Hart Mountain			Sheldon			
Cover type	Length (km)	Prop. length	No. plots	Length (km)	Prop. length	No. plots	Total plots
Meadow	39.0	0.29	7	42.7	0.52	9	16
Riparian Aspen	39.0	0.29	18	--	--	0	18
Snow Pocket Aspen	13.8	0.10	9	--	--	0	9
Willow	14.3	0.11	5	10.3	0.12	10	15
Nonriparian Shrub	12.2	0.09	8	24.3	0.29	1	9
Mixed Deciduous	16.1	0.12	0	5.7	0.07	2	2
Total	**133.9**		**47**	**82.9**		**22**	**69**

Plots were established in five cover types on five drainages on Hart (n = 47) and four cover types in six drainages on Sheldon (n = 22) (*table 1*). Of the 18 riparian aspen plots, all of which were on Hart, 14 were within multi-aged, mature stands; two were within decadent stands that had little or no regeneration and a large proportion of dead trees; and two were within a dense, even-aged stand that had burned in a 1972 wildfire. Stands of snow pocket aspen consist of trees that are shorter and more scrub-like than those in mature riparian aspen stands, but most also have some mature trees interspersed (Dobkin et al. 1995). Willow stands on riparian plots were typically narrow (<50 m) and varied substantially in sparseness and structural diversity. The two mixed deciduous plots, both along Idaho Creek on Sheldon, were in narrow, dense stands of mountain alder, red-osier dogwood, willow, and snowberry (*Symphoricarpos oreophilus*). Meadow plots varied from dry to moist to marshy and from narrow strips surrounded by non-riparian shrub to meadows extending the width of the plot. Seven meadow plots (4 in 1985 and 3 since 1993) and two willow plots (1990 and 1999) have undergone prescribed burning, and an additional 1 to 3 meadow plots were affected by a 1972 wildfire.

Methods

Each plot was 150 m long by 100 m wide, and most plots were at least 250 m apart. The width of the riparian vegetation on a plot ranged from <5 m to 100 m, but was typically less than the width of the plot. The centerline of the plot, which was marked at 50-m increments with permanent steel fence posts, ran near and parallel to the stream. Each plot was surveyed 3 times between 8 May and 24 June in 2000 and 17 May and 25 June in 2001. In 2001, four observers conducted surveys in a balanced design such that, except for a few exceptions, no person surveyed the same plot twice. Two observers conducted all surveys in 2000. In 1991-1993, each plot was surveyed six times, once on each of two consecutive days during each of 3 survey rounds between 7 May and 11 July (Dobkin and Rich 1998). In both 1991-1993 and 2000-2001, the order in which plots were surveyed within a day (and within a drainage) alternated between consecutive visits. During a survey, an observer walked slowly along the centerline recording the first occurrence of each individual seen or heard within the plot. Surveys were conducted between 0.25 and 3.5 hours after sunrise, and time allowed for a survey depended on cover type: 25 min in aspen, 20 in willow, and 15 in meadow or non-riparian shrub. Results provided an index to avian species abundance.

For each of the 69 plots, mean detections per visit were averaged among visits within a year, then among years within a phase (i.e., 1991-1993 and 2000-2001 are phases). The difference between phases was then calculated. The mean difference across all plots was calculated for each species and a paired t-test was used to determine whether the difference for each species was significantly different from 0. As a means of restricting the analysis to those species having a large enough sample to provide a reasonable power to detect a difference, only the 51 species with an average of ≥0.02 detections per plot-visit (equivalent to ≥1.3 detections/km^2) in either phase were used.

The comparison is restricted to passerines, doves, woodpeckers, and shorebirds that either nest or forage primarily in riparian habitat within the Hart-Sheldon landscape; shrubsteppe specialists are excluded because it is not clear how they would be expected to change as the riparian vegetation replaces shrubsteppe vegetation within plots but the shrubsteppe vegetation also improves. In three cases, "species" are combinations of species that were created to keep data recording and species identification consistent between phases. *Empidonax* includes Hammond's, Cordilleran, Pacific-slope, and Willow flycatchers, unidentified flycatchers, and the Olive-sided Flycatcher (genus *Contopus*); Dusky and Gray Flycatchers were analyzed separately. Hummingbird species include Broad-tailed, Calliope, and Rufous Hummingbirds, and unidentified hummingbirds. Sapsuckers include Red-naped and Red-breasted Sapsuckers, hybrids, and those recorded as unidentified. Scientific names for species mentioned in the text are given in *table 2*.

Species were assigned to primary habitats (aspen, willow, or meadow) based on the cover type in which its mean detections per plot-visit was highest in this study. Species were assigned to nesting guilds (ground/low cup, high cup, and cavity) and foraging guilds (ground/understory, overstory, aerial, and bark) based on Dobkin (1994) and Ehrlich et al. (1988). Within each guild, the proportion of species exhibiting a change was compared to 0.50, the proportion expected by chance, using a binomial test. Change in detections/km^2 (i.e., phase II – phase I) was calculated for each guild by pooling detections for all species within each guild and treating the plot as the primary sampling unit. Paired t-tests were used to determine whether the change in detections/km^2 was significantly different from 0 for each guild, and one-way ANOVAs were used to test for differences among guilds in change in detections/km^2. Standard errors are reported with means throughout the text and tables.

Table 2— *Species exhibiting significant increases and decreases in detections between 1991-1993 and 2000-2001. Changes in detections/km^2 are paired differences using the 69 original plots as sampling units; statistical significance based on paired t-tests with (*) $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Species categorized by foraging and nesting guilds based on Dobkin (1994) and Ehrlich et al. (1988). Habitat association is the habitat in which the species was most often recorded in this study. Species in bold are riparian species of concern based on BBS trends (1966-1999) and Partners in Flight prioritization (see Methods).*

Species	Scientific name	Change in detections per km^2	Foraging guild	Nesting guild	Habitat association
Increasing species					
Yellow Warbler	***Dendroica petechia***	**28.2 *** **	**Understory**	**Grnd/Low C**	**Willow**
White-crowned Sparrow	***Zonotrichia leucophrys***	**24.3 *** **	**Ground**	**Grnd/Low C**	**Aspen**
Song Sparrow	***Melospiza melodia***	**23.0 *** **	**Ground**	**Grnd/Low C**	**Willow**
Savannah Sparrow	*Passerculus sandwichensis*	17.9 **	Ground	Grnd/Low C	Meadow
Tree Swallow	*Tachycineta bicolor*	16.9 **	Aerial	Cavity	Aspen
Red-winged Blackbird	*Agelaius phoeniceus*	16.4	Ground	Grnd/Low C	Meadow
Dusky Flycatcher	***Empidonax oberholseri***	**12.2 *** **	**Aerial**	**Grnd/Low C**	**Aspen**
Warbling Vireo	***Vireo gilvus***	**9.4 *** **	**Overstory**	**High Cup**	**Aspen**
House Finch	*Carpodacus mexicanus*	8.5 **	Ground	High Cup	Aspen
Cliff Swallow	*Petrochelidon pyrrhonota*	7.7	Aerial	Other	Meadow
Common Snipe	*Gallinago gallinago*	5.9 *	Ground	Grnd/Low C	Meadow
Killdeer	***Charadrius vociferus***	**5.6 (*)**	**Ground**	**Grnd/Low C**	**Meadow**
Mourning Dove	***Zenaida macroura***	**5.5 ***	**Ground**	**Grnd/Low C**	**Willow**
MacGillivray's Warbler	***Oporornis tolmiei***	**3.9 ** **	**Understory**	**Grnd/Low C**	**Aspen**
Empidonax[a]	***Empidonax* spp.**	**3.7 (*)**	**Aerial**	**Grnd/Low C**	**Aspen**
Dark-eyed Junco	*Junco hyemalis*	3.7 **	Ground	Grnd/Low C	Aspen
Western Tanager	*Piranga ludoviciana*	3.4 *	Overstory	High Cup	Aspen
Brown-headed Cowbird	*Molothrus ater*	3.3	Ground	Other	Willow
Orange-crowned Warbler	***Vermivora celata***	**3.1 ***	**Overstory**	**Grnd/Low C**	**Aspen**
Spotted Towhee	*Pipilo maculatus*	3.1 **	Ground	Grnd/Low C	Aspen
Fox Sparrow	*Passerella iliaca*	2.2 (*)	Ground	Grnd/Low C	Aspen
Yellow-rumped Warbler	*Dendroica coronata*	2.1	Overstory	High Cup	Aspen
Mountain Bluebird	*Sialia currucoides*	1.8	Aerial	Cavity	Aspen
Yellow-breasted Chat	***Icteria virens***	**1.6**	**Ground**	**Grnd/Low C**	**Willow**
Black-headed Grosbeak	*Pheucticus melanocephalus*	1.3	Overstory	High Cup	Aspen
Say's Phoebe	*Sayornis saya*	1.2 *	Aerial	Other	Willow
American Robin	*Turdus migratorius*	1.0	Ground	High Cup	Aspen
Western Wood-Pewee	***Contopus sordidulus***	**0.6**	**Aerial**	**High Cup**	**Aspen**
Common Yellowthroat	*Geothlypis trichas*	0.5	Understory	Grnd/Low C	Willow
Hairy Woodpecker	*Picoides villosus*	0.5	Bark	Cavity	Aspen
Violet-green Swallow	*Tachycineta thalassina*	0.4	Aerial	Cavity	Meadow
Cassin's Finch	***Carpodacus cassinii***	**0.3**	**Ground**	**High Cup**	**Aspen**
Northern Flicker	***Colaptes auratus***	**0.3**	**Bark**	**Cavity**	**Aspen**
White-throated Swift	***Aeronautes saxatalis***	**0.2**	**Aerial**	**Other**	**Willow**
Sora	*Porzana carolina*	0.2	Ground	Grnd/Low C	Meadow
Barn Swallow	***Hirundo rustica***	**0.0**	**Aerial**	**Other**	**Meadow**
Decreasing species					
House Wren	*Troglodytes aedon*	-17.6 **	Understory	Cavity	Aspen
European Starling	*Sturnus vulgaris*	-13.3 **	Ground	Cavity	Aspen
Wilson's Phalarope	***Phalaropus tricolor***	**-11.0 (*)**	**Ground**	**Grnd/Low C**	**Meadow**
Bullock's Oriole	***Icterus bullockii***	**-4.0 *** **	**Overstory**	**High Cup**	**Aspen**
Willet	*Catoptrophorus semipalmatus*	-3.3 (*)	Ground	Grnd/Low C	Meadow

Table 2– *continued*

Species	Scientific name	Change in detections per km^2	Foraging guild	Nesting guild	Habitat association
Decreasing species (contd.)					
Brewer's Blackbird	***Euphagus cyanocephalus***	**-3.2**	**Ground**	**Grnd/Low C**	**Meadow**
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	-3.0	Ground	Grnd/Low C	Meadow
Ruby-crowned Kinglet	***Regulus calendula***	**-2.4 ****	**Overstory**	**High Cup**	**Willow**
Lazuli Bunting	***Passerina amoena***	**-2.2**	**Ground**	**Grnd/Low C**	**Willow**
Western Meadowlark	***Sturnella neglecta***	**-2.0**	**Ground**	**Grnd/Low C**	**Meadow**
Wilson's Warbler	***Wilsonia pusilla***	**-1.7 ***	**Understory**	**Grnd/Low C**	**Willow**
Hummingbird species[b]	***Selasphorus/Stellula* spp.**	**-0.8**	**Understory**	**Grnd/Low C**	**Aspen**
Swainson's Thrush	***Catharus ustulatus***	**-0.8**	**Understory**	**Grnd/Low C**	**Aspen**
Sapsuckers[c]	***Sphyrapicus nuchalis, S. ruber***	**-0.4**	**Bark**	**Cavity**	**Aspen**
Downy Woodpecker	*Picoides pubescens*	-0.2	Bark	Cavity	Aspen

[a]Includes: Hammond's Flycatcher (*Empidonax hammondii*), Cordilleran Flycatcher (*E. occidentalis*), Pacific-slope Flycatcher (*E. difficilis*), Willow Flycatcher (*E. traillii*), and one *Contopus*, the Olive-sided Flycatcher (*Contopus cooperi*).
[b]Includes: Broad-tailed Hummingbird (*Selasphorus platycercus*), Calliope Hummingbird (*Stellula calliope*), and Rufous Hummingbird (*Selasphorus rufus*).
[c]Includes: Red-naped Sapsucker (*Sphyrapicus nuchalis*) and Red-breasted Sapsucker (*Sphyrapicus ruber*) and those recorded as hybrid or unidentified sapsuckers.

Riparian species of concern, for the purpose of this study, are those riparian associates that had either (1) a significant declining trend on North American Breeding Bird Survey (BBS) routes within U.S. Fish and Wildlife Service Region 1, which includes California, Oregon, Washington, Nevada, and Idaho; (2) a significant declining trend on BBS routes in the Columbia Plateau physiographic area; (3) a Partners in Flight score for the Columbia Basin >20; or (4) an Oregon Management Index score >10. The latter two scores, obtained from Partners in Flight's Columbia Plateau Bird Conservation Plan (Altman and Holmes 2000), are based on relative abundance, population trend, threats on the breeding and wintering grounds, and the extent of the species' breeding and nonbreeding distributions.

Results

Preliminary results one decade after cattle removal, 1991 to 1993 compared to 2000 to 2001, indicate that 71 percent (36/51) of riparian species exhibited positive trends ($P < 0.01$, binomial test) and 76 percent (16/21) of species exhibiting a significant change (either positive or negative) increased ($P < 0.05$) (*table 2*). The average increase among the 51 species was 0.045 detections per plot or 3.0 detections/km^2 (a rate significantly greater than zero, paired t-test, $P < 0.01$). The 16 significantly increasing species were Yellow Warbler, White-crowned Sparrow, Song Sparrow, Savannah Sparrow, Tree Swallow, Dusky Flycatcher, Warbling Vireo, House Finch, Common Snipe, Mourning Dove, MacGillivray's Warbler, Dark-eyed Junco, Western Tanager, Orange-crowned Warbler, Spotted Towhee, and Say's Phoebe (*table 2*). The five significantly declining species were House Wren, European Starling, Bullock's Oriole, Ruby-crowned Kinglet, and Wilson's Warbler (*table 2*). Here we interpret the pattern of increasing species by primary habitat, nesting guild, and foraging guild.

Aspen and willow associates ($t = 2.86$, $P = 0.006$; and $t = 3.83$, $P < 0.001$), but not meadow associates ($t = 1.44$, $P = 0.16$), exhibited a significant increase in detections/km^2 (*table 3*). The change in detections/km^2 did not vary significantly among the three habitat association groups ($F = 0.76$, $P = 0.47$, *fig. 1*). Increasing species comprised a significant proportion (0.77) of significant changes among aspen species ($P < 0.05$) but not among willow or meadow associates (*table 3*).

Detections of ground/low-cup nesting species and high-cup nesting species increased significantly ($t = 6.12$, $P < 0.001$; $t = 2.23$, $P = 0.03$), but cavity nesting species exhibited little change ($t = 0.78$, $P = 0.44$, *table 3*). The change in detections/km^2 varied significantly among nesting guilds ($F = 22.0$, $P < 0.001$, *fig. 1*). Ground/low-cup nesting species increased significantly more than either high-cup nesters or cavity nesters, and cavity-nesting species increased the least. A similar pattern is evident in the proportion of increasing species. Increasing species comprised a significant proportion (0.92) of significant changes among ground/low-cup nesting species ($P < 0.01$) but not among other nesting guilds (*table 3*).

Table 3— *Mean change and percent change in detections/km^2, and proportion of species increasing by habitat, nesting, and foraging guilds for riparian species on the 69 original plots on Hart and Sheldon National Wildlife Refuges in 2000-2001 compared to 1991-1993. Paired t-tests with 68 df used to determine significance of change in detections/km^2; binomial test used to determine whether proportion of species increasing differed from 0.50 (* P < 0.05, ** P < 0.01, *** P < 0.001). Guilds were pooled for binomial tests if denominators were < 6 because statistical significance of P < 0.05 can't be achieved in such cases.*

Guild	Change in detections per km^2 (SE)	Percent change[a] in detections per km^2	Prop. species exhibiting positive trend[b]	Prop. significant changes that are increases[c]
Habitat				
Aspen	64.9 (22.7)**	19	0.74 (20/27)*	0.77 (10/13)*
Willow	57.3 (14.9)***	75	0.73 (8/11)	0.67 (4/6)[d]
Meadow	31.4 (21.9)	13	0.62 (8/13)	1.00 (2/2)[d]
Nesting				
Ground/low cup	132.9 (21.7)***	40	0.67 (18/27)	0.92 (11/12)**
High cup	20.1 (9.0)*	20	0.80 (8/10)	0.60 (3/5)[e]
Cavity	-12.1 (15.4)	-7	0.56 (5/9)	0.33 (1/3)[e]
Foraging				
Ground/Understory	96.1 (25.3)***	20	0.63 (26/41)	0.72 (13/18)
Aerial	44.7 (14.8)**	39	1.00 (10/10)**	1.00 (3/3)[f]
Overstory	12.8 (4.3)**	32	0.71 (5/7)[g]	0.60 (3/5)[f]
Bark	0.1 (3.4)	0	0.50 (2/4)[g]	0.00 (0/1)[f]

[a] Percent change = (change in detections/mean detections in 1991-1993) x 100%
[b] Number species increasing divided by total number species in the guild.
[c] Number of significantly increasing species divided by number of species exhibiting significant changes (either increases or decreases).
[d] Categories pooled for binomial test; 6/8 = 0.75, P = 0.29.
[e] Categories pooled for binomial test; 4/8 = 0.50, P = 1.0.
[f] Categories pooled for binomial test; 6/9 = 0.67, P = 0.51.
[g] Categories pooled for binomial test; 7/11 = 0.64, P = 0.55.

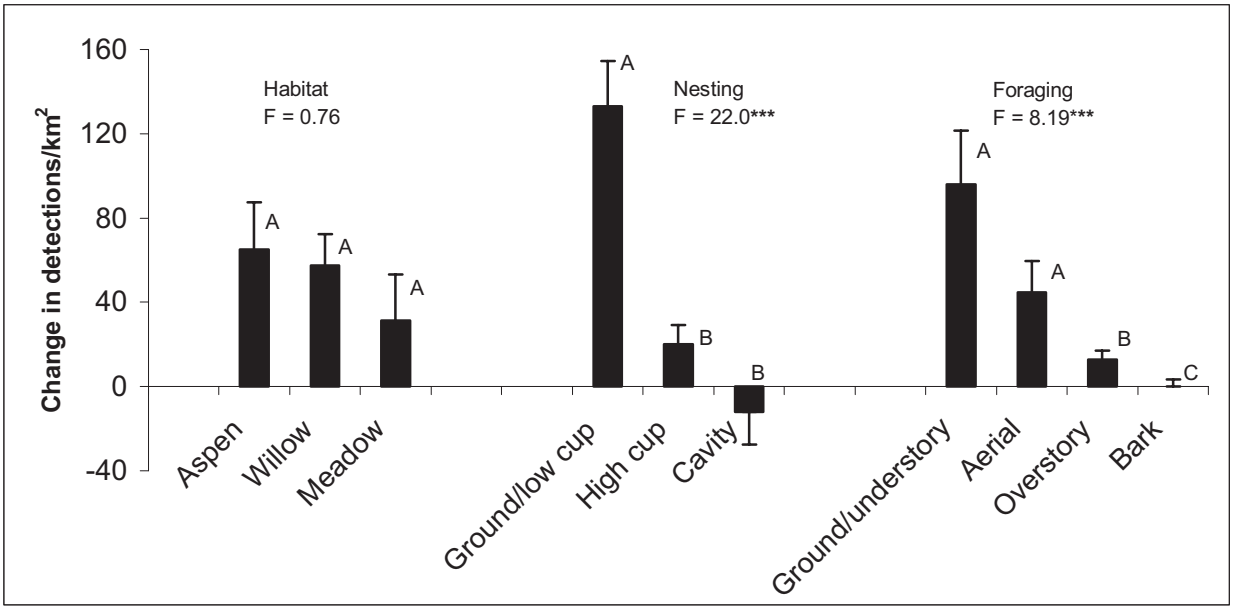


Figure 1— Change in detections/km^2 for riparian species within habitats of primary occurrence, nesting guilds, and foraging guilds. Change in detections is the difference between 2000-2001 and 1991-1993 detections pooled across species on the 69 original plots on Hart and Sheldon National Wildlife Refuges. Statistical tests are one-way ANOVAs (* P < 0.05, ** P < 0.01, *** P < 0.001). Within guild types, guilds with different letters above bars are those that differ significantly in detections/km^2 based on t-tests.

Ground/understory foraging species ($t = 3.79$, $P < 0.001$), aerial ($t = 3.02$, $P = 0.004$), and overstory foraging species ($t = 2.94$, $P = 0.004$) showed significant increases in detections, but bark-gleaning species did not ($t = 0.04$, $P = 0.97$, *table 3*). The change in detections/km^2 differed significantly among foraging guilds ($F = 8.19$, $P < 0.001$, *fig. 1*). Ground/understory foraging species increased significantly more than overstory foragers ($P = 0.002$) and bark gleaners ($P < 0.001$) and marginally more than aerial foragers ($P = 0.08$). Aerial foragers increased significantly more than overstory foragers ($P = 0.04$), and the change in detections of bark gleaners was significantly less than that of each of the other foraging guilds (all $P < 0.02$). Among ground/ understory foragers, increasing species comprised a marginally significant proportion (0.72) of significant changes ($P = 0.10$). Among aerial foragers, each of the ten species exhibited a positive trend, and the three significant changes were all increases (*table 3*).

Of the 26 riparian species of concern for which we had sufficient detections (*table 2*), 7 exhibited significant increases on original plots since the removal of cattle (Yellow Warbler, White-crowned Sparrow, Dusky Flycatcher, Warbling Vireo, MacGillivray's Warbler, Orange-crowned Warbler, and Mourning Dove). Three species of concern declined significantly since 1991-1993 (Bullock's Oriole, Ruby-crowned Kinglet, and Wilson's Warbler).

Discussion

Several patterns in the effects of grazing on avian communities have emerged. Saab et al. (1995) reviewed nine studies providing quantitative comparisons of species abundance in grazed and ungrazed systems (Page et al. 1978; Crouch 1982; Mosconi and Hutto 1982; Taylor 1986; Sedgwick and Knopf 1987; Medin and Clary 1990, 1991; Schulz and Leininger 1991; Knopf et al. 1988b). Species significantly affected by grazing, either across all studies or in at least one study, were primarily shrub nesting species (Red-winged Blackbirds, Common Yellowthroats, Willow Flycatchers, Yellow Warbler, American Redstart [*Setophaga ruticilla*], Gray Catbird [*Dumetella carolinensis*], and Yellow-breasted Chat) and ground or near-ground nesting species (Veery [*Catharus fuscescens*], Nashville Warbler [*Vermivora ruficapilla*], Fox Sparrow, Dark-eyed Juncos, White-crowned Sparrows, Savannah Sparrows, and Lincoln's Sparrows [*Melospiza lincolnii*]). As expected, habitat generalists, canopy nesters, and cavity nesters tended to be less directly affected by grazing. In a recent study, Krueper et al. (2003) documented dramatic changes in vegetation during the 5 years after cattle removal from the San Pedro River in Arizona and found that open cup nesters increased faster than cavity nesters, insectivores faster than omnivores, and neotropical migrants faster than residents. In a comparison across seven riparian systems in the western U.S., Tewksbury et al. (2002) found that open cup nesters, species nesting below 2.5 m, and long distance migrants were less abundant in grazed than ungrazed areas, but the difference was greatest for species nesting below 2.5 m.

In this study of riparian bird abundance one decade after cattle removal on Hart Mountain and Sheldon National Wildlife Refuges, we also found patterns of increases consistent with recovery from cattle grazing. Ground/low cup nesting species increased more than either high cup or cavity nesting species, and cavity nesting species increased less than either of the other two guilds. Ground/understory foraging species increased significantly more than overstory or bark foraging species, and bark foraging species increased significantly less than other foraging guilds.

Increases in this study were generally more widespread among species groups than might be expected. Significant increases were seen among aspen and willow associates, ground/low cup nesters, high cup nesters, and among ground/understory, overstory, and aerial foragers. Only meadow associates, cavity nesters, and bark gleaners did not increase significantly. Other studies also have found community-wide effects of cattle removal. Krueper et al. (2003) found significant increases in both open cup and cavity nesting species, both resident and Neotropical migrants, all foraging guilds (insectivores, omnivores, granivores), and all species groups categorized by vertical strata of occurrence (understory, midstory, and upperstory). Similarly, in a comparison of sites grazed for >50 years and sites free of grazing for >25 years along the Missouri River, effects were seen in both open-cup and primary cavity nesters, and low and high nesting species groups were equally affected (Tewksbury et al., 2002).

Widespread effects among foraging and nesting guilds illustrate the importance of understanding the mechanism by which cattle grazing affects avian communities. It is generally accepted that the species composition and structure of herbaceous and understory vegetation are affected by grazing. Presumably, this change in vegetation also affects the invertebrate population, and, as suggested by Krueper et al. (2003), it is likely that changes in the invertebrate population are not restricted to the lower layers of the vegetation. Studies of how invertebrate populations change with cattle removal, and how this affects avian communities, are largely lacking. However, our detailed vegetation measurements, collected in 1991-1993 and to be collected again in 2001-2002, will likely clarify the relationship between changes in particular aspects of plant species composition or structure and changes in avian abundance.

Regional rainfall may also have changed during the last decade. Cattle were removed from Hart Mountain and Sheldon National Wildlife Refuges at the end of a multi-year drought in the early 1990s. Since then, an increase in regional rainfall could have produced a positive response in riparian vegetation and a corresponding increase in riparian birds. One would expect any improvement due to regional rainfall patterns to be exhibited in other areas in addition to the refuges. To investigate this possibility, we compared our pattern of increasing species to that on Breeding Bird Survey (BBS) routes within the Columbia Plateau physiographic area and within U.S. Fish and Wildlife Service Region 1 during 1980-2001 (Sauer et al. 2002). Of the 16 significantly increasing species documented on the refuges in this study, 10 were sufficiently covered by BBS (i.e., observed on >14 routes) within the Columbia Plateau and all 16 were sufficiently covered within Region 1. Of the 10 sufficiently covered species within the Columbia Plateau, none was significantly increasing on BBS routes and 1 was significantly declining (Mourning Dove). Of the 16 sufficiently covered species within Region 1, only 1 was significantly increasing (Tree Swallow), but 3 were significantly decreasing (Common Snipe, Yellow Warbler, and Mourning Dove). Thus, the species increasing in abundance on Hart Mountain and Sheldon National Wildlife Refuges are not a reflection of regional patterns of species' increases. We will investigate this issue in more detail, by evaluating rainfall in relation to detections on the refuges and on BBS routes, after the final year of data collection.

Acknowledgments

This project was funded by the U.S. Fish and Wildlife Service, Region 1, Nongame Bird Program, and we thank M. Green and T. Zimmerman for their interest and guidance. We thank the observers in 2000 and 2001: D. Anderson, D. Moen, M. Schlenker, and A. Woodrow. Thanks to W. Pyle, A. Rich, M. Bray, J. Heltzel, J. Barnett, and J. Bart for useful suggestions throughout the study. The Sheldon-Hart Mountain National Wildlife Refuge Complex provided logistical support throughout; in particular, thanks to B. Reiswig, M. Nunn, J. Barnett, and C. Dippel for their support.

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Apparent Rates of Increase for Two Feral Horse Herds

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The Journal of Wildlife Management, Vol. 46, No. 2. (Apr., 1982), pp. 367-374.

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APPARENT RATES OF INCREASE FOR TWO FERAL HORSE HERDS

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Abstract: Rates of increase for 2 Oregon feral horse (*Equus caballus*) herds were estimated from direct aerial counts to be about 20% per year. These rates can be achieved only if survival rates are high, and reproduction exceeds that normally expected from horses. A population dynamics model suggests adult survival to be the key parameter in determining rates of increase, and there is some direct evidence of high adult survival rates. Management implications are discussed.

J. WILDL. MANAGE. 46(2):367–374

Widespread interest in feral horses, combined with differing management priorities, has led to substantial controversy about abundance and rates of increase of free-ranging herds. Counts of several Oregon herds in recent years have indicated high rates. This paper documents observations of horses on 2 such areas in Oregon, and compares estimates with potential rates. We do not propose that the observed rates in these herds are necessarily typical of feral horses in general. Because the observed rates are appreciably higher than might be expected on the basis of other experience with large mammals, we used a simple model of population dynamics to explore the range of vital parameters likely to be required if such rates are to persist.

The senior author was supported under Contract DE-AC06-76RLO-1830 with the U.S. Department of Energy. Useful suggestions from the editor and referees are gratefully acknowledged.

OBSERVED RATES OF INCREASE

Beaty's Butte Herd

The Beaty's Butte herd management unit is 78 km east of Lakeview, Oregon, on the Nevada border. The unit totals 176,900 hectares, of which 160,470 hectares are managed by the Bureau of Land Management. Topography varies from gently rolling hills to steep hills and buttes with a number of broad valleys and shallow or dry lakes. Big sagebrush (*Artemisia tridentata*) dominates virtually the entire area with an understory of Sandberg bluegrass (*Poa sandbergii*), Thurber needlegrass (*Stipa thurberiana*), bottlebrush squirreltail (*Sitanion hystrix*), bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and early season forbs. Livestock grazing and wildlife habitat are the primary public land values within the area.

Substantial numbers of horses have used the general area since the early 1900's. From the mid-1930's to the late 1940's there were approximately 2,500–3,000 horses present. By the mid-1950's numbers had been reduced to less than 50 head. The population increased slowly until the early 1970's, probably as a consequence of periodic removals. The first recorded aerial count was in 1969, and counts have continued to the present (Table 1). Fencing and natural barriers have limited ingress or egress of horses to and from the area. A fence to the south was down in 1972 (but repaired by November 1972), and the sharp increase in

Table 1. Feral horses censused on Beaty's Butte Management Unit, Oregon, 1969–80.

Date	"Adults"	Foals	Foals/ 100 "adults"	Totals
Oct 1969				142
Mar 1971				179
Oct 1971	190	44	23	234
Oct 1972	271	69	25	340
Apr 1973	279	25		365
Aug 1973	345	78	23	423
Jan 1974	328	85	26	413
Aug 1974	372	110	30	482
Aug 1975	494	117	24	611
Aug 1976	586	176	30	762
Aug 1977	690	189	27	879
Sep 1978	229	44	19	273
Sep 1979	251	54	22	305
Aug 1980	328	91	28	419

numbers from 1971 to 1972 may have been associated with ingress from the adjacent Sheldon Game Range herd.

Results of the aerial counts were plotted as a semi-logarithmic plot with a regression line fitted to the counts from 1972 to 1977 (Fig. 1). These counts, with 1 exception, were made by A. K. Majorowicz from a Cessna 182, using basically the same flight pattern during the first 4 or 5 hours of daylight. A total of 776 horses was removed from fall to spring 1977, and about 30 were moved into the area in "gathering" operations to the east. The regression estimate of the instantaneous annual rate of increase from 1972 to 1977 is 0.20 (95% CL = 0.18 to 0.23). Projecting this rate from 1978 to 1980 appears compatible with the observations for those years (Fig. 1).

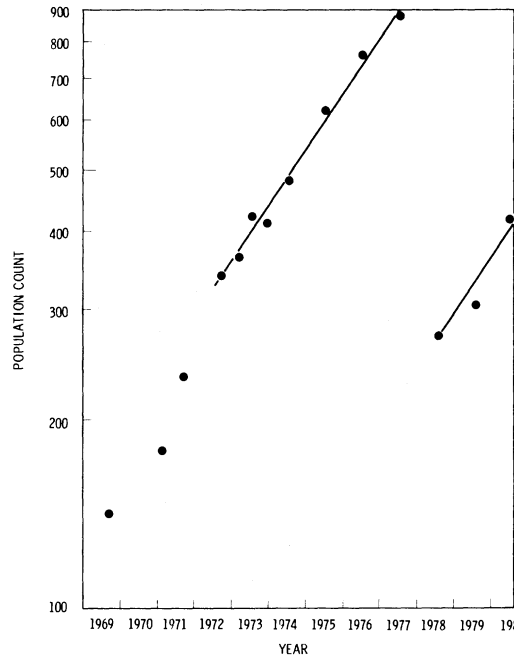


Fig. 1. Feral horse counts on the Beaty's Butte Management Unit. Regression line (log scale) calculated from 1972 to 1977 data, and projected to 1980.

Jackie's Butte Herd

The Jackie's Butte herd management unit is in southeastern Oregon, about 19 km southeast of Rome. The unit includes 31,600 hectares of which 98% is managed by the Bureau of Land Management. The topography is relatively flat, with gentle undulations. Jackie's Butte (1,340 m) is the only prominent landmark. Cover types are similar to those of the Beaty's Butte area, with big sagebrush, bluebunch wheatgrass and squirreltail as major vegetation types. Portions of the area have been seeded to crested wheatgrass (*Agropyron cristatum*), and the area is completely fenced.

This herd has been counted since 1969, with counts from 1974 to 1979 by J. A. Wilcox, who also participated in the 1969 and 1970 surveys (Table 2). A helicopter was used in 1970, and again from 1974 to 1980. Fixed-wing aircraft were used for counting in the other years. Three removals were made (Oct or Nov) from the area since 1969. These provide a check on the accuracy of the counts as the difference between the total count of 1 year and the "adult" category in the following year should equal the known removals plus any other losses.

For example, in 1970, 181 horses were removed as compared to the difference between 263 in September of 1970 and 78 "adults" in January of 1972, which was 185 horses. In 1976, 137 were removed while the corresponding difference was 135. A 1978 removal of 136 may be compared with a difference of 134. There thus is little reason to doubt the accuracy of the counts, although it is possible that a few early-season foals might have been classed as "adults", decreasing the apparent difference somewhat. The "adult" category includes all animals older than foals, due to the difficulties of classification from the air.

Estimating the rate of increase for the Jackie's Butte area was complicated by the removals and it was necessary to pool rates from 3 different time intervals, using a weighting scheme (Snedecor and Cochran 1967:432–436). The resulting value was an 0.18 instantaneous annual rate of increase. Using only the data from 1972 to 1976 (the longest period with no removals) gave a rate of 0.19.

Table 2. Feral horses censused on Jackie's Butte Management Unit, Oregon, 1969–80.

Date	"Adults"	Foals	Foals/ 100 "adults"	Totals
Mar 1969	175	50	28	225
Sep 1970	208	55	26	263
Jan 1972	78	16	20	94
Jan 1973	86	27	31	113
Mar 1974	113	27	24	140
Oct 1974	125	30	25	150
Apr 1975	186	36	19	222
Aug 1976	208	72	35	280
Nov 1977	145	56	39	201
Aug 1978	198	37	19	235
Dec 1979	101	27	27	128
Nov 1980	119	34	28	153

POTENTIAL RATES OF INCREASE

Biologists having extensive experience with large mammals are likely to view the above rates as improbable in terms of their experience. An important point, however, is that most such experience is with wild animals subject to mortality from a number of causes. In the horse herds considered here, few mortalities have been observed, and the likely sources of mortality are largely limited to disease (not yet observed) and an occasional accident (largely with fences). It is thus instructive to examine potential rates of increase with low mortality rates.

Any detailed appraisal of population dynamics requires a knowledge of both age-specific mortality rates and age-specific reproductive rates. Unfortunately neither of these requirements can be supplied for the herds considered here, beyond the little evidence of mortalities in the recent history of the areas, and the relatively high proportions of foals observed with the herds (Tables 1, 2). There are few suitable data on mortality rates for any feral horse herd, and surprisingly little data on reproduction for unconfined horses in comparable environments. Survival estimates for adult horses range from 70 to 80% per year (Wolfe 1980:Table 5) to 95% and higher (National Research Council 1980).

A number of foalings was observed in eastern Montana by Speelman et al. (1944) under range conditions. Their data yield a 60% foaling rate for 209 mares age 4 or older, observed over several breeding seasons. Peak rates were observed between 8 and 10 years of age, with a gradual reduction to age 20, and a sharp decline thereafter. Maximal reproductive rates for horses under good conditions are apparently not well established as domestic horses are rarely maintained in conditions permitting maximal possible foaling. We thus arbitrarily assume a maximal rate of 90% per year, to contrast

with the data of Speelman et al. (1944). Boyd (1979) observed an 86% foaling rate in animals 4 years of age and older on a Wyoming area in 1978, but the rate dropped to 54% in 1979, after a severe winter. Several additional sets of data on foaling rates are tabulated in the National Research Council (1980) report.

Undoubtedly both reproductive and survival rates decrease sharply in older animals. We assume that a decrease probably occurs at about 20 years of age, from experience with domestic horses and the observations of Speelman et al. (1944). The effects of old age probably are minimal for 2 reasons. One is that the herds have increased dramatically in a relatively short span of time (Tables 1, 2). The other is that the several reductions probably removed the oldest horses. This circumstance probably prevails in many managed areas, as the oldest animals are usually readily caught and are customarily not returned, if any animals are released back into the area.

The remaining issue in estimating potential rates of increase is age structure. The highest rates can be expected if the population is concentrated in the "prime" age classes, where reproductive rates are highest and mortality is minimal. Unfortunately, little is known about the age structure of the herds considered. However, the relatively short periods in which larger numbers of horses were present make it clear that the age structure has few old animals. This is supported by observations of the vigor of individuals in the annual surveys. For lack of a useful alternative, we assume that the age structure follows a "stable" age distribution, i.e., that established after a substantial period at a constant rate of change.

Although it seems clear that mortality was low in the herds concerned, it is a generally accepted principle that the youngest animals in most populations will show appreciably higher mortality than fully mature individuals. We have considered that a lower rate of survival needs to be incorporated for the younger animals, specifically from birth to 2 years of age. We thus used 2 survival rates, a single reproductive rate, and assumed a stable age distribution. The model is essentially that used by Leslie (1966), and seems to be the simplest practical approach in the absence of knowledge of the actual age-specific rates (as is often true in unconfined populations).

In Leslie's example, adult survival was such that the expected decrease in old age was not particularly important as relatively few animals survived to reach senescence. In the present situation, survival rates are quite high. However, animals in age classes beyond 20 are not likely to be present in any numbers, so we have simply truncated the age-structure at age 20. This can be thought of as either implying zero survival after age 20, or an effective cessation of reproduction at that age.

With the exception of the above truncation at age 20, the balance of our model follows that of Leslie, as adopted by Eberhardt and Siniff (1977). We assume the Lotka equation for a steady-state population:

$$1 = \sum_{0}^{\infty} \lambda^{-x} \ell_x m_x$$

$$= \lambda^{-a} P_0 P_1 P^{a-2} F \left[\frac{1 - (P/\lambda)^{w-a+1}}{1 - P/\lambda} \right],$$

where a = age of first reproduction, w = maximum age, ℓ_x = survival to age x (replaced in the 2nd equation by products of P_0, P_1, and P, which represent respectively survival in the 1st, 2nd, and subsequent years of life). Also m_x denotes the age-specific reproductive rate, ex-

pressed as female births per female which is replaced by a single rate, F, in the 2nd equation, and lambda denotes the finite population multiplier. Lambda is a multiplier denoting the size of the population 1 year after the current time. We assume an equal sex ratio at birth, so that F is one-half of the rates proposed above ($F = 0.3$ or $F = 0.45$).

Although the above model is greatly simplified from the Lotka equation, or the often-used Leslie matrix formulation, it nonetheless still contains several variables, making it difficult to evaluate potential rates of increase without making an explicit choice of values of these several variables. A convenient way to depict the possible solutions was used by Eberhardt and Siniff (1977). The equation is rearranged so that the ratio of the first 2 years' survival to adult survival can be denoted by K, that is:

$$K = \frac{P_0 P_1}{P^2}.$$

We can then plot K for various values of P and a choice of the age (a) of first reproduction. For present purposes we use $a = 3$ and $a = 4$. It should be noted that a denotes the age of the female when the first foal is born, and that available data indicate that relatively few females give birth at the earliest observed reproductive age. Consequently, the age assumed here is presumed to be that of the 2nd year, i.e., when $a = 4$ there will normally be a small proportion of females producing their first foal at age 3 (but this is neglected in the model). It is evident (Fig. 2) that the age of first breeding has a minor effect compared to that of adult survival rate, unless rates of increase are relatively high and juvenile survival is also high, as in the 2 herds considered here. The right-hand margins give values of lambda, the finite population multiplier.

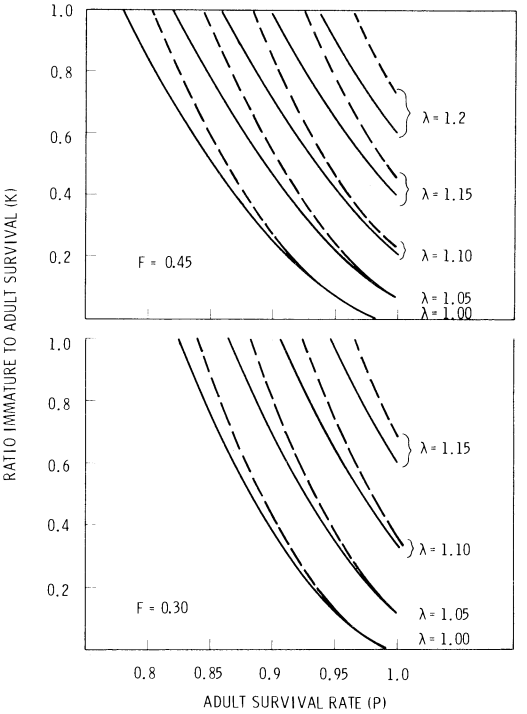


Fig. 2. Ratio of immature to adult survival (K) of feral horses plotted against adult survival (P) for various rates of population change (λ). Upper panel gives rates for annual reproductive rate (female births per female) of $F = 0.45$, lower panel for $F = 0.30$. First reproduction at age 3 (———); first reproduction at age 4 (— — —).

It can thus be seen that the values observed in the Oregon areas are rather improbable for $F = 0.3$, but are achievable at the higher reproductive rate ($F = 0.45$), providing adult survival exceeds 95% and survival for the first 2 years of life is 60–80% of adult survival. Conley (1979) gives results that are roughly comparable to ours (Fig. 2) but does not incorporate a separate survival rate for the first year, and truncates survival at age 14.

BIRTH AND SURVIVAL RATES

The data presently available on reproductive rates on the 2 areas are numbers of foals per 100 adults (Tables 1, 2). If there were no mortality of either adults or foals, then the ratio of foals to adults

would necessarily be equal to the observed rate of increase. However, we believe there is presently some small rate of adult mortality, and that the rate of foal mortality is necessarily higher than that for adults. Consequently, the reproductive rate must be higher than the rate of increase if the increase is to be maintained with some mortality. An estimate of the birth rate thus required can be obtained from eq. (2) of Eberhardt and Siniff (1977), using the same modification for truncation at age 20 as discussed above. It is also necessary to provide values of P_0 and P_0P_1. These were obtained by supposing that $P_1 = P$, and writing $P_0 = PK$ and $P_0P_1 = P^2K$ in the equation for birth rate. With these modifications, the parameters of Fig. 2 can be used to calculate birth rates corresponding to adult survival rates. This gives values in the range of 0.20–0.25, in general accord with the observed foal/adult ratios (Tables 1, 2). We have assumed an even sex ratio in the calculations, which may not be the situation in reality.

Survival rates have been calculated from wild horse age data (National Research Council 1980, Wolfe 1980). The method frequently used is that of Chapman and Robson (1960). This method assumes a constant survival rate exists over the age classes actually used in the calculations, and an unchanging population level. This then makes the age structure a geometric series, with parameter equal to the survival rate. However, if the population is increasing, the estimates will be biased, to a degree that may not be adequately appreciated by many users of the methods. In the present instance, age structure can be calculated from eq. (3) of Eberhardt and Siniff (1977):

$$c_x = \beta\lambda^{-x}P_0P_1P^{x-2} \qquad (\text{for } 2 \leq x < 20),$$

where β = birth rate per head (assumed constant). If $\lambda = 1$, this then gives the geometric series referred to above.

Various methods are used to estimate survival from age distributions, depending on the assumptions made about sampling error in the data. For examination of the bias, we can use the simplest method, i.e., the ratio of 1 class to the next youngest. This gives:

$$c_{x+1}/c_x = P/\lambda.$$

Hence when $\lambda = 1$, the true survival rate is estimated. However, if the population is increasing, survival is underestimated. For example, if $P = 0.98$ and $\lambda = 1.15$, the estimated rate is 0.85. Given such a biased estimate, one might erroneously conclude that the population would be unable to attain the rates of increase observed in this study. The logical conclusion, using the results displayed in Fig. 2, would be to expect little or no increase in the population under study, but that conclusion would be an artifact of the bias in the estimated rate.

Wolfe (1980) recognized this problem, but did not attempt corrections. Multiplying his estimates of survival (Wolfe 1980:Table 5) by estimates of λ from his Table 1 gives adjusted survival estimates for 4 areas. The average rate thus obtained is 0.94 annual survival for adult females (1 of the 4 samples is a composite of males and females).

A referee suggested calculating an approximate survival rate for the areas studied here by taking the ratio of the number of "adults" in 1 census to the number of "adults" plus foals in the previous year. For Jackie's Butte this procedure gives an average rate of 0.935, with individual rates ranging from 0.89 to 0.99. The Beaty's Butte data are rather more variable, but average 0.926. The rate thus estimated is a composite of "adult" and foal survivals. Using the total numbers of horses

tallied in the years suitable for estimates (excluding removals) for weights gives (Jackie's Butte):

$$798P + 212P_0 = 944.$$

This can be rearranged into an expression in K ($=P_0/P$) and P. The resulting curve is nearly coincident with that for $\lambda = 1.20$ and reproduction at age 3 in the upper panel of Fig. 2. We conclude that these survival estimates are compatible with the assumption that $F = 0.45$ and that reproduction occurs at age 3 on the areas studied.

DISCUSSION

It appears that the rates observed in the 2 Oregon areas may be compatible with the usual results of population dynamics models. When lambda is defined as e^r, where r is the rate of increase, an observed rate of, for example, 0.18 must be transformed to 1.20 for comparison with Fig. 2.

Some biologists with experience in studying large mammals may doubt the rates of increase documented here. The difficulty may be that wild mammals are rarely encountered in situations where mortality is greatly reduced and reproductive rates achieve maximal values. For example, Eberhardt and Siniff (1977) noted that marine mammals are unlikely to be able to achieve rates of growth in excess of 10% a year, although a number of pinniped species do show reproductive rates of about 90% per year. However, Payne (1977) documented a rate of increase for the Southern fur seal (*Halichoerus grypus*) exceeding 15% per year. The likely conclusion is that these seals were temporarily in a position of abundant food supplies, lacked crowding, disease, and appreciable predation. This is the situation with some feral horse herds.

There has been a generally skeptical attitude as to the reality of rates of increase of 20%/year in recent literature on feral horse herds (Frei et al. 1979, National Research Council 1980, Wolfe 1980), although the reports do cite data yielding such rates. One difficulty is that these reports use data collected by different methods and observers, on areas of sometimes uncertain boundaries, with topography or cover that may be unsuited for aerial surveys. As the present study is largely free of these problems and arrives at similarly high rates, there is clearly a need for a much more detailed assessment of the underlying population parameters. Data on age-specific pregnancy and survival rates needs to be obtained on herds having different range conditions.

While a year's difference in age at first reproduction can make an appreciable change in the first year survival required to achieve high rates of population increase, that difference is only equivalent to 2 or 3 percentage points in adult survival (Fig. 2). Adult survival is thus a key parameter, and needs to be determined accurately. Radiotelemetry may provide the most cost-effective method for that purpose. Foal survival is known to vary with annual weather conditions, and evidently (Fig. 2) is not as narrowly controlling as is adult survival.

MANAGEMENT IMPLICATIONS

It is important to stress that the herds studied should not be regarded as typical of all feral horse herds. There are situations in which the rates of increase are appreciably smaller than those reported here and herds in the same management districts as those reported here appear to have lower rates, but are unfortunately not as well documented as those described above. Generalizations about all herds should not be made from the ob-

served data, but research and management should be conducted in awareness that such rates are feasible and have been observed.

The management problem is basically that a herd with an annual rate of increase of 0.20 will more than double in size in 4 years. Substantial and continuing removals of feral horses must thus be made to sustain other uses of the affected rangelands, including cattle-grazing and wildlife uses. Under prevailing legislation, horses removed from Federal lands administered by the Bureau of Land Management cannot be sold, so that the bulk of the removals have been transferred to private ownership under an "Adopt a Horse" program. A "fact sheet" issued by BLM in June of 1981 reported that over 29,000 horses and burros (*Equus asinus*) have been removed and placed in private hands at an average cost of $300 per animal. Starting 1 October 1981, a flat fee of $200 per horse adopted will be charged, replacing a nominal fee in the past. The effect of this fee on adoption rates is as yet unknown. Current population estimates were reported as 56,000 feral horses and 17,000 burros on public lands.

Costs and numbers to be dealt with thus dictate a need for an efficient management scheme. Topography and cover conditions on many of the areas make censusing more difficult than on the 2 areas described here. Improvements in census methodology will at best provide better estimates of the numbers to be removed. Reduction of the total removals required can essentially be accomplished in 2 ways. One is to maintain the overall population at a low level. The other is to manipulate 1 or more of the parameters controlling rate of population growth. An approximate appraisal of the relative impacts of changes in the various parameters can be obtained from the model used here. Selective removals will change age structures, so a somewhat more complex analysis will ultimately be needed. Effective management requires both understanding of the processes resulting in population growth, and active use of that knowledge.

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Received 18 December 1980.
Accepted 17 September 1981.

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Biological Conservation 241 (2020) 108367

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Feral horse activity reduces environmental quality in ecosystems globally

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ARTICLE INFO

Keywords:
Ecosystem health
Degradation
Grazing
Disturbance
Burro
Mustang
Equus caballus

ABSTRACT

Feral horses occur on several continents, across a wide range of terrestrial biomes, and have had marked impacts on ecosystems worldwide. Despite their oft-reported negative impacts on plants and soils, a global synthesis of their effects has not been attempted. Here we present a meta-analysis of the global impacts of feral horses on ecosystem structure, function and composition using data from 78 studies across five continents. Two-thirds of these studies were from North America (47%) and Oceania (21%), and most studies examined feral horse effects on plants (58%) or soils (35%). Feral horse activity reduced environmental quality by 13% overall, and the magnitude of this decline increased with increases in the intensity of horse activity. Feral horse activity strongly reduced measures of ecosystem function by 19% on average, and had variable effects on composition, with measures of composition most strongly increased (by 21%) at arid sites. There were no overall effects of feral horse activity on ecosystem structure, with insufficient data to assess effects on plant height and cover. We found that feral horse activity had negative effects on soil, increasing erosion (by 31% on average) and reducing plant biomass and litter cover (by 25% and 31% on average respectively). Increases in soil physical properties generally intensified with increasing aridity. Given the generally negative effects of feral horses on ecosystems worldwide, resource managers and governments need to balance the needs of maintaining healthy functional ecosystems and their biota with social- and cultural-driven commitments to maintaining free-ranging herds of feral horses.

1. Introduction

Biological invasions have had profound effects on ecosystem properties and processes worldwide (Hooper et al., 2005). Introduced herbivores can have significant negative effects on ecosystems, both directly, by altering plant community structure and composition, such as the destruction of kelp forests by sea urchins (Johnson et al., 2005), or indirectly, by changing soil and microbial processes that feed back to alter ecosystem functions and biotic communities (Callaway et al., 2004). This can reduce environmental quality, which we define as the status of ecosystem characteristics in natural or human constructed systems that are important for sustaining all living organisms. For example, soil carbon and nitrogen pools have been severely reduced by introduced feral deer in New Zealand's native forests (Wardle et al., 2001). Managing introduced populations to minimise ecological damage can also be difficult because public perception is often organism- and culture-dependent (Coates, 2007). A classic example of an introduced herbivore is the feral horse (*Equus caballus*), which has presented considerable ecological and social problems for land managers on several continents (Nimmo and Miller, 2007; Davies and Boyd, 2019). While the scientific opinion is generally unified on the damaging role that feral horses have on a range of ecosystems (Robertson et al., 2015; Davies and Boyd, 2019; Driscoll et al., 2019), there have been few attempts to assemble a global synthesis of their net impacts on ecosystem processes worldwide. Here we attempt such a synthesis.

Feral horses are extremely adaptable and now occupy a wide range of terrestrial biomes including drylands (Symanski, 1994), wetlands (Turner, 1987), and riparian (Nimmo and Miller, 2007) and alpine (Dyring, 1990) environments. There is an extensive body of literature documenting their impacts on plant community structure and composition (Prober and Thiele, 2007), soil biology, stability and nutrient networks (Dyring, 1990; Davies and Boyd, 2019), and alterations to landscape hydrology via structural changes to the soil and vegetation (Worboys and Pulsford, 2013; Worboys et al., 2018). Feral horses threaten native wildlife directly by competing for resources, or indirectly, by reducing resource quality and thus altering the availability of food, water and habitat (e.g. polluting streams, reducing grass cover, trampling nests; Hall et al., 2016; Eldridge et al., 2019; Davies and

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https://doi.org/10.1016/j.biocon.2019.108367
Received 10 July 2019; Received in revised form 21 November 2019; Accepted 22 November 2019
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Boyd, 2019). Evidence suggests that horses disproportionately use some landscape positions such as streambeds and open areas more intensively than others, thereby heavily concentrating their impacts in riparian areas and grasslands or meadows (Crane et al., 1997; Hampson et al., 2010). Horse-induced changes to vegetation structure in a range of systems, including streambank stability in riparian areas, have been shown to facilitate the invasion of exotic plants and impact multiple species including aquatic fauna (Levin et al., 2002), invertebrates (Ostermann-Kelm et al., 2009), small mammals (Beever and Brussard, 2004) and birds (Zalba and Conzzani 2004). Given their widespread impacts on a range of systems, it is important to synthesize the breadth and depth of feral horse impacts globally.

Studies of feral horses impacts to date have been restricted to specific regions or systems such as the semi-arid rangelands of the western United States (Baur et al., 2017) or the Australian Alps (Robertson et al., 2015), areas where their impacts have garnered substantial political and community attention (Garrott, 2018). As with any large exotic herbivore (Hobbs, 1996), there are likely to be a range of direct and indirect effects of horses on ecosystem structure, function and composition. For example, trampling by horses has been shown to cause irreversible damage to soils and streambanks in alpine riparian systems in Australia (Driscoll et al., 2019). In sagebrush (*Artemisia* spp.) steppe systems in Nevada (USA), there were no differences in perennial grass, biocrust or litter cover between horse grazed and ungrazed exclosures five years after horses were removed (Davies et al., 2014). These conflicting effects of horse activity make it extremely difficult to reach a general consensus of the extent to which they contribute to the degradation of terrestrial systems. It is likely that their impacts vary with changes in abiotic variables such as soil type and climate (Hobbs, 1996). Riparian areas appear to be particularly susceptible to horse impacts year-round (Ostermann-Kelm et al., 2008), but in drylands (rangelands), the magnitude of their effects is likely to be strongly dependent on animal densities (grazing intensity), plant community and annual rainfall (Milchunas et al., 1988). Furthermore, at the global scale, there are large gaps in our understanding of their impacts, with many studies from North America (Beever and Brussard, 2000; Scasta et al., 2016; Davis and Boyd 2019), but relatively few published studies from other continents (though see Turner, 1988; Linklater et al., 2004; Zalba and Cozzani, 2004; Mallon and Zhigang, 2009; Hampson et al., 2010; Odadi et al., 2011).

In this study, we combined a structured, qualitative search of global literature with a quantitative meta-analysis to explore the net effects of feral horses on ecosystems worldwide. We retrieved 4261 observations from 78 publications that reported quantitative data on the effects of feral horses on 64 ecosystem response variables such as plant community composition and cover; soil chemistry and soil stability, that together give us a measure of environmental quality. Studies of feral horse impacts are unevenly distributed across continents affected by feral horses, with a strong emphasis on a few ecosystems. We expected that sites subjected to a higher intensity of horse activity would show the greatest changes in ecosystem structural, functional and compositional variables. Similarly, we expected that, as horse impacts vary widely among widely different ecosystems, any impacts would likely be mediated by changes in soils (clay content) and climate (aridity). Erosion, for example, might be expected to be more severe on finer-textured soils (Robertson et al., 2015). Similarly, changes in plant composition would likely be more pronounced in drier (more arid) systems where plant cover is sparse and their recovery is more protracted (Noy-Meir, 1982). Understanding the general trends in horse impacts improves our understanding of how horses might affect ecosystems and therefore how they can be managed more effectively, helping land managers, administrators, governments and policy advisers to make appropriate decisions to mitigate their impacts.

2. Methods

2.1. Database construction

To compile a comprehensive list of publications on ecosystem impact of feral horse across the globe, we searched multiple databases (e.g., Web of Science, Scopus, Proquest Science & Technology, Infromit Online, Environment Complete, Biosis and Geobase/georef) for studies of ecosystem impacts by feral horse populations. We used the following search string to search for relevant papers by searching for key terms that fell within five words (NEAR/5) of the word horse: Topic = (horse NEAR/5 ecosystem OR horse NEAR/5 environment OR horse NEAR/5 ecolog* OR horse NEAR/5 soil* OR horse NEAR/5 plant* OR horse NEAR/5 vegetation OR horse NEAR/5 hydrolog* OR horse NEAR/5 crust OR feral NEAR/5 horse). We supplemented this dataset by including unpublished government reports (e.g. National Research Council, 1980) and student theses. This resulted in 1182 unique studies, which were then screened using the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) procedure (Liberati et al., 2009) in the revtools package (Westgate, 2018) within R (R Core Team, 2018) (Appendix A). Revtools allows bibliographies to be systematically and efficiently screened based on the frequency of keywords within abstracts, titles and keywords (Westgate, 2018). Studies that were included were based on the following criteria: 1) a focus on wild, free-roaming, introduced horses occurring within the environment unrestrained or uncontained; 2) quantitative data were reported; 3) data were relevant to ecosystem responses to feral horse activity, including grazing (i.e., herbivory, consumption of plant material) and disturbance (i.e., non-trophic, engineering effects associated with changes in the physical environment of the soil or plant structure, such as defecation pollution, trampling disturbance); 4) reported values represented feral horse impacts only (i.e. not combined with additional herbivore impacts); and 5) comparison data were provided for different levels of feral horse activity (i.e., no activity, low activity, moderate activity and high activity). By activity, we refer to any effects of horses that influence environmental quality including soil disturbance, pugging, vegetation destruction, and herbivory. Based on these criteria, studies were refined to 78 publications (Appendix B).

2.2. Data collection

From each study, we recorded the location, the intensity of horse activity (i.e., no activity, low, moderate or high activity as described in relative terms by the data source), sample size, the mean and the standard deviation for each ecosystem-related attribute, for all available measures of feral horse activity treatments. We also extracted data on environmental variables that were indicative of increases or declines in environmental quality in order to explore potential ecological impacts of feral horses under different environmental contexts. The Aridity Index (AI = precipitation/potential evapotranspiration) was derived from the Consortium for Spatial Information (CGIAR-CSI) means of the 1950–2000 period (Zomer et al., 2008) (http://www.cgiar-csi.org/data/global-aridity-and-pet-database) and soil properties were obtained from the Harmonized World Soil Database (1 km resolution) (http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/). In this study, we defined aridity as 1 minus Aridity Index so that increases in aridity corresponded to greater dryness. Numeric data from figures were extracted using the software Engauge Digitizer V 4.1. Our final database consisted of 64 ecological response attributes, which were categorised into 12 broad categories (animal richness, animal abundance, bacterial abundance, plant biomass, litter cover, plant abundance, plant cover, plant richness, soil physical, soil chemistry, soil organics, soil erosion; Appendix C).

2.3. Estimating mean effect size and constructing the variance matrix

We calculated a log response ratio as the effect size to determine the effect of feral horse on ecological attributes: $\text{LnRR} = \ln(\overline{x}_t / \overline{x}_c)$ (Hedges et al., 1999) where $\overline{x}_t$ is the mean value of the ecological variable in the horse activity plot (i.e. treatment), and $\overline{x}_c$ is the mean value of the ecological variables in either the plot with no horse activity or the plot with the lower intensity of horse activity (i.e. control). Thus, positive values indicate an increase in the measure of environmental quality with greater feral horse activity and vice versa. The LnRR is used as the response in calculating the overall effect size of the ecosystem responses and the interaction with moderators in the meta-regression models. Our final dataset contained 4261 contrasts between intensity levels of horse activity (i.e. several treatments and controls). Where increases in an ecological response indicated a reduction in ecosystem function (e.g. increases in soil erosion, greater surface runoff, etc.), the LnRR values were multiplied by −1 (i.e. 'coined', Eldridge et al., 2016b) to allow consistency among positive values and to place all values in a common direction. We realise that this approach might have potential shortcomings given our assumption that increases in a given attribute (e.g. shrub cover, soil carbon) indicate an increase in functionality and therefore greater environmental quality. However, in the absence of the additional information on how an increase in a particular attribute affects function, we assume increases lead to greater ecosystem function.

We used random effects models to estimate mean effect sizes for feral horse impacts. All of our models had an intercept of zero and included random factors to structure a variance matrix to account for three potential sources of non-independence: i) data collected from the same study, ii) residuals of each observation from calculations of the variance and the potential bias from sample size, and, iii) shared controls among observations from a single study that reported multiple levels of feral horse activity but only a single control (e.g., lower activity level or no activity plot). To control for any potential lack of independence within and among studies we included a unique ID for each reference as a random factor. To account for non-independence in the construction of our model and the potential bias from sample size, we included another random factor to account for the order of the data within the data file. To control for the potential influence of shared controls, we included a coded group used to identify shared controls (Nakagawa and Santos, 2012).

2.4. Calculating measures of ecosystem structure, function and composition

We used a relatively novel approach of pooling a number of related ecological attributes into three categories that provide measures of ecosystem structure (landscape architecture), function (measures that support ecosystem processes), and composition (measures of diversity, richness etc). This allowed us to pool attributes that would otherwise occur at different spatial or measurement scales to calculate a meaningful, scaled up assessment of the response of ecosystems to feral horse activity. For example, we pooled together plant cover and density as structure, and biota diversity and richness as composition, while soil organics, soil physics and plant biomass were pooled into function. This approach has been used elsewhere to examine ecosystem effects of shrub encroachment (Eldridge et al., 2013; Ding and Eldridge, 2019), soil disturbing animals (Mallen-Cooper et al., 2019) and mammalian herbivores (Eldridge et al., 2016a) on structural, functional and compositional attributes in global and regional studies.

2.5. Meta-regression model approach

Our modelling approach involved three stages. First, we ran four intercept-only (null) models for 1) the total dataset, and its separate components of ecosystem 2) structure, 3) function, and 4) composition. We then ran 12 separate models for their subset of attributes (i.e. for the individual measures, or categories, that comprised structure, function and composition) using LnRR as our response variable, and included the variance matrix and random factors described above. The null models allowed us to estimate the mean effect sizes for an overall ecological response. The significance of the estimated effect sizes was examined using a *t*-test, testing whether the estimated effect size was significantly different from zero in the random effect model at $P < 0.05$. Secondly, to explore the influence of the intensity of feral horse activity on different ecosystem response variables, we ran meta-regression models that included the variance matrix described above for the total dataset, with LnRR as the response variable and a comparison of different intensities of horse activity (i.e., no activity to high activity, low to high, no activity to medium, medium to high, low to medium, no activity to low) as fixed effects. We then used the modified version of I^2, a heterogeneity statistic based on intra-class correlation, to determine the total level of heterogeneity among effect sizes (Nakagawa and Santos, 2012). Our high I^2 (0.983) indicated significant heterogeneity within our model despite accounting for data variance and random factors, and justified the inclusion of moderators to explain this variance. We selected the aridity as explanatory variables that might account for the observed heterogeneity. Aridity gives us insights into whether effects are consistent from mesic to arid areas, and clay is the soil fraction that is most susceptible to compaction, most sensitive to pugging (indentations in damp soil resulting from hoof action), and contains most of nutrients. Thus the consequences of erosion of clay soils is likely to be more pronounced. Thirdly, to explore which explanatory variable might explain the observed heterogeneity, we ran two separate meta-regression models that included the variance matrix described above, with LnRR as the response variable and each explanatory variable separately (i.e. aridity, soil clay content) as the fixed effects for the total dataset, and datasets for ecosystem structure, function, composition, and, 12 subset attributes. Meta-analyses were performed using the 'metafor' package (Viechtbauer, 2010) in R 3.4.1 version (R Core Team, 2018). To assess any potential publication bias, we used funnel plots, Egger regression and 'trim and fill' approaches (Nakagawa and Santos, 2012) across the whole dataset, and for ecosystem structure, function and composition subsets (Appendix D). An important caveat from our publication bias results was the inconsistent evidence from publication bias tests, with two of the three tests suggesting some publication bias in the ecosystem function dataset. These tests indicated that our results for the ecosystem function may be overestimated to some extent, despite including 78 publications and 4261 rows of data from across the world. The possibility of publication bias would likely result from heterogeneity in the unexplained residuals from our data such as other measures of environmental factors (climate variability, soil fertility, topography), horse populations, plant communities and interactions with livestock (e.g. cattle, sheep, goats, etc). Our results therefore require conservative interpretation.

3. Results

Most observations of feral horse effects on ecosystems were from North America (47%), followed by Oceania (21%), Europe (17%) and South America (12%; Fig. 1). Fifty-eight percent of observations were of plants (58%), followed by measures of soil (35%) and fauna (7%; Fig. 2a & 2b). Averaged across all 4261 observations, the mean log response ratio (LnRR) was close to zero (-0.044 ± 0.025; mean ± SE), indicating a 4% decline over all attributes. However, when our data were coined to place all response variables in the same direction to represent an increase in environmental quality (e.g., erosion and runoff multiplied by −1), the overall effect of feral horses was strongly negative (-0.121 ± 0.132) and left skewed (skewness = −0.24, kurtosis = 8.94). The mean LnRR for the coined data represented a 13% decline in overall environmental quality due to horse activity (Fig. 3). Our coined data also indicate that the log response ratio declined with increasing contrast between any two levels of horse activity (Fig. 3). The effects of feral horse activity on ecosystem composition and

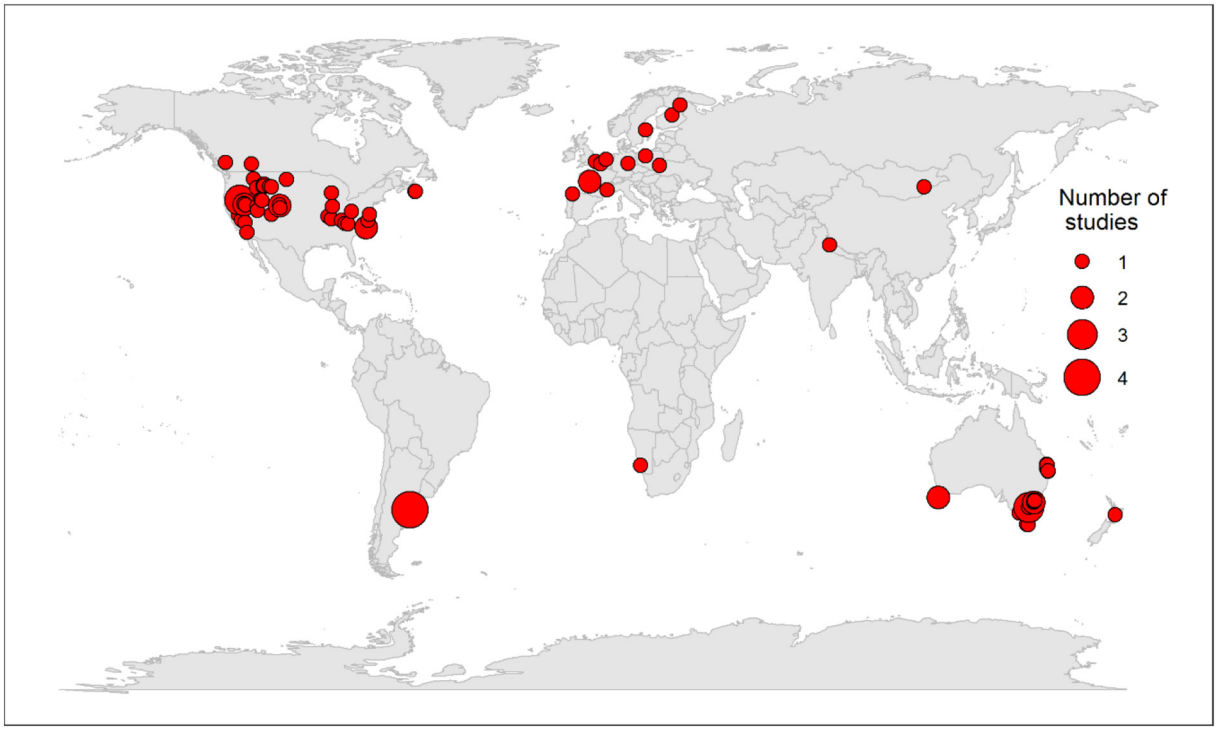


Fig. 1. Global distribution of studies of feral horse activity on ecosystem properties.

structure did not differ significantly from zero, but feral horse activity reduced ecosystem function by 19% (LnRR = −0.21, P = 0.020, 95% CI: −0.39 to −0.03, Fig. 4).

When we examined the individual responses to increasing horse activity, we found consistent negative outcomes on environmental quality (Fig. 4). For example, microbial abundance declined by 78% (LnRR = −1.511, P = 0.004, 95% CI: −2.536 to −0.485, n = 31), animal richness by 59% (LnRR = −0.886, P = 0.092, 95% CI: −1.917 to 0.144, n = 42), plant biomass by 25% (LnRR = −0.294, P = 0.071, 95% CI: −0.613 to 0.025, n = 324) and litter cover by 31% (LnRR = −0.378, P = 0.056, 95% CI: −0.766 to 0.010, n = 115; Fig. 4). Predictably, soil erosion increased by 31% compared with treatment plots (LnRR = 0.377, P < 0.001, 95% CI: 0.190 to 0.565, n = 627). We also detected some interactions with aridity, with greater increases in composition (LnRR = 0.239, P < 0.001, 95% CI: 0.432 to 0.047, n = 1087) and soil physical properties (LnRR = 0.336, P = 0.002, 95% CI: 0.548 to 0.124, n = 202) due to feral horse activity at more arid sites (Fig. 4). However, we found no significant interactions with soil clay content.

4. Discussion

We examined the global published literature on the effects of feral horse activity on a range of ecosystem response variables and found that their overall effect was a 13% decline in environmental quality, which we interpreted as a decline in the status of ecosystem characteristics that are important for sustaining living organisms. Furthermore, the magnitude of this decline increased markedly with

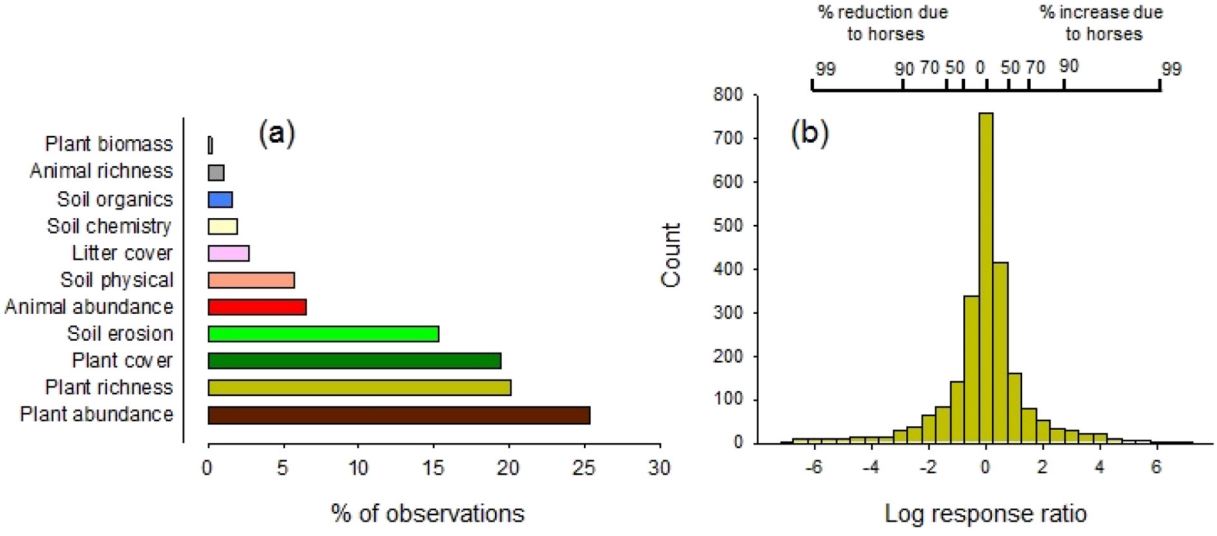


Fig. 2. (a) Percentage of observations for each of the 11 main attributes and (b) frequency distribution of all effect sizes using coined data. Note the greater number of observations of LnRR < 0.

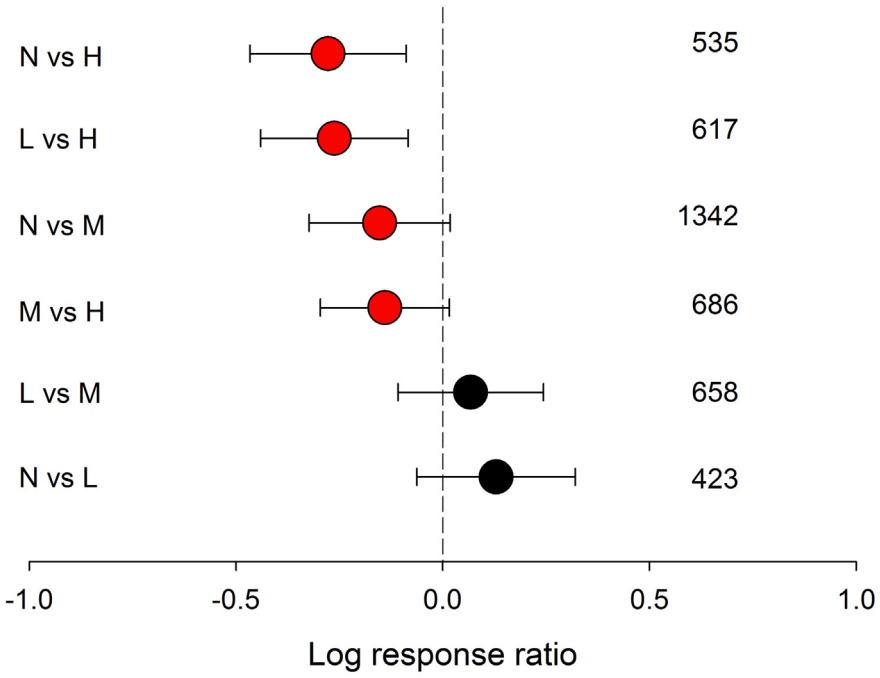


Fig. 3. Estimates (± 95% CI) of the log response ratio for all coined data arranged in order of increasing horse activity contrast, i.e. for the lowest contrast (no activity to low activity) to the highest difference in the intensity of horse activity. N = no activity, L = low activity, M = moderate activity, H = high activity. Red symbols represent a significant decline in the log response ratio for those activity contrasts ($P < .05$); grey symbols indicate no significant effect ($P > .05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

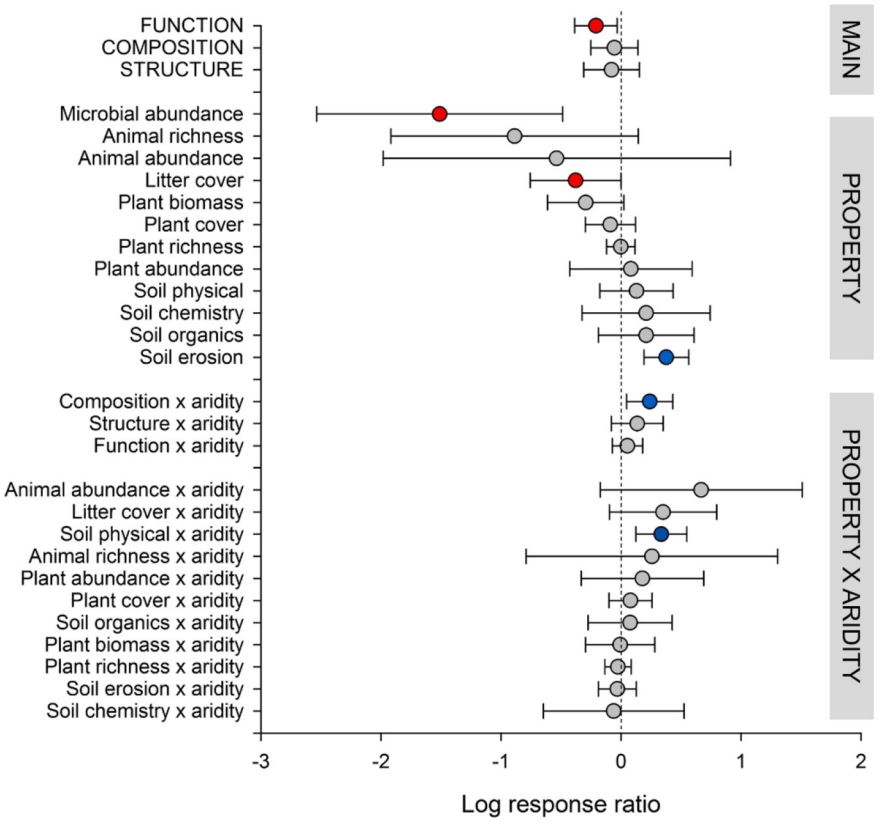


Fig. 4. Results of meta-regression with three moderators (aridity, ecosystem property and the interaction of property and aridity. Blue circles represent response attributes that increase significantly ($P < .05$) under greater horse activity, red points those that decline ($P < .05$), and grey points represent insignificant responses ($P > .05$). Error bars represent 95% confident intervals. As all of the observations of microbial abundance came from the same section of the aridity gradient, there are no interactions with aridity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increases in the intensity of horse activity and became strongly negative with comparisons between low and moderate horse stocking rates. We found three main results. First, low activity (i.e. comparing no activity with low activity scenarios) had neither positive nor negative environmental outcomes (i.e. the log response ratio was not significantly different from zero), though the mean effect of feral horse activity was highly variable, and overall had an insignificant positive effect (13% increase compared to lower horse activity). However, the difference between moderate and high activity contrasts resulted in clear and significant reductions (~15%) in environmental quality, suggesting that increases above moderate activity likely result in marked reductions. Our study results are largely consistent with recent reviews indicating substantial reductions in soil, vegetation, and ecosystem health in areas grazed by feral horses (Nimmo and Miller, 2007; Beever and Aldridge, 2011, Worboys et al., 2018; Beever et al., 2019; Davies and Boyd, 2019). Our results also demonstrate the fact that the global

effects of feral horses are consistent with the results of more regional or local impacts.

Notwithstanding these results, we acknowledge that additional data might reveal a significant positive effect of very low levels of activity compared with no activity, consistent with the literature on ungulate grazing activity elsewhere (e.g. cattle; Scasta et al., 2016), particularly in areas where large-bodied, hard-hooved ungulates have co-evolved with soils and vegetation (Beever and Brussard, 2000) such as in Europe or the Americas. Such a scenario is unlikely, however, in continents with a short evolutionary history of grazing or that lacked large ungulates (e.g. Australia), which were under-represented in our data. Similarly, an important caveat from the results of the publication bias tests is that our results may underestimate the effects of horses, given the relatively small number of global studies. Second, the main effects of feral horse activity were related to reductions in plant biomass and litter cover, and increases in soil erosion, with some evidence that feral horse activity reduced microbial abundance and animal richness. Declines in microbial biomass are likely to have marked cascading effects to ecosystem functions associated with nutrient availability and the processing of organic matter. Thirdly, we found that, although individual components of ecosystem composition were unaffected by changes in aridity, the effect of feral horse activity on overall composition became more positive as aridity increased. The most parsimonious explanation is an increase in grazing-insensitive plants (e.g. exotic plants, forbs) with increasing horse activity. Similarly, soil physical effects became more positive, indicating a greater increase in bulk density due to horse activity with increases in aridity.

For those studies that also reported specific rates, feral horse stocking rates varied from approximately 6.7 horses ha^{-1} in mesic environments in Poland (Chachaj and Seniczak, 2005) to as few as 0.002 horses ha^{-1} for a range of environments in Europe (Belgium and France; Cosyns and Hoffmann, 2005) and the USA (Baur et al., 2017). However, estimates of free-ranging horse numbers can vary substantially due to problems of access and therefore animal detection. For example, aerial surveys over extensive areas (2860 km^2) of grassland and forest in the Australian Alps have assessed feral horse numbers to be about 2.7 horses km^{-2} (Cairns and Robertson, 2015), though these densities are likely to be larger given the remoteness, nature of the terrain and therefore the difficulty of detection. Poor detection can make surveys of large areas problematic and can be a major issue when dealing with free-ranging animals. However, free-ranging feral horses tend to congregate in favoured locations such as riparian areas and grasslands, so that average densities are not indicative of the true stocking rate and impacts in habitats favoured by horses. In our study, we could not ascribe exact stocking rates to much of our data, either because these data were not provided in the studies we accessed, or studies were conducted across large areas and therefore average stocking rates would be misleading. Rather, we relied upon the subjective assessment of the intensity of feral horse activity reported by individual authors to assign rates to each study. This technique has been shown to be highly correlated with empirical measures of stocking intensity in other grazing studies (e.g. Eldridge et al., 2016a).

4.1. Feral horse activity leads to substantial reductions in biomass

We found a significant and relatively large (19%) reduction in ecosystem function associated with feral horse activity, and smaller, yet highly variable, non-significant declines in composition (5%) and structure (8%; Fig. 4). Our functional declines indicate a reduction in the capacity to support critical ecosystem functions such as the plant biomass production or carbon and nitrogen sequestration in soils (soil organic matter), and analyses of individual functions revealed that this decline is driven strongly by reductions in plant production of about 25% overall. This result is not unexpected, given that a major impact of horses would be plant removal either directly by herbivory (e.g. Wood et al., 1987; Seliskar, 2003; de Villalobos and Zalba, 2010) or indirectly by trampling-induced soil damage (Turner, 1987; Beever et al., 2008). For example, using sites across a rainfall and temperature gradient, Baur et al. (2017) showed that feral horses reduced biomass by > 47% in Nevada and Utah (arid) but only 6% in North Dakota (humid) and Colorado (dry subhumid). Most of the effects were due to changes in the biomass of grasses (Baur et al., 2017), the preferred food item of horses (McInnis and Vavra, 1987; Scasta et al., 2016). Feral horses have a stronger preference for graminoids than forbs and shrubs (Scasta et al., 2016), and grazing can lead to a conversion of grasslands to shrublands because shrubs are generally not consumed (Van Rees and Holmes, 1986). Reductions in grass cover could also lead to long-term reductions in grass production (e.g. de Villalobos et al., 2011).

Reductions in plant biomass, height and structure resulting from increasing horse activity (Turner, 1987; de Villalobos and Zalba, 2010) could lead to a number of potential outcomes such as: 1) alteration to plant cover, richness and composition (Lopez et al., 2017); 2) reduced vegetation structure and therefore habitat quality (Martin and Fahrig, 2012), which has been shown to alter ant community composition for example (Beever and Herrick, 2006), 3) reduced capacity for production of litter and organic matter, and thus increased soil erosion risk (Weaver and Dale, 1978), and 4) reduced organic matter inputs into the soil, with feedback effects on soil biota, microbially-mediated decomposition and therefore soil nutrient pools (Six et al., 2004). Although there are some studies of the impacts of horses on plant height and structure (e.g. de Villalobos and Zalba, 2010; Lopez et al., 2017), we did not find significant evidence of feral horses reducing plant cover or height in our database largely because there were insufficient data to undertake a global assessment. However, declines in plant biomass have been linked to changes in vegetation height, which have been shown to affect habitat quality for a range of grassland-dependent biota. For example, broad-toothed rats (*Mastacomys fuscus mordicus*) are highly dependent upon large, dense, native grasses for habitat and foraging, particularly in winter (Carron et al., 1990). Increasing feral horse activity has been shown to reduce habitat quality for broad-toothed rats by reducing grass height (Schulz and Green, 2018; Eldridge et al., 2019). Horses may also influence larger herbivores such as elk by displacing them at watering points (Hall et al., 2016). Feral horse activity has also been shown to affect invertebrates (Ostermann-Kelm et al., 2009), small mammals (Beever and Brussard, 2004), birds (Zalba and Cozzani, 2004) and estuarine fauna (Levin et al., 2002), some through changes in vegetation structure.

Reduced biomass likely equates with lower litter levels, which we found declined by 31% under feral horse activity (Fig. 4), consistent with other studies (Freedman et al., 2011; though see Davies et al., 2014). In functional ecosystems, litter plays a critical role by regulating soil temperature, protecting the soil surface against raindrop action, and providing organic compounds, enzymes and nutrients to the soil (Facelli and Pickett, 1991). Livestock grazing has been shown to redistribute surface litter (Daryanto et al., 2013), increasing the connectivity of bare patches and the potential for overland flow to move sediment, organic material and nutrients off-site. The depth of litter is also important for a range of biota. Scheele and Foster (2018) showed that horse activity reduced litter depth to a level that was sub-optimal for nest construction for the endangered corroboree frog (*Pseudophryne pengilleyi*), potentially exacerbating any effects of egg desiccation that lead to reproductive failure (Scheele et al., 2012).

Despite their preference for graminoids (Scasta et al., 2016), we found highly variable effects of feral horse activity on measures of plant composition such as richness, evenness or diversity, yet no significant net effect as grazing-induced declines in one species are typically accompanied by compensatory increases in other species. Grazing by feral horses might lead to the persistence of prostrate plants or unpalatable plants or species with short life cycles, rosette-forming habits, or species associated with grazing lawns at the expense of more erect and palatable, often native species. For example, in the Australian Alps, feral horse grazing has been shown to be associated with increases in light-

dependent herbs, particularly exotic species, and exotic European grasses such as *Holcus lanatus*, but marked declines in the native perennial sedge *Carex gaudichaudiana* (Prober and Thiele, 2007). Thus, although we found no significant changes in richness, a component of composition, overwhelming evidence suggests major changes in composition with prolonged horse grazing such as declines in dominant perennial grasses or sedges and increases in short stature plants (e.g. Fahnestock and Detling, 1999; Bai et al., 2001). Plant community richness has been shown to increase under horse grazing in the coastal grasslands in France (Loucougaray et al., 2004; Marion et al., 2010), but declines in more arid environments in the western United States (Beever and Brussard, 2000; Davies et al., 2014). In gorse shrublands in northern Spain, feral horse grazing led to a reduced abundance of woody species, which was compensated by an increase in herbaceous species (Lopez et al., 2017).

4.2. Feral horse activity increases erosion risk

The impacts of horses on erosion are highly variable and, like the effects of cattle, are likely to vary with factors such as vegetation type, stocking rate, soil properties, slope and level of utilisation, to name a few. We found evidence that feral horses increased erosion by pugging and streambed widening in riparian areas (Robertson et al., 2015; Prober and Thiele, 2007) and that high levels of recreational horse activity lead to considerable erosion (e.g. Summer, 1986; Newsome et al., 2002). Overall, our analyses showed that soil erosion increased by 31% (Fig. 4), which is likely to lead to instability and further declines in function.

Patch creation by large-bodied herbivores is an important process driving plant community composition and leading to increases in spatial heterogeneity (Bakker and Olff, 2003). However, the extent to which large patches of disturbed soil such as dust baths and wallows created by feral horses lead to positive ecosystem benefits is unknown. These effects are likely to be predominantly negative in environments with a short evolutionary history of grazing by horses. The effects of horses on erosion are also likely to be indirect, by reducing plant cover and biomass or increasing bare ground, which lead to substantial declines in soil aggregate stability (Davies et al., 2014). Erosion also has flow-on effects to ecosystem functions, reducing the capacity of the soil to produce biomass, or changing plant composition by altering soil seed banks. We did not find that erosional effects varied with aridity, though the implications of erosion are likely greater in more sensitive alpine areas (e.g., alpine bogs) where soil formation rates are extremely low in the production of peat, the main component of alpine soils (Hope and Nanson, 2015).

Finally, the effect of feral horse activity on animals was highly variable. We did not test for feral horse effects on mammals specifically because most research has focused on plants and soils (Fig. 2a), and animal effects have focused mainly on specific iconic species such as the greater sage-grouse (*Centrocercus urophasianus*; Davies et al., 2014), corroboree frog (Scheele et al., 2012), mountain pigmy possum (*Burramys parvus*; Bates, 2018), a range of vertebrates and invertebrates (Davies and Boyd, 2019), or behavioural interactions between horses and other vertebrates (Ostermann-Kelm et al., 2008), to name a few. However, studies from the Australian Alps have documented substantial negative effects of feral horses on a range of threatened fauna from reptiles to fish and amphibians (Worboys et al., 2018). There are some specific environments where it is likely that the reductions we observed in biomass, litter cover and erosion would translate into reduced richness and abundance of other unstudied biota. Future studies need to consider how functional and structural shifts in ecosystems will alter biotic communities. Further work could also benefit from exploring the large variation we found surrounding some results and consider potential sources that led to positive publication bias test results for our models. Future work may consider different measures of environmental quality (climate, soil texture, topography) or account for horse populations, specific plant communities and interactions with other herbivores.

5. Concluding remarks

Our results provide strong evidence that feral horses have marked effects on ecosystems and are associated with reductions in overall function, but also specific reductions in soil health associated with reduced litter cover and greater erosion. Our data do not allow us to provide specific grazing or activity rates that could be advocated to prevent declines in environmental quality due to feral horse activity, largely because of the paucity of data on specific grazing rates for many of these studies due to an emphasis on large scale studies of free-ranging horses. There are three clear conclusions that arise from our review. First, there are surprisingly few empirical data on horse effects on vertebrates, particularly those associated with riparian areas. Second, we know little about whether a sustainable level of feral horse activity is possible or even feasible, but given that total control is unlikely in most areas, this should be a high priority for resource managers. Finally, the feral horse issue is as much a social and political issue as it is an ecological issue. We echo a call by others (e.g. Nimmo and Miller, 2007) to involve the community and stakeholder groups in feral horse management. It is only by engaging all sectors of the community that we can hope to find a balance between the needs of maintaining healthy functional ecosystems and their biota, and societal needs of supporting free-ranging herds of feral horses to meet cultural and social outcomes.

Author contribution

DJE designed the study and methods. DJE and SKT wrote the manuscript drafts. JD and SKT collected the data and built the database. JD performed the data analyses and revised manuscript drafts.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Acknowledgements

We thank Shinichi Nakagawa for assistance with the meta-analysis and Max Mallen-Cooper for assistance with R code. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. Thanks to Eloise Stephenson @ elle_stephenson for drafting the graphical abstract.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108367.

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Growth Rates of Feral Horse Populations
Author(s): Robert A. Garrott, Donald B. Siniff, L. Lee Eberhardt
Source: *The Journal of Wildlife Management*, Vol. 55, No. 4 (Oct., 1991), pp. 641-648
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3809513
Accessed: 09/03/2009 11:04

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Received 29 May 1990.
Accepted 13 March 1991.
Associate Editor: Morrison.

GROWTH RATES OF FERAL HORSE POPULATIONS

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Abstract: We studied growth rates of feral horse (*Equus caballus*) populations in the western United States by consolidating aerial count records for 103 management areas administered by the Bureau of Land Management (BLM). Data from most areas could not be used because of free exchange of horses between neighboring areas and/or inadequate or incomplete data. Twenty-two areas provided data that were used to assess the accuracy of aerial counts with the index-removal method. Most (24/31) aerial counts consistently detected a large proportion (85–105%) of the horses. Replicate index-removal estimates provided little evidence of progressively higher sighting probabilities that would inflate growth rate estimates, and we concluded that aerial counts could be used to obtain reliable estimates of population growth rates. We used log-linear regression to estimate finite annual growth rates (λ). Estimates of λ for 12 areas with adequate data ranged from 1.15 to 1.27 with a mean of 1.21. Population simulations from age-specific reproduction and survival data collected independent of our study produced a similar range of growth rates. We concluded that many feral horse populations are currently being maintained at levels below which density-dependent responses operate and are, therefore, increasing at or near their biological maximum.

J. WILDL. MANAGE. 55(4):641–648

Equids became extinct in North America 8,000–11,000 years ago, but were reintroduced with the arrival of European settlers. With the aid of the American Indian, horses spread throughout the western United States during the 17th and 18th centuries, and they persist in many areas as feral populations (Berger 1986). There are currently a minimum of 45,000 feral horses, primarily in the Great Basin of Nevada, southeastern Oregon, and the Red Desert of Wyoming (BLM 1990). Although substantial populations of feral horses have occupied these regions for centuries, they received almost no scientific study until passage of the Wild and Free-Roaming Horse and Burro Act in 1971. This law established federal ownership of feral horses on most public land and prohibited the commercial exploitation that had previously limited their populations. Expanding horse populations soon created conflicts with the livestock industry, which demanded that their numbers be controlled (Wagner 1983). The ensuing controversy about management of feral horse populations found federal agencies, horse protection groups, and the livestock industry with little data to support their positions.

Most feral horse populations in the western United States reside on public lands administered by BLM. After feral horses received federal protection, the BLM began to monitor trends in horse populations by conducting periodic aerial surveys intended to count all horses within each management unit (Boyles 1986). Preliminary studies of these data suggested that growth rates of many horse populations approached or exceeded 20% annually (Nat. Res. Counc. 1980). Several investigators questioned the quality of the aerial counts because the growth rate estimates appeared unrealistically high, suggesting that overestimates may have been caused by improvements in counting techniques which resulted in progressively higher sighting probabilities (Nat. Res. Counc. 1980, Wolfe 1980). Using aerial counts extending over 10 years,

Eberhardt et al. (1982) also estimated annual growth rates of 20% for 2 feral horse populations in southeastern Oregon. However, they cautioned that such high growth rates might not be typical.

Our study was undertaken to extend the work of Eberhardt et al. (1982) to populations throughout the range of feral horses in the western United States. The first objective was to investigate the allegation that growth rates calculated from a series of aerial counts are unrealistically high due to progressively higher sighting probabilities caused by refinements in counting techniques (Frei et al. 1979, Wolfe 1980). The second objective was to calculate growth rates directly from census data for all populations with adequate data. The final objective was to calculate generalized growth rates from an age-structured population model and from published age-specific fecundity and survival schedules to determine if these data corroborate growth rates calculated directly from census data.

We are indebted to many BLM employees throughout the western United States who provided access to their data and shared their knowledge of horse biology. J. R. Tester and T. C. Eagle facilitated interactions with BLM personnel and the data collection. F. K. Larntz advised us on statistical analysis, and A. M. Starfield provided assistance on population modeling. All these individuals reviewed early drafts of our manuscript and provided useful suggestions for improving the study and its presentation. Funding was provided by BLM contract USDI-AA852-CT5-29. The efforts of L. L. Eberhardt were supported by the Office of Health and Environmental Research of the U.S. Department of Energy under contract DE-AC06-76-RLO1830.

METHODS

Aerial counts and removal histories were compiled from 15 BLM administrative districts, including 23 management units in Oregon, 62 in Nevada, 17 in Wyoming, and 1 in Idaho. Of these 103 management units, 22 and 12, respectively, contained records that could be used to estimate the proportion of horses observed on aerial counts and to estimate growth rates directly from count data. The basis for exclusion of most management units from analysis was free exchange of horses with neighboring units. Although few data on movements of marked horses were available, the knowledge of district BLM personnel was usually corroborated by aerial counts that fluctuated erratically for management units where horses were believed to commonly cross boundaries. In contrast, aerial counts from units that were completely fenced or isolated from other horse populations usually displayed consistent and explicable trends. Inadequate or infrequent aerial counts were also a major problem that resulted in the exclusion of many management units.

Assessing Sighting Probability Trends

Periodic removal of large numbers of horses from many management units allowed use of the index-removal method (Eberhardt 1982) to estimate proportions of animals detected during aerial counts and to address the possibility of temporal trends in sighting probability. This technique requires 2 counts, one before and one after the removal. The "apparent" number of animals removed (difference between the counts) divided by the actual number removed yields an estimate of the proportion of animals actually counted during aerial surveys, assuming that the same proportion was counted in both surveys (Eberhardt 1982).

Two situations provided data useful for index-removal calculations. The first, when both counts occurred within 1–2 months of the removal, allowed the apparent number of horses removed to be calculated simply as the difference between the 2 counts ($n = 12$). In the second situation, postremoval counts were not conducted until after a subsequent foaling season ($n = 15$). In these cases the apparent number of horses removed was calculated as the difference between the preremoval count and the number of adult horses in the postremoval count. We obtained additional estimates of the proportion of horses detected during the aerial counts when all animals were removed from a management unit ($n = 4$). In these situations the proportion of animals detected was calculated as the number of horses counted prior to removal divided by the number of horses removed.

Growth Rate Estimates from Count Data

A preliminary review of count data indicated that growth of feral horse populations appeared to be geometric. The basic model for geometric population growth is

$$N_t = N_0\lambda^t \quad (1)$$

where N_0 is the initial number of animals in the population, N_t is the number of animals in the

population at time t, and λ is the finite population multiplier. Taking natural logarithms of equation (1) yields

$$\log N_t = \log N_0 + t \log \lambda, \quad (2)$$

which is the form of a linear regression model. The slope of a regression line fitted to a series of such log transformed counts estimates the instantaneous annual rate of increase (r), and the antilog of r estimates λ (Eberhardt 1987). Because $N_t = N_{t-1}\lambda$, $\lambda = 1.00$ for a stationary population, whereas a λ of 1.20 indicates a population increasing at 20% annually. Estimating λ was complicated for populations that had undergone ≥ 1 removal. For these herds we used pooled regression techniques to fit lines with a common slope to the intervals between removals (Snedecor and Cochran 1980). We used the F-test (Snedecor and Cochran 1980) to compare the fit of the pooled regressions to results obtained by fitting each interval separately. The F-test employed a mean mean square error for individual segments that was calculated by summing sum squares error of all individual regressions and dividing by the total number of degrees of freedom.

Growth Rate Estimates from Population Simulations

We used equations presented by Siler (1979) and Eberhardt (1985) and data from Garrott and Taylor (1990) and Garrott et al. (1991) to conduct population simulations by constructing a variety of age-specific survivorship and fecundity schedules. The survivorship equation is

$$l_x = \exp\{-a_1 - a_2 x - a_3[\exp(b_3 x) - 1]\}, \quad (3)$$

where l_x is the proportion surviving from birth to age x, a_1 is a coefficient describing juvenile survival (birth to 1 yr, S_j), a_2 is a coefficient for adult survival (S_a), and a_3 and b_3 are senscence coefficients that describe the rapid decrease in survival associated with old age. Coefficients a_1 and a_2 can be converted to annual survival rates ($S_j = \exp[-(a_1 + a_2)]$, $S_a = \exp(-a_2)$) and, conversely, survival rates can be converted into the coefficients ($a_1 = -\log(S_j/S_a)$, $a_2 = -\log(S_a)$). The fecundity equation is

$$m_x = a\{1 - \exp[-b(x - x_0)]\} \cdot \exp\{-a_3[\exp(b_3 x) - 1]\}, \quad (4)$$

where m_x is the number of female young produced per year by females of age x, a is a coefficient describing the maximum reproductive rate, b is a coefficient describing the rate of increase of the reproductive rate during the early reproductive years, x_0 is the age prior to first reproduction, and a_3 and b_3 are coefficients describing reproductive senescence. Garrott (1990) reported that feral horse sex ratios at birth were near parity so reproductive rates reported in the literature as number of young produced per female were halved.

The population model used in the simulations was that derived by Lotka (1907) and modified by Cole (1954) for populations where births are concentrated in a short interval annually. The basic equation was

$$1 = \sum_{x=a}^{w} \lambda^{-x} l_x m_x, \quad (5)$$

where the summation ranges from the age of first reproduction (a) to the maximum age in the population (w), and λ is the finite annual rate of increase. Population growth rates were determined for various combinations of l_x and m_x schedules by using a spreadsheet program to solve equation (5).

We used equation (3) and equation (4) and published data on survival and reproduction to construct 4 l_x and 4 m_x schedules. The l_x values used in equation (5) generally refer only to female survival, but the only age-specific survival data available in the literature combined both sexes (Garrott and Taylor 1990). Garrott (1990) discussed age-specific changes in sex ratios that suggest that l_x schedules for males and females may differ substantially; however, lacking better empirical data, we developed the 4 l_x schedules used in the population simulations from the general survivorship schedule presented by Garrott and Taylor (1990). The l_x schedule S1 was identical to the fitted schedule developed from 11 years of survival data from the Pryor Mountain herd in Montana (Garrott and Taylor 1990). The other 3 schedules were constructed by varying the coefficients for juvenile (a_1) and adult survival (a_2) to produce 1 schedule near the maximum likely survivorship (Smax) and 2 schedules in which survival was lower than that observed for the Pryor herd (Fig. 1). The survival senescence coefficients a_3 and b_3, derived from the Pryor data, were used in all 4 schedules (Table 1). The coefficients used to generate m_x schedules F1 and F2 are those presented by Garrott et al. (1991) for reproductive rates derived from 2 independent sources of data. The Fmax schedule used the same coefficients as F1 with the exception that the maximum reproductive rate (a) was increased slightly; the F3

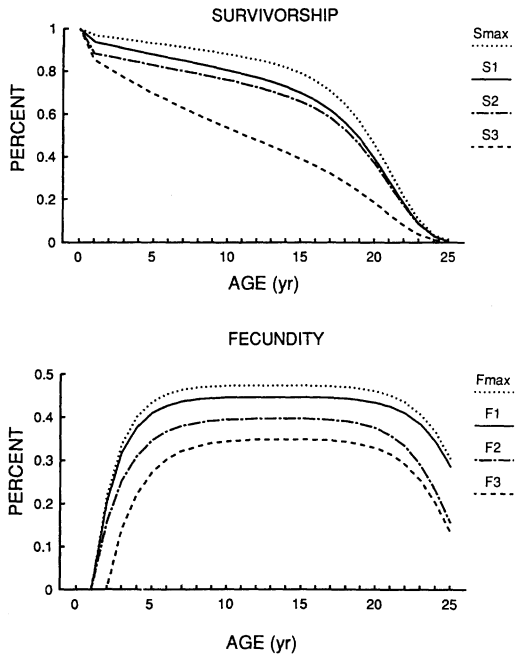


Fig. 1. Age-specific survivorship (l_x) and fecundity (m_x) schedules for feral horse populations. The l_x schedule S1 and m_x schedules F1 and F2 are curves fitted to data presented by Garrott and Taylor (1990) and Garrott et al. (1991). We produced the remaining schedules by changing various parameters in the l_x and m_x equations to approximate both lower and higher survival and fecundity rates. We consider the Smax and Fmax schedules to be biological maximums for the species.

Table 1. The values of coefficients used to generate 4 survivorship (l_x) and 4 fecundity (m_x) schedules. The coefficients a_1 and a_2 can be interpreted as juvenile and adult annual survival rates of 0.97 and 0.99 for Smax; 0.94 and 0.98 for S1; 0.89 and 0.98 for S2; and 0.86 and 0.95 for S3; respectively.

	Coef. values			
Model	a_1	a_2	a_3	b_3
Survivorship				
Smax	0.0202	0.0101	0.00012	0.42265
S1	0.0468	0.0164	0.00012	0.42265
S2	0.1054	0.0164	0.00012	0.42265
S3	0.1054	0.0513	0.00012	0.42265

	Coef. values				
	a	b	x_0	a_3	b_3
Fecundity					
Fmax	0.48	0.6178	1	0.0000008	0.52910
F1	0.43	0.6178	1	0.0000008	0.52910
F2	0.40	0.5053	1	0.0000013	0.53908
F3	0.35	0.5053	2	0.0000013	0.53908

schedule used the same coefficients as F2 except for a, which was decreased, and x_0 (age prior to first reproduction), which was raised to 2 (Table 1, Fig. 1). The Smax and Fmax schedules were constructed to approximate the biological maximums possible for feral horses.

RESULTS

The index-removal analysis indicated that large proportions of the horses were normally observed during aerial counts with 24 of 31 estimates between 85 and 105% (Table 2). One estimate was 41% (1978–79, Three Fingers, Oreg.); in this instance we suspect that the number of horses removed included animals taken from a neighboring unit during the same period. Evidence of possible trends in counting proficiency was gained from examining sighting probabilities for the 7 management units where data allowed 2 or 3 index-removal calculations (Table 2). Estimated sighting probabilities remained consistently high for 4 of these management units (Paisley, Beaty Butte, Jackie Butte, and 15 Mile), whereas estimates for the Three Fingers, McCullough, and Challis units were inconsistent.

Plots of log-transformed aerial counts for each herd were approximately linear (Fig. 2), indicating the simple model for geometric growth was appropriate. For those herds where removals interrupted population growth, fitting lines to the individual segments did not result in better fits than did pooled regression techniques ($F = 0.68$; 14,38 df; $P < 0.05$) therefore, only results of the pooled regressions are presented. Estimates of λ for the 12 management units with adequate data to perform log-linear regressions ranged from 1.15 to 1.27 (Table 3) with an unweighted mean of 1.21. Widths of 95% confidence intervals ranged from 0.02 to 0.04 for estimates calculated from at least 10 counts, whereas regressions using only 5 counts resulted in confidence intervals >0.10. The confidence intervals (Table 3) are derived from the variance of the regression coefficient, which might underestimate the true variability of the trend lines. Although Harris (1986) and Gerrodette (1987) present alternatives for calculating confidence intervals that may be more appropriate, estimates of the coefficient of variation of the aerial counts are needed for their approach. Because such estimates were lacking for horse counts these techniques were not used.

Growth rate estimates obtained with the Lotka/Cole equation and all possible combinations of the l_x and m_x schedules (Table 4) produced values similar in range to those obtained from log-linear regressions of count data (Table 3).

Table 2. Estimates of the percentage of animals detected during aerial counts of feral horse management units in the western United States based on the index-removal method (Eberhardt 1982).

State	Management unit	Yr	No. animals removed	Aerial counts		Estimated %	
				Preremoval	Postremoval	Removed	Detected
Oreg.	Paisley	76–77	235	307	100[a]	67	88
	Paisley	81	183	244	81	66	89
	Beaty But.	81	272	391	150	62	89
	Beaty But.	84	260	382	134	65	95
	Palomino	86	173	183	30	84	88
	3 Fingers	75–76	256	424	186[a]	56	93
	3 Fingers	78–79	342	244	103[a]	58	41
	Jackie But.	70–72	181	263	78[a]	70	102
	Jackie But.	76–77	137	280	145[a]	48	99
	Jackie But.	78–79	136	235	101[a]	57	99
	Monger	75	178	169		100	95
	Stockade	78	81	74		100	91
Nev.	Eugene Mtn.	85	346	349		100	101
	Buffalo H.	79–80	494	623	194[a]	69	87
	Sonoma Ran.	85	349	391		100	112
	Humboldt	85	665	609	5	99	91
	East Range	80–81	931	1,044	252[a]	76	85
	Fox-Lake	86	478	913	493	46	88
	Flanigan	85	351	704	320	55	109
	Pah Rah	84–85	1,139	1,075	107	90	85
	Pine Nuts	86	208	437	273	38	79
	New Pass	86	783	1,880	1,105[a]	41	99
	Bald Mtn.	81–82	401	686	326[a]	52	90
	Fish Creek	80	600	907	293	68	102
Wyo.	McCullough	83–84	307	459	208[a]	55	82
	McCullough	87–88	152	290	121[a]	58	107
	15 Mile	78–79	154	302	155	49	95
	15 Mile	84–85	360	429	94[a]	78	93
Id.	Challis	79–80	148	650	545[a]	16	71
	Challis	80	309	617	319	48	96
	Challis	83–84	311	499	223[a]	47	89

[a] Used the number of adults instead of total count to remove effects of foaling season between pre- and postremoval counts.

Projection of these growth rates resulted in population doubling times ranging from 3 to 7 years with populations growing at intermediate rates (1.19–1.21) doubling in 4 years.

DISCUSSION

The generally high sighting probabilities calculated in our study contrast markedly to average observability estimates of 30–66% reported for other large North American herbivores (LeResche and Rausch 1974, Bartmann et al. 1986). High observability of horses was apparently due to the lack of tree cover and arid climate that exposed horses and their dust trails. Horse management units in some mountainous regions, however, contained extensive woodlands that can substantially reduce observability of horses (Siniff et al. 1982). Few such areas are represented in our data; hence, the high sighting probabilities we report should not be applied in areas with extensive woodlands.

Eberhardt (1982) and Siniff et al. (1982) discussed biases that affect sighting probabilities derived with the index-removal method. The most important bias in our data could have been the long interval between many of the pre- and postremoval counts. Approximately half the sighting probabilities (Table 2) were calculated from counts conducted nearly a year apart. Ideally, counts should be conducted close to the removal period to reduce the possibility that additional animals were lost from the population because of undetected mortalities (Eberhardt 1982), which would inflate sighting probabilities. The magnitude of this bias, however, was apparently not large, as sighting probabilities from counts conducted a year apart were similar to those calculated from counts conducted close to the removal dates (Mann-Whitney $U = 98$; 15,16 df; $P > 0.20$). Data on horse survival support this hypothesis because most foal mortality occurs within the first 1–2 months

Table 3. Estimates of finite annual growth rates (λ) of feral horse populations based on log-linear regression of aerial counts conducted over 5–17 years. Where >1 line segment was fitted we used pooled regression techniques to obtain a single slope estimate. Lambda was calculated as the antilog of the regression slope.

Management unit	No. Counts	No. Yr	No. Line segments	λ estimate	95% CI
Jackie Butte	15	16	5	1.23	1.22–1.24
McCullough	14	17	3	1.22	1.20–1.24
Beaty Butte	13	14	3	1.24	1.23–1.25
Paisley	13	14	3	1.27	1.26–1.29
Challis	10	12	3	1.15	1.13–1.16
Stockade	7	7	1	1.16	1.14–1.19
15 Mile	7	7	1	1.17	1.13–1.21
Lander Complex	6	6	1	1.23	1.19–1.27
Riddle Mtn.	6	13	2	1.25	1.23–1.27
Cold Springs	5	7	1	1.18	1.09–1.28
Monger	5	5	1	1.21	1.16–1.29
Goshute	5	7	1	1.19	1.12–1.27

(Boyd 1979, Berger 1986), and thus, occurs prior to the time aerial counts were usually conducted. Furthermore, adult mortality is typically very low (Berger 1986, Siniff et al. 1986, Garrott and Taylor 1990).

Although biases might have influenced the calculated sighting probabilities, they would not influence estimates of population growth rates derived from a series of aerial counts unless the magnitude of the bias changed in a consistent direction over time (Harris 1986, Gerrodette 1987). Several authors have suggested that growth rates calculated from a series of aerial counts are overestimates because changes in census techniques such as increased observer experience, switching from fixed-winged aircraft to helicopters, and refinement of counting techniques have resulted in progressively higher sighting probabilities (Frei et al. 1979, Wolfe 1980). Studies of feral horse census techniques, however, do not support these concerns. Siniff et al. (1982) found no significant difference between the abilities of experienced and inexperienced observers. In addition, comparisons of aerial counts conducted with helicopters (Bell B-2) and fixed-winged aircraft typically used by BLM personnel (Piper Supercub, Cessna 180) found that both types of aircraft performed similarly in some areas, whereas helicopter flights in other areas resulted in slightly higher counts (Siniff et al. 1982).

Inconsistent sighting probability estimates were detected for 3 of 7 management units that provided multiple estimates; however, the low values in 2 of these areas were probably aberrations. As discussed earlier, the low 1978–79 Three Fingers estimate was believed to be an error in the records. The low 1979–80 Challis sighting probability was probably due to the small number of horses removed (16%); Eberhardt (1982) cautioned that index-removal estimates are highly variable when the proportion of the population removed is low. The 96% sighting probability calculated after approximately half the population was removed the following year supports this contention. The McCullough data, therefore, provide the only evidence that counting proficiency may have increased over time. Thus, we conclude that the growth rate estimates derived from aerial counts (Table 3) are reliable.

Several authors have used log-linear regression to estimate growth rates of feral horse populations from aerial counts with similar results. The National Research Council (1980) calculated a weighted mean λ of 1.16 for aerial count data from 25 management units in 5 states. Wolfe (1980) tabulated data from 12 management units representing 6 states and calculated λ's ranging from 1.08 to 1.30 with an unweighted mean of 1.22. Both these sources, as well as Conley (1979), used modifications of the Leslie matrix (Leslie 1945) or Lotka's (1907) equation in population simulations to determine the demographic characteristics needed to produce population growth rates similar to our log-linear regression estimates. Various combinations of fecundity and survival schedules produced growth rates ranging from 1.04 to >1.20; however, all 3 sources concluded that the high reproduction and survival needed to produce growth rates approaching or exceeding 1.20 were not realistic.

At the time these early simulations were conducted, females were thought to produce their

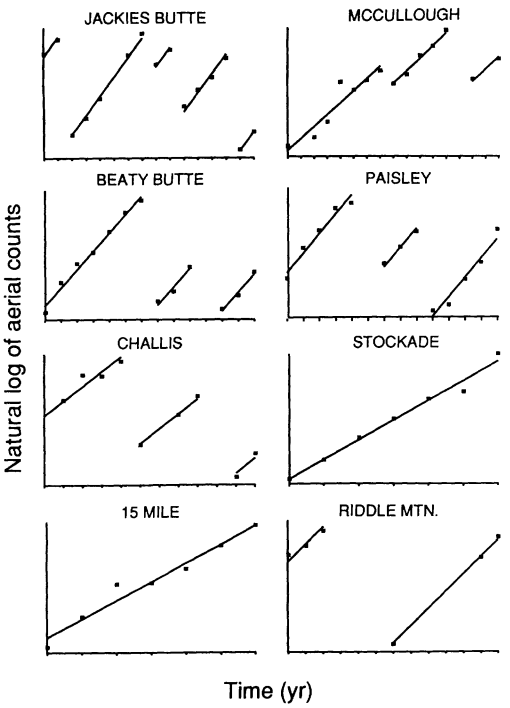


Fig. 2. The apparent growth of 8 feral horse populations based on aerial counts conducted over variable time spans. Log-linear regressions were used to fit the lines and to provide estimates of finite population growth rates (λ). Tick marks on *x* axis indicate yearly intervals, but scale of *y* axis varies for each plot.

first foals at 3–5 years, possibly only foaling in alternate years, and becoming reproductively senescent between 10 and 15 years of age. Adult survival rates exceeding 0.90 were also believed unrealistic, and foal mortality was assumed to be relatively high (Boyd 1979, Conley 1979, Nat. Res. Counc. 1980, Wolfe 1980). Recent reproductive studies, however, demonstrate that age of first foaling is usually 2–3 years with females commonly producing foals in consecutive years (Seal and Plotka 1983, Berger 1986, Siniff et al. 1986, Wolfe et al. 1989, Garrott et al. 1991). Females also remain reproductively active throughout their lives with only a slight reduction in foaling rates in the oldest age classes (Garrott et al. 1991). In addition, studies by Berger (1986), Siniff et al. (1986), and Garrott and Taylor (1990) indicate that survival of both foals and adults is usually high, with annual survival rates of adults commonly exceeding 0.95. Incorporating these higher reproductive and survival estimates into similar population models resulted in population growth rates that corroborate our log-linear regression estimates (Table 4).

Table 4. Finite population growth rates (λ) calculated by solving Lotka's (1907) equation for all possible combinations of 4 age-specific survivorship and fecundity schedules (Fig. 1).

Fecundity schedules	Survival schedules			
	Smax	S1	S2	S3
Fmax	1.27	1.26	1.24	1.20
F1	1.26	1.24	1.23	1.19
F2	1.22	1.21	1.20	1.16
F3	1.17	1.16	1.15	1.11

Such high annual growth rates appear unusual for populations of long-lived vertebrates that experience delayed sexual maturity and produce only 1 young per reproductive cycle. However, growth rates approaching or exceeding 20% have been documented for colonizing populations of elk (*Cervus elaphus*) (Eberhardt 1987, Gogan and Barrett 1987, McCorquodale et al. 1988), bison (*Bison bison*) (Eberhardt 1987), muskox (*Ovibos moschatus*) (Reynolds 1989), and sea otter (*Enhydra lutris*) (Estes 1990).

We conclude that feral horse populations are increasing at or near their biological maximum. Apparently many feral horse populations are currently being maintained at levels below which density dependent responses in reproduction and survival operate. Such high growth rates dictate that horse populations be managed to prevent severe overpopulation and a concurrent deterioration in range conditions. Assuming a population of 45,000 animals (BLM 1990) and a 20% annual growth rate, 9,000 horses must be removed annually to maintain a stable population; BLM normally removes 5,000–10,000 animals annually. However, federal laws and pressure from horse advocacy groups have made disposal of these surplus animals difficult (Boyles 1986, BLM 1990). In response to this dilemma a variety of contraceptive techniques have been developed for reducing reproduction (Kirkpatrick et al. 1982, Siniff et al. 1990); but, little effort has been devoted to determining how to apply these new tools to population management or if they will prove practical. The survival and fecundity schedules we developed appear to reasonably approximate the key components of feral horse demography. We suggest simulation studies to explore possible management alternatives for controlling feral horse populations.

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Received 30 July 1990.
Accepted 18 April 1991.
Associate Editor: DeYoung.

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Genetics and Paleogenetics of Equids

DNA, or deoxyribonucleic acid, is the molecule of life that determines morphology, function, and development of all living things. The study of both the information contained in these molecules and their transmission (i.e., genetics) allows us to describe phenotypic traits of a species as well as reconstruct its evolution, diversity, and relationship to other species. Genetic analyses are an invaluable and complementary part of the research necessary to understand the biology of a species and to aid in its preservation.

The genus *Equus* is the only remaining branch of a bushy evolutionary tree covering 55 million years. Within this genus, only the domesticated forms (the caballine horses and the donkeys) are spread over the planet and not endangered. The plains zebra (*Equus quagga*) is locally common in Africa, as is the kiang (*E. kiang*) in parts of Asia, but all the other equid species (African and Asiatic wild ass [*E. africanus* and *E. hemionus*, respectively], Przewalski's horse [*E. przewalskii*, also known as *E. ferus przewalskii*], mountain and Grevy's zebra [*E. zebra* and *E grevyi*, respectively]) are more or less at the edge of extinction. A deeper understanding of the phylogeny, genome evolution, and genetic diversity of these species is important for their conservation. In this chapter, we present an overview of the present-day knowledge concerning these topics. The mitochondrial DNA diversity and phylogeny of these species are shown as a phylogenetic tree based on whole mitochondrial genomes (fig. 7.1) (Vilstrup *et al.* 2013).

Despite a long-standing interest of paleontologists in the complex evolutionary history of the equids, the taxonomic relationships of the fossil forms are still not clear. Studies of equid chromosomes show a high rate of evolution within this genus, which has led to a large variety of different karyotypes that do not prevent gene flow (Jónsson *et al.* 2014). These karyotypic changes are not reflected in the morphology because extant equids rather strongly resemble each other, confirming the accelerated evolution that is also seen at the sequence level underlying the rapid radiation found among equid populations (Vilstrup *et al.* 2013).

The application of the extreme power of the latest DNA sequencing methods to the analysis of genetic material preserved in fossils has made it possible to revisit the most recent part of the phylogenetic relationships and the taxonomy of the equids with relatively high precision, leading to a taxonomic reappraisal and to the demise of several species present in

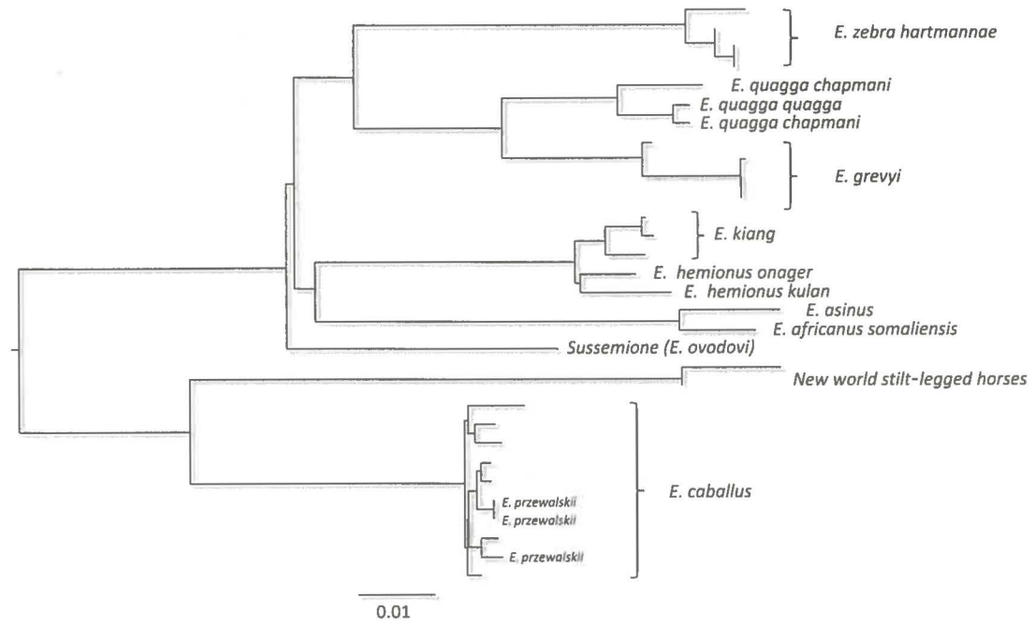


Fig. 7.1 Phylogenetic tree of whole mitochondrial genomes (after Vilstrup *et al.* 2013). The scale bar represents 0.01 nucleotide substitutions per site.

the Pleistocene (Orlando *et al.* 2003, 2008, 2009; Geigl and Grange 2012; Vilstrup *et al.* 2013). The most recent sequencing of whole genomes of several extinct and extant equid species allowed for the recalibration of the equid phylogeny, which now date the most common recent ancestor to around four million years (Orlando *et al.* 2013). In addition, the analysis in ancient equid remains of phenotypic traits—such as coat color—have increased our knowledge of the physical appearance of ancient horse populations beyond body size and shape. Because coat color is also one of the phenotypic traits that changed during the domestication process, when humans started to select for certain behavioral or physical characteristics, its analysis allowed the dating of the onset of the domestication of horses.

Whole genome sequence data from Pleistocene fossils now unequivocally assign domestic (*E. caballus*) and Przewalski's horses to two distinct evolutionary lineages (Orlando *et al.* 2013). This distinction was not clear before, as the Przewalski's horse, whose populations went through a dramatic bottleneck that almost led to its extinction, was sometimes considered to be the ancestor of the domestic horse.

The increasing power of paleogenetic and paleogenomic studies contributes considerably to a deeper understanding of the evolution and taxonomy of equids, which is also important in designing efficient strategies for the conservation of the relic populations, such as the Asiatic wild asses. If combined with the analysis of extant populations living in their natural habitat or in reserves where they have been (re)introduced, these phylogeographic studies can lead to the revision of conservation strategies so that they account for the past geographical range of the species. This type of genetic study is also advisable to better understand the evolution of reintroduced populations in a given area, such as the Asiatic wild ass in Israel, and will be invaluable for conservation biologists seeking to optimize strategies to rescue these threatened populations.

Genetic analyses of small populations of equids whose habitats are difficult or dangerous to access, such as in the case of the Somali wild ass (*E. a. somaliensis*), can be performed at present in a noninvasive manner using feces that have been collected in the wild. Such an approach can be used to better characterize the African wild ass and show that the Somali wild ass was probably not the ancestor of the domestic donkey. Microsatellite markers can also help demonstrate that until recently gene flow occurred between populations from Eritrea and Ethiopia, which by now are separated.

It is important to draw the attention of those who decide conservation policies to the results of these studies, since conservation strategies, which often neglect the genetics of the populations they aim to rescue, risk being ineffective, as in the example of the Cape mountain zebra. This is even true for the populations of feral horses (*E. caballus*) in North America. Although currently not endangered, a recently noticed reduction of the genetic variation of these horses could indicate a threat to their long-term survival.

This chapter aims to shed light from various angles on the genetics of various extant and extinct equid species, their evolution, their past and present distribution, and the consequences of population reduction on genetic diversity.

Karyotype Evolution and Genome Plasticity in the Genus *Equus*

With Contributions by Elena Giulotto and Elena Raimondi

In spite of their recent evolutionary divergence, morphological similarity, and capacity to interbreed (although infertile offspring are produced), equid species differ greatly at the karyotype level (Ryder 1978; Yang *et al.* 2003, 2004). The variation involves both the structure and the number of chromosomes, which ranges from 32 in *Equus zebra* to 66 in *E. przewalskii*. Using cross-species chromosome painting, Trifonov *et al.* (2008) calculated the rate of evolutionary chromosomal rearrangements, showing that it was extremely low in all ceratomorphs (<0.3 rearrangements per million years), while it was very rapid in the lineage of equids, ranging from 2.92 to 22.2 rearrangements per million years. According to these calculations, the equid genome evolution is one of the most rapid observed in nonrodent mammals (Trifonov *et al.* 2008).

In total, 53 chromosome fusion events occurred during the evolution of extant equids. In this genus, the majority of fusions are of the centromere-centromere type (33/53). Most chromosomes originating via centric fusions maintained the centromere at the site of fusion, although some underwent "centromere repositioning" or pericentric inversion. Centromere repositioning consists of the shift, during evolution, of centromere position on the chromosome without DNA rearrangement (Montefalcone *et al.* 1999; Rocchi *et al.* 2012). We discovered that, in the genus *Equus*, centromere repositioning played a crucial role in the extensive and rapid karyotype evolution. Using a comparative cytogenetic approach, we demonstrated that at least nine centromere repositioning events took place during the evolution of equids, six of which occurred in *E. asinus* (donkey) and one in horse chromosome 11 (ECA 11) (Carbone *et al.* 2006; Piras *et al.* 2009). These observations demonstrate that this phenomenon was exceptionally frequent in equids because such a high frequency of centromere repositioning has never been reported in any other evolutionary lineage.

Centromeres are essential for the proper chromosomal segregation in meiosis and mitosis. They are the sites of kinetochore assembly and spindle fiber attachment, and consist of protein-DNA complexes, in which the DNA component is typically characterized by the presence of extended arrays of tandem repeats (satellite DNA), but these do not specify centromere function or identity. There is general agreement that the centromere's genetic identity is determined epigenetically by proteins rather than the DNA they contain (Allshire and Karpen 2008). We performed an extensive analysis of the chromosomal distribution of centromeric satellite tandem repeats in *E. caballus* (ECA), *E. asinus* (EAS), *E. grevyi* (EGR), and *E. quagga* (EBU). Our results demonstrated that the organization of such sequences is atypical: several centromeres lack satellite DNA, at least at the fluorescence in situ hybridization (FISH)-resolution level, while satellite repeats are often present at noncentromeric termini, probably corresponding to relics of ancestral, now inactive, centromeres (Piras *et al.* 2010; Raimondi *et al.* 2011). In one instance, the centromere of horse chromosome 11, we proved the total absence of satellite repeats at the sequence level (Wade *et al.* 2009). Taking advantage of the availability of the horse genome sequence, we carried out a chromatin immunoprecipitation (ChIP)-on-chip assay: an array of the ECA11 centromeric region was hybridized with horse chromatin, immunoprecipitated with an antibody against the kinetochore proteins CENP-A or CENP-C. Using this approach, we demonstrated that the centromeric function resides within a DNA sequence totally devoid of satellite DNA (Wade *et al.* 2009).

The rapidly evolving *Equus* species gave us the opportunity to catch snapshots of evolutionarily new centromeres in different stages of "immaturity." On the basis of these observations, we propose a model for the birth, evolution, and complete maturation of centromeres (Piras *et al.* 2010). The first step would consist in the shift of the centromeric function to a new position lacking satellite DNA, while the satellite DNA from the old centromere remains in the ancestral position, as we observed in a number of donkey and zebra chromosomes; a subsequent step would be the loss of the leftover satellite DNA; and finally, at a later stage, satellite repeats would colonize the new centromere, giving rise to "mature" centromeres. Thus, in the case of ECA 11, we may surmise that it is a "young,"

evolutionarily new centromere, as suggested by the complete lack of satellite DNA.

The satellite-less equid centromeres represent a new and powerful model system offering a clear advantage with respect to other artificial or clinical model centromeres: they are natural centromeres, stably present in all individuals of a given species, and can therefore be used as an ideal tool to study the normal mammalian centromere. The nonrepetitive nature of these centromeres and the availability of the complete sequence of the horse genome provide the chance to analyze centromere architecture and plasticity at the molecular level with particular reference to protein-binding domains (Purgato *et al.* 2014), nucleosome organization, and DNA methylation; in fact, while the roles of many of these components in mitosis have been documented, relatively little is known about the detailed structure of the chromatin fiber that underlies these functions.

The uncommon evolutionary plasticity of the equid genome is also proved by the high mobility of insertion DNA elements, such as numts (nuclear sequences of mitochondrial origin). Insertion of mitochondrial DNA fragments into nuclear chromosomes—together with the insertion of transposons, retroviruses, and telomeric-like sequences—is a driving force in evolution. Indeed, numts, similarly to transposons and interstitial telomeres (Salem *et al.* 2003; Nergadze *et al.* 2004, 2007; Hazkani-Covo *et al.* 2010), have been successfully used in several studies as evolutionary markers. We analyzed mitochondrial DNA insertions in the horse reference genome sequence (Nergadze *et al.* 2010) and found that insertion polymorphisms are exceedingly high in the horse with respect to the human genome. Our results support the hypothesis that the genome of equid species is in an ongoing evolutionary state.

Depicting Wild Horses of the Past with Ancient DNA

With Contributions by Mélanie Pruvost

The study of the evolution of horses, and in particular of their domestication process, is complicated by the fact that the mitochondrial DNA (mtDNA) and nuclear microsatellite diversity of present-day horse populations is high and lacks significant geographic structure and that the diversity of the pseudoautosomal region of the Y chromosome is extremely low (Lippold *et al.* 2011; Achilli *et al.* 2012). This finding indicates that several maternal lineages had been domesticated, but a higher level of resolution of the domestication event could not be achieved. The recent publication of the sequence of the genome of a Middle Pleistocene horse, the oldest full genome sequence so far (560,000–780,000 years before present; Orlando *et al.* 2013), allowed a reappraisal of the evolution of equids in the Pleistocene. Such studies are so far limited to few samples owing to the high costs and the difficulties of the sequencing of ancient genomes, restraining it to well-preserved fossils and often preventing insights into the diversity of past populations. Therefore, until these approaches are less costly and challenging, well-chosen genetic markers give a useful picture of certain aspects of the evolution and of the migration of populations.

Shifts in phenotypic trait markers can be valuable indicators for alterations in both natural selection (climatic shifts causing changes of forest coverage or nutrition) and artificial selection (domestication). Domestication boosted major phenotypic changes in domesticates compared to their wild ancestors (Cieslak *et al.* 2011), for example, and coat color is likely to have been selected by humans during the domestication of horses. To identify a change in the phenotypes occurring during domestication, one needs to know the situation before domestication. The phenotype of undomesticated horses during the Late Pleistocene could be deduced from parietal art because horses are the most represented animals in caves during the Upper Paleolithic in Europe. They are depicted most of the time in natural, everyday postures such as standing, feeding, fighting, running, and trotting, which indicates that humans had a good knowledge of the behavior of horses in their natural environment. Horses represented in cave paintings show various coat colors, in particular, brown, black, and spotted (dark spots on white coat). Moreover, by analyzing basic coat color, pelage length, and seasonal patterns in horses represented in Paleolithic art throughout Europe, a regional cline in pelage change was reconstructed and concluded that living wild horses (*E. przewalskii*) have similar pelage characteristics (Guthrie 2006). Using a paleogenetic approach, we analyzed whether these coat colors corresponded to the coats of Pleistocene horses and whether there was a change in colors over time from the Late Pleistocene to the domestication of the horse during the Bronze Age.

The genetic systems underlying the large amount of phenotypic variations in coat color observed in modern horses has been well characterized, and >300 genes and associated loci have been identified thus far (Rieder 2009). The skin and hair of horses contain only two different kinds of pigments called

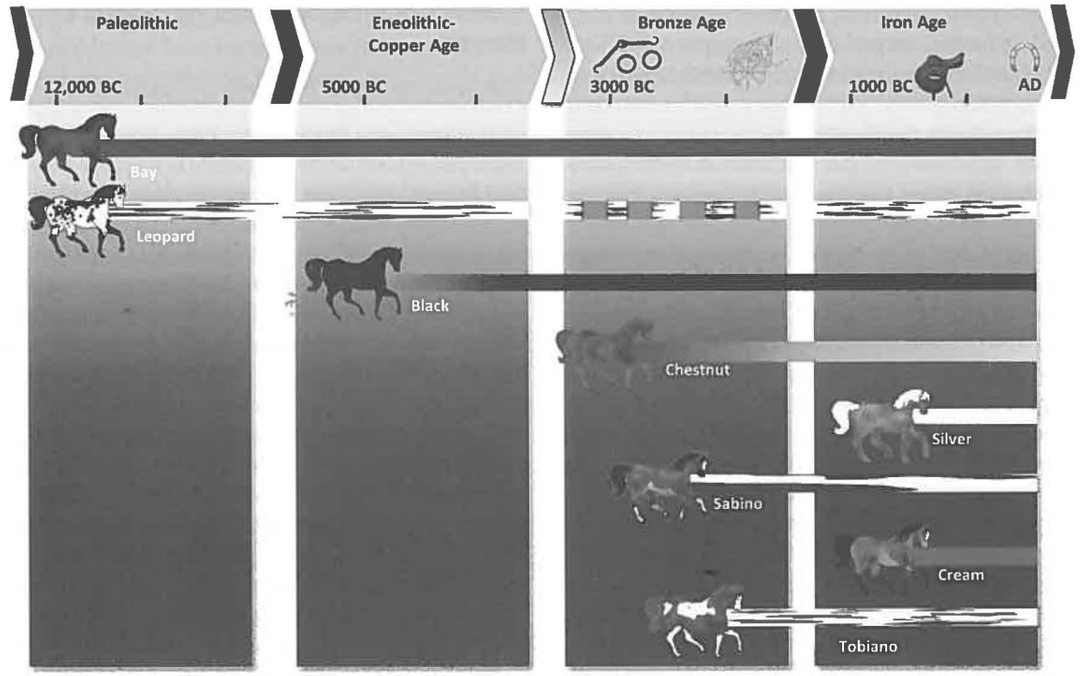


Fig. 7.2 Schematic representation of the first occurrence of coat colors in horses before and after domestication based on genetic markers in ancient remains.

pheomelanin (yellow) and eumelanin (black). These two pigments are distributed in various ways, determining the various coat colors. All coloration genes affect either the production or the distribution of these two pigments. To determine the ancient coat colors, we targeted the mutations controlling the basic coat color ("bay," "black," and "chestnut") and others responsible for the dilution of these basic colors ("silver," "cream," and "champagne"), leading to a lighter color, as well as white spotting ("tobiano," "sabino," "leopard," and "overo") patterns. For some coat colors, however, the responsible mutation is still unknown, especially for the "dun" coat color of the Przewalski's horses. Modern domestic horses show a high variability in coat coloration. No color is confined to a single breed, and the same mutation is responsible for a certain color variant across breeds, supporting the idea that mutations producing the color variants occurred prior to breed formation and may be valuable indicators for artificial selection during the domestication process.

By selecting short DNA regions including the point mutation on each gene involved in the coat colors, we analyzed the coat coloration of ancient horses using fossil remains (Pruvost *et al.* 2012). We showed that Pleistocene horses in Siberia and Germany displayed the basic bay coat color (Ludwig *et al.* 2009), which is the most common painted phenotype in Paleolithic art (fig. 7.2). At the beginning of the Holocene and until the end of the Copper Age, wild horses present both black and bay coat colors, with a slight predominance for bay (Ludwig *et al.* 2009), and so far no chestnut color has been found among predomestic horses (fig. 7.2). None of the mutations responsible for dilution (cream, champagne, silver) or the white spotting pattern was found in wild horses except for the mutation linked to the leopard spotting pattern phenotype (fig. 7.2). We estimated the frequency of the leopard allele to be higher than 0.1% in the western European horse population from the Pleistocene and suggested that this phenotype was not rare (Pruvost *et al.* 2011). The leopard complex spotting pattern is characterized by white spots that range from a few white flecks on the rump to a coat color that is almost completely white. A similar phenotype is depicted in the paintings of the "dappled horses" in the cave of Pech-Merle, France, dated to 24,700 years ago, featuring spotted horses in a frieze that includes hand outlines and abstract patterns of spots. The spotted pattern had been considered until now more symbolic than realistic because of the

juxtaposition of abstract elements and the unlikelihood of finding spotted coat phenotypes in wild animals, but this interpretation might need to be revisited, as genetics indicates the existence of such a coat color in horses during the Pleistocene.

The distribution of the coat color in ancient horse populations seems to change with domestication because we could demonstrate a significant shift and an increase of coat color variants, including dilutions and spotting patterns other than leopard from Bronze Age horse bone remains. The first chestnut phenotype observed dates to the third millennium BCE in a Siberian horse, and its frequency increased rapidly, reaching a proportion of 28% in Bronze Age horse bone assemblages (Ludwig *et al.* 2009) (fig. 7.2). The three basic coat colors (bay, black, and chestnut) seem to be equally common among ancient domestic horses (Ludwig *et al.* 2009; Svensson *et al.* 2012) from Europe and Siberia (fig. 7.2).

Mutations responsible for dilution or spotting phenotypes appear later in domestic horses (fig. 7.2). Date and location of their appearance are so far known only from the study of Ludwig *et al.* (2009) and therefore are just an approximation. The sabino pattern is the first spotting phenotype found, appearing during the third millennium BCE in Siberia. It was still present in Armenia and Moldavia during the middle Bronze Age, while today it is found only in North American horses. The tobiano genotype, which is widespread today, was observed in an eastern European horse (1500–1000 BCE), demonstrating its ancient history. Both "cream dilution" (buckskin) and "silver dilution" (black silver) were not found in horse bones older than 800 BCE, which could indicate that the diluted colors were not selected at the beginning of the domestication and only appeared later. So far, only two phenotypes, champagne and overo, were not found among the ancient domestic horses tested (Ludwig *et al.* 2009; Svensson *et al.* 2012). This is not a surprising result given that overo is lethal in a homozygous state and would therefore have been under strong negative selection, and champagne is known as a recent mutation.

The analyses of genetic markers linked to coat color are a first step to the phenotypic characterization of ancient horse populations going beyond skeletal properties. Moreover, the sudden and rapid increase in coat color variation at the beginning of domestication allowed for the first time a clear-cut distinction of the onset of the domestication of horses. In the future, whole-genome analyses of ancient horse remains will allow both a much more comprehensive phenotypic characterization of ancient horses and a refined understanding of their evolution.

Genetics of Mongolian and Przewalski's Horses

With Contributions by Tsendsuren Oyunsuren

Mongolia today is home to two horse populations, the native Mongolian domestic horse (*E. caballus*) and the wild Przewalski's horse. The native Mongolian domestic horse population, estimated at >2.6 million (National Statistical Office of Mongolia 2014), consists of five main lines named Galshir, Tes, Myangad, Datkhad, and Shankh. These lines differ in body conformation, size, coat colors, speed, and endurance. The Przewalski's horse became extinct in the wild in the 1960s but was reintroduced into its native habitat in Mongolia in 1992.

The genetic diversity and evolutionary relationship of domestic and Przewalski's horses have been studied and debated for decades. A variety of genetic studies have been performed targeting the mtDNA control region (the fastest-evolving DNA region known in mammals), microsatellite loci, and single nucleotide polymorphisms (SNPs) to assess the evolutionary relationship between domestic and Przewalski's horses (George and Ryder 1986; Ishida *et al.* 1995; Oakenfull and Ryder 1998; Goto *et al.* 2011). Interestingly, these horses can breed and produce viable offspring (Short *et al.* 1974) despite their karyotype differences (chromosome number of Przewalski's horse 2n = 66, domestic horse 2n = 64) (Bernischke *et al.* 1965; Ryder 1978; Trommerhausen-Smith *et al.* 1979; Ryder 1994). Contradictory hypotheses were proposed regarding the question of whether the Przewalski's horse was the direct ancestor of the domestic horse (Mohr 1959; Ryder 1994; Bowling *et al.* 2003; Lau *et al.* 2009). It was shown that the estimated mtDNA nucleotide sequence divergence between domestic and Przewalski's horses is 0.05–0.5%, suggesting a relatively ancient genetic divergence of these two types of horses (Ryder 1994). However, the ancestral status of the mtDNA of the Przewalski's horse, based on studies of the mtDNA control region, was not confirmed (Ishida *et al.* 1995).

Recently, full mitochondrial genomes and a part of the nuclear genome of Przewalski's and domestic horses have been sequenced using massively parallel sequencing technology, showing that the Przewalski's horse population has a higher diversity than expected. The mean autosomal diversity was determined to be 0.195%, thus higher than that of the thoroughbred horse (0.05%) (Goto *et al.* 2011). These analyses suggested that Przewalski's and domestic horse have both retained joint ancestral genes since their divergence.

The complete mitochondrial genomes of six Przewalski's horses have been sequenced in two studies published simultaneously (Goto *et al.* 2011; Achilli *et al.* 2012). In one study (Goto *et al.* 2011), four Przewalski's mitochondrial genomes were obtained and assigned to three haplogroups named I, II, and III. Haplogroups I and II are similar and cluster with the Przewalski-specific F haplogroup, which Achilli *et al.* (2012) defined on the basis on the analysis of the mitogenomes of two Przewalski's and eighty-one domestic horses across Asia, Europe, the Middle East, and America, whereas haplogroup III is most closely related to the J and K haplogroups of domestic horses from Europe and the Middle East. Thus, when a large number of mitochondrial genomes of horses are analyzed such as in the study of Achilli *et al.* (2012), it is clear that the mitochondrial genome sequences of the Przewalski's horses are contained within the diversity of the domestic horses. This result indicates that there was gene flow between the ancestors of the present-day populations or common ancestry.

The high variability of microsatellites is useful for revealing genetic diversity and has been used to explore the genetic relationship among Przewalski's horses (Breen *et al.* 1994; Oakenfull and Ryder 1998). Twelve microsatellite loci were examined for parentage testing and were shown to discriminate two Przewalski's individuals with a probability of 99.3% (Munkhtuya 2005). Moreover, this study also showed that the heterozygosity in the Przewalski's horse population was moderate compared to most domestic horse breeds (He = 0.63; Munkhtuya 2005).

Based on the sequence of 14.3 kb of the Y chromosome of 52 horses of 15 breeds and of one Przewalski's horse, it was shown that the Przewalski's horse belongs to a distinct lineage because no sequence variability was observed among all domestic horses, whereas the Przewalski's sequence differed by six nucleotides (Lindgren *et al.* 2004). Thus it was estimated that the divergence between the Przewalski's horse and the domestic horse occurred between 120,000 and 240,000 years ago (Lindgren *et al.* 2004).

Pairwise genetic distance and multidimensional scaling of genome-wide SNP analyses of domestic and Przewalski's horses showed that they are genetically distinct from all domestic horses, including the native Mongolian horse, despite a close evolutionary relationship (McCue *et al.* 2012). Finally, a recent study where whole genomes of ancient horses (about 560,000–780,000 and 43,000 years old) were sequenced, as well as the genomes of a domestic and a Przewalski's horse, showed that the domestic and the Przewalski's horse are distinct lineages and estimated that the two populations diverged between 38,000 and 72,000 years ago (Orlando *et al.* 2013). Furthermore, in the genome of the Przewalski's horse that was sequenced in that study, no traces of gene flow from domestic horse breeds were detected. The final conclusion has to await the sequencing of more genomes, wild and domestic ones, and in particular those of the Mongolian breeds.

Even though the diversity of the Mongolian horse population has not yet been fully explored with the most advanced techniques, the combination of various studies involving the analysis of microsatellite loci, inter simple sequence repeat (ISSR) markers, and nuclear SNPs indicated that Mongolian horses have the highest heterozygosity and genetic diversity among all domestic horse breeds analyzed so far (Tozaki *et al.* 2003; Voronkova *et al.* 2011; McCue *et al.* 2012; Tsendsuren *et al.* 2013*b*). This is also seen at the level of the mitochondrial control region because the Mongolian horse population harbors 53 mitochondrial haplotypes (Tsendsuren *et al.* 2013*a*). All of these findings suggest that the Przewalski's horse is not the ancestral type of the domestic horse, but that the two belong to sister lineages within the genus *Equus*, which originated 4.0–4.5 million years ago (Orlando *et al.* 2013).

One Hundred Thousand Years of Phylogeography of the Eurasiatic Wild Ass Based on Ancient DNA

With Contributions by E. Andrew Bennett, Thierry Grange, and Eva-Maria Geigl

Paleogenetics, the analysis of traces of DNA preserved in fossilizing calcified tissue of the remains of organisms, provides a temporal perspective on the evolution of the genetic diversity of populations. These data can be invaluable for the design of conservation biology strategies. They also complement paleontological studies, which are often made difficult owing to the scarcity of bone remains, the lack of reference skeletons, and other taphonomic and morphological biases (for a review, see Geigl and Grange 2012).

The Asiatic wild ass is on the way to extinction before having been well studied (International Union for Conservation of Nature 2013). Asiatic wild asses hold a distinct biological, ecological, and cultural importance in arid and high-altitude plains and deserts. In order for a large herbivore to be able to survive in such barren environments and to develop their characteristic extreme endurance, enormous physiological

adaptations are necessary; however, many of these remain to be explained.

The global population of Asiatic wild asses is estimated at ~54,000 individuals, with the largest population in the Mongolian Gobi (commonly referred to as *E. h. hemionus* or "dziggetai") and much smaller populations in India (*E. h. khur*), Turkmenistan (*E. h. kulan*), and Iran (*E. h. onager*), which have been assigned subspecies status because of some morphological differences and geographic isolation (Denzau and Denzau 1999; Groves and Grubb 2011). Kiang (*E. kiang*) are currently considered a different species and seem still numerous on the high-altitude plains of the Tibetan Plateau, with an estimated number of between 60,000 and 200,000 (St-Louis and Côté 2009).

To unravel the phylogeographic history of the Asiatic wild ass, the kiang, and their extinct European counterpart *E. hydruntinus*, we analyzed around 250 samples—archaeological bones, museum specimens, and modern animals from both zoos and the wild—ranging in time and space over a period of 100,000 years and the entire Eurasian continent, from western France to India and Mongolia. We concentrated our analysis on the mitochondrial hypervariable region, the high mutation rate of which guarantees a high-resolution phylogenetic analysis and reveals the evolution of maternal lineages. Moreover, this DNA sequence is characterized by a deletion of 28 nucleotides that is specific for the Asiatic wild ass and can be used as a bar code. We obtained 145 DNA sequences, 8 of which were older than 10,000 years and one ~100,000 years old. Fifty-eight of our samples originated from southwest Asia, including regions within the present-day borders of Syria, which contain climatic conditions that are highly unfavorable for DNA preservation (Bennett *et al.*, in review). Thus DNA from these samples is extremely degraded, and only short DNA fragments at minimal quantities are preserved, if at all. The surprisingly high success rate of our study is to be attributed to a continuous and profound effort to adapt and optimize DNA extraction and analysis methods and to eliminate contamination with modern DNA, which is a major problem of ancient DNA analyses (Pruvost and Geigl 2004; Pruvost *et al.* 2005; Champlot *et al.* 2010; Bennett *et al.* 2014).

The DNA sequences we obtained were subject to Bayesian phylogenetic reconstructions (Drummond and Rambaut 2007) and spatial principal component analysis (Jombart *et al.* 2008). The ancient DNA sequences in particular allowed us to identify nine distinct clades (haplogroups) showing a clear phylogeographic structure (Bennett *et al.*, in review). Our analyses reveal multiple aspects of the evolution of this species. First, the highest diversity over the last 8,000 years was found with three distinct clades in the area of present-day Iran, suggesting that the radiation of the hemiones took place in this area and that colonization of Eurasia started from here. One clade that seems to have gone extinct as recently as the Bronze Age comprises the population that once inhabited the Caucasus and northern Iran. The other clade that had diverged from the latter one several hundreds of thousands of years ago comprises the present-day Iranian onagers, a population that roamed the highlands of Iran in prehistoric times but still is present today in the reserve of Bahram-i-Goor. The hemiones from northern Iran and Turkmenistan belong to a third clade that diverged earlier from the two others more than half a million years ago. The fact that they belong to the same clade demonstrates that these populations, which are currently assigned to different subspecies or even species—that is, *E. h. onager* and *E. h. kulan* (Groves and Grubb 2011)—are not separated and have experienced gene flow throughout the past until recently. The individuals that were introduced in Israel in the first half of the 1990s founding the breeding core in the Hai-Bar Yotvata Reserve were from Iran and Turkmenistan, respectively, and were found to belong to the Iranian and the Iran-Turkmen clades, respectively. The Indian khurs cluster in a distinct clade that is related to the Turkmen-Iranian kulans but separated from the latter ones for hundreds of thousands of years.

The conquest of the Tibetan and Mongolian Steppes appears to have occurred in two waves. The first wave seems to represent the continuation of the migration of the ancestors of the Asiatic wild asses out of Africa that is dated, on the basis of the fossil record, to one million years ago (Forsten 1992; Eisenmann 2004; Bernor *et al.* 2010). All other clades diverged later from the clade in which the present-day Tibetan kiangs and some lineages of the Mongolian dziggetais (populations of Asiatic wild ass) cluster. The subbranches of this clade are found in both the kiang and the dziggetai populations. The fact that kiang and dziggetai share a common clade shows that gene flow occurred recently between these two populations, thus questioning the assignment of *E. kiang* as a distinct species (Groves and Grubb 2011). There is a second clade of dziggetais that is related to the Iranian haplogroups and reflects a more recent colonization event from southwest Asia. We did not detect any kiang lineage in this clade, which suggests that it is the result of a second migration wave of hemiones out of Iran that did not reach the Tibetan highlands and did not hybridize with the kiangs. Altogether these data suggest the direction of interbreeding between kiangs and dziggetais: it could be explained with female kiangs migrating back from the Tibetan Plateau to Mongolia and interbreeding with the dziggetais.

Syria was inhabited in the past by a distinct clade that separated from the Caucasian-Iranian onagers around 300,000 years ago and much earlier from the hemiones from neighboring Turkey. This clade went extinct in the twentieth century when the last Syrian onagers, the *E. h. hemippus*, died in European zoos. The Syrian hemippus had a distinctive physical appearance with short ears and was the smallest and most gracile of all hemiones. We showed that bigger animals present in Syria 4,000 years ago belonged to the same clade, indicating that size reduction was a recent phenotypic evolution of the species in an ecological pessimism due to impoverished living conditions, possibly following climatic changes and competition with domestic life stock (Bennett *et al.*, in review).

Since the Middle Pleistocene, Europe was populated by the now extinct *E. hydruntinus*, a gracile wild ass that disappeared some time during the Holocene, and for which paleontological determination is particularly difficult (Geigl and Grange 2012). We genotyped several Pleistocene bone remains from western France, Romania, and Turkey that were assigned on morphological grounds to this species. The results clearly demonstrate that *E. hydruntinus* is a hemione, as all analyzed remains showed the hemione-specific 28-bp deletion. Moreover, the individual that lived 100,000 years ago in western Europe, classified as *E. hydruntinus*, clustered together with an early twentieth-century Iranian onager to form a clade, which had diverged from the eastern European / Anatolian clade roughly half a million years ago. This latter clade is constituted by Holocene hydruntines, which lived in Romania and Anatolia roughly 7,000 years ago. This clade is sufficiently distinct from the other clades in that it could well have the characteristic morphological features that are commonly attributed to *E. hydruntinus*, suggesting that Europe was colonized by hemiones through at least two colonization waves before and after the last two glaciation maxima. We conclude from this finding that the Magdalenian cave art representations, like the famous "Panneau de l'Hémione" in the Lascaux cave in France, were indeed representations of contemporaneous animals and not inaccurate or symbolic representations of horses, as some currently believe on the basis of the assumption that hemiones were not present in western Europe at this time (Bennett *et al.*, in review).

Genetic Diversity of the Reintroduced Asiatic Wild Ass in Israel: From the Breeding Core to the Current Wild Population

With Contributions by Shirli Bar-David, Sharon Renan, Tomer Guieta, Edith Speyer, Naama Shahar, Gili Greenbaum, Idan Goodman, Amos Bouskila, and Alan Templeton

The endemic Middle East subspecies of Asiatic wild ass (*E. h. hemippus*) became extinct at the beginning of the twentieth century as a result of hunting and habitat loss (Groves 1986). In 1968, the Israel Nature and Parks Authority (INPA) established a breeding core of the Asiatic wild ass at the Hai-Bar Yotvata Reserve from six Persian wild asses (*E.h. onager*; three males, three females), and five from the Turkmenian subspecies (*E. h. kulan*; two males, three females). The animals were kept at the reserve and were allowed to interbreed (Saltz and Rubenstein 1995). Between 1982 and 1993, the INPA released the wild ass from the breeding core into the Negev Desert: 28 wild asses (14 males, 14 females) were reintroduced to Makhtesh Ramon and 10 wild asses (3 males, 7 females) to the Paran area, about 35 km south of Makhtesh Ramon. Prior to the Paran reintroduction (in 1991), a genetic study of the animals in the breeding core (17 males, 13 females; referred as the founding population) was conducted (Sinai 1994), and blood samples have been preserved since then. Since the reintroduction onset, the wild ass population has grown and expanded its range. The current population (wild population) is estimated at >250 individuals in the Negev Desert and Arava Valley.

The samples of the founding population provide a unique opportunity to explore the genetic and evolutionary processes that have occurred in the wild ass population since reintroduction. We compared the genetic diversity of the wild population with that of the founding population, four generations since reintroduction onset (generation time is 7.4 years; Saltz and Rubenstein 1995). We further examined the spatial-genetic structure of the wild population in order to understand the course of development of genetic structure and the factors affecting it.

The study was conducted by analyzing 30 blood samples of the founding population, and fecal samples of the wild population collected in the field, during 2009–2012 using noninvasive genetic techniques. DNA from the samples was extracted and amplified by a set of mtDNA (Gueta *et al.* 2014) and microsatellite primer pairs (Nielsen *et al.* 2007), following the techniques of Renan *et al.* (2012). Expected heterozygosity (H_E) and observed heterozygosity (H_O) of the founding

population, calculated on the basis of nine microsatellites, were compared to measures of the *E. h. onager* from the European breeding groups documented previously (Nielsen *et al.* 2007). Both H_E and H_O of the founding population were significantly higher than the corresponding values found in the European *E. h. onager* breeding cores. The mean number of alleles per locus among the founders was lower than the European breeding cores, however. The relative high genetic diversity in the founding population in terms of heterozygosity measures is due to admixture between the subspecies/subpopulations, while the low diversity in terms of allele numbers is probably due to the recent population bottleneck in Israel (S. Bar-David *et al.*, unpublished data).

Fifty-nine samples of the wild population were analyzed using six microsatellite markers (Renan 2014). The number of alleles per locus did not differ significantly between the founding and wild populations. Most of the alleles in these loci of the founding population remained in the wild population, but there was a significant difference in the allele frequencies between the populations (Renan 2014). The wild population experienced considerable genetic drift, as indicated by substantial shifts in allele frequencies in most alleles. Model simulations suggest that the polygamous mating system of the Asiatic wild ass could induce the increased genetic drift, affecting the population's genetic diversity (Renan 2014). Decrease in the genetic diversity over time could have significant consequences for the long-term persistence of the wild ass in Israel.

We examined the spatial-genetic structure of the wild population and related it to landscape features within the wild ass range of distribution (Nezer 2011; Davidson *et al.* 2013). We collected 393 fecal samples of the wild population from 79 documented sites in the Negev Desert and Arava Valley and analyzed them using mtDNA markers. Three mtDNA haplotypes were identified in the wild population, the same haplotypes as in the founding population (Gueta *et al.* 2014). Two of these haplotypes were found mostly among the Turkmenian, and the other mostly among the Persian wild ass sequences (Bennett *et al.*, in review).

Fecal samples were delimitated to six "subpopulations" according to their geographical locations. The mtDNA haplotype frequency was calculated for each subpopulation. The "east subpopulation," at the wave front of the wild population's distribution, was reported to be significantly different than the rest of the population in terms of haplotype frequencies (AMOVA, $\Phi ST = 0.13$, $P = 0.04$). The east region is characterized by high-quality habitat patches (high density of *Acacia spp.* trees) and low landscape connectivity to the rest of the area. These landscape features possibly led to the relative isolation of the east subpopulation. Dispersers from the release area probably initiated the subpopulation and remained in the "new area" (Gueta *et al.* 2014).

Spatial-genetic structure, following a founder effect, can arise when a population is expanding its range, as demonstrated by theoretical models (e.g., Excoffier and Ray 2008) and a few empirical studies (e.g., Neuwald and Templeton 2013). It might diminish over time owing to gene flow and additional range expansion. Yet even a temporary genetic structure may influence the response of the population to selection and help maintain genetic diversity in the total population, thereby affecting the population's long-term persistence.

Life on the Edge: What We Know—and Don't Know—about the Genetics of the African Wild Ass

With Contributions by Sónia Rosenbom and Albano Beja-Pereira

The African wild ass was once distributed across a wide geographic range—north and west into Sudan, Egypt, and Libya—but the species is now circumscribed to the Horn of Africa (the deserts of Ethiopia, Eritrea, and Somalia and possibly Sudan) (Moehlman *et al.* 2008). Historically, three subspecies were recognized according to both geographic distribution and morphology. The Atlas wild ass (*E. a. atlanticus*) was found in the Atlas region of northwestern Algeria and adjacent parts of Morocco and Tunisia; the Nubian wild ass (*E. a. africanus*) inhabited the Nubian Desert of northeastern Sudan, from east of the Nile River to the shores of the Red Sea, south to the Atbara River and into northern Eritrea; and the Somali wild ass (*E. a. somaliensis*) lived in regions of southern Eritrea, Ethiopia, and Somalia (Moehlman *et al.* 2008). The Atlas wild ass is believed to have gone extinct in historic times (Groves 1986) as a result of intensive hunting, and the Nubian wild ass is probably now extinct in the wild or extremely rare. Populations of the Somali wild ass subsist in Ethiopia and Eritrea; however, anthropogenic pressures and possible hybridization with the domestic donkey have been driving the African wild ass to the brink of extinction. Currently, the number of African wild asses in the wild is estimated at <600 animals (see chap. 12).

The few molecular studies that included African wild ass were designed either to assess the *Equus* genus phylogeny (George and Ryder 1986; Oakenfull *et al.* 2000) or to unravel the putative ancestor of the domestic donkey (Beja-Pereira *et al.* 2004; Kimura *et al.* 2011). Up to now, however, no studies focusing exclusively on the genetics of extant African wild ass populations have ever been published. Such a fact might be mainly attributed to two reasons: the near-inaccessibility of extant populations in remote and harsh habitats in northeast Africa, and the limitations to sample collection imposed by current Convention on International Trade in Endangered Species (CITES) Appendix I status.

Nonetheless, the first study using samples belonging to free-ranging African wild ass individuals from Sudan (as well as three captive individuals) allowed the identification of this species as the likely ancestor of the domestic donkey; more specifically, it identified the Nubian wild ass as the probable ancestor of one domestic donkey lineage (termed Clade 1) and a relative of the Somali wild ass, probably already extinct, as the ancestor of the other lineage (termed Clade 2) (Beja-Pereira *et al.* 2004).

More recently, a study published by Kimura *et al.* (2011) was the first to include a relevant number of noninvasive (fecal) samples of free-ranging African wild ass belonging to populations in Ethiopia and Eritrea. This study analyzed mtDNA data from modern, historical, and ancient African wild ass and domestic donkey specimens in order to clarify questions regarding donkey ancestry and domestication. Median-joining network of obtained haplotypes revealed two distinct mitochondrial domestic donkey haplogroups previously reported (Chen *et al.* 2006; Kimura *et al.* 2011), and a third clade incorporating all 33 modern Somali wild ass specimens and previously published Somali wild ass sequences. Sequences belonging to ancient and historic Nubian wild ass (identified on the basis of morphology) fell inside the wider variation of a domestic donkey Clade 1, reinforcing the hypotheses of this subspecies as a possible ancestor of the domestic donkey. Four new haplotypes were found in the thirty-three analyzed specimens, and haplotype diversity of the Somali wild ass clade was only 0.7417 + 0.0444 (compared with 0.9309 + 0.0102 and 0.8212 + 0.0268 for domestic donkeys' Clades 1 and 2, respectively), suggesting a low genetic variability among present-day Somali wild ass. The observed haplotypes shared by both Eritrean and Ethiopian populations reveals the absence of geographical structure at the mitochondrial level. A historic Somali specimen from Berbera, Somalia, from the late nineteenth century yielded amplifiable mtDNA, and the obtained sequence was identical to that of a contemporary haplotype from Eritrea and Ethiopia, demonstrating a degree of continuity in the mitochondrial variability of Somali wild ass within this region over the last 120 years.

In a recent study by Rosenbom *et al.* (2015), three African wild ass populations in Ethiopia (Afdera and Hillu) and Eritrea (Asmera) as well as several Asiatic wild ass populations (representing both *E. hemionus* and *E. kiang* species) were sampled using a noninvasive approach. Given the current geopolitical scenario in areas where the Nubian wild ass may still occur, sampling of this subspecies was not achievable. Sequence analyses of a 410-base-pair fragment of the fast-evolving mitochondrial DNA control region revealed the Eritrean population of Asmera as presenting the highest values of both haplotype and nucleotide diversity among African wild ass populations.

Clear differentiation among available Nubian and obtained Somali haplotypes was found; however, three out of four haplotypes belonging to *E. a. somaliensis* were shared between populations in Eritrea and Ethiopia, confirming no geographical structure for this subspecies. Despite the sampling effort ($n = 85$), no new haplotypes were found, which is a clear indication that variability in the wild was most probably fully captured in this study. Demographic dynamics analyses revealed that populations in Ethiopia and Eritrea remained relatively stable over time but at lower maternal effective population sizes when compared with focal populations of *E. hemionus* in Iran and China.

Given the actual scenario of decreasing numbers and extreme endangerment, the next step for the African wild ass will necessarily be the assessment of relevant parameters for the conservation and management of this emblematic species. In this way, the same populations in Ethiopia and Eritrea are now being further investigated. Previously tested horse microsatellites (Rosenbom *et al.* 2012) are being used in order to assess levels of genetic diversity, effective population size, geographic structure, and migration. Preliminary results corroborate the level of diversity of the Eritrean population of Asmera being considerably higher than for both Ethiopian populations. This value is also in line with previously reported values for a captive population of the Somali wild ass, using a similar set of microsatellite loci (Rosenbom *et al.* 2012). Obtained results for geographic structuring corroborates the idea of weak structuring among Eritrean and Ethiopian populations of the African wild ass, as previously observed in mitochondrial DNA haplotypes, with only 14% of the captured variation being attributed to differences among populations. These results raise the possibility that up until recently gene flow still existed among studied populations.

Future perspectives on genetic studies on the African wild ass include the increase in the number of sampled individuals from extant populations and, more importantly, the use of new genomic tools that will allow the analyses of genome-wide data in order to continue answering questions regarding this critically endangered equid species.

Has Genetic Conservation Been as Successful as "the Numbers"? The Conservation of Cape Mountain Zebra Genetics

With Contributions by Halszka Hrabar and Eric H. Harley

Mountain zebra are divided into two subspecies, the Cape mountain zebra (*E. z. zebra*) of South Africa and Hartmann's mountain zebra (*E. z. hartmannae*) of Namibia (Moodley and Harley 2005). The individual population histories of these two subspecies differ significantly in scale and intensity. Hartmann's mountain zebra underwent a serious decline in the first half of the 1900s (Novellie *et al.* 2002), yet the arid conditions in Namibia prevented large-scale human settlements and hence limited habitat destruction. In the last two decades, tight control of hunting and the installation of artificial watering points resulted in an increase in Hartmann's mountain zebra numbers such that the total population size in 2002 was estimated to be over 25,000 (Novellie *et al.* 2002).

By contrast, in South Africa, where Cape mountain zebra were once widespread in the mountains of the western and eastern Cape provinces (Millar 1970*a*,*b*), excessive hunting and habitat loss to agriculture (intensive human settlement dates to the seventeenth century) left their numbers in a critical status in the 1950s, with <80 individuals remaining in only three relic populations. Since the 1950s, numbers have gradually increased through active conservation programs, with a metapopulation approach through translocations to ensure continued population growth (Novellie *et al.* 2002) (see chap. 14).

Despite the improved status, however, the security of the subspecies is still questionable, as a lack genetic biodiversity is still a key threat. A primary concern is that all reintroduced subpopulations except for one (De Hoop Nature Reserve) originate from only one of the natural relic populations (Mountain Zebra National Park [MZNP]). Two-thirds of the entire genotype is therefore located in just two populations (Moodley 2002), namely, the Kammanassie and Gamka populations (which together make up <7% of individuals in the metapopulation). It is also a problem that all Cape mountain zebra populations are isolated from one another because of fencing (i.e., there is no gene flow between populations).

The level of genetic variation in each individual relict population is lower than in the subspecies overall, which implies that higher levels of diversity still exist within the Cape mountain zebra gene pool. For example, De Hoop, the population of mixed (MZNP/Kammanassie) origin, have the highest genetic variation for any Cape mountain zebra population (Moodley and Harley 2005). Translocations from the Kammanassie and Gamka populations have not occurred in the past, as the management aim has been to first allow the populations to increase sufficiently in size (to around 90 individuals in Gamkaberg). Despite formal protection since 1923 and 1971, respectively, however, both populations still consist of <50 individuals and are at risk owing to limited suitable habitat availability (Watson *et al.* 2005). For a decade now, it has been recognized that the populations can no longer be managed in a hands-off manner, and viable management options need to be implemented urgently (e.g., purchasing or leasing neighboring land to increase the available suitable habitat) to reduce the risk of quasi-extinction of the population (Watson *et al.* 2005). But progress has been minimal, and the previously less favored option of translocating the populations to other protected areas within the region with more suitable habitat is now a necessary consideration. The situation has reached a point where the need to expand these genetically valuable populations outweighs the ideal to conserve them in their original habitat.

An additional concern is the large number of small populations (particularly on private land) because the risk of inbreeding depression and increasing loss of genetic diversity from genetic drift is higher in small populations (Frankham 1996; Bowland *et al.* 2001). The total heterozygosity in the Cape mountain zebra population, based on measurements at 15 microsatellite loci, was only 0.236 (Moodley and Harley 2005), which equates to about three-quarters of gene loci being homozygous and compares with a total heterozygosity of 0.476 for Hartmann's mountain zebra. Apart from the resulting decreased evolutionary potential from the lack of adequate genetic variation, inbreeding depression may result in decreased fecundity and especially increased susceptibility to disease. This problem appears to be already manifesting itself in the Cape mountain zebra population, where there is marked increase in the prevalence of equine sarcoids (Sasidharan 2006; Sasidharan *et al.* 2011).

Of the 52 populations, 11 are smaller than the recommended minimum founder size of 14 individuals (Novellie *et al.* 2002), and 31 populations consist of fewer than 30 individuals. The recommendation that reinforcement of existing populations receive priority over the establishment of new populations, and that one or two animals be added to subpopulations once every five to ten years in order to avoid inbreeding depression (Novellie *et al.* 1996, 2002), has also not been adhered to. This is largely because of the cost of investing in a large number of animals (according to personal communication with private land owners).

The problem of low genetic diversity in Cape mountain zebra populations is exacerbated by their social structure, whereby the behavior of the males tends to reduce the effective population size (a fraction of the males can dominate matings for an extended period of time). Females within a breeding herd are usually unrelated, however, thereby increasing the potential genetic diversity of offspring produced by a single harem. The loss of genetic integrity through human-driven hybridization between the two subspecies has been considered to be a threat in the past (Novellie *et al.* 2002). A permit system for the transportation of wildlife, maintained by provincial conservation agencies, has reduced this threat, however, as the system ensures that Hartmann's mountain zebras cannot legally be introduced into the range of the Cape subspecies. The capacity of provincial conservation agencies to undertake the necessary measures to enforce such segregation is questionable, though, and cases of hybridization are still reported.

No restrictions exist for the co-occurrence of plains zebra and Cape mountain zebra, as historic records show the two species did occur in sympatry when the Cape mountain zebra moved onto the flats from time to time for grazing (Skead 2007, 2011). The threat from hybridization between the two species has also not been a great concern, as fertile hybrids are thought to be unlikely owing to the relatively large difference in the number of chromosomal pairs (44 vs. 32 in plains zebra vs. Cape mountain zebra, respectively) compared to plains and Grevy's zebra (44 vs. 46), which do produce fertile hybrids (Ryder 1978; Cordingley *et al.* 2009). In 2014, hybrids were recorded in Mountain Zebra National Park, however, which serves as a key source population. All plains zebra and known hybrids have subsequently been culled from this population, but the two species still coexist in at least six other populations. Hybridization is most likely to occur in poor habitats or small populations, where low mate availability and skewed sex ratios may lead to exclusion of some individuals from mating (Mace and Waller 1998; Jansson *et al.* 2007), which is the case for a number of Cape mountain zebra populations. It is therefore vital that the fertility of Cape mountain zebra–plains zebra hybrids be determined so that the potential degree of threat in coexisting populations can be assessed. Regulations regarding their coexistence also need to be reassessed, and a system needs to be in place to test for hybridization in individuals so as to ensure that no movement or sale of hybrids occurs (many private owners will already only purchase DNA-tested animals).

In conclusion, conservation efforts to decrease the threat of hybridization and increase genetic diversity within the entire Cape mountain zebra metapopulation remains an urgency, as the current distribution of two-thirds of the entire genotype in just 2 of the 52 populations leaves the population highly vulnerable to genetic loss. Much of the population is at risk of inbreeding depression owing to the small size of many populations and the isolated nature of all populations. We therefore advocate a management strategy that (1) entails the mixing of relic populations, (2) focuses on increasing the size of small populations, (3) ensures gene flow between populations, and (4) addresses the threat of hybridization with plains zebra.

Genetic Diversity in Populations of Feral Horses on Public Lands in the Western United States

With Contributions by E. Gus Cothran, Brian W. Davis, Anas Khanshour, Eleanore Conant, Reid C. Booker, and Rytis Juras

Feral horses are domestic individuals that have returned to a free-living condition, either through escaping from a controlled domestic environment or by being released into the wild by owners who can no longer care for them. Many species of domestic animals have undergone this feral transition, and in most cases the free-living animals quickly return to what are essentially native phenotypes and behaviors. We examined 12 autosomal microsatellite markers distributed across the horse genome to evaluate genetic variation in feral horse populations in the United States. These 175 populations consisted of over 7,000 total horses and ranged over 10 states, with some populations being represented two or more times over the sampling time period.

Observed heterozygosity, which is a measure of individual genetic variation, ranged from 0.49 to 0.87, which spans the range of variation for domestic breeds. The same could be said for all variability measures, however; on average, genetic variation levels tend to

be lower in the feral horse populations. A variety of factors can influence genetic variability in these relatively small populations. In addition to variability measures, we obtained estimates for the percentage of individuals sampled within the population that do not fit the genetic profile of the remainder of the population and may represent recent immigrants into the herd. We also obtained the appropriate management level (AML) for each herd. This is the manager-calculated number of horses that the herd area can support. It is thus an estimate of target population size (actual census numbers are almost never available). The herd will increase in size above the AML between "gathers" (roundups of horses, which are mainly used to remove what are considered to be excess animals), but the population size is usually reduced to a number well below the AML at the time of a gather.

Variability was significantly associated with population size as measured by AML. Population sizes of the herds have fluctuated over time. When a herd was sampled on more than one occasion, levels of variation at the different time periods were compared. In most cases no change was evident, mainly because sampling periods spanned less than a generation interval. There also was a significant association between the estimated number of migrants in a population and genetic variation, with variation increasing as the number of migrants increased. Various measures of genetic distance and genetic differentiation among the populations were examined, and genetic distance was compared to geographic distance based upon GPS coordinates for each herd (supplied by the US Bureau of Land Management). In general, there is no strong correlation between genetic distance and geographic distance, but those herds that are geographically closest to each other average lower genetic distances between them. Some herds show no close relationship to any other herd or to any domestic breed. These are mostly herds with variability levels outside those near the mean herd values.

Possible ancestry of each feral herd from domestic breeds was estimated by comparison to 65 domestic horse breeds, focusing on those from the New World. Most herds appeared to be of widely mixed ancestry with no definitive breed ancestor. This result is consistent with the history of most areas where the feral herds are located. When a clear ancestral breed could be identified, it was almost always a common North American breed such as the Quarter Horse or Morgan. Only a handful of herds show evidence of Spanish ancestry, with these herds tending to be more isolated than others. This is significant because the first feral horses of the American West were of Spanish origin, but most of the Spanish influence now appears to be gone.

The general management trend for feral herds on public lands has been a reduction in population size. Based upon the analyses conducted, this practice will inevitably lead to a long-term loss of genetic variability within individual Herd Management Areas. This loss of variation can be mitigated by a low level of exchange of individuals from geographically close herds. This process will tend to homogenize the herds, but it would take many generations. Some consideration should be made to manage a few of the herds to preserve them as they are for historical conservation, or to retain breed type in the cases of the small number of herds with evident Spanish horse ancestry.

Conclusion

Genetic analysis has enabled the description of both the evolution of wild equid populations in the present and in the recent and more ancient past, as well as revealed the consequences of conservation policies. Much remains to be done. In particular, the reduction of the costs of next-generation sequencing renders possible the genomic analyses of many individuals. Including multiple markers would allow expanding on this current work to complete our understanding of the past demography of populations and the relationships between them to an extent beyond what can be achieved solely through mitochondrial or microsatellite markers. This opportunity should be taken quickly to obtain a global view of these populations, which would allow for a more enlightened approach to future conservation management.

ACKNOWLEDGMENTS

While the opening page of this chapter lists the lead author of each section, many talented contributors also coauthored this chapter. The authors also wish to thank anonymous referees for their comments and corrections.

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8

The Roles of Humans in Horse Distribution through Time

SANDRA L. OLSEN

The human–horse relationship has been a key factor in alterations of the horse's range, its introduction to new regions, and its redistribution in areas previously occupied before the Holocene (12,000 BP to present). This chapter provides a synopsis of the ways in which the changing roles of the horse in human societies and the movements of people have combined to produce the current geographic coverage of this amazingly adaptable species. Today, horses are found on every continent in the world with the exception of Antarctica, but this has not always been the case. Before human intervention, wild equid species dispersed from one landmass to the next via land bridges when sea levels were low. Mountains, deserts, and rainforests impeded the expansion of wild equids, as grasslands are typically their preferred habitat, but large bodies of water presented the most challenging barriers. After domestication, humans became the dominant agent of dispersal, introducing them into radically different environments.

Horses played a variety of vital roles in societies, including those related to diet, transportation, work, religious, property/commodity, military, and sports. Because horses conveyed people, either on their backs or in vehicles, the dispersal of the two species was often synchronized. The movement of horses from one region to the next was accomplished through migration, exploration, colonization, trade, marriage exchanges such as dowry and bride price, theft and counting coup, military campaigns, war booty, gifts or tribute, and accidents such as shipwrecks. Numerous innovations facilitated horse transport, with the most significant being improved roads and shipping methods. Domestication of grain provided a supply of fodder when needed, especially in marginal environments, but horses can survive on relatively poor-quality pastures. Documenting the presence of horses in a region is accomplished through identification of their remains or trappings in archaeological contexts, images in art, and written accounts. Tracking the arrival of horses in new lands beyond their original Holocene native range is not always easy or reliable, however, because it is often dependent on inconsistent or incomplete records. The spread of horses is reported here with the goal of shedding light on the timing of their initial occurrences around the world and their lasting impact.

The first equid to be associated with hominins in the archaeological record was *Hipparion*. *Hipparion* was a relatively large (about 13 and a half hands) grazing horse that retained four toes, although three were

© 2016 Johns Hopkins University Press
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Printed in the United States of America on acid-free paper
9 8 7 6 5 4 3 2 1

Johns Hopkins University Press
2715 North Charles Street
Baltimore, Maryland 21218-4363
www.press.jhu.edu

Library of Congress Cataloging-in-Publication Data

Wild equids : ecology, management, and conservation / edited by Jason I. Ransom and Petra Kaczensky.
pages cm
Includes bibliographical references and index.
ISBN 978-1-4214-1909-1 (hardcover : alk. paper) — ISBN 978-1-4214-1910-7 (electronic) — ISBN 1-4214-1909-2 (hardcover : alk. paper) — ISBN 1-4214-1910-6 (electronic)
1. Equidae. 2. Wild horses. 3. Horses. 4. Zebras. I. Ransom, Jason, editor. II. Kaczensky, Petra, editor.
QL737.U62W526 2016
599.665—dc23 2015022981

A catalog record for this book is available from the British Library.

Special discounts are available for bulk purchases of this book. For more information, please contact Special Sales at 410-516-6936 or specialsales@press.jhu.edu.

Johns Hopkins University Press uses environmentally friendly book materials, including recycled text paper that is composed of at least 30 percent post-consumer waste, whenever possible.

For Liam, Nicky, and Una:
Part of the next generation to share the earth with wild equids



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Acknowledgments

THIS BOOK WOULD NOT HAVE BEEN POSSIBLE IF IT WEREN'T FOR THE participants and sponsors of the International Wild Equid Conference held in Vienna, Austria, in 2012. Many of the participants contributed to this book, but the work herein reflects the efforts of many talented scientists that continue to work for the conservation of wild equids. Not all could contribute to this effort, but their work is enormously appreciated. We must thank the sponsors of that conference for starting this work in progress and ultimately helping to fund publication: University of Veterinary Medicine–Vienna, Colorado State University's Center for Collaborative Conservation, Vienna Business Agency, Ms. Evelyn Haim-Swarovski, International Takhi Group, US Geological Survey, World Associations of Zoos and Aquariums, and Vectronic Aerospace. Thank you also to the Austrian Science Foundation (FWF) for funding wild equid research in the Mongolian Gobi since 2001. Many outcomes of that work contributed substantially to this book.

A special thanks is owed to the many peer reviewers who donated their time to provide critical comments for this book's chapters, as well as to the anonymous reviewers solicited by the publisher to critique the book as a whole. Your comments, criticisms, and insights have improved the content of this volume, and it is this kind of dispute that ultimately drives good science. Thank you also to Vincent Burke, Catherine Goldstead, and Kathryn Marguy at Johns Hopkins University Press for pursuing this book to publication and keeping the administration and technical aspects of the book in line. Thanks also to Ashleigh McKown for her careful and thoughtful editing contributions.

Lastly, a sincere thank-you to each of the friends, family, and colleagues who shared their work, time, opinions, insights, and often data, to form this book. We don't always agree on methodologies or conclusions, but move forward nonetheless. This book is a testament of your dedication to the academic pursuit of knowledge and your belief in conserving the world's equids. Thank you.

Journal of Arid Environments 138 (2017) 38–43

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

The impact of feral horses on pronghorn behavior at water sources

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ARTICLE INFO

Article history:
Received 11 May 2016
Received in revised form
23 September 2016
Accepted 29 November 2016
Available online 12 December 2016

Keywords:
Antilocapra americana
Equus caballus
Interference competition
Behavioral change
Vigilance behavior
Water source

ABSTRACT

Feral horses (*Equus callabus*) occur throughout the world on all continents except Antarctica. In North America, feral horses occupy 31.6 million acres throughout western North America. Throughout their range, feral horses often share habitat with American pronghorn (*Antilocapra americana*). Since horses are larger and more aggressive than pronghorn, they are considered socially dominant. In the Great Basin of western North America, pronghorn often access water sources where horses occur since habitat preferences are similar. If pronghorn are excluded where water is used by both species, pronghorn fitness may be impaired, especially during dry or droughty periods. The purpose of this study was to investigate interference competition between pronghorn and feral horses at water sources within the Great Basin. We observed horses and pronghorn at high-use water sources and recorded all occurrences and outcomes of pronghorn/horse interactions. We assessed differences in pronghorn behavior in the presence or absence of horses. Pronghorn invested more time on vigilance behavior and less time foraging or drinking in the presence of horses than in their absence. Nearly half of pronghorn/horse interactions resulted in pronghorn exclusion from water. We conclude that as feral horse numbers increase, competition for water will subsequently increase.

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1. Introduction

Feral (free-roaming) horses (*Equus caballus*) inhabit 18 countries across all continents except Antarctica (Beever et al., 2008). In semi-arid rangelands of western North America, feral horses may compete with pronghorn (*Antilocapra americana*) and other sympatric native species for limited water, food resources, and habitat (Meeker, 1979; Beever and Brussard, 2004; O'Gara and Yoakum, 2004; Beever and Herrick, 2006; Nevada Department of Wildlife, (2008); U.S. Fish and Wildlife Service, 2008; Davies et al., 2014; Zeigenfuss et al., 2014; Perry et al., 2015; Hall et al., 2016). According to Perry et al. (2015), aggressive interactions occur between horses and elk (*Cervus elaphus*) as water availability decreases. Several studies have examined forage overlap between horses and pronghorn to assess the potential for exploitative competition between these species (McInnis and Vavra, 1987; Meeker, 1979; Smith et al., 1998). However, little information is available regarding the potential for interference competition between feral horses and pronghorn.

Interference competition most often occurs when resources are not only limited but concentrated spatially. This resource concentration can create an aggregation of animals where direct contact between competing species is more common, increasing the likelihood of interference behavior (Valeix et al., 2008; Atwood et al., 2011). In arid and semi-arid ecosystems, water sources are ideal locations to investigate the influence of interference competition on mammal individuals or populations since they represent a scarce and concentrated resource (Valeix et al., 2008; Atwood et al., 2011).

Interference competition has been observed between individual feral horses at water (Stevens, 1988; Perry et al., 2015). In a study of interactions with desert bighorn sheep (*Ovis canadensis nelsoni*), domestic horses were experimentally placed near water sources which resulted in no direct aggression, however, the mere presence of horses resulted in a 76% decline in bighorn use of water holes at those locations (Ostermann-Kelm et al., 2008). Others have reported observing aggressive interactions in which horses chased pronghorn from water sources (Nevada Department of Wildlife,

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http://dx.doi.org/10.1016/j.jaridenv.2016.11.012
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(2008)). In contrast, while observing water sources within our same study area, Meeker (1979) concluded there was no evidence of negative interactions between horses and pronghorn and suggested that such interactions were positive with pronghorn possibly using horses as a predator avoidance tactic.

Feral horses have been found to be typically dominant in their social interactions with native Great Basin ungulates, due to their large size (typically 1.3–1.6 m tall at the shoulder and weighing 315–450 kg) and often aggressive behavior (Berger, 1985). Even solitary horses have been shown to displace groups of deer (*Odocoileus hemionus*), California bighorn sheep (*Ovis canadensis*), and pronghorn (Berger, 1985). Social dominance is key in interference competition, with subordinate species often displaced by larger, more aggressive competitors (Valeix et al., 2007). The expected response by the subordinate species would be a change in behaviors (Atwood et al., 2011). Interference competition can occur directly in interactions between species through aggression which results in flight response (Ping et al., 2011; Vahl et al., 2005). Interference competition can also occur indirectly through changes in activities when other species are present, such as avoidance or increased vigilance behaviors (Ping et al., 2011; Vahl et al., 2005; Valeix et al., 2008).

We evaluated direct and indirect interference competition between feral horses and pronghorn at water sources with the assumption that pronghorn would be the subordinate species. We assessed the behavioral responses of pronghorn during horse interactions by determining 1) changes in pronghorn foraging and vigilance behaviors in the presence of horses and 2) the outcomes of pronghorn-horse interactions.

2. Methods

2.1. Study area

The Sheldon National Wildlife Refuge (Refuge, SNWR), administered by the US Fish and Wildlife Service (FWS), is located in northwest Nevada. It stretches across 232,694 ha (575,000 acres) of high desert sagebrush-steppe habitat (41.867995, −119.015493). The SNWR ranged in elevation from 1280 to 2223 m with an annual precipitation of 15–33 cm, and 2011–2012 summer temperatures ranging from −0.6 °C to 39.4 °C. For the duration of this study, the SNWR supported large numbers of sympatric pronghorn and feral horses. Minimum population estimates of pronghorn and horses on the SNWR during this study were estimated at 1727 and 1,236, respectively (Collins, 2010). Water resources on the SNWR were scarce and typical of high-desert habitats, and the majority of available surface water was in the form of small, isolated springs and seeps. Prior to this study, nearly 80% of the Refuge's springs and 44% of stream reaches had been classified as receiving heavy to severe use by horses (U.S. Fish and Wildlife Service, 2008). All livestock grazing was eliminated from SNWR in the mid-1990s.

2.2. Behavior observations

We collected data on pronghorn behavioral responses during interactions with horses via field observation. We deployed 22 remote cameras at representative sites in summer 2011 to assess relative horse and pronghorn use; based upon that information we selected three field observation sites (site 138 [West Catnip], site 142 [WRB_142], and site 32 [Little Buckaroo]) in proximity to spring-fed riparian systems (Appendix A, Fig. 1). We chose these sites because they regularly maintained available surface water from spring through fall, and supported both high horse and pronghorn use. We made observations from June to September 2012. We randomly assigned observation order, observing sites in one-week intervals before relocating to the next site. We observed each site once within a three-week block before observing any site again, repeated four times for a total of 12 weeks of observations.

We made observations in teams of two observers from 0700 to 1900 h, with alternating 6 h morning or evening "half" days and 12 h "full" days to prevent observer fatigue. Observers were concealed within a camouflaged blind 150–300 m away from the riparian habitat. Binoculars and spotting scopes were used for observing animals. We documented animal behaviors within a 500 m radius of the riparian habitat, and any animals outside of this observation area were not counted in our scans. We defined riparian habitat as the area within 5 m of riparian vegetation or water (Ostermann-Kelm et al., 2008). All other areas were considered uplands habitat and outside the scope of this paper.

We divided pronghorn observations within riparian habitats into group visits, or "observation sessions." An observation session began when the first pronghorn of a group entered the riparian habitat, and ended when the last pronghorn left and none other entered for at least 1 min. Solitary pronghorn constituted a group of one. We defined a horse/pronghorn interaction as any time one species came close enough to the other that we could observe the outward signs of one reacting to the others' presence, while acknowledging that unseen responses may have occurred at even greater distances (the overt response distance) (Smith et al., 2012). Based on preliminary observations, we chose 120 m as the overt response distance.

We used a scan sampling method (Altmann, 1974) to record pronghorn behaviors. During each observation day, we scanned the area every 15 min, recording the time of day and all pronghorn and/or horses present. When pronghorn and/or horses were spotted we recorded their estimated distance from water, location, and group size. Additionally, we recorded each individual pronghorn's sex and estimated age (young [<1 year old] vs adult), distance from nearest horses (in meters), and behavior (defined below). Whenever pronghorn entered a riparian area, we began scan sampling every minute. However, whenever horses were within a distance that interactions could occur with pronghorn, we sampled every 30 s. We recorded all occurrences of aggression or alarm by either horses or pronghorn during interactions (Altmann, 1974). We considered animals to be in the same group if they were within 100 m of each other (Ostermann-Kelm et al., 2008). Since the majority of the pronghorn in our study were not uniquely marked, we made no attempt to identify individual animals, but groups were assigned temporary identification numbers as long as they were visible for recording purposes.

Based on preliminary observations recorded in 2011 we determined that horse and pronghorn interactions within riparian habitats often occurred too quickly for direct field observation, particularly when animals were in large groups. Subsequently, we recorded all observations of pronghorn within the riparian habitats via video recorder for later viewing and analysis, supplemented with a digital voice recorder as a backup in case of video failure. Videos were later analyzed using Noldus Observer XT® software.

2.3. Pronghorn behavior

We created a pronghorn ethogram (Appendix A), with mutually exclusive main primary behaviors (i.e. standing, walking, running, or bedding) and modifiers to further define those primary behaviors (e.g. standing/vigilant or standing/foraging). We then selected and analyzed two specific behavior modifiers: vigilance and foraging. Vigilance was defined as any time the pronghorn had its head above shoulder height while scanning the surroundings, and foraging was defined as any time an individual was consuming vegetation, drinking, or searching with their head below shoulder

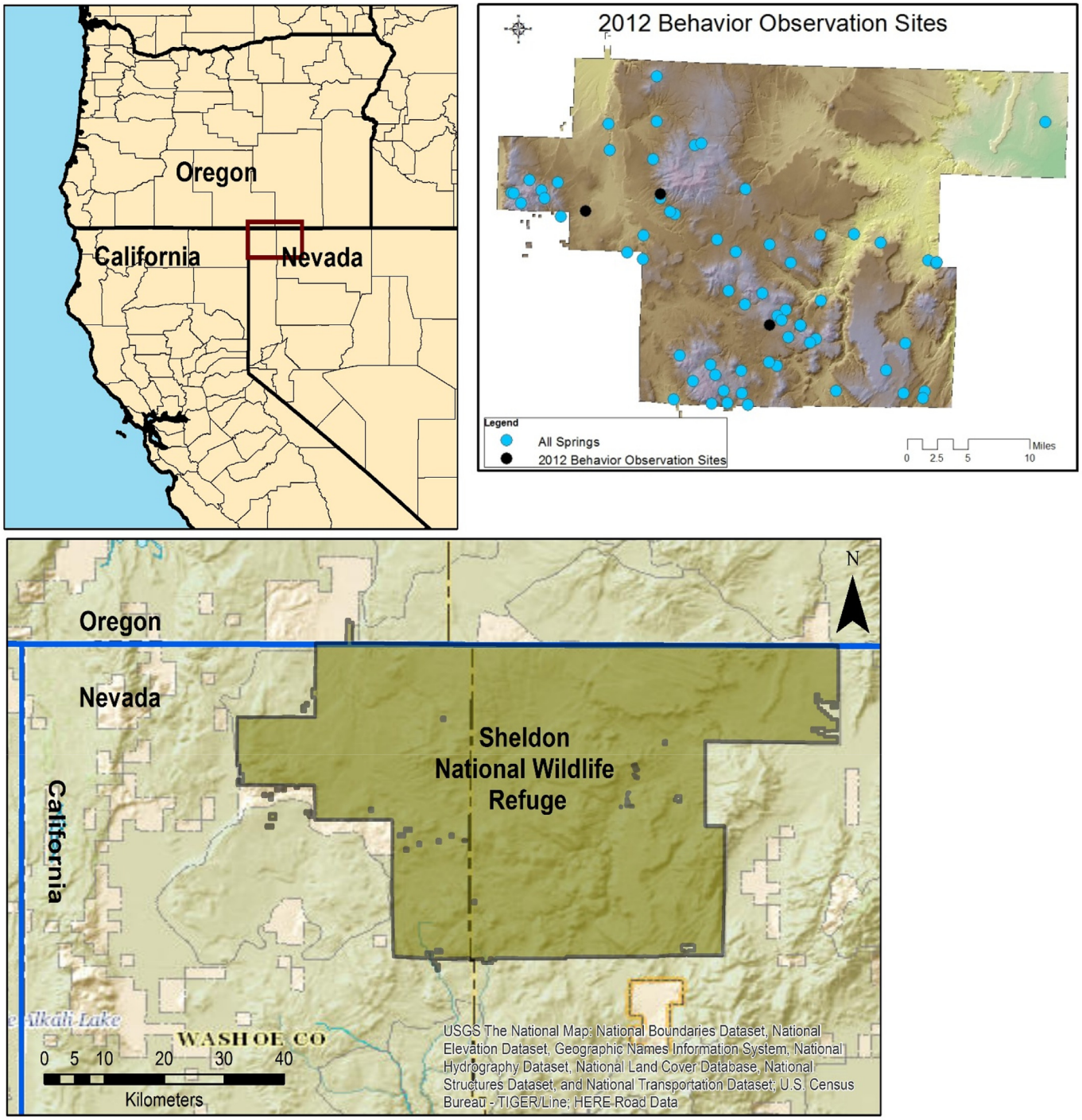


Fig. 1. Maps show the location of the Sheldon National Wildlife Refuge in northwest Nevada (top left and bottom). The 2012 behavioral observation sites were located throughout much of the Sheldon National Wildlife Refuge (top right).

height. (Gavin and Komers, 2006; Appendix A).

2.4. Outcomes of interactions

For each pronghorn-horse interaction, we recorded the date and time, which species initiated the interaction (horse or pronghorn), the type of approach (e.g. walking or running in, and walking directly towards or to the side of the animals already in the riparian); individual pronghorn age (young [<1 year old]) vs. adult), sex, and group size; individual horse age (young [<1 year old]) vs. adult), and group size; and the minimum distance between horses and pronghorn during the interaction measured in meters. We defined each interaction as neutral, negative, or positive. We categorized an interaction as neutral when pronghorn exhibited no outwardly detectable, costly negative reactions to the presence of horses (i.e. no detectable reaction, or minor reactions categorized as: raising their heads, moving a few meters but remaining in the riparian area, or leaving the riparian area but quickly returning). We categorized an interaction as negative when pronghorn left the riparian area as horses entered or immediately after, or when

pronghorn left some time after horses entered but in direct response to horse actions (e.g. aggression, activity, or approach). We also considered an interaction negative when the pronghorn stopped foraging and drinking due to horse activity, and did not resume foraging or drinking while there were horses present (Valeix et al., 2007). We categorized an interaction as positive if pronghorn waited outside the riparian area until horses entered first, and then entered the riparian area along with the horses.

Video and voice recordings were used to provide observations that are otherwise difficult to code on standardized data sheets during observations. Having both forms made it possible to accurately and efficiently collect and analyze data which is often too complex to capture on data sheets. These data were also used to validate the quality of data collected on datasheets.

2.5. Data analysis

We used logistic regression to explore the potential effects of site, pronghorn cohort, the presence of pronghorn young, pronghorn sex (adults), pronghorn group size, horse group size, time of day, distance to horses (from 0 to 120 m), and the presence of horses on pronghorn behavior. We selected 5 categories of pronghorn cohorts for analysis: 1) solitary adults, 2) groups of all adult females, 3) groups of adult females with young, 4) groups of all adult males, and 5) mixed sex/age groups (Ping et al., 2011). Additional variables included the presence of pronghorn young (yes, no), and sex (male, female, unknown). We selected 3 time categories: morning (0700–1059 h), day (1100–1459 h), and evening (1500–1900 h). We included a variable representing the presence of horses (yes, no) within the interaction distance (120 m) as well as the distance between pronghorn and the nearest group of horses (in meters).

We ran a model for each behavior of interest (vigilance and foraging). All variables were counted as fixed effects except site, which was a random effects model. We used backwards selection to eliminate the non-significant variables and identify the best model. We made no attempt to identify individuals, but since individuals were likely sampled multiple times over the course of each observation session, the data were blocked by observation session to correct for this lack of independence. We considered individual pronghorn observation sessions as a statistical unit. We performed these analyses using SAS statistical software. We considered a p-value <0.05 significant.

3. Results

Between June 25 and September 14, 2012, we collected a total of 492 observation hours, averaging 164 h per site ($n = 3$ sites). We recorded a total of 166 pronghorn observation sessions, 20% of which included interactions with horses accessing riparian areas ($n = 34$), and documented 12,186 instances of pronghorn behavior ($x = 4062$ instances per site; Table 1). We excluded individual observations in which pronghorn behaviors were influenced by observer presence, and we also excluded whole observation sessions which consisted mostly of observer-biased observations. Due to time constraints, we subsampled the data collected from the video and voice recorders from June 25–July 14 ($n = 102$ total observation hours; $x = 34$ observation hours per site; Table 2).

Table 1
Summary of observations for three sites within the Sheldon National Wildlife Refuge, Nevada. Information included the number of hours of observation, the number of hours analyzed and the total number of pronghorn observations.

Site				
	West Catnip	WRB_142	Little Buckaroo	Total
Hours of Observation	162	162	168	492
Hours Analyzed	42	24	36	102
Pronghorn Observations	8940	1566	1680	12,186

3.1. Behavior analysis

Distance to horses and horse presence were determined to be highly correlated variables, therefore only the significant variable (distance to horses) was included. Neither site nor horse group size were found to be significant variables, and thus, were also not included in the model. The best model for vigilance included the variables pronghorn sex (F-value = 51.52, $p < 0.0001$), with young being vigilant less of the time than adult males ($p < 0.0001$) or adult females ($p < 0.0001$); time of day (F-value = 51.09, $p < 0.0001$), with pronghorn being vigilant more often in the morning than in the day ($p < 0.0001$) or afternoon ($p < 0.0001$); distance from horses (F-value = 13.49, $p = 0.0002$), with the probability of pronghorn vigilance decreasing 0.3% for each 1 m increase in distance from horses; pronghorn cohort (F-value = 6.52, $p < 0.0001$), with groups of adult females with young being less vigilant than groups of adult females without young ($p = 0.0469$, groups of adult males ($p = 0.0031$), mixed sex/age groups ($p = 0.0041$), or solitary adult pronghorn ($p = 0.0016$); and horse group size (F-value = 5.51, $p = 0.0189$), meaning that for each additional horse, there was a 2.3% increase in the probability of pronghorn vigilance.

Distance from horses was the most important variable influencing foraging behaviors. The influence of horse group size was not significant, and it was not included in the model (Table 3). Distance to horses and horse presence/absence were highly correlated variables. Both were initially included in each model, but the less significant variable of the two was removed. This was consistently the “horse presence” variable. The best model for foraging included the variables distance from horses (F-value = 67.28, $p < 0.0001$), with the probability of foraging increasing 0.6% for each 1 m increase in distance from horses; time of day (F-value = 17.05, $p > 0.0001$), with pronghorn in the day foraging less often than pronghorn in the morning ($p < 0.0001$); pronghorn sex (F-value = 6.55, $p = 0.0002$), with adult females spending more time foraging than either adult males ($p = 0.0087$) or young ($p = 0.0187$); and pronghorn cohort (F-value = 2.49, $p = 0.0412$), with groups of adult females with young foraging less than mixed sex/age groups ($p = 0.0493$).

3.2. Outcomes of interactions

During recorded interactions ($n = 34$) between pronghorn and horses, pronghorn individuals within groups responded in a consistent manner 88% of the time. Thus, we summarized pronghorn responses based on group response. In those instances, where all individuals did not respond similarly, we used the response of the majority of pronghorn in the group as the group response. Of the pronghorn/horse interactions we recorded, 41% ($n = 14$) were negative, 3% were positive ($n = 1$), and 47% ($n = 16$) were neutral. Three additional interactions were classified as “unknown,” due to other factors (e.g. coyotes) where we could not confidently attribute pronghorn responses to the presence of horses. All negative interactions were classified as costly as they resulted in the pronghorn being prevented from drinking ($n = 1$) or leaving the riparian area entirely which prevented them from drinking ($n = 13$).

Horses initiated 47% of interactions ($n = 16$) and pronghorn initiated 53% ($n = 18$). Of the horse-initiated interactions, 75% ($n = 12$) were negative, 19% ($n = 3$) were neutral, and 6% ($n = 1$)

Table 2
Significant results from the differences of least squares means from all variables included in the foraging and vigilance behavior models. Adjustment for multiple comparisons: Tukey-Kramer.

Foraging						
Variable Type	Variable 1	Variable 2	Estimate	SE	t-value	Adj p-value
Cohort	Female with Young	Mixed	−0.1243	0.04548	−2.73	0.0493
Time of Day	Afternoon	Day	0.1957	0.08395	2.33	0.0517
Time of Day	Day	Morning	−0.231	0.03962	−5.83	<0.0001
Pronghorn Age/Sex	Adult	Male	0.2921	0.09225	3.17	0.0084
Pronghorn Age/Sex	Adult	Young	0.2425	0.08715	2.78	0.0277
Pronghorn Age/Sex	Female	Male	0.1705	0.05402	3.16	0.0087
Pronghorn Age/Sex	Female	Young	0.121	0.0415	2.91	0.0187
Vigilance						
Variable Type	Variable 1	Variable 2	Estimate	SE	t-value	Adj p-value
Cohort	All Female	Female with Young	0.204	0.07416	2.75	0.0469
Cohort	All Male	Female with Young	0.4591	0.128	3.59	0.0031
Cohort	Female with Young	Mixed	−0.1574	0.04485	−3.51	0.0041
Cohort	Female with Young	Solitary	−0.2588	0.06887	−3.76	0.0016
Time of Day	Afternoon	Morning	−0.4194	0.08417	−4.98	<0.0001
Time of Day	Day	Morning	−0.362	0.03942	−9.18	<0.0001
Pronghorn Age/Sex	Adult	Female	−0.4601	0.09292	−4.95	<0.0001
Pronghorn Age/Sex	Adult	Male	−0.5474	0.09813	−5.58	<0.0001
Pronghorn Age/Sex	Female	Young	0.4399	0.04158	10.58	<0.0001
Pronghorn Age/Sex	Male	Young	0.5272	0.05379	9.8	<0.0001

Table 3
Effect of distance to horses and horse group size on pronghorn vigilance and foraging behavior.

Foraging				
	Estimate	Standard error	t-value	p-value
Distance to horses	0.0063	0.0008	8.2	<0.0001
Vigilance				
	Estimate	Standard error	t-value	p-value
Distance to horses	−0.003	0.0007	−3.67	0.0002
Horse Group Size	0.0225	0.0096	2.35	0.0189

were positive. An initiation was defined as the species making the approach was the initiator (e.g. if horses were already in the riparian area, and pronghorn approached the horses, then pronghorn were the initiators. Of the pronghorn-initiated interactions, 11% ($n = 2$) were negative, 72% ($n = 13$) were neutral, 17% ($n = 3$) were unknown, and none were positive. We also documented 6 instances of horse aggression during which pronghorn were present. In 50% of the instances ($n = 3$), horses were directly aggressive towards pronghorn, and resulted in a negative outcome (e.g., horses chased pronghorn from the area). For the remaining instances ($n = 3$), the horses were aggressive towards other targets such as other horses or coyotes. In two of those instances, the outcome of the aggression, although not directed at the pronghorn, was still negative for the pronghorn present. The third instance was neutral where the individual pronghorn initially fled the area following horse aggression, but then returned.

4. Discussion

Our work supports the findings of others (e.g. Berger, 1985; Meeker, 1979) that direct aggression is rare, however feral horses were found to be affecting pronghorn vigilance and foraging behaviors at water sources through interference competition. This is in contrast to conclusions by Meeker (1979), however, both the feral horse and pronghorn populations occupying the Refuge during the mid-1970s were substantially smaller, averaging less than half (42%, $x = 521$ horses) and less than a third (29%, $x = 502$ pronghorn) of recent population estimates, respectively (G. Collins, unpublished data). It is reasonable to expect that increases in numbers and density of both species would result in increases in competition for scarce resources. As such, we observed increased vigilance and decreased foraging behaviors by pronghorn in the presence of feral horses. Further, nearly half of the pronghorn/horse interactions we observed were negative and resulted in pronghorn being excluded from the water source as a result of horse activity.

Directly measuring the consequences of these interactions on pronghorn water consumption and fitness was outside the scope of this study, therefore we cannot ascribe significance to these negative interactions. However, since about 40% of interactions resulted in pronghorn exclusion from water, these pronghorn/horse interactions are likely associated with some costs of fleeing (the cost of leaving the water source prematurely and the energy expended on departure; Frid and Dill, 2002) for pronghorn. Increased vigilance behaviors in the presence of horses represented opportunity costs, as seen by the decrease in time spent foraging and drinking, and may result in decreased consumption of water and forage (Frid and Dill, 2002; Wakefield and Attum, 2006). These effects could have detrimental impacts on pronghorn fitness and population dynamics, particularly under adverse conditions when surface water availability is limited and monopolized by horses.

Previous observations of horse and pronghorn interactions have suggested that interference competition at water in North America was unlikely (Meeker, 1979; Berger, 1985). However, our study supports findings by others that interference competition may occur between feral horses and native wildlife (Ostermann-Kelm et al., 2008). Hall et al. (2016) found that water sources experienced lower wildlife richness and diversity when associated with horse use. They suggest that horses have a competitive advantage over smaller wildlife species. Subsequently, native wildlife species visited water sources less frequently reducing the ability of wildlife to access limited water on arid environments. Horses have also been shown to displace even larger bodied animals such as elk in areas with water limitations (Perry et al., 2015). These data suggest that aggressive interactions by horses will increase as water becomes more limited. Competition has the potential to reduce the fitness of pronghorn and other native wildlife populations in areas with limited resources which are also impacted by high concentrations of feral horses. These impacts should be carefully considered when making management decisions.

Acknowledgments

We appreciate the Sheldon National Wildlife Refuge for lodging, transportation, and staff support. We appreciate the Sheldon NWR, Brigham Young University, and the Nevada Department of Wildlife (Michael Cox) for providing research funding. We appreciate Dr. Randy Larsen from Brigham Young University for his statistical consultation and assistance. We also appreciate the many technicians and volunteers who helped with data collection and lab analysis. We thank Brian Day, manager of the Sheldon NWR, for assistance with logistics and housing. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Pronghorn Ethogram

We composed a pronghorn ethogram, separating behaviors into main primary behaviors and secondary modifiers. Primary behaviors described the activity state of a pronghorn: standing, walking, running, or bedding. Secondary modifiers further defined the primary behaviors, and were defined as follows:

- Vigilance was defined as “any time the pronghorn had its head above shoulder height while scanning the surroundings” (Childress and Lung, 2003).
- Foraging was defined as: “Any time an individual [was] consuming vegetation or searching with their head *below* shoulder height.” (Lipetz and Bekoff, 1982). Whether the animal was consuming forage or drinking could not always be distinguished, so these two behaviors were combined.
- Linked urination-defecation was defined as a sequence of behaviors used by territorial bucks, with the sequence proceeding as follows: (1) Sniff and paw the ground, (2) Stretch and urinate in the scrape, and (3) Squat and defecate (Kitchen, 1974).
- Marking/thrashing was defined as when a “male rubs its cheek scent gland on vegetation or thrashes vegetation with its horns” (Maher, 1991).
- Travelling was defined as “walking, trotting, or running with head at shoulder level” (Childress and Lung, 2003).s
- Chasing/following was defined as a dominance-oriented social interaction in which the dominant animal drives (at a walk) or chases (at a lope or run) the subordinate animal (Kitchen, 1974).
- Forcing up was defined as “A dominant pronghorn … forcing up a bedded subordinate by approaching, lowering its head, and sniffing and/or butting the reclining individual” (Kitchen, 1974).
- Sparring was defined as any interaction between pronghorn individuals that involved touching horns, ranging from brief horn contact to actual fights.
- Herding was defined as males, positioned to the rear of females, with lowered heads walking towards the females, and/or blocking the flight path of the females in a broadside threat position (Kitchen, 1974).
- Courting was defined as the any of the progressive behaviors in the courtship sequence, which involves rump sniffing, chest touching, attempted mounting, and mounting (Kitchen, 1974)
- Other social behavior
- Other behavior.

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Equine vet. J. (1988) **20** (3), 189-193

External balance of water and electrolytes in the horse

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Summary

The components of the daily external water and electrolyte balances of five normal Standardbred geldings with a mean body weight of 427 kg, were determined over 14 day periods. The mean value of daily total water intake (a summation of free, combined and metabolic water intake) for the group was 27.6 litres, that is, 64.4 ml/kg body weight, while mean values for ambient temperature and humidity ranged from 16 to 25°C and 55.4 to 75.5 per cent, respectively. The mean daily urine volume of 9.9 litres (23.2 ml/kg) for the group, was found to exceed the mean faecal water output of 7.2 litres (16.9 ml/kg). The mean output of sodium for the five animals, in urine and faeces, was 780 mmol or 79 per cent of the intake. The mean output of potassium, chloride, calcium and magnesium were 3163, 2521, 1824 and 1448 mmol or 95, 84, 74 and 75 per cent, respectively of intake. The sodium and potassium not accounted for in urine and faeces may well have been lost in sweat. Results are discussed and compared with those of a previous external balance study in the horse.

Introduction

A KNOWLEDGE of the components of the daily intake and output of water and electrolytes particularly sodium, potassium and chloride, in the resting horse provide a basis for formulating dietary requirements in the normal animal and for establishing the fluids needed for replacement and daily maintenance in clinical disturbances of body fluids. Although there has long been a general appreciation of the daily free (drinking) water requirements of the horse (Hinton 1978), the only previously reported study of external water, sodium and potassium balances was that of Tasker (1967). Using four horses each for two, 7 day periods, Tasker (1967) observed a mean daily free water intake of 23.6 litres (53.8 ml/kg body weight) and a combined water intake of 1.1 litres. In addition, the estimated mean value for water of metabolism was 2.7 litres, giving a mean total daily water intake of 27.4 litres (62.4 ml/kg body weight). The mean values for daily water output via urine, faeces and estimated evaporative loss, respectively, were 4.9, 14.0 and 8.5 litres. Tasker (1967) also found mean daily sodium intake and output to be 329 and 123 mmol, respectively, with the mean daily potassium intake and output being 3930 and 3189 mmol. The mean daily urine output of sodium and potassium were 7 and 2196 mmol, respectively, and faecal output 116 and 993 mmol. The ambient temperature during the latter study ranged between 5 and 12°C.

As a basis for further studies in a warm temperate climate and to supplement the work of Tasker (1967), measurements of the components of daily water and electrolyte balances were made in the normal horse at rest. Also, because evaporative loss (respiratory and cutaneous water loss) form a large component of total daily water output, the values obtained were correlated with the environmental temperature and humidity.

Materials and methods

Animals and management

Five adult, gelded Standardbred pacers with mean body weights ranging from 408 to 462 kg were used. Temperamentally, this breed is well-suited to wear the harness employed in the collection of urine and to accept confinement in a metabolism stall without stress. Studies were undertaken intermittently, as suitable horses became available, over a period of 22 months. Each horse was subjected to an initial physical examination to evaluate the blood (haematology, renal and hepatic function) and urine and faecal samples to ensure that it was in good health and free of intestinal parasites. External balance studies of 14 days duration were conducted on three occasions in one horse **(Horse A)** and on one occasion in each of the other four horses **(Horses B to E).**

The metabolism stall was similar to that used by Tasker (1966) It was located indoors in a well ventilated area with ample room to move around the stalled animal. Horses were given a period of at least 10 days in the metabolism stall, with full collection harness attached, before external balance measurements were begun. The animals were tied short for limited movement other than that required for easy access to feed and water. The horses were removed from the stall once daily, weighed (to nearest 1.0 kg) and hand walked for a brief period.

Each horse was fed a weighed amount of good quality lucerne chaff twice daily and residues present prior to the next feeding were weighed. Some spillage of feed occurred, but a catchment area was designed to reclaim this so that the total daily feed intake was accurately recorded to within 50 g. Deionised drinking water was offered so that its electrolyte content did not have to be measured. Fresh water was provided twice daily, at which time residual volumes from the previous watering were measured. Daily free water intake was determined to within 50 ml.

Collection and storage of samples

The urine collection harness was modelled on that employed by Tasker (1966). Each horse was harnessed with a breastplate, girth and crupper while stalled; the harness for urine collection was suspended from both girth and crupper, so that the collec-

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tion bag covered the preputial area of the ventral abdomen. All horses accepted this harness and in all experiments urine was collected without loss. When voided, the urine drained quickly from the collection bag, via pliable plastic tubing, to a large plastic container positioned at the side of the stall. Daily urine volumes were measured (to nearest 10 ml) and aliquots of daily output, for subsequent electrolyte determinations, were diluted 1:50 with electrolyte free water and stored at –1°C.

Faeces were collected twice daily from a faecal collection bin fitted at the rear of the stall, weighed (to nearest 10 g) and representative samples collected for subsequent analyses. Dry matter was determined by drying milled samples, to constant weight, in an oven at 100 ± 2°C. Aliquots of dried samples were stored, pending analyses for electrolyte content. A representative sample of chaff was obtained from each bag and its water content determined using the same method as for faecal water content. Aliquots of dried chaff were also stored pending analyses for electrolyte content.

Venous blood samples were collected at three day intervals during each 14 day external balance period. They were immediately centrifuged and plasma was refrigerated pending analyses for electrolyte concentrations.

Analytical methods

The determination of sodium and potassium concentrations in feed, faeces and urine were measured by flame photometry (Model 100; Evans Electraselenium Ltd, Halstead, Essex) as described by English and Becvar (1971). Chloride concentrations in feed and faeces were determined by techniques of alkaline digestion, protein precipitation and perborate oxidation (Cotlove 1964), with modifications described by English and Becvar (1971). The urine concentrations of chloride were measured using an EEL chloride meter, (Model 92; Evans Electroselenium Ltd, Halstead, Essex). To determine calcium and magnesium concentrations in feed and faeces, those samples subjected to acid digestion for sodium and potassium analysis were examined (Willis 1960 a & b) by atomic absorption spectroscopy (Series AA6; Techtron, Melbourne, Australia). Calcium and magnesium concentrations in urine were measured by the same methods after the sediment had been dissolved by acidification with acetic acid.

Plasma concentratons of sodium, potassium and chloride were also measured using techniques previously described (English, Hardy and Holmes 1969) and those of calcium and magnesium by atomic absorption spectroscopy (Willis 1960 a & b).

Other procedures

In determining the volume of water in feed (combined water) and the amount of water of metabolism available to the animal from daily feed intake, methods described previously (English 1966) were used. Also in deriving values for evaporative water loss, it was assumed that the insensible water loss (Benedict and Root 1926; Leitch and Thompson 1944) and the evaporative water loss would be equal, as the respiratory quotients in the normal animals studied would have approached 1 (Dale 1977). The values for daily mean maximum and minimum temperatures and relative humidities at 09.00 h and 15.00 h were made available by the Queensland Bureau of Meteorology for the seven, 14 day periods of the study.

Results

To gain an appreciation of the within animal variation in mean values for the components of the daily external water balance, these values were determined in one horse **(Horse A)** for three, separate 14 day periods extending over eight weeks (Table 1); mean daily body weights for each of these three periods are also presented as are values for dry matter intake and output, and for environmental temperature and humidity, as they relate to water requirements.

The mean values for the components of daily external water balance measured in each of four additional horses (**B** to **E**) for 14 days to obtain information with respect to between animal variations are presented in Table 2. The components of the external water balance for the first of the three periods in **Horse A** are included so that mean values ± se for the group of five horses could be determined. Much of the within and between animal variation present could have been accounted for by the seasonal variations in temperature and humidity.

The mean values for environmental temperature and relative humidity for each of the five, 14 day external water balance periods (Table 2), were derived from the daily maximum and minimum temperatures and the relative humidity readings at 09.00 h and 15.00 h, after it was found that they were similar to those derived from hourly temperature and relative humidity readings. No free sweating was observed throughout the study.

To provide a guide for the estimation of maintenance needs in fluid therapy in the horse under similar environmental conditions, the mean values determined for the components of daily external water balance (Table 2) have been converted to ml/kg body weight. The mean value for the components of the total daily water intake for the five horses was 64 ml/kg, composed of the mean values of 55.0, 2.6 and 6.8 ml/kg for free, combined and metabolic water, respectively. Mean values for the components of total water output in urine, faeces and evaporation were 23.2, 16.9 and 23.4 ml/kg, respectively. From Table 2, it can also be determined that the mean daily free water intake of the individual animal ranged from 46 to 71 ml/kg body

TABLE 1. Mean values (±sd) for the components of daily external water balance, dry matter turnover, and the environmental temperature and relative humidity determined in three separate 14 day periods in Horse A

Period	Body-weight	Water Intake (1) Free	Combined	Metabolic	Total	Water Output (1) Urine	Faeces	Evapor. Loss*	Total†	Mean Daily DM (kg) Intake (feed)	Output (faeces)	Temp. (C°)	Relative humidity (%)
1	437 (4.7)	26.0 (5.97)	1.6 (0.33)	3.0 (0.60)	30.6 (6.53)	13.9 (1.72)	5.1 (1.61)	11.8 (8.14)	30.2 (6.73)	7.9 (1.60)	2.0 (0.75	19.0 (4.20)	55.4 (14.29)
2	446 (7.0)	33.2 (8.35)	1.7 (0.22)	2.9 (0.28)	37.8 (8.45)	14.6 (2.03)	5.5 (1.08)	17.9 (9.75)	37.1 (8.85)	7.9 (0.94)	2.4 (0.47)	18.5 (5.39)	56.2 (17.18)
3	441 (3.9)	29.5 (10.94)	1.3 (0.21)	2.7 (0.43)	33.0 (10.46)	11.9 (2.36)	4.8 (1.88)	16.4 (13.47)	32.9 (12.02)	7.2 (1.16)	2.3 (0.64)	20.5 (4.74)	53.5 (13.89)

*Daily evaporative loss, determined by subtracting the sum of the daily urine and faecal water output from the estimated total daily water output; †Daily change in body weight used in combination with urine and faecal output, to estimate total water output

TABLE 2. Mean values (±sd) for the components of daily external water balance, dry matter turnover, and the environmental temperature and humidity determined in each of the five horses over a period of 14 days

Horse	Body-weight	Water Intake (1) Free	Com-bined	Meta-bollic	Total	Water Output (1) Urine	Faeces	Evapor. Loss*	Total†	Mean Daily DM (kg) Intake (feed)	Output (faeces)	Temp. (C°)	Relative humidity (%)
A	435.0 (4.7)	26.0 (5.97)	1.6 (0.33)	3.0 (0.60)	30.6 (6.53)	13.9 (1.72)	5.1 (1.61)	11.8 (8.14)	30.2 (6.73)	7.9 (1.60)	2.0 (0.75)	19.0 (4.20)	55.4 (14.29)
B	462 (6.1)	24.1 (3.82)	0.7 (0.29)	3.1 (0.22)	27.6 (3.75)	11.3 (0.81)	7.0 (0.96)	9.3 (7.30)	27.7 (6.58)	8.2 (0.59)	2.4 (0.54)	22.1 (3.65)	60.5 (18.51)
C	409 (4.8)	28.9 (7.84)	1.6 (0.30)	3.5 (0.63)	33.9 (8.35)	10.0 (1.19)	10.3 (2.07)	13.7 (7.14)	34.1 (6.70)	9.2 (1.85)	4.0 (0.96)	25.0 (3.73)	75.5 (11.37)
D	422 (7.3)	19.9 (6.41)	1.1 (0.26)	2.5 (0.54)	23.6 (6.49)	6.8 (1.71)	6.4 (2.43)	8.5 (9.95)	21.7 (9.15)	6.8 (1.44)	2.6 (0.86)	18.8 (4.10)	73.5 (13.90)
E	408 (4.0)	18.8 (5.79)	0.7 (0.26)	2.6 (0.49)	22.1 (5.92)	7.7 (0.74)	7.0 (1.26)	6.8 (9.45)	21.7 (8.99)	7.0 (1.32)	3.0 (0.51)	16.3 (4.93)	64.1 (15.42)
M±se	427 (22.23)	23.5 (4.2)	1.1 (0.45)	2.9 (0.40)	27.6 (0.87)	9.9 (2.85)	7.2 (1.92)	10.0 (2.73)	27.1 (5.42)	7.8 (0.97)	2.8 (0.76)	20.2 (3.36)	65.8 (8.55)

***Mean evaporative loss determined by subtracting mean daily water output in urine and faeces from estimnated total daily water output; †Daily change in body weight used in combination with urine and faecal output, to estimate total water output**

weight (**Horses E and C**), with the mean total daily water intake ranging from 54 to 83 ml/kg (**Horses E and C**). The mean components of water output in urine ranged from 16 to 32 ml/kg (**Horses C and A**), in faeces from 12 to 25 ml/kg (**Horse A and C**), and in evaporative loss from 17 to 33 ml/kg (**Horses E and C**).

In obtaining the mean values for the components of daily external balances of sodium, potassium and chloride (Table 3), one of the three 14 day periods for **Horse A** was again included. Some, but not all, of the between animal variation in these electrolytes would have been accounted for by seasonal variations in environmental temperature and humidity (Table 2).

The mean output of sodium in urine and faeces for the five horses (Table 3) was approximately 79 per cent of its mean intake; whereas these values for potassium and chloride, respectively, were 95 and 84 per cent. In mmol/kg body weight, mean values for intake of sodium and potassium were 2.3 and 7.7 and those for output were 1.8 and 7.4. Loss of most of the sodium and potassium not accounted for in the urine and faeces could have occurred via insensible sweat loss.

As external balances of calcium and magnesium are not as important in fluid therapy as are those of the principle cations sodium and potassium and of the anion chloride, their overall mean daily values are presented rather than the tabulation of mean values for individual animals. The overall mean daily external balance values for the five horses showed that calcium and magnesium intake were 2466 ± 358.3 and 1939 ± 397.6 mnol, respectively, and their output was 1824 ± 549.9 and 1448 ± 730.0 mmol. Some of the output not accounted for may have been present in the form of insoluble salts in the urine or faeces, particularly in the latter. The mean daily intake of calcium and magnesium, in mmol/kg body weight, would have been 5.7 and 4.5, respectively, with their loss in urine and faeces being 74 and 75 per cent of total intake.

The pooled mean values for plasma electrolyte concentrations in mmol/l, observed during the study, were sodium 135.2 ± 3.26, potassium 3.8 ± 0.29, chloride 100.0 ± 1.88, calcium 3.1 ± 0.15 and magnesium 0.8 ± 0.05.

Discussion

For the three separate 14 day periods in **Horse A** (Table 1), the variations in the components of external water balance were small. The constant dietary regime and low levels of mus-

TABLE 3. Mean values (±sd) for the components of daily external sodium (Na), potassium (K) and chloride (Cl) balances in each of the horses over periods of 14 days

Horse	Body (kg)	Na Intake (mmol)	Na Output (mmol) Urine	Faeces	Total	K Intake (mmol)	K Output (mmol) Urine	Faeces	Total	Cl Intake (mmol)	Cl Output (mmol) Urine	Faeces	Total
A	446 (7.0)	225 (71.4)	168 (94.7)	15 (4.3)	183 (95.8)	2267 (293.7)	2236 (429.0)	443 (96.3)	2679 (423.8)	4451 (700.0)	3060 (492.3)	235 (88.7)	3296 (453.2)
B	462 (6.1)	1257 (259.8)	783 (225.5)	351 (134.2)	1141 (267.5)	3696 (294.1)	3009 (386.0)	639 (110.1)	3612 (364.4)	3233 (352.4)	3074 (356.6)	169 (38.3)	3243 (356.7)
C	409 (4.8)	1225 (367.3)	636 (344.4)	426 (191.1)	1061 (452.4)	3795 (822.4)	3021 (612.1)	531 (176.7)	3566 (769.6)	2561 (655.9)	2012 (394.6)	198 (54.5)	2210 (411.6)
D	422 (7.5)	1076 (227.6)	380 (139.4)	231 (84.8)	611 (153.5)	3509 (739.2)	2448 (644.2)	419 (136.7)	2882 (724.2)	2453 (516.7)	1676 (501.7)	95 (28.1)	1771 (521.4)
E	408 (4.0)	1117 (328.7)	667 (197.5)	243 (64.8)	903 (219.6)	3334 (627.0)	2590 (462.8)	488 (77.5)	3078 (483.4)	2344 (440.8)	1912 (294.0)	174 (42.5)	2087 (328.2)
M±se	429 (23.8)	986 (415.4)	527 (248.8)	253 (155.5)	780 (390.3)	3320 (614.8)	2661 (347.0)	504 (86.8)	3163 (413.7)	3008 (877.7)	2347 (688.7)	174 (51.4)	2521 (701.7)

cular activity would have contributed to this, as would the small variations in mean temperature and mean relative humidity between periods. However, a direct relationship was observed between increases in free water intake and estimated evaporative loss. This suggested that the diurnal variations in ambient temperature and humidity, during the second and third trials, may have been sufficient to raise the evaporative loss and increase free water intake for short periods, on a number of days, without obvious sweating. The ratios of mean daily urine/faecal water output for each of these three periods were 2.7, 2.7, and 2.6, respectively. These values were higher than those observed in the other four horses.

The between horse variations in the components of external water balances observed in the five animals (Table 2), understandably, were greater than those within the individual animal (Table 1). Again, a direct relationship was found between values for mean free water intake and those for estimated evaporative loss in each of the animals, as well as for the group. In turn, values for evaporative loss can be seen to have been smallest when the mean environmental temperatures were lowest and, importantly, when mean relative humidities were also low. This would be so because, regardless of its humidity when inspired, all air is saturated when expired. The ratio of the urine/faecal water loss (Table 2) varied between animals from 0.97 in **Horse C** to 2.7 in **Horse A** with a mean ratio for the group of 1.4.

Under the conditions of the study, the mean values for daily water output in urine were equal to those for the evaporative loss. However, should these horses have been subjected to markedly high ambient temperatures and/or work, there would have been a sharp rise in evaporative water loss (Hinton 1978). Thus, particularly in warm temperate or tropical climates, evaporative loss could be responsible for much more than half the total daily water output. The greatest part of the 10.7 per cent reduction in body weight observed in horses deprived of water in high environmental temperatures (Carlson, Rumbaugh and Harrold 1979) would have been due to evaporative loss. The changes in the body weights of the five experimental horses (Tables 1 and 2) during the 14 day periods of the present experiments were small, as the standard deviations in body weight of 1 to 1.5 per cent in individual animals indicates. As food intake in all horses was consistent throughout the experiments, the mass of gut contents found to be 10 to 12 per cent of total body weight in the normal horse (Robb *et al* 1972; Webb and Weaver 1979), was unlikely to have altered sufficiently to have been responsible for these small weight variations.

In prescribing body fluid therapy in the horse, veterinary clincicians (Waterman 1977; Rose 1981) have used the value of 54 ml/kg body weight, being the free water intake determined by Tasker (1967), to establish daily maintenance requirements, although the mean total daily water requirements of the horse were found by the latter to be 62 ml/kg. It was anticipated that under the conditions of the present experiments (mean ambient temperature 16 to 25°C), total daily water losses, and consequently requirements, would have been much greater. This was found not to be the case, the mean total daily intake being 64 ml/kg, with a range over the five horses (Table 2) of 54 to 83 ml/kg body weight. However, in estimating the daily water requirements in the horse, as in other homeothermic animals, it should be borne in mind that there is a direct relationship between normal water turnover and metabolic weight. The latter was shown (Kleiber 1947) to be body weight in kg $^{0.75}$. Thus, under similar environmental conditions, large horses would normally require less water per kg body weight and ponies more.

The mean daily faecal water losses in the present study (Table 2) were invariably lower than the mean urine water losses. In the study conducted by Tasker (1967), the reverse was the case, with mean faecal water output being 2.5 times that of mean urine volume. As a result, the assumption in veterinary literature that faecal water loss invariably exceeds urinary loss (Waterman 1977; Carlson 1979) in the normal animal, may need revision. There would appear to be a wide variation in faecal water content in the normal horse, dependent on ration composition and individual animal variation.

Different lots of lucerne chaff have been shown to vary considerably in their sodium, and potassium and chloride concentrations (English and Becvar 1971) and such would have been the case in the present study. The mean sodium and potassium intakes of 2.3 and 7.7 mmol/kg per day, respectively, would have been well in excess of those of 0.2 and 0.4 mmol probably necessary for maintenance. The mean sodium output in faeces and urine was 79 per cent of the intake, a value significantly higher than the 35 to 40 per cent determined by Tasker (1967) in the resting horse. It is possible that a large part of the 21 per cent unaccounted for in the present study would have been lost in the sweat (Kerr and Snow 1982), despite the fact that sweating was never obvious in these animals.

The mean daily potassium intake of 3,320 mmol, in the present study, as well as being greatly in excess of maintenance requirements, is largely absorbed from the intestines and excreted via the urine. The mean urine/faecal output ratio for potassium of 5.3 was much higher than the ratio of 2.21 calculated from the components of potassium output observed by Tasker (1967). External balances of chloride have not previously been reported in the horse and the mean output in urine in this study was over 13 times that lost via the faeces. Of the 16 per cent of chloride not accounted for in the mean external balance values presented, it is likely that most could have been excreted with sodium in sweat.

The mean daily calcium intake of 5.7 mmol/kg body weight, in the present study, was well in excess of the daily requirements of 1.25 mmol/kg (Schryver, Craig and Hintz 1970). Loss of calcium via faces and urine were only 74 per cent of the total intake, most (92 per cent) of this loss occurring via the urine. The 26 per cent of the calcium output not accounted for in the external balances may have resulted from the presence of some insoluble calcium salts in the faeces, as well as a small amount of calcium not accounted for in the sweat. The mean daily intake of magnesium of 4.5 mmol/kg body weight was also clearly in excess of the minimum requirement of 0.58 mmol/kg for maintenance in the horse (Hintz and Schryver 1972). Losses determined via faecal and urinary routes were similar but the 25 per cent of output not accounted for in faeces and urine would have been much greater than could have been lost via the skin.

Acknowledgements

The project was funded by the Queensland Equine Research Foundation and the authors were most grateful for this support. They also wish to thank the Queensland Bureau of Meterology for making available the climatic data used.

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Received for publication 4.11.86
Accepted 11.5.87

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Journal of Arid Environments 127 (2016) 100–105

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment

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ARTICLE INFO

Article history:
Received 3 November 2014
Received in revised form
9 November 2015
Accepted 17 November 2015
Available online 30 November 2015

Keywords:
Communities
Equus caballus
Exotic species
Horse
Semi-arid
Water source

ABSTRACT

Introduced species can impact native communities by altering competition dynamics. Large exotic species, such as the horse (*Equus caballus*), may have a competitive advantage over smaller native species and could exclude them from access to limited resources. Our objective was to determine the influence of the exotic horse on the use of water by native species in a semi-arid environment where availability of water is limited. From July 2010 to August 2011, we used remote cameras to monitor water sources in the Great Basin Desert where horses had drinking access and where horses were excluded (with fencing) to compare 1) composition of native communities and 2) water usage by native species. We captured 96,601 images representing 40 species of birds (29,396 images) and 13 species of mammals (67,205 images). Of the 67,205 images of mammals, 79% contained horses. Horses were associated with decreased richness and diversity of native species at water sources. Furthermore, native species had fewer visits and spent less time at water sources frequented by horses. Our results indicated that horses displaced other species at water sources providing evidence of a negative influence on how communities of native wildlife access a limited resource in an arid environment.

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1. Introduction

Competition for limited resources influences the organization and structuring of biotic communities (Schoener, 1974; Carothers and Jaksić, 1984). Where species co-occur and compete for resources there are often mechanisms that enable coexistence and community stability. Because species differ in their competitive abilities, some species outcompete others for access to resources (Côté, 2005). To ensure coexistence in multi-species environments, subordinate competitors often partition resources with dominant competitors (MacArthur, 1958; Barot and Gignoux, 2004). However, mechanisms that stabilize community structure (e.g., resource partitioning) typically evolve over long periods of time.

Consequently, communities with species that have co-evolved over relatively long periods of time likely have better developed strategies for coexistence than newly formed communities. For example, within the community of native herbivores in semi-arid Africa, there is evidence that the large-bodied elephant (*Loxodonta africana*) influences community structure at waterholes (Valeix et al., 2007). Smaller herbivores that compete with elephants tend to avoid peak times of elephant visitation to waterholes. These smaller herbivores have co-existed with elephants over millions of years and have likely evolved strategies for temporal resource partitioning to minimize competition. In native communities, dominance hierarchies are typically well established, helping to stabilize community organization (Schuette et al., 2013). In communities where relatively new competitors have been introduced (i.e., exotic species), dominance hierarchies and competition dynamics may be altered, negatively influencing resource partitioning and the structure of native communities.

The introduction of exotic species is a global phenomenon that has had far-reaching implications for the stability of native communities (Wolfe and Klironomos, 2005; Lach, 2008; Kenis et al., 2009). Many exotic species have a competitive advantage over

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http://dx.doi.org/10.1016/j.jaridenv.2015.11.008
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native species due to a variety of factors related to life history and physiology (e.g., growth rate, reproduction rate, lack of natural predators and/or competitors; Humphrey and Schupp, 2004; Côté, 2005; Preston et al., 2012). In addition, physical attributes such as body size further enable some exotic species to outcompete native species (Gherardi and Cioni, 2004; Reed et al., 2012). Exotic species that are large-bodied and behaviorally dominant can disrupt native communities due to competitive advantages over native species.

The horse (*Equus caballus*) is a large, exotic ungulate that has been introduced around the world since its domestication (Clutton-Brock, 1981; Mills and McDonnell, 2005). Horses have been shown to negatively influence soil, vegetation, small vertebrates and invertebrates in a variety of systems (Beever and Brussard, 2000; Zalba and Cozzani, 2004; Beever and Herrick, 2006; Parvage et al., 2011; Davies et al., 2014). Exotic horses (and burros [*Equus asinus*]) have also displaced native ungulates from preferred habitats and at water sources (Ostermann-Kelm et al., 2008; Attum et al., 2009; Girard et al., 2013; Gooch, 2014). Species inhabiting arid or semi-arid environments rely on the availability of water (Rautenstrauch and Krausman, 1989; Cain III et al., 2006; Cain III et al., 2012; Bock, 2015) and there may be implications for species that compete with horses for access to water. Horses are gregarious, behaviorally dominant, and water-limited (an individual horse can drink up to 33 L of water/day; Berger, 1985; Groenendyk et al., 1988; Stevens, 1988) and these characteristics may compound competition for native species at water sources. Moreover, horse populations have increased dramatically in arid regions of western North America over the past several decades and are currently exceeding management objectives in many areas (Palmer et al., 2013; Davies et al., 2014). Little is known, however, concerning the degree to which horses compete with communities of native species for water in environments where water is scarce or how increased populations of horses may influence native communities.

Our objective was to determine the influence of horses on the use of water by communities of native wildlife in the semi-arid Great Basin Desert. We monitored water sources where horses had drinking access (horse included; hereafter HI) and water sources where horses were excluded with fencing (hereafter HE) to determine if there were differences in 1) composition of native communities or 2) use of water sources by native species. We expected native species to alter use of water (indirect evidence of competition) to minimize overlap with horses. We predicted that communities of wildlife would 1) be less species-rich and less diverse and 2) spend less time at HI water sources compared to HE water sources.

2. Materials and methods

2.1. Study area

We conducted this study on 631 km^2 of land managed by the United States Department of Defense, United States Army Dugway Proving Ground located in the Great Basin Desert of western Utah, USA. Valley terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats which were dominated by black greasewood (*Sarcobatus vermiculatus*). Along mountain foothills, big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), juniper (*Juniperus osteosperma*), and cheatgrass (*Bromus tectorum*) were common plants. Annual weather consisted of mean air temperatures of 12.3 °C (range: −20.0–40.6 °C) and mean precipitation of 146 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). Unlike typical neighboring land managed by the United States Department of the Interior, Bureau of Land Management, this study area had not been grazed by domestic livestock for more than 60 years allowing us to assess the influence of exotic horses on wildlife communities at water sources without this potential confounding influence. Recent estimates of the horse population in and around our study area suggested herd size was 464 horses (Bureau of Land Management, 2012).

2.2. Sampling design & data collection

We monitored 12 HI water sources and 13 HE water sources during June 2010 through August 2011. Water sources included water developments targeted for wildlife (13), overflow ditches and ponds from water treatment facilities (2), and natural springs (10). The majority of water sources were small (mean surface area = 2.6 m^2) with the exception of the two overflow water sources (mean surface area = 1620 m^2). To exclude horses at water sources, but not native species, HE water sources were enclosed with a two-tier, barbless cable fence in the late 1990s (AGEISS Environmental, 1998). Different strategies have been used so that perimeter fencing surrounding water sources does not exclude native ungulates such as mule deer (*Odocoileus hemionus*) or pronghorn (*Antilocapra americana*) (Larsen et al., 2011). In our study area, perimeter fencing was ≥5 m from the water source, with the top cable 92 cm from the ground, the bottom cable 44 cm from the ground, and a 48 cm space in between both cables, allowing native ungulates ample space to crawl underneath or jump over the fencing. Both native ungulates regularly occurred at HE water sources.

To sample species visitation to water sources, we used Reconyx PC900 covert infrared cameras (Reconyx, Inc., Holmen, Wisconsin) at all water sources. We mounted each camera to a metal post and positioned it 40 cm above ground level and approximately 3 m from the water source. Cameras were preset to detect motion and heat and were set to record an image at a minimum interval of 30 s. We checked cameras for proper function, battery status, and replaced memory cards every two weeks. We used Exifer v.2.1.5 (www.friedemann-schmidt.com/software/exifer) software to extract metadata (date and time stamps) from each image file. With date and time information for each image, we then sorted photos into species visits. We defined separate “visits”as consecutive images of a species separated by at least 30 min (Hall et al., 2013).

Water sources (and fences) were in place prior to our study (AGEISS Environmental, 1998), thus we did not have experimental control over location of water sources. This lack of experimental control created the potential for location and surrounding habitat features to influence species use of water sources and confound our results (Burger and Gochfeld, 1992; Larsen et al., 2007, 2012). To address this limitation, we collected a suite of habitat variables associated with each water source. We measured vegetation and topographic characteristics up to 100 m around each water source. We estimated cover and density of shrubs with a Random T-Square sampling approach (Krebs, 1999). To measure vegetation height, we used a Robel pole (Robel et al., 1970) and recorded vegetation measurements at 10, 20, 50, 75, and 100 m intervals radiating away from the water source in all four cardinal directions. We also used ocular estimation to classify the area surrounding each water source with the two dominant types of vegetation present at each site. To further describe each water source, we used ArcGIS (ArcMap, version 10.2, Environmental Systems Research Institute, Redlands, California) to calculate slope, aspect, and ruggedness (Sappington et al., 2007) around water sources using a 10 m resolution digital elevation model.

2.3. Data analyses

To address potential differences in wildlife community composition, we compared species richness and Simpson's indices of diversity for birds, mammals, and all species combined among treatments using *t*-tests. We also assessed similarity/dissimilarity of wildlife community composition across treatments (HI or HE) using Non-metric Multi-Dimensional Scaling (NMDS) on a Bray–Curtis similarity matrix (Bray and Curtis, 1957). We used ANOSIM to further support NMDS results and assess variation in community composition between treatment groups (Clarke, 1993). In addition, we used an NMDS analysis to determine if habitat characteristics were different between HE and HI sites. We then compared the number of visits/day (mean visits per site/number of days monitored), duration of visits (min; time from initial photo in a visit subtracted from the time of the last photo), and overall duration/day (min) of wildlife species at HI and HE water sources with *t*-tests. We also compared the amount of time (min/day) spent at all water sources for horses and all native species combined with a Mann–Whitney *U*-test. We performed statistical analyses using Program R and the community analysis package "vegan" (R Development Core Team, 2011; Oksanen et al., 2015). For series of statistical analyses, we used a Holm-Bonferroni correction to avoid type I errors (Holm, 1979; Gaetano, 2013). We set the family-wise alpha level for all significance tests at = 0.05.

3. Results

We captured 96,601 images representing 53 species of vertebrates including 40 species of birds (29,396 images) and 13 species of mammals (67,205 images). Approximately 0.2% of images (N = 198) did not contain sufficient information to confidently identify species. Of the total 67,205 images of mammals, 79% (53,091) contained exotic horses. Horses visited all 12 water sources that did not have exclusionary fencing and were photographed outside fencing at all 13 HE water sources.

Species richness at HE water sources was greater than at HI water sources (Overall: t = 8.20, P < 0.001, N = 25, Fig. 1a; birds: t = 8.98, P < 0.001, Fig. 1b; mammals: t = 3.91, P < 0.001, Fig. 1c). Similarly, species diversity was greater at HE water sources compared to HI water sources (Overall: t = 3.41, P = 0.002, N = 25, Fig. 2a; birds: t = 5.89, P < 0.001, Fig. 2b; mammals: t = 2.60, P = 0.016, Fig. 2c). We detected a difference between wildlife community composition between treatment groups (HI and HE) with noticeable between-group compactness (Global R = 0.77,

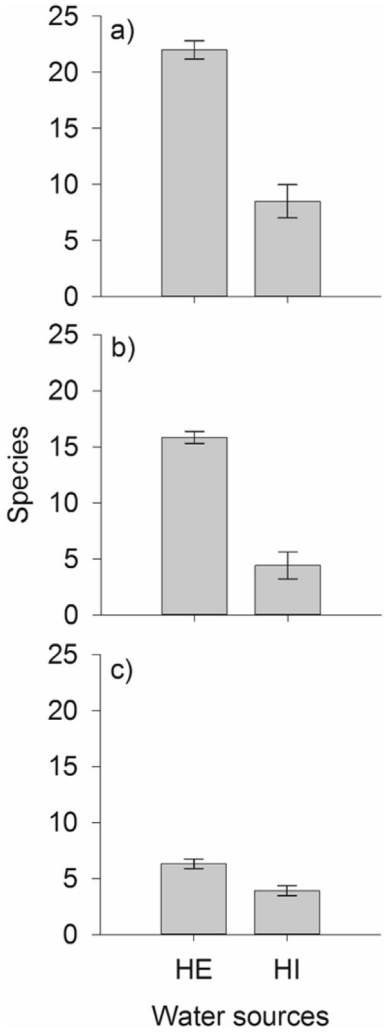


Fig. 1. Mean (±SE) species richness of a) all species, b) birds, and c) mammals that appeared in images captured by remote cameras at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

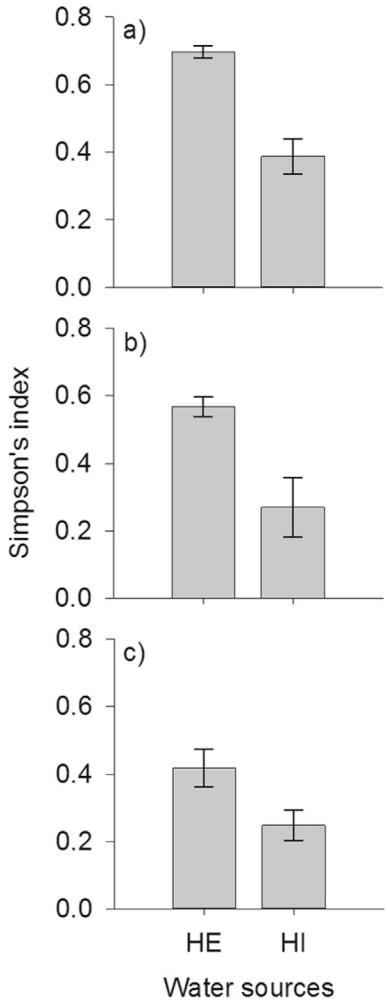


Fig. 2. Mean (±SE) Simpson's diversity of a) all species, b) birds, and c) mammals that appeared in images captured by remote cameras at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

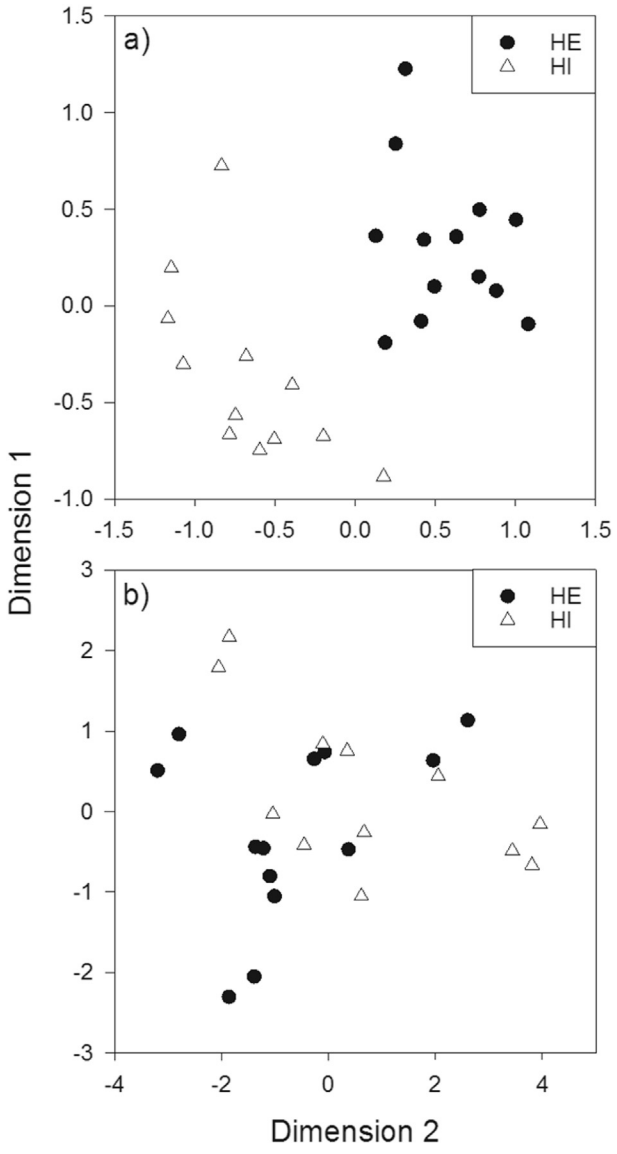


Fig. 3. Non-metric Multi-Dimensional Scaling (NMDS) ordination map of similarity/dissimilarity for species composition of wildlife communities (panel a) and habitat characteristics (panel b) at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

$P = 0.001$, Fig. 3a). We did not, however, detect any differences between habitat characteristics that accounted for the differences we observed in wildlife community composition (Global $R < 0.001$, $P = 0.38$; Fig. 3b).

Native wildlife visited HE water sources on average over three times more per day than HI water sources (Table 1). We did not, however, detect consistent differences in duration of native wildlife visits between HE and HI water sources, with exception of our "other birds" and "small mammals" taxonomic groups (Table 1). The overall time/day that native wildlife spent at HE water sources was nearly three times greater than at HI water sources; "raptors" were the only taxonomic group that did not significantly differ in time/day between HE and HI water sources (Table 1). On a daily basis, horses were present at water sources almost 10 times longer than all species of wildlife combined ($U = 0.00$, $P < 0.001$, $N = 25$, Fig. 4).

4. Discussion

Exotic species can disrupt the stability of biotic communities by altering how limited, communal resources are partitioned by multiple species. Our study illustrated that horses displaced native species from access to water in a semi-arid environment. Native species tended to avoid times when horses were present at water sources, providing some indirect evidence for interference competition, similar to what has been observed for interactions between bighorns (*Ovis canadensis*) and feral horses (Ostermann-Kelm et al., 2008). We only detected a few instances where native species and horses simultaneously occurred at the same water source. This observation could result from one or several of the following reasons: 1) large body size can confer a competitive advantage (Berger, 1977; Robertson, 1998; Palomares and Caro, 1999), 2) frequent physical intraspecific disputes among horses may deter other species from approaching (Berger, 1977; Stevens, 1988), and 3) the sheer number of horses at nearly all of the available space for drinking.

Competition from a large dominant species may drive niche partitioning of other species (Carothers and Jaksić, 1984; Ziv et al., 1993; Schuette et al., 2013). For example, small African herbivores avoided visiting water sources during peak times of visitation by the larger African elephant (Valeix et al., 2007). Likewise in our study, native species avoided water sources occupied by horses. Generally, niche partitioning enables two (or more) competing species to share resources while minimizing potentially costly interspecific interactions (Case and Gilpin, 1974; Schoener, 1974). However, during times of greatest physiological stress (increased temperature, decreased precipitation), horses monopolized access

Table 1
Mean (±SE) temporal metrics of all species of native wildlife (separated into taxonomic groups) at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

Group	Visits/day			Minutes/visit			Minutes/day		
	HE	HI	*p*	HE	HI	*p*	HE	HI	*p*
All wildlife	7.29 (±0.27)	2.67 (±0.12)	<0.001*	1.94 (±0.09)	1.67 (±0.06)	0.175	14.30 (±1.09)	4.45 (±0.27)	<0.001*
Birds	4.92 (±0.24)	1.68 (±0.07)	<0.001*	1.75 (±0.12)	1.31 (±0.15)	0.175	8.77 (±0.81)	2.23 (±0.28)	<0.001*
Passerines	2.69 (±0.23)	1.31 (±0.04)	<0.001*	1.28 (±0.12)	0.90 (±0.12)	0.180	3.61 (±0.61)	1.17 (±0.15)	0.001*
Raptors	0.11 (±0.02)	0.03 (±0.02)	0.028*	2.17 (±0.33)	1.47 (±0.24)	0.224	0.27 (±0.07)	0.09 (±0.06)	0.064
Other birds[a]	2.05 (±0.13)	0.34 (±0.02)	<0.001*	1.95 (±0.18)	1.07 (±0.18)	0.016*	4.23 (±0.59)	0.37 (±0.06)	<0.001*
Mammals	2.37 (±0.17)	0.99 (±0.09)	<0.001*	2.50 (±0.12)	2.11 (±0.13)	0.180	6.08 (±0.65)	2.15 (±0.26)	<0.001*
Ungulates	1.76 (±0.17)	0.87 (±0.08)	<0.001*	3.02 (±0.17)	2.86 (±0.19)	0.551	5.34 (±0.62)	2.57 (±0.36)	0.004*
Carnivores	0.47 (±0.07)	0.08 (±0.01)	<0.001*	1.20 (±0.09)	0.63 (±0.05)	<0.001*	0.58 (±0.11)	0.05 (±0.01)	<0.001*
Sm. Mammals	0.14 (±0.03)	0.04 (±0.01)	0.002*	1.24 (±0.25)	0.66 (±0.06)	0.118	0.22 (±0.08)	0.03 (±0.01)	0.031*

*Denotes significance at $p < 0.05$.
[a] Other birds included mourning dove (*Zenaida macroura*), chukar (*Alectoris chukar*), northern flicker (*Colaptes auratus*), common poorwill (*Phalaenoptilus nuttallii*), American coot (*Fulica americana*), killdeer (*Charadrius vociferus*), spotted sandpiper (*Actitis macularius*), and white-faced ibis (*Plegadis chihi*).

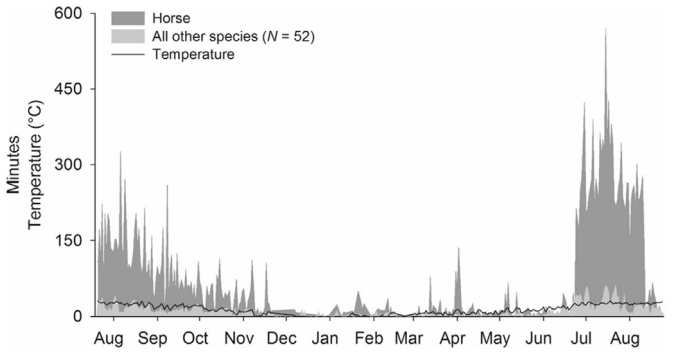


Fig. 4. Mean duration of time (min/day) spent at water sources by all species of native wildlife compared to that of horses (*Equus caballus*) in the Great Basin Desert, Utah (USA). Diel activity at water sources is presented in relation to mean air temperature and month.

to water sources where they were present up to 73% of the day, leaving limited time for other species. The potential for an exotic species, such as the horse, to outcompete native species for a limited communal resource during peak need raises concern for native communities in water-limited environments.

The availability of a limited resource can dictate the competitive environment between species (Dolman, 1995; Hasui et al., 2009). Though elephants have been implicated in altering the temporal niche of other herbivores (Valeix et al., 2007), these subordinate herbivores did not avoid waterholes used by elephants (Valeix et al., 2009). The discrepancy between what was observed in Zimbabwe, Africa and what we observed is likely due to at least two factors. First, communities of African wildlife have evolved in the presence of elephants and therefore have likely adapted strategies of minimizing potential conflict. Second, the size (diameter) of water sources in Zimbabwe was on average 14 times larger than the water sources in our study area. Large water sources provide greater availability of shoreline edge where animals can access water, likely minimizing interspecific competition. The relatively small water sources in our study area could accommodate one to a few horses at a time, leaving little to no space for other species to drink. Moreover, the species of wildlife in our study have co-occurred with exotic horses for a relatively short time and likely have not completely adapted to the presence of a large, gregarious mammal with high water demand (Groenendyk et al., 1988).

Our results have implications for the conservation of water sources in arid and semi-arid regions. Recent projections of climate change in desert regions, particularly western North America, predict increased temperatures and decreased precipitation (Seager et al., 2007; Mamtimin et al., 2011; Ault et al., 2014; Borsa et al., 2014; Cook et al., 2015). Furthermore, ever increasing anthropogenic use of water and modification of arid landscapes has caused dramatic reductions of water availability which is only predicted to increase in the future (Barnett et al., 2008; Bruins et al., 2012). Increased aridity and reduced availability of water in already water-limited landscapes may magnify the competitive pressures that large exotic species have on smaller native species at water sources.

In addition to the effects we observed, horses may also indirectly alter the quality of water and habitat for native species. At unfenced water sources, disturbance to water and trampling of the immediate habitat surrounding water sources was prevalent, corroborating other work (Turner, 1987; Stevens, 1988; Davies et al., 2014). Furthermore, some of our photos depicted horses urinating and defecating either in or adjacent to water sources and we commonly found dung piles near water sources. The addition of bodily waste from horses to water sources could also have contributed to the lack of use by wildlife compared to water sources where horses were excluded. There may also be bottom-up effects for aquatic ecosystems due to mechanical (trampling, grazing) and chemical alteration by horses (Levin et al., 2002; Beever and Herrick, 2006; Loydi and Zalba, 2009).

We provide novel information concerning the influence of the exotic horse on community use of water by native wildlife in a semi-arid environment. We recognize that our study was observational in nature and that we cannot infer causality. Additional efforts, such as monitoring survival, productivity, and recruitment by native species, are needed to determine if horses exert a biological relevant impact via competition for water. Despite these shortcomings, however, our study is the first to provide a community-level perspective regarding temporal and spatial use of water by native species in the presence of horses. We found strong differences between water use patterns and communities of wildlife at fenced (horses excluded) and unfenced water sources. At water sources where horses had access, wildlife spent less time and communities were less species-rich and less diverse compared to water sources where horses were excluded. Our results indicate that horses displaced other species at water sources providing evidence of a negative influence on how communities of native wildlife access a limited resource.

Acknowledgments

We thank R. Williams, D. Smedley, R. Hamilton, and J. Huber for assistance in the field and the lab. We also thank R. Rader for assistance with statistical analyses. We appreciate the valuable insight and critique from two anonymous reviewers that greatly improved this manuscript. Funding for this project was provided by the U.S. Army Dugway Proving Ground (contracted through the Utah Division of Wildlife Resources, contract #106298).

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Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment

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Citation: Hall, L. K., R. T. Larsen, R. N. Knight, and B. R. McMillan. 2018. Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment. Ecosphere 9(1):e02096. 10.1002/ecs2.2096

Abstract. The horse (*Equus caballus*) is a feral ungulate that currently exceeds target population sizes in many areas of western North America. Horses are behaviorally dominant over native ungulates and outcompete the latter for access to water sources. However, a better understanding of the broader spatial and temporal implications of horse-induced competition on access to water by native ungulates will enable better conservation and management of native species. Our objective was to determine whether pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) spatially or temporally altered their use of water to minimize interactions with horses. From 2010 to 2014, we used remote cameras to monitor ungulates at 32 water sources in the Great Basin Desert. We evaluated spatial and temporal partitioning by these species at water sources using generalized linear models, mixed-effects models, and Mann–Whitney *U* tests. We found that both native ungulates used water sources less often where horse activity at water sources was high, indicating that spatial avoidance occurred. Further, we observed significant differences in peak arrival time for pronghorn, but not mule deer at horse-occupied sites versus sites where horses were absent or uncommon, indicating that temporal avoidance may be more important for pronghorn than mule deer. Because mule deer are primarily crepuscular and nocturnal whereas horses are largely diurnal, we did not expect to observe a temporal shift for mule deer. We also found strong support for the interactive negative effect of elevated temperature and subsequent increased activity of horses at water sources on drinking patterns of pronghorn and mule deer. Our findings indicate that feral horses further constrain access to an already limited resource for native species in a semi-arid environment.

Key words: competition; horse; mule deer; pronghorn; temperature; ungulates; water.

Received 13 October 2017; accepted 29 December 2017. Corresponding Editor: James W. Cain III.
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INTRODUCTION

The horse (*Equus caballus*) is an exotic and feral ungulate that was introduced to North America during the 16th century (Mills and McDonnell 2005). Since its introduction, the horse has become widespread in western North America. Numbers of horses currently exceed appropriate management levels by almost 46,000 animals and can increase by 15–20% per year (Palmer et al. 2013, Bureau of Land Management 2017). However, because horses are federally protected and share close relationships with humans, management options are limited, costly, and controversial (Linklater et al. 2002, Taggart 2008, Bies et al. 2011, Garrott and Oli 2013). In fact, the management of feral horses is often met with public debate and criticism (Symanski 1996, Linklater et al. 2002). Because public opinion and sentiment can take priority over conservation needs for ecosystems, the ability to mitigate the negative effects of large populations of horses on western rangelands can

be compromised (Linklater et al. 2002, Bies et al. 2011). Despite efforts to manage populations of horses, current practices and methodologies appear inadequate to achieve target population sizes in much of western North America (Palmer et al. 2013, Bureau of Land Management 2017).

Increased numbers of horses are associated with negative impacts to arid and semi-arid landscapes and some of the species inhabiting these environments (Beever 2003, Beever and Aldridge 2011, Davies et al. 2014, Hall et al. 2016*b*). Horses can degrade habitat features (e.g., soil and vegetation) via trampling, excessive nutrient deposition, and overgrazing (Loydi and Zalba 2009, de Villalobos et al. 2011, Parvage et al. 2011). Horse-related shifts in soil and vegetation are linked to altered community composition of fossorial invertebrates and small vertebrates (Beever and Brussard 2004, Beever and Herrick 2006). Increased grazing by horses can result in higher rates of predation for some species by removing vegetative cover used for concealment (Levin et al. 2002, Zalba and Cozzani 2004). While evidence suggests that horses can influence habitat components and relatively small animals, there is substantially less information supporting the idea that horses affect larger species (e.g., native ungulates). Because desert environments are generally resource-poor areas, increased numbers of horses may influence resource acquisition by native ungulates (Ostermann-Kelm et al. 2008, Perry et al. 2015, Gooch et al. 2017).

Water is a limiting resource for horses and native ungulates such as pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). Horses have a relatively high water demand (up to 33 L/d; Groenendyk et al. 1988). During periods of water stress (e.g., increased temperatures), horses visit water sources more often and for longer periods (up to 73% of the day; Miller 1983, Stevens 1988, Hall et al. 2016*b*). Pronghorn and mule deer drink less water than horses (pronghorn up to 3.4 L/d, mule deer up to 6 L/d; Hazam and Krausman 1988, Fox et al. 2000), but depend on water during periods of water stress (e.g., lactation during summer months; Bowyer 1984, Clemente et al. 1995, Boroski and Mossman 1996, Fox et al. 2000, McKee et al. 2015). Unfortunately, when the physiological dependence on water is greatest for ungulates during the hot and dry summer months, water is often least available. Reduced availability of an already limited resource, such as water, could heighten competitive interactions between horses and native ungulates during stressful summer conditions (Perry et al. 2015, Gooch et al. 2017).

Horses are dominant over native ungulates (Berger 1985) and can negatively influence their use of water. For example, horses have excluded desert bighorn sheep (*Ovis canadensis*) from water (Ostermann-Kelm et al. 2008), chased elk (*Cervus elaphus*) away from water (Perry et al. 2015), and increased vigilance behavior in pronghorn at water sources (Gooch et al. 2017). Understanding the broader spatial and temporal implications of horse-induced competition for water with native ungulates will facilitate conservation and management of native species. As water is projected to become even more limiting in western North America over the course of this century (Cook et al. 2004, 2015, Seager et al. 2013), a better understanding of how non-native feral species negatively influence the conservation of native species is imperative. Furthermore, a more developed comprehension of the interacting effects of increased temperatures and subsequent high activity of horses near water (Hall et al. 2016*b*) on drinking patterns of native ungulates will enhance our ability to better manage native species and natural resources in light of oncoming environmental change.

Our objective was to determine whether horses influenced spatial and temporal drinking patterns of native ungulates. If horses excluded native ungulates from water as suggested by previous work, we would predict the latter to avoid water sources used by horses or alter arrival times to minimize interactions with horses. Because mule deer are primarily crepuscular and nocturnal whereas horses are largely diurnal, we did not predict as large of a difference in visitation times to water in response to presence of horses, compared to pronghorn. We also predicted that the interactive effects of high temperatures and subsequent increased activity of horses (Hall et al. 2016*b*) would negatively affect the use of water by native ungulates.

Methods

Study areas

We conducted this study in the Great Basin Desert of western Utah, USA (Fig. 1). Our study area consisted of 1200 km^2 of land managed by the U.S. Department of Defense, U.S. Army

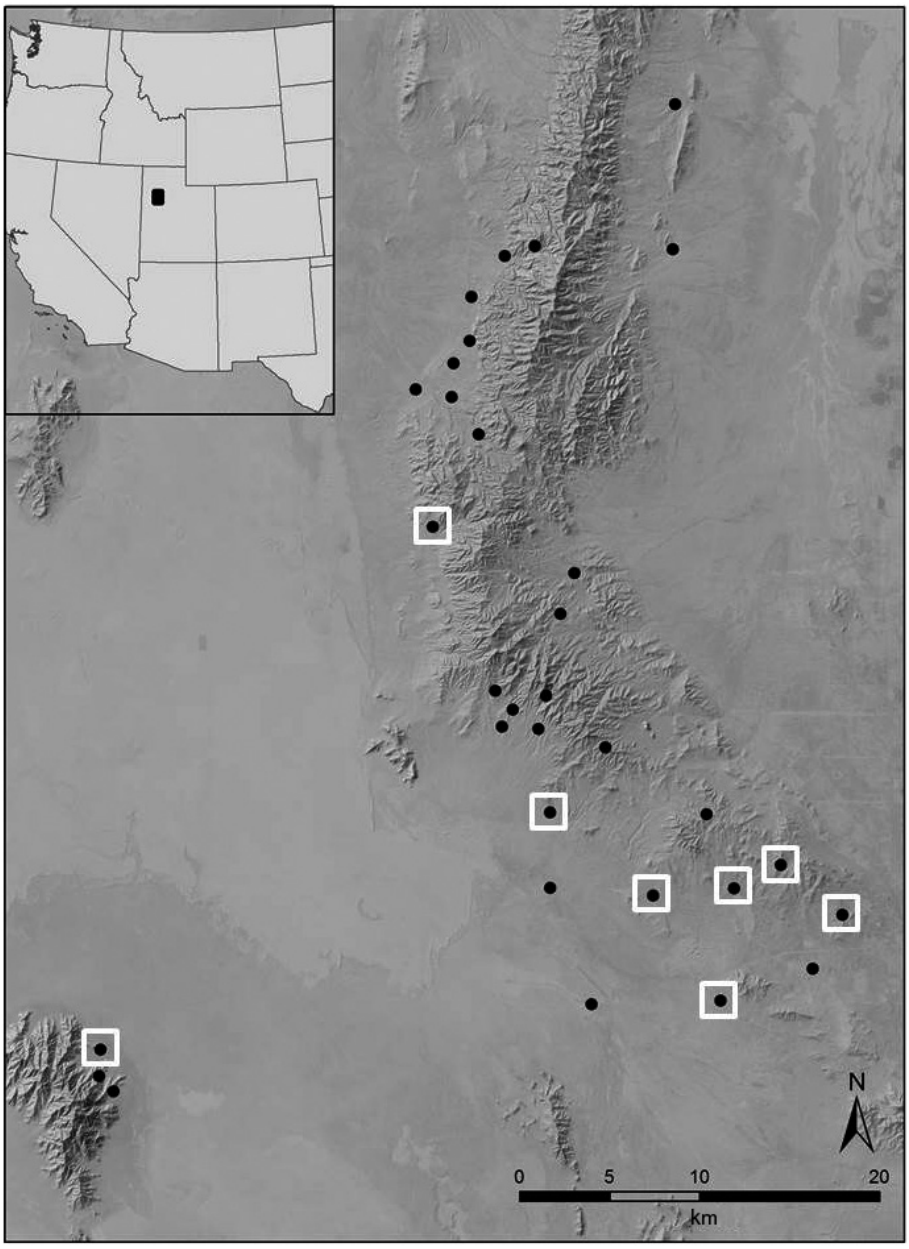


Fig. 1. Distribution of water sources that were monitored with remote cameras for pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and horses (*Equus caballus*) in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014. White squares around water sources indicate horse-exclusionary fencing.

Dugway Proving Ground and the U.S. Department of the Interior, Bureau of Land Management. Elevations across the study area ranged from 1300 to 1850 m. The terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats dominated by black greasewood (*Sarcobatus vermiculatus*). Along the foothills, invasive annual grasslands (*Bromus tectorum*) were commonly mixed with desert shrubs (*Chrysothamnus* spp.), sagebrush (*Artemisia* spp.), and juniper (*Juniperus osteosperma*), transitioning to pinyon (*Pinus edulis*)-juniper woodlands at higher elevations. Annual weather consisted of mean air temperatures of 13.6°C and mean precipitation of

160 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center).

Data collection

We used infrared-triggered cameras (Reconyx PC900 Hyperfire, Holmen, Wisconsin, USA) to monitor ungulate activity at 32 water sources in our study area (Fig. 1). These water sources consisted of nine water developments for wildlife (i.e., guzzlers), eight livestock troughs, 11 natural springs/seeps, and four ponds. Seven water developments and one spring had exclusionary fencing for livestock that prevented horses from accessing water sources. To encourage use by native ungulates, perimeter fencing was ≥5 m from the water source, with the top cable 92 cm from the ground, the bottom cable 44 cm from the ground, and a 48 cm space in between both cables. Based on documented occurrence from prior research, these fence dimensions provided ample space to crawl underneath or jump over the fencing and both pronghorn and mule deer regularly occurred at fenced water sources (Hall et al. 2016*b*).

We secured cameras to metal posts and placed them approximately 3 m from the edge of water where animals accessed water for drinking. At water sources with multiple locations of drinking access (e.g., paired tanks of water, ponds), we placed cameras at a minimum of two locations where animals could drink. We considered proximity to trails and recent ungulate sign (i.e., tracks, pellet droppings) to determine the location of cameras at larger ponds or springs. Despite our efforts to optimally place cameras at large sources, our estimates of water usage are likely conservative as we may have missed the existence of other trails used by native ungulates. We checked the battery status, changed memory cards, and performed any necessary maintenance to cameras approximately every two weeks. Cameras were set to trigger on both motion and heat following which they recorded an image every 30 s. We monitored 16 water sources from June to October, 2010–2014, and monitored an additional 16 water sources (for a total of 32 water sources) from June to October, 2013–2014. This seasonal window captured periods of increased temperatures and decreased precipitation where visitation rates to water by ungulates were greatest (Shields et al. 2012).

To determine relative patterns of visitation by ungulates, we first summarized the images of ungulate species captured by remote cameras. We extracted the time and date associated with each camera image. With date and time information, we then sorted camera images into species visits. Due to the difficulty of identifying individuals (particularly females and juveniles), we followed the methodology of previous research using remote cameras to monitor wildlife and defined independent visits as consecutive images of a species separated by at least 30 min (Michalski and Peres 2007, Hall et al. 2016*b*).

To account for the potential influence of site characteristics on the use of water by wildlife (Larsen et al. 2012, Hall et al. 2013), we measured vegetative and topographical characteristics within a 1785 m radius around each water source (Larsen et al. 2011). We selected a 1785 m radius based on summer home range sizes and daily distances traveled for pronghorn and mule deer (Gregg 1955, Kitchen 1974, Yoakum 1978, Hoskinson and Tester 1980, Garrott et al. 1987, Hayes and Krausman 1993, O'Gara and Yoakum 2004). We used tree cover and topographical ruggedness (terrain roughness) as our primary habitat variables to follow what has been done with pronghorn and mule deer at water sources in the Great Basin Desert (Larsen et al. 2011). We derived tree cover using vegetative cover types available in LANDFIRE (Landscape Fire and Resource Management Planning Tools) data provided by the U.S. Department of Agriculture Forest Service and the U.S. Department of the Interior. We defined tree cover as the proportion of pixels within a 1785 m radius around water sources containing vegetation dominated by trees (Larsen et al. 2011). Using ArcGIS (ArcMap, version 10.3; Environmental Systems Research Institute, Redlands, California, USA), we calculated ruggedness within the 1785 m radius buffer around water sources using a 30-m resolution digital elevation model. We used the vector ruggedness metric and set the ruggedness neighborhood to a 3×3 cell size (Sappington et al. 2007).

Statistical analyses

We employed a two-stage modeling approach to determine whether spatial partitioning occurred between horses and native ungulates. In the first stage, we identified the most appropriate statistical distribution (Gaussian, Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial [ZINB]) for visitation rates

(counts) of mule deer and pronghorn (Larsen et al. 2011). Count data for wildlife at water sources can often result in data that do not meet the assumptions of normality for standard linear models. These data are often not easily normalized via transformations due to the presence of large numbers of zero counts (where no target species were detected). Within the last two decades, however, statistical distributions designed to handle non-normal data with large numbers of zeros have been identified and used in ecological modeling. To determine the best distribution for ungulate data, we used model selection and Akaike's information criterion, corrected for sample sizes (AIC_c) model weights to evaluate the relative performance of a simple model (ungulate visits as a function of elapsed sampling time [number of camera days; EST]) with each of the distributions.

In the second stage of our analysis, we created two sets of models to measure any influence that horses may have on the selection of water sources by native ungulates (Larsen et al. 2011). One model of each set contained a habitat covariate such as tree cover or ruggedness (or both). The other model of each set was identical to the first but included horse activity (number of pictures of horses at a water source) as an additional parameter. We included EST in each model to account for differences in total sampling time across water sources over the 5 yr as some water sources were sampled the entire time and others for only two years. Because EST was included in every model, we did not need to standardize horse photographs by the number of days cameras were operable. We limited our models to no more than three variables considering our overall sample size of water sources was rather modest ($n = 32$) and the general rules of thumb regarding model selection and linear models (Burnham and Anderson 2002). We intentionally excluded any variables referencing time (e.g., temperature, year) to explicitly test for spatial avoidance and therefore used only a single photograph count of ungulates at each sampled water source in this stage of analysis. Prior to model selection, we conducted correlation analyses with all variables. In the case where variables were highly correlated ($|r| > 0.6$), we retained the variable that was associated with a model having the lower AIC_c score. Using AIC_c model weights (w_i), we ranked competing models (Burnham and Anderson 2002). We considered models to be competing if they received ≥5% of the cumulative AIC_c model weight. We then evaluated both the AIC_c model weight and log-likelihood associated with top models to identify any models with uninformative parameters. We judged parameters as uninformative when competing models differed from the top model by a single parameter and little to no improvement in log-likelihood was evident (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). Where we encountered multiple competing models, we did not model average to acquire β coefficients, but instead calculated predicted values with 85% confidence intervals and then averaged these values based on relative AIC_c weight of the top models (Cade 2015). This model comparison coupled with the β estimates from supported models allowed us to evaluate the relative influence of horses on the spatial use of water by native ungulates after accounting for known habitat factors.

We then determined whether native ungulates experienced temporal shifts or altered time usage (Valeix et al. 2007) at water sources where activity of horses was high. For this analysis, we identified the hour of peak arrival for pronghorn and mule deer at each water source. We then compared hour of peak arrival for native ungulates at water sources where horses were common and absent (or rare) using Mann–Whitney *U* tests. We considered water sources as horse common if horses visited more than once per day. This categorization resulted in a natural break in water sources based on horse activity and resulted in 17 that were horse common and 15 that were horse absent or rare. On average, activity of horses was 16.5 times greater at horse common water sources compared to horse absent or rare water sources.

We constructed several generalized linear mixed models to determine whether the interactive increase of temperature and activity levels of horses negatively influenced daily visitation to water by native ungulates. In these models, we limited ourselves to a ZINB distribution for pronghorn and mule deer photograph counts, due to the excess numbers of zero counts occurring across days and sites. These models were similar to the spatial partitioning models in that we included tree cover and ruggedness at the summer home range scale to account for known habitat characteristics, but we also included maximum daily temperature (°C) and daily photograph counts of horses. We

then included a temperature × horse variable to capture the interaction between daily maximum temperature and daily activity of horses (number of pictures/d). A potential concern for our interaction term could arise from a correlation between horse activity and daily temperature, but the correlation coefficient was low ($r = 0.17$) and well below generally accepted thresholds for correlation coefficients of $|r| > 0.6$. To account for variation between water sources and years, we included these variables as random effects in these models. We then followed the same evaluation as before and compared AIC_c model weights, log-likelihoods, and β estimates of candidate models with and without the horse × temperature interaction to determine whether the multiplicative effects of increased temperatures and high horse activity better explained drinking patterns of native ungulates. We performed all analyses using Program R (R Development Core Team 2014). We used the glmmADMB package (http://glmmadmb.r-forge.r-project.org/) to run generalized linear mixed models in Program R. We set the level of significance for all statistical tests at $\alpha = 0.05$.

Results

From 2010 to 2014, we accrued a total of 29,666 pictures of pronghorn and 39,605 pictures of mule deer in 27,700 camera days. Of these pictures, there were 7465 visits of pronghorn and 7363 visits of mule deer. Horses accounted for an additional 780,452 pictures comprising 20,202 visits. All three ungulates occurred at the majority of water sources that we sampled. Pronghorn visited 26 of the 32 water sources (81%), mule deer visited 29 water sources (91%), and horses visited 23 water sources (72%).

From stage one of our modeling, we determined that a ZINB distribution best fits the pronghorn data and a negative binomial distribution best fits the mule deer data (Table 1). In stage two of our modeling (to determine spatial selection of water sources), we found that in nearly all analyses, the models that contained horse activity were best supported by the data. In fact, models with the horse activity covariate comprised 93% of model weight for pronghorn and 76% of model weight for mule deer (Table 2). Our models revealed that horse activity was negatively associated with visitation to water by pronghorn and mule deer (Figs. 2, 3).

Table 1. AIC_c scores for the statistical distribution of camera trap images for pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) at water sources.

Species	Distribution	AIC_c
Pronghorn	ZINB	381
	Negative binomial	386
	Gaussian	462
	ZIP	8355
	Poisson	11,423
Mule deer	Negative binomial	393
	ZINB	396
	Gaussian	472
	ZIP	11,648
	Poisson	13,076

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes; ZINB, zero-inflated negative binomial; ZIP, zero-inflated Poisson. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

Table 2. Model selection results evaluating overall spatial partitioning of water sources by pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) with horses (*Equus caballus*).

Model†	*K*‡	LL§	ΔAIC_c¶	w_i#
Pronghorn				
EST + Trees + Horse	8	−207.20	0.00	0.76
EST + Rugged + Horse	8	−208.90	3.38	0.14
EST + Trees	7	−212.60	5.09	0.06
EST + Horse	7	−213.30	6.47	0.03
EST + Rugged	7	−214.50	8.91	0.01
EST	5	−219.80	10.23	0.00
Mule deer				
EST + Rugged + Horse	4	−181.72	0.00	0.63
EST + Rugged	3	−184.65	3.24	0.13
EST + Trees + Horse	4	−183.68	3.72	0.10
EST + Trees	3	−184.98	3.90	0.09
EST + Horse	3	−186.00	5.93	0.03
EST	2	−187.64	6.77	0.02

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

† EST, elapsed sampling time; trees, proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse, log base 10 of activity (no. of pictures) of horses; rugged, ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model.

‡ Number of parameters; pronghorn models contained nearly 2× as many parameters compared to mule deer models because of the zero-inflated distribution model counts and excess zeros with separate estimates.

§ Model log-likelihood.

¶ Change in AIC_c value compared to top model.

AIC_c weight.

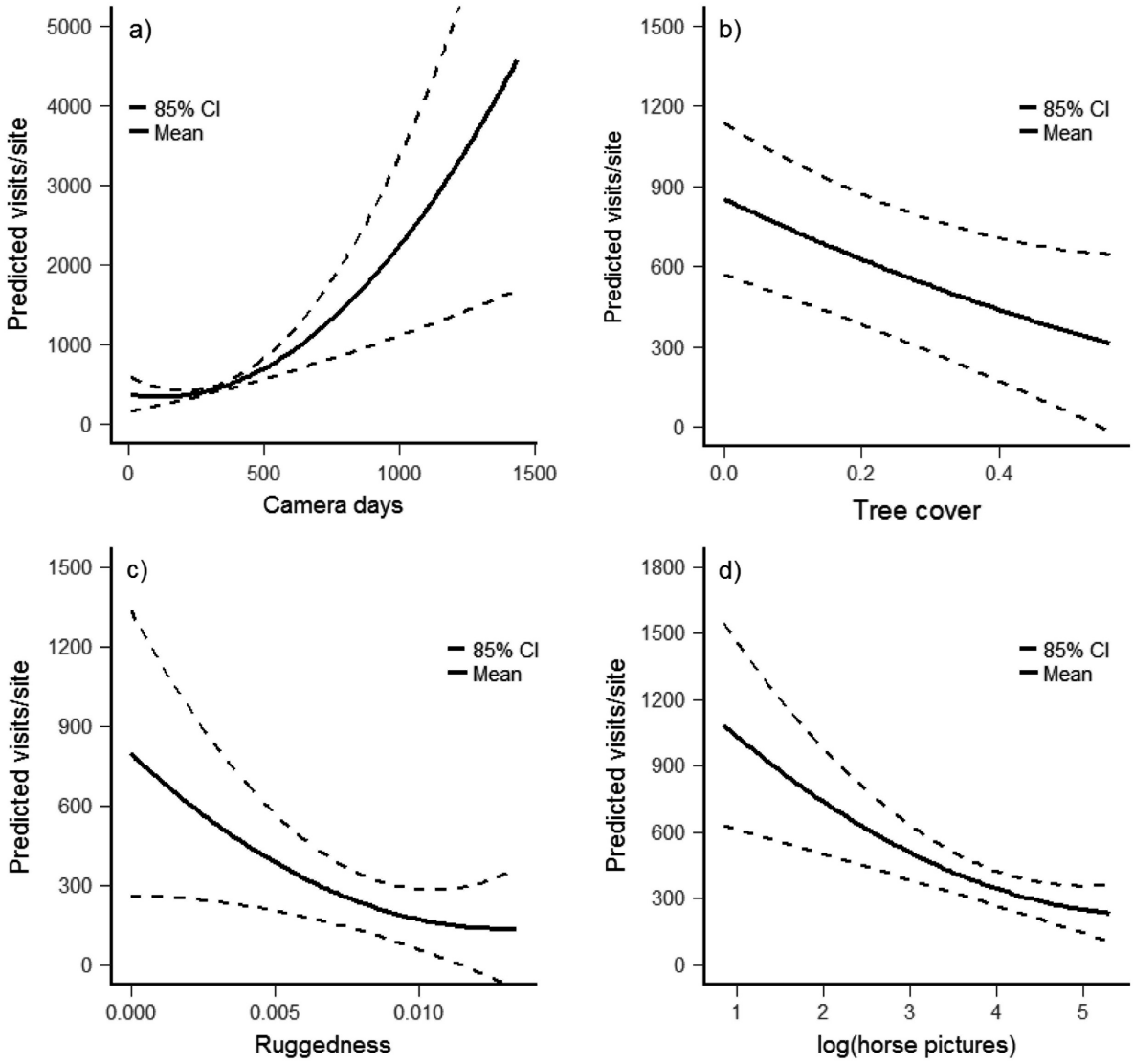


Fig. 2. Predicted visits (with 85% confidence intervals) to water by pronghorn (*Antilocapra americana*) based on variables from the top generalized linear models evaluating spatial partitioning with horses (*Equus caballus*). Camera days = number of camera-sampling days; tree cover = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); log(horse pictures) = log base 10 of activity (no. of pictures) of horses; and ruggedness = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

Native ungulates exhibited relatively distinct patterns of temporal activity at water sources, whereas horses were active throughout day, but most active during diurnal hours (Fig. 4). Horse activity did not appear to influence arrival times to water by pronghorn and mule deer in the same fashion. At water sources where horses were common, pronghorn exhibited differences in arrival times compared to water sources where horses were absent or rare ($U = 81.00$, $P = 0.04$; Fig. 5). Pronghorn also experienced a greater amount of variation in arrival times where horses were common (Fig. 5). Alternatively, there were no differences in arrival time to water for mule

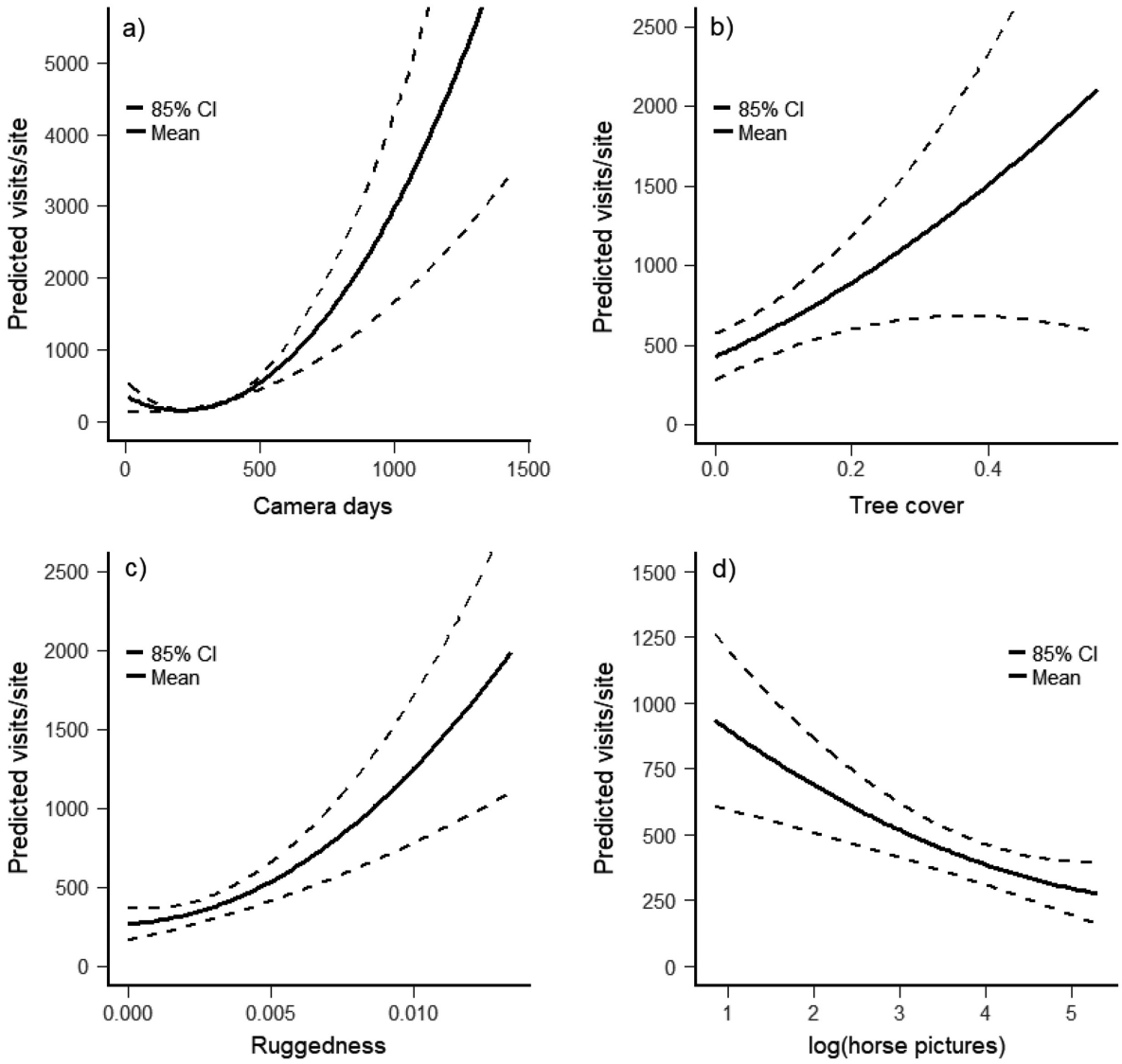


Fig. 3. Predicted visits (with 85% confidence intervals) to water by mule deer (*Odocoileus hemionus*) based on variables from the top generalized linear models evaluating spatial partitioning with horses (*Equus caballus*). Camera days = number of camera-sampling days; tree cover = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); log(horse pictures) = log base 10 of activity (no. of pictures) of horses; and ruggedness = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

deer, regardless of horse activity ($U = 159.00$, $P = 0.95$; Fig. 6).

With our mixed-effects models, we found strong support for the temperature × horse interaction. Pronghorn models containing the temperature × horse interaction accounted for 95% of the cumulative model weight (Table 3). While the individual model estimates for horse and temperature variables were both positively correlated with water use by pronghorn, the estimate for the interaction of these variables had a negative correlation with the use of water by pronghorn (Fig. 7). Similar to pronghorn, mule deer models with the temperature × horse

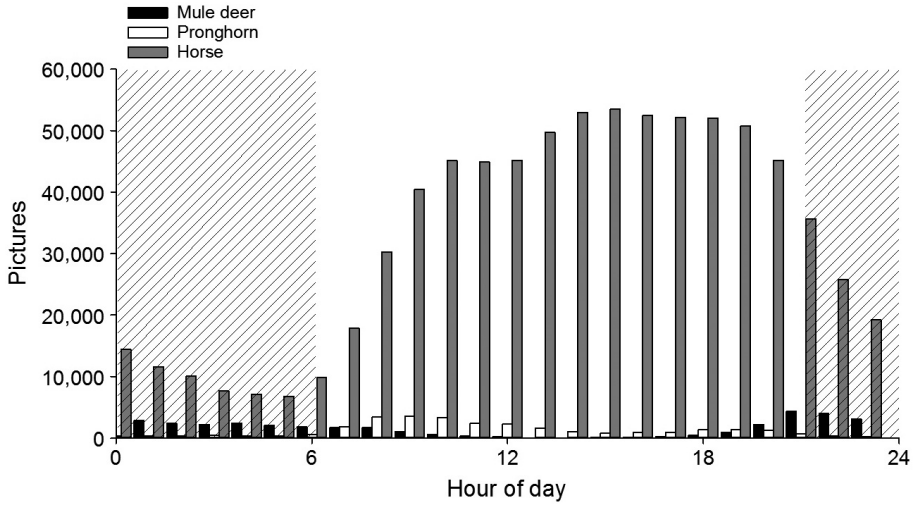


Fig. 4. Temporal activity (number of pictures from remote cameras by hour of day) of pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and horses (*Equus caballus*) at water sources in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014. Hatched (shaded) regions depict nocturnal hours.

interaction accounted for nearly all (99%) of the cumulative model weight and that interaction was negatively correlated with use of water by mule deer (Table 3, Fig. 8).

Discussion

Our study demonstrated that horses negatively influenced how pronghorn and mule deer accessed a limiting resource. Our findings also provided corroborating evidence that horses outcompeted native ungulates for water (Miller 1983, Ostermann-Kelm et al. 2008, Perry et al. 2015, Gooch et al. 2017). We observed resource partitioning (indirect evidence of competition) between horses and native ungulates; specifically, we found evidence for spatial partitioning as pronghorn and mule deer avoided water

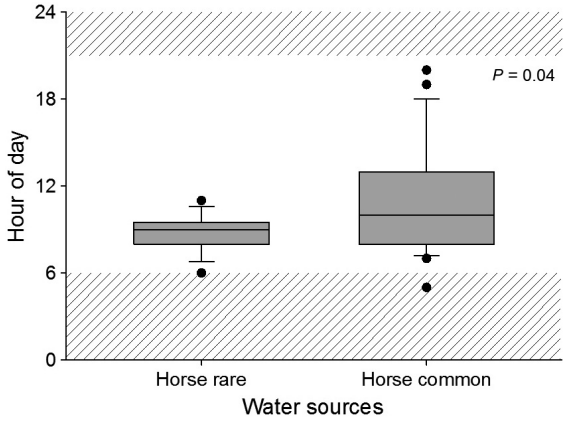


Fig. 5. Peak arrival hour for pronghorn (*Antilocapra americana*) at water sources where horses (*Equus caballus*) were rare (or absent) and where horses were common. Hatched (shaded) regions depict nocturnal hours. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

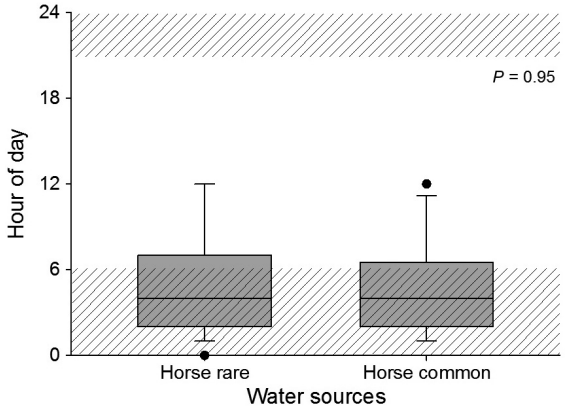


Fig. 6. Peak arrival hour for mule deer (*Odocoileus hemionus*) at water sources where horses (*Equus caballus*) were rare (or absent) and where horses were common. Hatched (shaded) regions depict nocturnal hours. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

Table 3. Model selection results evaluating the interactive effect of daily temperature and horse activity on daily visitation to water by pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*).

Model†	*K*‡	LL§	ΔAIC_c¶	w_i#
Pronghorn				
Trees + Temp + Horse + Temp × Horse	9	−14,257.20	0.00	0.65
Trees + Rugged + Temp + Horse + Temp × Horse	10	−14,257.20	2.00	0.24
Rugged + Temp + Horse + Temp × Horse	9	−14,259.80	5.20	0.05
Trees + Temp + Horse	8	−14,261.20	6.00	0.03
Temp + Horse + Temp × Horse	8	−14,261.70	7.00	0.02
Trees + Rugged + Temp + Horse	9	−14,261.20	8.00	0.01
Rugged + Temp + Horse	8	−14,263.70	11.00	0.00
Trees + Temp	7	−14,287.20	55.99	0.00
Trees + Rugged + Temp	8	−14,287.20	58.00	0.00
Rugged + Temp	7	−14,289.80	61.19	0.00
Trees + Horse	7	−14,376.40	234.39	0.00
Trees + Rugged + Horse	8	−14,376.40	236.40	0.00
Rugged + Horse	7	−14,379.00	239.59	0.00
Mule deer				
Rugged + Temp + Horse + Temp × Horse	9	−16,654.60	0.00	0.45
Trees + Rugged + Temp + Horse + Temp × Horse	10	−16,654.00	0.80	0.30
Trees + Temp + Horse + Temp × Horse	9	−16,655.30	1.40	0.22
Temp + Horse + Temp × Horse	8	−16,658.70	6.20	0.02
Rugged + Temp + Horse	8	−16,660.30	9.40	0.01
Trees + Rugged + Temp + Horse	9	−16,659.70	10.20	0.00
Rugged + Temp	7	−16,662.00	10.79	0.00
Trees + Temp + Horse	8	−16,661.00	10.80	0.00
Trees + Rugged + Temp	8	−16,661.40	11.60	0.00
Trees + Temp	7	−16,662.80	12.39	0.00
Rugged + Horse	7	−16,805.70	298.19	0.00
Trees + Horse	7	−16,806.00	298.79	0.00
Trees + Rugged + Horse	8	−16,805.10	299.00	0.00

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

† Trees, proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse, activity (no. of pictures) of horses; rugged, ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Temp, maximum daily temperature.

‡ Number of parameters.

§ Model log-likelihood.

¶ Change in AIC_c value compared to top model.

AIC_c weight.

sources more heavily used by horses. We also observed temporal shifts in water use by pronghorn in response to increased activity of horses. However, we did not detect temporal shifts for mule deer in response to horse activity; likely due to horses being primarily diurnal, while mule deer accessed water during crepuscular or nocturnal periods, suggesting horses may impact pronghorn more than mule deer.

Large herbivores can influence patterns of water use by smaller, less competitive species (Valeix et al. 2007, 2008, Hall et al. 2016*b*). For example, relatively small African herbivores generally avoided times of peak visitation to waterholes by elephants (Valeix et al. 2007). Desert bighorn sheep exhibited a similar pattern using alternative water sources when a horse was present at a regularly used water source (Ostermann-Kelm et al. 2008). Similarly, Nubian ibex (*Capra nubiana*) avoided water sources that had been recently used by feral donkeys (*Equus africanus asinus*) in northern Africa (Attum et al. 2009). In a more direct fashion, horses were observed on multiple occasions actively preventing elk (*Cervus elaphus*) from accessing water (Perry et al. 2015). In each of these examples, larger dominant herbivores outcompeted smaller herbivores for water. Moreover, the latter three studies highlighted how a feral equid

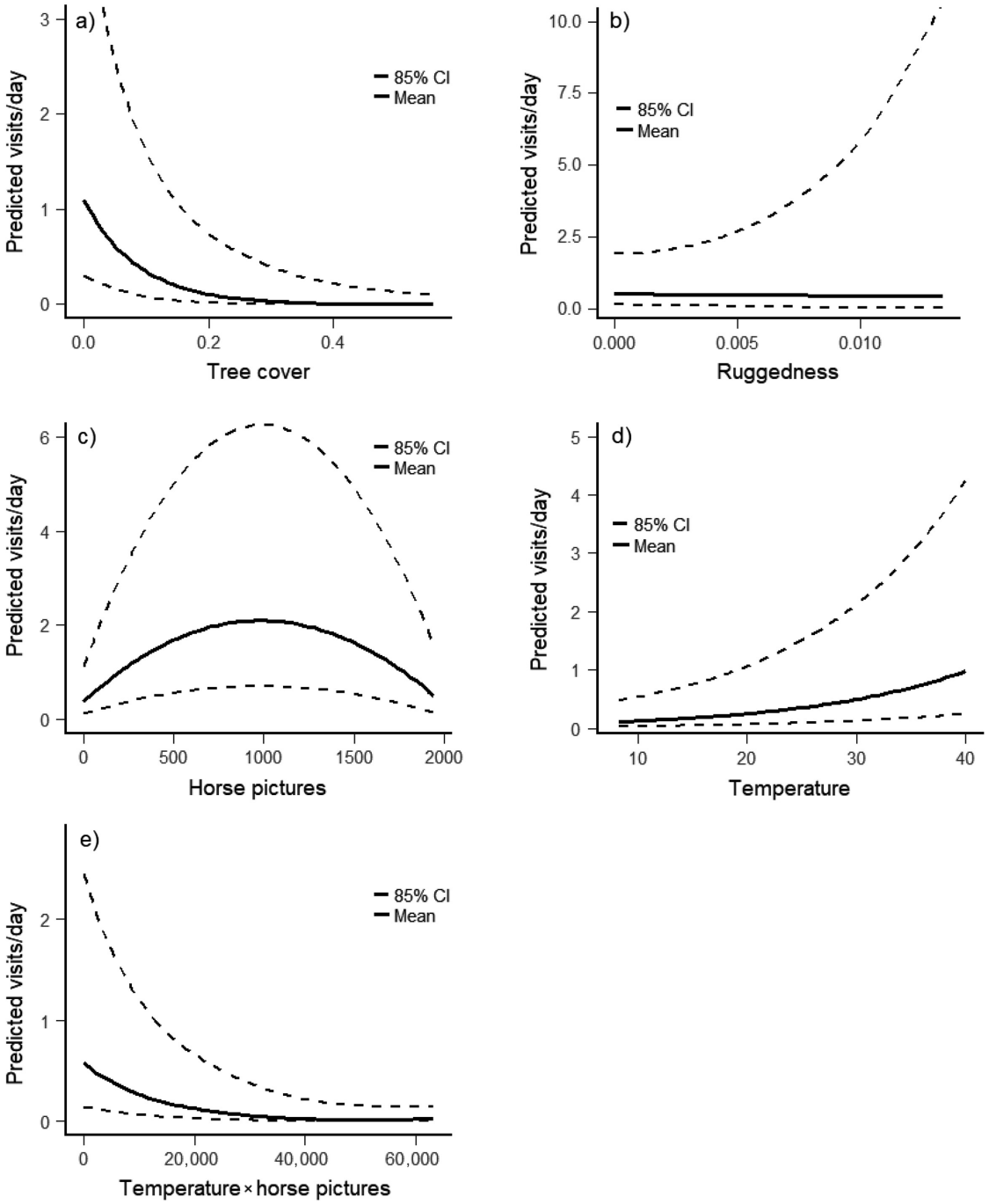


Fig. 7. Predicted visits (with 85% confidence intervals) to water by pronghorn (*Antilocapra americana*) based on variables from the top generalized linear mixed models evaluating the interactive effect of daily temperature and horse (*Equus caballus*) activity. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014. Tree cover = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse pictures = activity (no. of pictures) of horses; and ruggedness = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

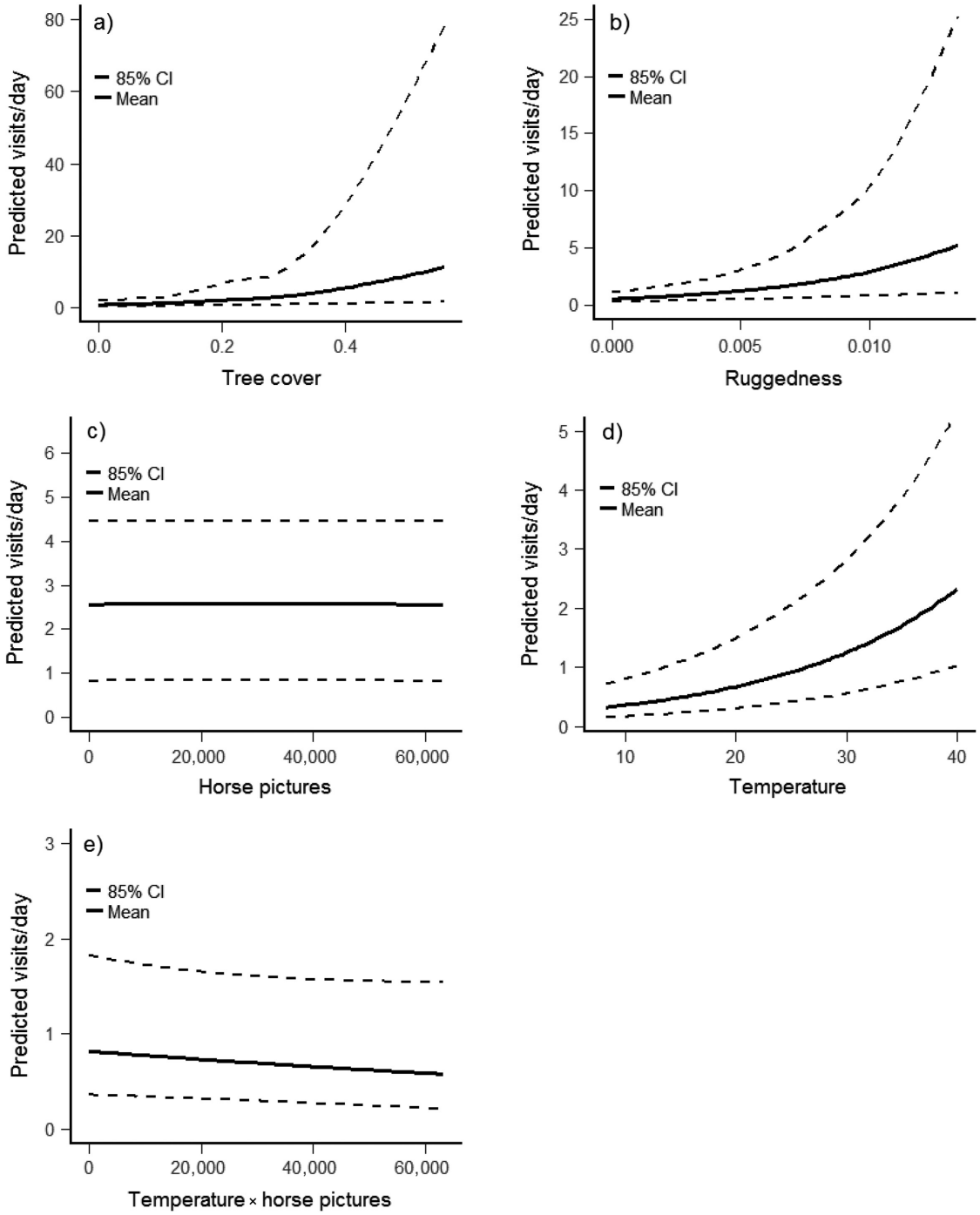


Fig. 8. Predicted visits (with 85% confidence intervals) to water by mule deer (*Odocoileus hemionus*) based on variables from the top generalized linear mixed models evaluating the interactive effect of daily temperature and horse (*Equus caballus*) activity. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014. Trees = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse = activity (no. of pictures) of horses; and rugged = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

can influence patterns of resource acquisition by smaller native species (Ostermann-Kelm et al. 2008, Attum et al. 2009, Perry et al. 2015).

Competing for limiting resources can result in trade-offs for the species involved. In arid and semi-arid regions, many species face a trade-off associated with accessing limited water resources and minimizing conflict with more competitive species (Atwood et al. 2011, Edwards et al. 2015). In our study system, there may be fitness costs associated with the trade-off of directly competing with horses versus using different water sources or allocating use at different times, when horses are absent. Prior work conducted in the Great Basin Desert on use of water by horses and pronghorn found the latter devoted more time to vigilance behavior and foraged and drank less in the presence of horses (Gooch et al. 2017). While the long-term implications of this behavioral modification are largely unknown and may be negligible, our work supports previous research, indicating that horses can alter the drinking patterns of pronghorn.

The intense use of water by horses during periods of increased temperatures and physiological stress (Perry et al. 2015, Hall et al. 2016*b*) raises conservation concerns for native species that compete with horses for water. Based on our mixed-effects models, visits to water sources for pronghorn and mule deer were reduced on particularly hot days when activity of horses was high. With models of global climate change predicting increased temperatures and aridity in many deserts, water will likely become less available for species inhabiting these areas (Ault et al. 2014, Cook et al. 2014, Wanders et al. 2015). While reduction of water availability is not a novel challenge for desert species, the rapid loss of water in these systems (due to contemporary climate change) will likely pose additional challenges for desert biota (Hall et al. 2016*a*). Water already serves as a major selective force in warm and dry environments (Noy-Meir 1973). Further loss of water from the environment combined with competition with increasing populations of feral species will likely create additional conservation and management issues for native species.

Our study provides a multi-year perspective on how a behaviorally dominant, feral species such as the horse can alter the spatial and temporal use of a limiting resource by native species. While we did not experimentally manipulate the density of horses to identify a causal relationship for the patterns that we observed, we capitalized on differences already occurring in horse activity across water sources. We also monitored multiple water sources for five years providing extensive spatial and temporal context to our findings. We provide evidence that horses competed with and spatially displaced pronghorn and mule deer from water sources. Horses also temporally displaced pronghorn from water sources, but not mule deer. In addition, we found strong support for the interactive negative effect of increased temperature and activity of horses on drinking patterns of pronghorn and mule deer. Our findings indicated that feral horses further constrained access to an already limited resource for native species in a semi-arid environment.

Acknowledgments

We thank the many technicians that assisted in the field and laboratory (analyzing pictures) over the course of this 5-yr study. We appreciate the comments from two anonymous reviewers that greatly improved this manuscript. Funding for this study was provided by the U.S. Army Dugway Proving Ground and the Utah Division of Wildlife Resources (contract no. 106298).

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Equine vet. J. (2010) **42** (Suppl. 38) 582-586
doi: 10.1111/j.2042-3306.2010.00203.x

Distances travelled by feral horses in 'outback' Australia

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Keywords: horse; feral horses; GPS; distance; water frequency

Summary

Reasons for performing study: **The distance travelled by Australian feral horses in an unrestricted environment has not previously been determined. It is important to investigate horse movement in wilderness environments to establish baseline data against which the movement of domestically managed horses and wild equids can be compared.**

Objectives: **To determine the travel dynamics of 2 groups of feral horses in unrestricted but different wilderness environments.**

Methods: **Twelve feral horses living in 2 wilderness environments (2000 vs. 20,000 km^2) in outback Australia were tracked for 6.5 consecutive days using custom designed, collar mounted global positioning systems (GPS). Collars were attached after darting and immobilising the horses. The collars were recovered after a minimum of 6.5 days by re-darting the horses. Average daily distance travelled was calculated. Range use and watering patterns of horses were analysed by viewing GPS tracks overlaid on satellite photographs of the study area.**

Results: **Average distance travelled was 15.9 ± 1.9 km/day (range 8.1–28.3 km/day). Horses were recorded up to 55 km from their watering points and some horses walked for 12 h to water from feeding grounds. Mean watering frequency was 2.67 days (range 1–4 days). Central Australian horses watered less frequently and showed a different range use compared to horses from central Queensland. Central Australian horses walked for long distances in direct lines to patchy food sources whereas central Queensland horses were able to graze close to water sources and moved in a more or less circular pattern around the central water source.**

Conclusions: **The distances travelled by feral horses were far greater than those previously observed for managed domestic horses and other species of equid. Feral horses are able to travel long distances and withstand long periods without water, allowing them to survive in semi-arid conditions.**

Introduction

Movement and the distances travelled by domestic horses (*Equus caballus*) may affect general health. Domestic horses have become more sedentary since the industrial revolution, with many now kept in small paddocks and stables as land available for horse maintenance has declined. The athletic Thoroughbred racehorse, for example is typically boxed in a stable for 23 h/day and moved to the training track for a short gallop once daily (Richards *et al*. 2006). Hampson *et al*. (2010) found that horses kept in small yards travelled only 1.1 km/day and those housed in a 16 hectare paddock travelled a mean of 7.2 km/day. The psychological, physiological and musculoskeletal consequences of this relatively sedentary lifestyle are not fully understood, but the low level of mobility from an early age may adversely affect musculoskeletal health. Domestication of the horse has not only affected mobility but has been associated with an altered diet. Horses in training are routinely fed high energy diets twice daily and may have an abundance of pasture and water (Southwood *et al*. 1993). Confinement and altered feeding patterns parallel the modern human lifestyle that is thought to be responsible for endemic levels of obesity, cardiovascular disease, arthritis and diabetes (Johnson *et al*. 2004; Perkins *et al*. 2005; Richards *et al*. 2006; Lepeule *et al*. 2009).

Global positioning system (GPS) technology has been shown to be able to accurately measure horse movement, including distance travelled, range use and watering patterns of wild/feral equids. This method was used previously by the current research team in a pilot study to monitor 3 feral horses in Australia and found that the mean daily distance travelled was 17.9 km (Hampson *et al*. 2010). This was significantly further than wild asses (*E. hemionus*) (8.3 km/day; Kaczensky *et al*. 2008) and wild Przewalski horses (*E. przewalskii*) (3.5 km/day; Kaczensky *et al*. 2008) in Mongolia. However, female zebras (*E. burchelli*) were documented to walk approximately 15 km over a 12 h period between water and their feeding region, where they remained for 3–4 days before walking back to water (Brooks *et al*. 2007).

A total published sample size of 3 individual free roaming horses is not representative of the population and does not allow robust comparison of movement patterns to other equids. Since there appears to be substantial variation within and between equid species in locomotory habits, the aim of this further work was to monitor free-ranging feral horses in order to compare feral horse movement with the movement ecology of other equid species and managed domestic horses.

Materials and methods

Twelve feral horses were tracked using GPS data loggers to determine movement and watering patterns.

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[Paper received for publication 04.01.10; Accepted 01.07.10]

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GPS data logger

The University of Queensland Equine GPS data logger was constructed from a Wintec G-Rays GPS unit (G-Rays 2 WBT-201data logger)[1]. The store-on-board GPS unit was modified by the addition of a circuit board which controlled the power input from an additional 3 AA battery pack. The total weight of the GPS, battery, collar and a very high frequency (VHF) location beacon was 700 g. The GPS unit was mounted on a neck collar with a full sky view, counterweighted by the battery pack and VHF beacon, which hung under the horse's neck. The 130,000 position storage capacity of the unit and the life of a single battery power source (6.5 days) allowed data logging at the rate of one position every 5 s (Hampson *et al*. 2010).

Data defining both horizontal and vertical positions were downloaded via Google Earth Plus[2]. The Wintec software was used to perform distance calculations from the raw GPS positional data. The pattern of travel was also superimposed on Google Earth satellite photographs of the study area and checked for plausibility and data error. In a previous study (Hampson *et al*. 2010) the same GPS unit was determined to be sufficiently accurate to measure domestic horse movement in small paddocks and feral horse movements in large paddocks with no 'outlier' data points.

Subjects

Twelve mature feral horses, from different family bands (8 mares, 4 stallions), living in 2 different wilderness environments, were tracked for 6.5 consecutive days. Four mares and 4 stallions were tracked at one location, which was semi-arid country on a large cattle property (Babbiloora) in central Queensland (latitude –25.18, longitude 147.49). The area receives a mean annual rainfall of 528.5 mm, and 157 mm had fallen in the 6 months prior to data collection (Bureau of Meteorology, Australia). The area had a large body of feed in all areas of the paddock accessed by the horses. Four mares were tracked at the second location, which was a semi-arid environment near Kings Canyon in central Australia (latitude –24.50, longitude 132.10). This 20,000 km^2 area consists of a valley system bordered by high prominent escarpments and is surrounded by vegetated and nonvegetated sand dunes measuring 15 m in height. Mean annual rainfall is 335 mm and rainfall was 331 mm in the 6 months prior to data collection (Bureau of Meteorology, Australia). There was high competition for feed resources in this area between feral cattle, horses and camels. Vegetation was scarce within 15 km of the single permanent water hole. All other semi-permanent waterholes in the area were dry at the time of the study as confirmed by the local indigenous people and stockmen. Ground and aerial searches from helicopter also confirmed that all animal tracks converged at this single waterhole. Feral horses have inhabited both areas for in excess of 140 years (Berman 1991) and experience very little pressure from human intervention. The breed origins of the horses were uniform with influence from early Thoroughbred, Arab and station hack horses.

GPS collar placement

In order to apply the collars, horses were darted i.m. with 0.7 ml etorphine hydrochloride (Imobilon)[3] when they approached water. When the horse became laterally recumbent, the collar was attached to the upper neck and the immobilising agent reversed using 1.4 ml diprenorphine hydrochloride (Revivon)[3] injected i.v. Horses returned to their usual band within 15 min of darting and appeared unaffected by the neck collar and the initial human contact. After a minimum of 6.5 days, the same feral horses were relocated using the VHF beacon on their collar and again immobilised by darting. The collars were removed, the immobilising agent reversed and the horses released.

Watering frequency

Both study locations had only one watering point available to the horses at the time of the study. Watering frequency was determined by the frequency that horses approximated the position of the water point on the Google Earth satellite photograph of the study area.

Statistical analysis

Distances travelled were compared between groups depending on sex and location of the horses using a nonparametric Wilcoxon *t* test. Statistical significance was set at 0.05. All values are presented as mean ± s.e.

The project was approved by the University of Queensland Animal Ethics Committee (AEC-PCA) monitoring compliance with the Animal Welfare Act (2001) and The Code of Practice for the care and use of animals for scientific purposes (approval number SVS/393/07/AHF).

Results

GPS analysis of travel distance

Mean daily distances travelled by all horses over the 6.5 day period of GPS tracking are presented in Figure 1. There was a large range of mean daily distances (8.1–28.3 km) covered by the horses. The mean daily distance travelled by all horses combined was 15.9 ± 1.9 km. During the period of tracking, stallions (18.2 ± 2.91 km/day) tended to travelled further on average than mares (14.8 ± 2.5 km/day) but this difference was not significant due to the small sample size. Mean daily distance travelled was 16.8 ± 1.71 km by central Queensland horses and 14.7 ± 4.17 km for central Australian horses. The mean daily distance travelled, regardless of gender was not significantly affected by location. However, central Queensland horses tended to travel a similar distance each day and

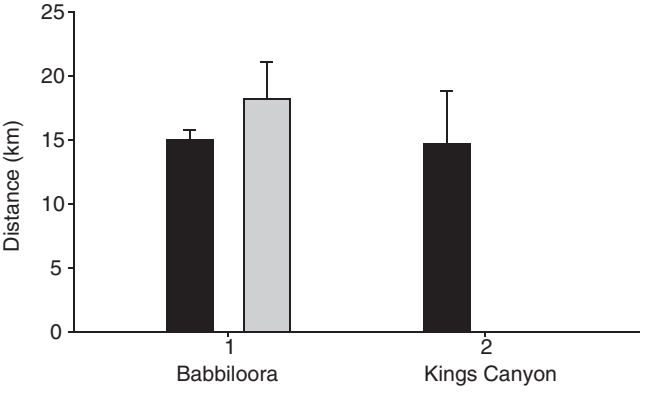


Fig 1: Mean ± s.e. daily distance (km) travelled by female (■) and male (□) feral horses in 2 inland Australian locations, Babbiloora (central Queensland) and Kings Canyon (central Australia). Distances travelled were measured by GPS tracking collar. Stallions did not travel significantly further than mares.

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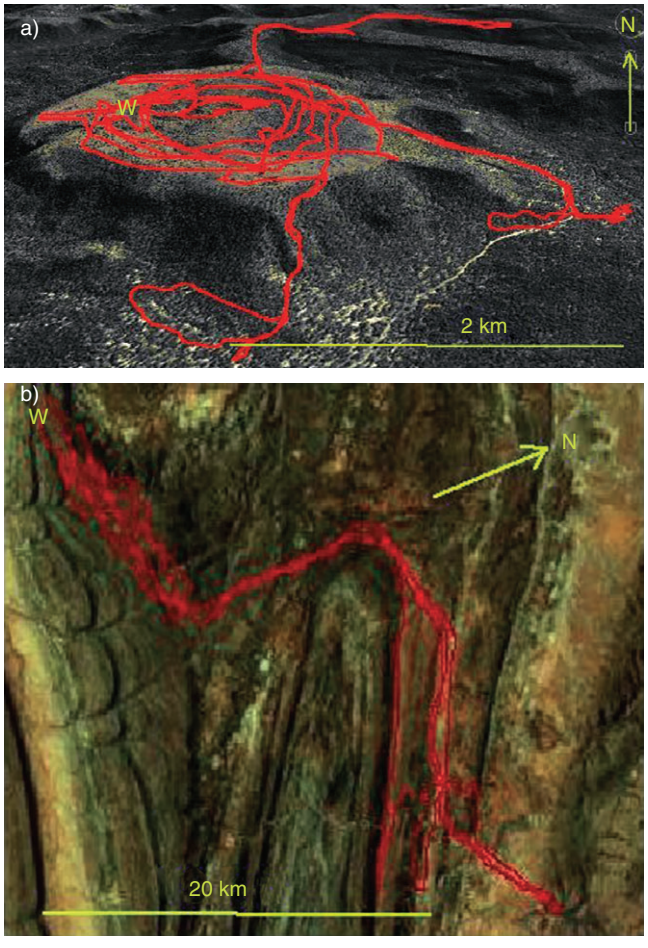


Fig 2: Comparison of typical ranges of horses in the 2 different environments. a) Shows the GPS path of a band stallion in prime grazing country. Each daily travel distance is consistent and within 3.5 km of a central waterhole (W). b) Shows the GPS path of a desert mare with a young foal at foot. Water (W) is at one end of the path and the preferred feeding ground is a distance of 22.5 km from water. True North is shown by 'N'. The end of the path is around 40 km in a straight line from the marked water.

never more than approximately 8 km from water. Central Australian horses travelled significantly greater single day distances when travelling to and from water and were frequently recorded at distances of 15–55 km from water. Long distance travelling days (mini-migrations), to and from water, were followed by short travelling days within good feeding locations (Fig 2).

Watering frequency

The mean watering frequency of central Queensland horses was 2.1 ± 0.9 days (range 1–3 days). Central Australian horses watered less frequently and this difference was significant ($P<0.05$). Their mean watering frequency was 3.2 ± 0.8 days (range 2–4 days).

Discussion

There is a large variability of range use ecology within the Equid family. There have been several previous studies reporting the home range size of feral horses determined by repeated sightings during ground based observations. The accuracy of observation vs. GPS data logging has not been established but observation has previously been the gold standard for animal ecologists (Linklater *et al*. 2000). Since the introduction of accurate and reliable GPS, animal ecologists are now able to monitor animals regularly for long periods without risk of interference. Linklater *et al*. (2000) reported a home range size for Kaimanawa feral horses of 0.96–17.7 km^2 for 48 horse bands (horse groups). Kaimanawa horses have a similar breed origin to the Australian feral horses (Halkett 1996). Linklater *et al*. (2000) found that all band home ranges overlapped with others and were located within an area of approximately 7 × 4 km. Similar spatial organisation of feral horses was reported by Klingel (1975), Salter and Hudson (1979) and Feist and McCouough (1975) in feral horse populations confined in small ranges. However, the study of arid and semi-arid habitat horses in Nevada (Berger 1986), western Alberta (Salter and Hudson 1982) and Wyoming (Miller 1983), have reported larger home ranges. These studies relate the increased size of the home ranges to resource demand. Kaczensky *et al*. (2008) were the first to report equid movement and home range size using GPS technology. Over a 4 year period in Mongolia, wild Przewalski horses had ranges of 152–826 km^2, significantly larger than reported for feral horses elsewhere. Over this 4 year period Przewalski horses travelled approximately 60 km from one end of their range to the other but the mean daily distance was 3.5 ± 0.9 km. On average, Przewalski horses ventured only 9 ± 2.9 km from the nearest water. The same study reported home ranges of 4449–6835 km^2 with a mean daily distance of 8.3 ± 0.7 km for Asiatic wild asses. Asses ventured a mean of 13.5 ± 0.9 km away from water. Other *Equidae* studied include the plains zebras which were recorded using GPS trackers walking up to 15 km away from water to feed and returning to water at 3–4 day intervals (Brooks *et al*. 2007). The current study used GPS technology to determine feral horse movement and watering patterns. We found that central Australian and central Queensland feral horses travelled larger mean daily distances than other equids reported previously. Central Australian horses, in particular, travelled up to 55 km from water and had large interwatering intervals.

The current study found that even though the average daily distance did not vary significantly between the 2 populations from contrasting habitats, the day by day routine of the horses was quite different and appeared to be dependent on resource location. In central Queensland, there was little requirement for horses to travel large distances between food and water. Pasture was widespread and pasture quantity close to water was similar to that at a distance away from water. However, in central Australia, resource distribution was scarce and patchy. Feed tended to grow solely along gully floors and low lying areas where water may have pooled and soaked the ground for several days following infrequent rain. Berman (1991) studied the ecology of feral horses in the same study area in the mid 1980s and measured the herb cover at distance intervals from the same permanent water source used by horses in the current study. Herb cover increased relative to the distance away from water (Fig 3), indicating the large competition for food resources close to water. Berman (1991) found evidence of horses 65 km away from the only available water source.

The current study located horses 55 km from Berman's (1991) water point. In consideration of the long walks the horses must make to access water from distant feed grounds it is not surprising that watering frequencies were as low as every fourth day. Scheibe *et al*. (1998) found that Przewalski horses drank less frequently than domestic horses and drank a higher volume of water relative to body size. They suggested that drinking frequency was not as

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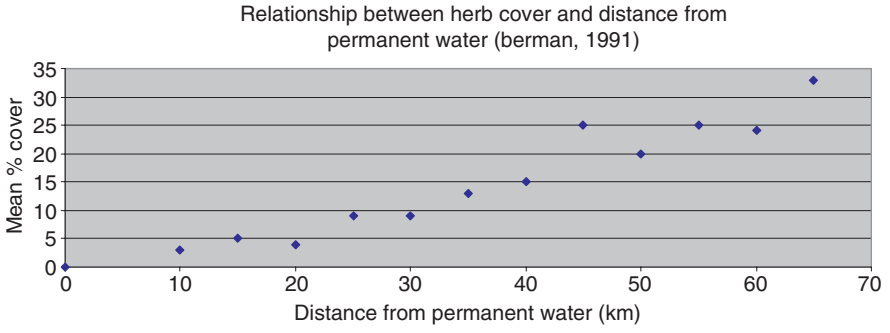


Fig 3: The relationship between herb cover and distance from permanent water in the desert horse habitat recorded by Berman (1991). Horses had to travel long distances from water to access feeding grounds. Feed within a range of 20 km from water was minimal. A similar situation existed in this location during the present study. This graph was drawn from data from Berman (1991) with permission from the author.

important to wild horses as the amount of water consumed. Horses that drank less frequently also ingested larger volumes of water. These authors, as well as Bouman and Bouman (1994) and Sneddon *et al*. (1991) all suggested that desert-dwelling horses are genetically adapted to hot and dry climates as part of the evolutionary strategy of the species. Other equid species have apparently also adapted to arid conditions. Maloiy (1970) subjected Somali donkeys (*E. asinus*) to heat stress and dehydration. Donkeys survived water loss equivalent to 30% of their original bodyweight in temperatures up to 40°C and survived up to 12 days without water. Donkeys were able to drink enough water (24–30 l) in 2–5 min to restore the deficit. Maloiy (1970) concluded that these observations represented a thermal and metabolic adaptation of desert mammals to heat and aridity. This adaptation did not totally eliminate the need to drink water, but permitted a considerable degree of dehydration. Donkeys are capable of living and reproducing in arid habitats similarly to camels in the Middle East, northern and eastern Africa and central Asia.

Central Australian horses may also be genetically adapted to arid conditions. The population of feral horses in the semi-arid areas of central Australia can be reduced by up to 75% in times of severe drought (Berman 1991). The ability to travel up to 65 km from water to access feed (Berman 1991) and survive for at least 4 days without water (present study) may represent a physiological adaptation of the original domestic horse stock that were the founders of the feral horses over 140 years ago. The strong pressure of the frequent severe droughts in central Australia for natural selection may have driven a genetic change. In contrast, domestic horses travel very small distances compared to their feral relatives (Hampson *et al*. 2010), generally have free access to water and have been documented to drink several times daily (Scheibe *et al*. 1998). Scheibe *et al*. (1998) suggested that the high water consumption of domestic horses may be a learned behaviour acquired under conditions of abundance.

The current study determined the range of 12 adult feral horses in 2 different wilderness environments over a 6.5 day period. Mean distance travelled was 15.9 ± 1.9 km/day (range 8.1–28.3 km/day). Horses in the central Queensland habitat, with plentiful pasture, tended to remain close to water (maximum 8 km from water). Central Australan horses were recorded up to 55 km from water and some horses walked for 12 h to reach water. Feed was scarce within a range of 15 km from the water point in the central Australian habitat due to competitive grazing by large numbers of feral horses, feral cattle and feral camels. These horses watered less frequently (3.2 ± 0.8 days; range 2–4 days) than central Queensland horses. Central Australian feral horses travelled longer mean daily distances and recorded longer watering intervals than other wild equids (Rubenstein 1989; Berman 1991; Scheibe *et al*. 1998; Adriansen and Nielson 2005; Brooks *et al*. 2007; Kaczensky *et al*. 2008). The unique ecology of the central Australian horse, as shown by this study, warrants further study.

The ability to survive the extreme environment of central Australia may be within the phenotype of all horses and simply a testament to the versatility of *E. caballus* as a species. On the other hand the central Australian population, subjected to the extreme selection pressure of the harsh environment, may have already inherited traits that set them apart from their domestically managed cousins.

Conflicts of interest

The authors have declared no potential conflicts.

Manufacturers' addresses

[1]Wintec Wireless Electronics, Taiwan.
[2]Google Earth Plus, google.com.
[3]Novartis SA (Pty) Ltd. Base, Switzerland.

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The Nutritional Basis for Food Selection by Ungulates

THOMAS A. HANLEY

Abstract

A conceptual framework is outlined for understanding the reasons why ungulates select the kinds of foods that they do. It consists of four morphological parameters: (1) body size and (2) type of digestive system (cecal or ruminant) determine the overall time-energy constraints within which the ungulate may forage selectively; (3) rumino-reticular volume to body weight ratio determines the type of food the ruminant is most efficient in processing; and (4) mouth size determines the ability of the ungulate to harvest selectively plant parts of individuals. Principal premises are the following: (1) large ungulates and cecal digestors are more limited by time than are small ungulates and ruminant digestors; (2) high rumino-reticular volume to body weight ratio is an adaptation to exploiting thick cell-walled, high cellulose diets (i.e., graminoids); and (3) low rumino-reticular volume to body weight ratio is an adaptation to exploiting thin but lignified cell-walled diets (i.e., browse).

The composition of diets selected by wild and domestic ungulates has long been of interest to range and wildlife ecologists. Numerous tabulations of diet composition data are available in the literature. However, diet composition data alone are not satisfactory for explaining the reasons for observed diet differences between animal species. A knowledge of the reasons why ungulates select the foods that they do is necessary for an understanding of the forage needs of range animals and the underlying basis of competitive interactions among them.

The theory of optimal foraging strategies has provided a means of examining resource partitioning in consumer communities. It is a theory based on the assumption that natural selection acts on phenotypic variation within populations with the result that greatest genetic fitness is conferred to individuals which feed most efficiently (i.e., prefer an optimal diet). The primary objective of the theory is to specify the complex of behavior and morphology which best suits a particular animal to a particular environment (Schoener 1971). A prerequisite of devising tests of this hypothesis is that the optimal diet can be defined. The problem of determining an optimal diet under a given set of circumstances consists of three major parts: (1) choosing the most appropriate currency to be maximized (e.g., energy); (2) determining the most appropriate constraints imposed on the animal; and (3) solving for the optimum solution to the cost-benefit functions (Shoener 1971). This has most commonly resulted in the following algorithm for determining the optimal diet (defined as the diet which maximizes the net rate of energy or mass intake in a fine-grain situation): potential food items are ranked by their net values, i.e., ratio of food value (however defined) to handling time; abundances of food types and total time for foraging are taken into account; and the optimal diet is then determined by beginning with the food type of highest net value and adding food types in rank order to the diet as long as the net rate of food intake is increased by the inclusion of the additional food type in the diet (Pyke et al. 1977). Optimal diets determined in this manner have three properties in common: (1) whether or not a food type is included in the optimal diet is independent of the abundance of that food type and depends only on the abundance of higher quality food types; (2) as the abundance of a preferred food type increases, less preferred food types drop out of the optimal diet; and (3) any food type within the optimal diet is either eaten whenever encountered or passed by whenever encountered (unless differential nutrient constraints also are considered; e.g., Pulliam 1975) (Pyke et al. 1977). This theory has centered on the strategic aspects of feeding and seldom has dealt with the tactical aspects. Although numerous papers have dealt with optimal foraging strategies (Emlen 1966, 1968; MacArthur and Pianka 1966; Levins 1968; Levins and MacArthur 1969; Schoener 1969, 1971; Tullock 1971; Rapport 1971; Cody 1974; Pulliam 1974, 1975; Katz 1974; Westoby 1974; Estabrook and Dunham 1976; Ellis et al. 1976; Pyke et al. 1977; Hughes 1979; Stenseth and Hansson 1979; Sih 1979), the applicability of this theory to ungulate food selection remains unsatisfactory (Westoby 1978). The existing theory largely has developed around data on food selection by carnivores, granivores, and frugivores, all of which prey upon food items occurring as discrete "packages." Large, generalist herbivores, on the other hand, select food items from a chemically heterogeneous spectrum, and what constitutes an individual food item is often not evident. Chemical description of the food item is itself a difficult task, each plant being highly variable, depending on plant part (Gwynne and Bell 1968, Halls and Epps 1969, Blair et al. 1977), plant vigor (Cook et al. 1962), habitat (Halls and Epps 1969), phenology (Laycock and Price 1970), and intraspecific variation (Garten 1978). Furthermore, different species of plants differ greatly in their content of specific nutrients (Cowan et al. 1970) as well as toxins and digestion inhibitors (Levin 1976, Feeny 1976, Rhoades and Cates 1976, Jung 1977, Laycock 1978), the so-called secondary plant compounds. A large, generalist herbivore therefore must select a diet within the constraints of minimal levels of specific plant nutrients (Halls 1970, Westoby 1974) as well as maximal levels of specific secondary plant compounds (Freeland and Janzen 1974).

To apply existing optimal foraging models to ungulate food selection it must be assumed that large, generalist herbivores can rank potential food items according to their net value. Furthermore, the animal must be able to keep track of the constantly changing values of the food items and adjust their ranked values as a function of differing phenologies and habitats. The foraging ungulate would have to detect the values of individual species while consuming continuous multi-species meals. The ruminant herbivore would be confronted with the additional complication of differing nutritional value of a food item as a consequence of other food items in the rumen (Church 1975). The tactical difficulties of such a scenario have been addressed by Westoby (1978), who concluded that the underlying assumptions of current optimal

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Manuscript received July 31, 1980.

foraging models were not met satisfactorily by the case of the large generalist herbivore. Even if this were not so, the difficulties of quantifying the necessary parameters are great. However, although we are not yet able to predict the "optimal diet" in quantitative, taxonomic terms for a given ungulate, it would appear feasible to predict the general type of diet that an ungulate, given a choice, will select. Ruminant nutritionists, and more recently ecologists, have developed a body of knowledge and a conceptual framework for understanding food selection and food resource partitioning in ungulate communities. The purpose of this paper is to review this framework and to identify some implications for competition theory and habitat management.

Forage Selection Framework

The framework consists of four morphological parameters: (1) body size, (2) type of digestive system (cecal or ruminant), (3) rumino-reticular volume to body weight ratio, and (4) mouth size. The hypothesis is that a knowledge of the values of these parameters is sufficient for prediction of the types of foods a given ungulate is most efficient in exploiting; or conversely, knowledge about the types of food available in a given habitat is sufficient to predict values of these morphological parameters for the type of ungulate(s) most efficient in exploiting them. Briefly, the idea is that body weight and type of digestive system determine the overall time-energy constraints within which the ungulate must secure its food. Rumino-reticular volume determines the type (characteristics of) food items the ruminant is most efficient in processing. Mouth size determines the degree of selectivity that is mechanically possible for the forager to exhibit and the time and energy costs of selectively foraging on specific plant parts or individuals.

Body Size

The food requirements of mammals increase with increasing body weight as a result of increasing costs of maintenance and production (Moen 1973). The increase is not linear, however (Cordova et al. 1978). Kleiber (1961) estimated that the basal metabolic rate (kcal/day) of mammals is approximately seventy times the three-fourth power of their body weight (in kg). Thus although larger mammals require more nutrients per day than smaller mammals do, their *relative* requirements (per unit weight of body tissue) are lower. The relative value of large body weight in the food selection process is dependent upon the availability of nutritious forage (Case 1979). A larger mammal, requiring a greater absolute quantity of nutrients during a day, has less time per nutrient unit to spend selectively foraging than does a smaller mammal with a lower absolute requirement. The larger mammal has a lower relative requirement, however, and therefore can meet its nutritional needs with relatively lower quality forage. Thus, Bell (1969, 1971) has generalized that where forage *quantity* is limiting, small body size is advantageous; where forage *quality* is limiting, large body size is advantageous. The "limiting" nature of the forage quantity or quality is determined by the time-energy constraints upon the forager. A smaller forager has relatively more time to spend foraging (and therefore can be more selective in what it chooses to eat); but the benefits of spending more time foraging must outweigh the costs. Energy cost for the foraging ruminant is a direct function of the time spent foraging (Osuji 1974).

Digestive System

Although the cellular contents of plants are high digestible, the plant cell wall poses digestive difficulties for herbivores (Van Soest 1965a, 1965b; Smith et al. 1971, 1972). Two major types of digestive systems have evolved in ungulates to enable them to digest plant cell walls by anaerobic fermentation and to subsist on relatively high fiber diets. These are the ruminant and the cecal digestive systems (Janis 1976). The ruminant system has evolved in the Artiodactyla and is found in most species of this group. All species of the Perissodactyla are cecal digestors. The actual process of fermentation is very similar in the rumen and the cecum (Janis 1976); and the rate of digestion of a cotton string in the cecum of a horse is comparable to that in the rumen of a cow (Alexander 1952). However, horses are only about 70% as efficient as cattle and sheep are in digesting cellulose (Heinlein et al. 1966, VanderNoot and Gilbreath 1970, Janis 1976).

The ruminant digestive system has two principal advantages. One is that the regurgitated "cud" can be chewed repeatedly, thereby grinding the food to a smaller particle size. The other is that food is digested by microbes *before* entering the true stomach (abomasum). Plant material is digested by bacteria and protozoa in the rumen and converted to microbial tissue or waste products which are absorbed there or ultimately digested by the ruminant in the abomasum. This has advantages in terms of nitrogen cycling and digestive efficiency (Houpt 1959, Mugerwa and Conrad 1971, Nolan and Leng 1972, Robbins et al. 1974). In the cecal digestive system, microbial fermentation takes place *after* the food has passed through the stomach, and very little microbial protein can be recycled (Janis 1976). The principal disadvantage of the ruminant digestive system is that in order for food to pass from the rumen into the rest of the digestive tract, it must be broken down to a relatively small particle size (Hungate 1966). Very fibrous forages, therefore, limit the rate of food passage through the gastrointestinal tract of the ruminant and restrict consumption of additional forage (Fontenot and Blaser 1965, Van Soest 1965a, Weston 1966, Ammann et al. 1973). The cecal digestor, however, is not limited by such a constraint (Janis 1976). It may be less efficient at digesting the fibrous cell walls of plants but can pass much more plant material through its system daily. The ruminant must be a more selective forager than the cecal digestor must be; but being a more efficient digestor, it requires a lower absolute quantity of forage. It therefore has been generalized that where forage *quantity* is limiting, a ruminant digestive system is advantageous; whereas where forage *quality* is limiting, a cecal digestive system is advantageous (Bell 1969, 1971; Janis 1976). This is analogous to the relative value of body size and therefore is similarly important in determining the overall time-energy constraints on the foraging ungulate.

Rumino-reticular Volume

The most basic subdivision of plant material is between cellular contents and cell walls (Van Soest 1965b, 1967; Van Soest and Wine 1967). The cellular contents are highly digestible, generally about 98% digestible (Goering and Van Soest 1970), but the cell walls are much less so. Plant cell walls are composed primarily of cellulose, hemicellulose, and lignin. Cellulose is digestible by rumen and cecal microbes; hemicellulose may or may not be digestible, depending on the type of hemicellulose; and lignin is generally considered nondigestible (Goering and Van Soest 1970; Smith et al. 1971, 1972). Plant species and plant parts differ in their proportions of cellular contents, cellulose, hemicellulose, and lignin. Rapidly growing plant tissue and the leaves and new stem production of shrubs and forbs generally have relatively thin cell walls and a high proportion of cellular contents (Short 1971, Segelquist et al. 1972, Cook 1972, Albersheim 1975, Blair et al. 1977, Milchunas et al. 1978:8, Short 1981). Mature grasses and woody tissue, however, generally have thick cell walls, composed primarily of cellulose in grasses, and relatively high in lignin in shrubs (Short 1971, Johnston et al. 1968, Segelquist et al. 1972, Cook 1972, Albersheim 1975, Blair et al. 1977, Milchunas et al. 1978:8, Short 1981).

Plant cellular contents, therefore, are the most valuable food source for herbivores, but their relative availability is seasonal and/or dependent upon the degree of selectivity that the herbivore can exercise. Cellulose is potentially a high energy food source and is relatively abundant where grasses comprise a substantial proportion of the vegetation. Cellulose digestion, however, is a time dependent process with a sigmoidal response curve (Hungate 1966, Torgerson and Pfander 1971), presumably due to the increased rate of digestion as long fibers are broken into many shorter fibers by enzyme action.

Cellulose digestion and the rate of food passage through the rumen are closely related aspects of ruminant digestion (Nagy et al.

1969). In order to benefit from a high cellulose diet, food must be retained in the rumen for a sufficient time to digest the cellulose. For an animal with a relatively small rumen, rumen fill is reached in a relatively short time during feeding (Purser and Moir 1966), and consequently voluntary intake would be greatly restricted on a high cellulose diet. An animal with a large rumen, however, would have a relatively slow rumen turnover rate, thereby keeping a given food particle in the rumen for a longer time period despite a relatively high rate of food consumption. Voluntary intake would not be as greatly restricted as for the animal with the small rumen. Thus, a large rumen is advantageous for subsisting on a high cellulose (i.e., graminoid) diet (Nagy et al. 1969).

The proportion of lignin in a forage is an important factor affecting the nutritional quality of a forage. Lignin is not only virtually nondigestible, but also interferes with cellulose digestion (Head 1961; Smith et al. 1971, 1972; Robbins and Moen 1975), presumably by decreasing the amount of cellulose accessible for bacterial action. It therefore would be disadvantageous for an animal with a large rumen to consume a diet relatively high in lignin (e.g., browse). A slow rumen turnover rate in such a case would greatly reduce the efficiency of rumen fermentation (Hungate 1966, 1975). On the other hand, a high rumen turnover rate would be advantageous for an animal with a diet relatively high in lignin. Plant cellular contents are digested very rapidly (Van Soest 1965a; Hungate 1966, 1975), and the rapid passage of the lignified cell walls would be beneficial. For a ruminant to subsist on such a diet, however, it must be able to obtain a diet relatively high in cellular contents and not waste time and energy processing lignin and cellulose.

The rumino-reticular volume to body weight ratio (l/kg) of a ruminant therefore determines the type of food the ruminant is most efficient in digesting. High rumino-reticular volume to body weight ratio is an adaptation to a high cellulose content diet, typically a diet consisting primarily of grasses. Low rumino-reticular volume to body weight ratio is an adaptation to a high cellular content and/or high lignin diet, typically a diet consisting primarily of young grasses, forbs, and browse (Nagy et al. 1969, Hofmann and Stewart 1972). Rumino-reticular volume to body weight ratios of North American ungulates typically range from about 0.10 (e.g. deer, *Odocoileus* spp.) to 0.25 (e.g. domestic sheep, *Ovis aries,* and cattle, *Bos* spp. (See Hanley and Hanley (1982), for an analysis of diet selection by these species).

Hofmann (1973) studied the diet composition and stomach morphology of 26 species of African ruminants. On the basis of data collected from 263 animals, he classified African ruminants into three major groups based on stomach structure and food selection: (1) concentrate selectors, (2) bulk and roughage eaters, and (3) intermediate feeders. The concentrate selectors had very small rumens and diets of fruit, forb foliage, and tree and shrub foliage. The bulk and roughage eaters had very large rumens and diets of grasses. The intermediate feeders had intermediate size rumens and diets of grasses, forbs, and tree and shrub foliage. In studies of digestive efficiency, Maloiy et al. (1970) found that red deer *(Cervus elaphus),* with a smaller rumino-reticular volume to body weight ratio than sheep *(Ovis aries),* were less efficient cellulose digestors than sheep. On the other hand, white-tailed deer *(Odocoileus virginianus),* with a smaller rumino-reticular volume to body weight ratio than cattle (*Bos* spp.), have been reported to be more efficient than cattle in utilizing browse forages (Short 1963). Similar results for deer and sheep have been reported by Longhurst et al. (1968). Differences in rumen volume and turnover rate have been suggested as being important factors in resource partitioning in ungulate communities (Hungate et al. 1959, Milchunas et al. 1978).

Mouth Size

The degree of selectivity that *can* be exercised by a large herbivore, within its time-energy constraints, is determined largely by mouth size. Animals with small mouths are more capable of being selective of plant parts than animals with large mouths are (Meyer et al. 1957, McClymont 1967, Jarman 1974). Mouth size and bod size, however, seem to be highly correlated, presumably because c the overall time-energy constraints on forage selectivity. Data fror fistulated animals show that sheep obtain a higher quality diet tha cattle do by selecting higher quality plant parts when both speci have access to the same forage (Cook et al. 1963, Church 1975:54 Empirical observations of differential effects of grazing antelop bitterbrush *(Purshia tridentata)* by cattle, sheep, and deer als demonstrate the importance of mouth size. Whereas grazing b cattle results in a club-shaped or mushroom-shaped, heavil hedged shrub, grazing by sheep or deer results in a tall, straggl growth form. The difference is due to the consumption of ol woody tissue along with the current annual growth by cattl compared to the selective removal of only the current annu growth by sheep and deer (Hormay 1943). Observations of tam Rocky Mountain elk *(Cervus elaphus)* and mule deer *(Odocoileu hemionus)* foraging in the same habitats indicated an average bit size (oven-dry weight) of about 0.4 to 0.6 grams for elk (Collins a al. 1978) compared to 0.1 grams for deer (Deschamp et al. 1979 Whereas deer were highly selective when browsing shrubs an removed only the leaves and current annual growth, elk, with the larger mouths, removed both old and new growth with each bit (W.B. Collins and J.A. Deschamp, personal correspondence).

Relationships between Parameters

Several relationships between parameters have been mentione already. In terms of the time-energy constraints imposed on th foraging ungulate, large body size and cecal digestive system hav similar effects. Mouth size probably is influenced largely by th time-energy constraints.

The relationships between rumen turnover time, fermentatic rate, and increasing relative metabolic requirements with decrea ing body size have prompted the suggestion by some autho (Hungate et al. 1959, Nagy et al. 1969, Hoppe 1977) that sma ruminants meet their relatively high metabolic requirements b having a small rumen volume, short turnover time, high ferment tion rate, and highly selective diet. While this may be true in mar cases, notable exceptions to the rule demonstrate that body si and rumen volume are not necessarily dependent upon or another. Rather, the relationship is dependent upon the nutrition characteristics of the forage resource that is exploited. The elan antelope *(Taurotragus oryx),* for example, is a very large (400–8(kg) African ruminant with a relatively small rumen (rumin reticular volume to body weight ratio of about 0.110) Hofman 1973:267). It is "best suited for rapidly fermenting plant materia (Hofmann 1973:267) and is a selective forager, primarily eatin dicotyledonous forage (Hofmann 1973). The domestic sheep o the other hand, is a relatively small (about 50 kg) ruminant with very large rumen (rumino-reticular volume to body weight ratio about 0.250). It has a relatively long rumen turnover time (Maloi et al. 1968), and eats a diet consisting of a substantial proportion grasses (Olsen and Hansen 1977, Stuth and Winward 1977, Hanle and Hanley 1982). The domestic sheep is very well adapted t producing on poor quality rangeland—its small body size an ruminant digestive system minimize the time-energy constrain and provide a relatively large amount of time to forage selectivel (Lofgreen et al. 1957; Arnold 1960, 1962); the large rumen volum enables it to exploit the relatively abundant sources of fermentab carbohydrates (Maloiy et al. 1970); and the small mouth siz enables it to be highly selective of the plant parts and individua taken (Arnold 1960, 1962; Cook et al. 1963; Eadie 1969; Churc 1975:54). The combination of small body size and large rume volume, however, has an obvious disadvantage in terms of escap from predators.

The ability to forage selectively (determined by the time-energ constraints and mouth size) is very important when browse is bein eaten. Whereas leaves and current annual growth of browse speci may be about 65% cell solubles and 10% lignin, older twigs may b only 30% cell solubles and 20% lignin (Blair et al. 1977). The abilit to harvest selectively the leaves and current annual growth witho

also harvesting the older twigs therefore is important in determining the relative value of a browse forage to an herbivore. Such ability has been mentioned frequently for small-mouthed ruminants such as sheep, pronghorn, and deer (Cook and Harris 1950; Meyer et al. 1957; Weir and Torell 1959; Arnold 1960, 1962a, 1962b, 1964; McClymont 1967; Eadie 1969; Healy 1971; Short 1977), but seldom mentioned for large-mouthed ungulates such as cattle or horses. Rather, cattle do not appear to be capable of such a fine degree of selectivity, as evidenced by their browsing effects on the growth form of antelope bitterbrush (Hormay 1943). Rocky Mountain elk are smaller than either cattle or horses yet also apparently are incapable of harvesting only leaves and current annual growth from shrubs that are routinely browsed in this manner by mule deer (W.B. Collins and J.A. Deschamp, personal correspondence).

The relatively high degree of intraspecific variation in forage quality within browse species is another important aspect of the relationship between forage selectivity and the desirability of browse forages. Large differences in palatability have commonly been observed within browse species (Smith 1950; Oh et al. 1967; Nagy and Tengerdy 1967, 1968; Longhurst et al. 1968; Nagy and Regelin 1977) but are seldom reported for graminoids. Existing evidence is that these differences are due to the presence of plant volatile oils (Nagy et al. 1964, Nagy and Regelin 1977), which are recognizable by smell or taste (Longhurst et al. 1968, Nagy and Regelin 1977). If a foraging ungulate must take the time to smell or taste each individual of a particular species to determine its volatile oil content, then certainly herbivores that are more restricted by time-energy constraints (large ruminants and cecal digestors) would be more negatively influenced by the presence of volatile oils in some plant individuals than herbivores with more relaxed time-energy constraints would be. The large herbivore should "view" the plant species more in relation to its mean nutritional value; whereas the small herbivore may take the time necessary to seek out and consume only the most nutritious individuals.

The foregoing discussion has emphasized the forage selection, harvesting, and processing aspects of the ungulate herbivore. There are advantages and disadvantages associated with the possible values of each of the four major parameters: body size, type of digestive system, rumino-reticular volume, and mouth size. The optimal combination of values, however, is dependent not only upon the nature of the forage resource, but also upon the constraints of climate (Moen 1973, Western 1975) and predation (Geist 1974), as well as the potential for social organization to modify these factors (Jarman 1974, Geist 1974). The wide array of existing species of ungulates represents the numerous possible solutions to this optimization problem.

This is not meant to imply that other forage nutritional parameters or secondary plant compounds are not important factors in ungulate forage selection. It is suggested that these are of secondary importance, however, and are more important at a finer grain of resolution beyond the framework presented here. The roles of these factors are probably those of minimum nutrient constraints (Westoby 1974) and maximum secondary plant compound constraints (Freeland and Janzen 1974) in determining the species composition of the optimal diet.

Competition and Habitat Management

Although the present framework for understanding forage selection by ungulates is not sufficient for prediction of the species composition of optimal diets, it does provide much more insight into competition and resource partitioning in ungulate communities than has been provided by current models of optimal foraging strategies. It should provide a useful basis for understanding food selection in other herbivore communities as well, where cecal digestion and coprophagy are important nutritional aspects (see Janis 1976). Food resource partitioning, however, is only one dimension of niche separation (Schoener 1974). An understanding of the temporal and spatial components of habitat selection will further refine and extend the applicability of the present framework.

Dietary overlap is not sufficient evidence for exploitative competition (Colwell and Futuyuma 1971, Pianka 1976). For example, the present framework suggests that systems analogous to the facilitative grazing systems described for the Serengeti Plains of East Africa (Gwynne and Bell 1968; Bell 1969, 1971; McNaughton 1976) may operate in range livestock-wildlife relationships in North America. Early greening spring grasses are important components of mule deer diets in the Rocky Mountain and intermountain regions of North America (Willms and McLean 1978, Carpenter et al. 1979). While heavy livestock use at that time may result in exploitative competition for this forage resource, light or moderate use, particularly by cattle, conceivably may be beneficial to deer due to the compensatory growth responses by the grazed plants and a prolongation of the time period of active leaf growth (McNaughton 1979).

Where exploitative competition for the forage resource does exist, the present framework may provide insight into expected equilibrial outcomes. The appropriate model for competition between cattle and deer, for example, is most likely along the lines of Schoener's (1974) model for exploitative competition where each species has exclusive resources. Competition between sheep and deer, however, may be more similar to Miller's (1964, 1967) "included niche" model. The equilibrial outcomes of these two models can be entirely different. Whereas competition in Schoener's model always results in a stable node equilibrium, with the population levels of both species depressed, competition in Miller's model can yield either a stable node or competitive exclusion, depending on whether or not individuals of the narrow-niched species (deer) are sufficiently better than those of the broad-niched species (sheep) at exploiting the overlapping resources and whether those resources are sufficiently abundant to permit coexistence.

The present framework is also useful for predicting the consequences of management actions aimed at habitat improvement. The revitalization of decadent antelope bitterbrush ranges, for example, is a frequent objective in the management of the intermountain rangeland of North America. If bitterbrush decadence has resulted from excessive use by cattle, then the present framework suggests that simple reductions in the number of cattle permitted to graze the range will not solve the bitterbrush problem unless sufficient high quality grass forage is made available so that bitterbrush drops out of the optimal diet for cattle. If bitterbrush remains in the optimal diet, then use of bitterbrush by cattle will increase with any improvement in bitterbrush growth form. In such a situation, a rest-rotation grazing management system probably would be more effective in yielding the desired results.

An understanding of the forage needs of wild and domestic ungulates and the competitive relationships among them is important for wise management of these renewable resources. The brief review outlined here highlights only some of the research that has focused on this need.

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Feral Burro Impact on a Sonoran Desert Range

THOMAS A. HANLEY AND WARD W. BRADY

Highlight: Impact of feral burros on native desert vegetation was studied in the Havasu Resource Area, Lower Colorado River Valley, California-Arizona. Browse utilization ranged from heavy to light with increasing distance from the Colorado River. Overgrazing occurred near the Colorado River but decreased to light or moderate use at distances greater than 2.5 km from water. Overgrazing decreased the canopy cover of *Ambrosia dumosa* from about 2.26 to 0.04%, and decreased total canopy cover for all species from 8.64 to 2.80%. No plant species appear to act as increasers or invaders under grazing pressure by burros on the study area.

The feral burro (*Equus asinus*) has become a common member of the fauna in many areas of the southwestern United States. McKnight (1958) first called attention to potential range problems related to this animal. Recent ecological investigations of feral burros have centered on animal behavior and population parameters (Moehlman 1974; Woodward 1976). Woodward and Ohmart (1976) have reported on habitat use and dietary preferences in the Havasu Resource Area, California. However, quantitative information concerning feral burro impact on native vegetation has not been available. Perennial vegetation communities were identified and related to patterns of browse utilization in the present study.

Study Area

The study area is located in the Havasu Resource Area, 27 km north of Parker, Ariz. The Colorado River has been impounded at Parker Dam, forming Lake Havasu, which borders the study area on the southeast. Arizona State Highway 95 borders the study area on the north. Soils are entisols and aridisols, ranging in texture from sand to sandy loam. The study area is bisected by the Aubrey Hills, volcanic extrusions rising 100 to 150 m above the gentle sloping alluvial plain, and extending from the Bill Williams River about 25 km northwest to Lake Havasu City, Ariz. A major wash, called Standard Wash, also runs approximately north to south through the study area. When referred to in this paper, the study area will be called the Standard Wash study area.

Vegetation of the washes is dominated by foothills paloverde (*Cercidium microphyllum*), white bursage (*Ambrosia dumosa*), cheesebush (*Hymenoclea salsola*), and creosotebush (*Larrea tridentata*). The interfluves are sparcely vegetated with creosotebush and scattered chollas (*Opuntia* spp.). Riparian vegetation, dominated by salt cedar (*Tomarix* spp.), mesquite (*Prosopis juliflora* and *P. pubescens*), and arrowweed (*Pluchea sericea*), fringes the lake shore at the mouths of the washes. Perennial grasses are absent from the flora. Herbaceous cover varies with precipitation, but is dominated by the winter annual, wooly Indianwheat (*Plantago insularis*).

Approximately 50 feral burros inhabit the Aubrey Hills (Woodward 1976). A few desert bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) are also present. No livestock are grazed in the study area.

Elevation of the study area ranges from 140 to 330 m above sea level. Mean annual precipitation for Parker, Ariz., is 116 mm. Ambient air temperatures generally range from winter lows around 0°C to summer highs around 42°C. The Colorado River is the only permanent source of water for all large animals.

Vegetation communities, patterns of browse utilization, precipitation, and soil moisture relationships were investigated as part of a

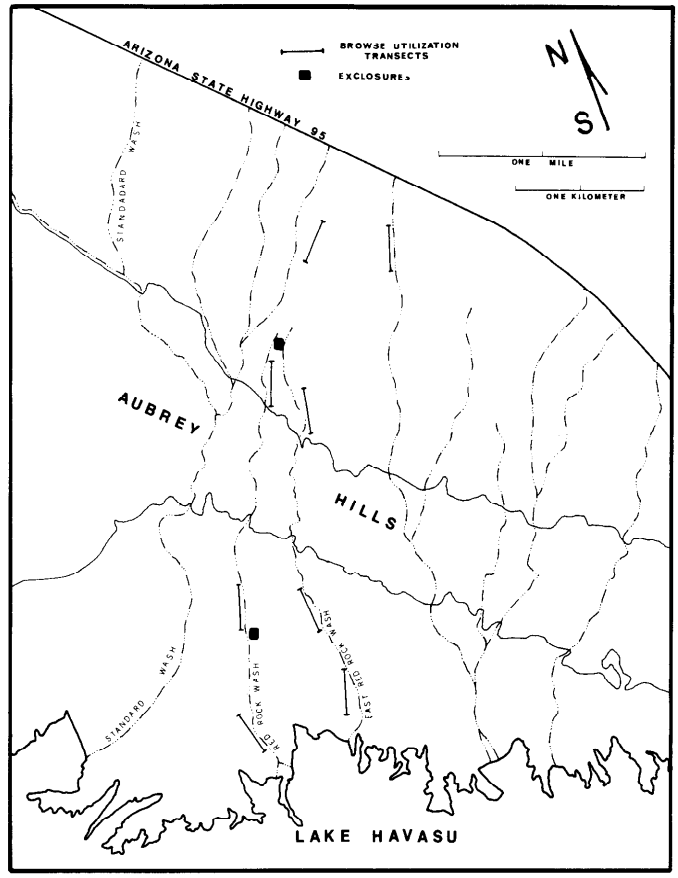


Fig. 1. *Location of exclosures and paired plots and utilization transects in the Standard Wash study area.*

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This research was sponsored by the Department of the Interior, Bureau of Land Management, under contract 52500-CT4-318.

Manuscript received October 26, 1976.

study of carrying capacity relationships conducted in1974 and 1975 (Hanley 1976).

Methods

Precipitation and soil moisture were monitored in two exclosures and two paired plots measuring 70 by 20 m, at distances of 1.25 and 3.25 km from the lake (Fig. 1). Both exclosures were located in secondary washes (i.e. washes in which flows of water were less frequent and intense than in major or primary washes). Precipitation was collected in a rain gauge located in each exclosure. Soil moisture was measured with gypsum electrical resistance blocks buried at depths of 20, 40, 60, and 80 cm at each of two sampling sites in each exclosure and paired plot. Precipitation and soil moisture data were collected biweekly in winter and spring, monthly in summer and fall, from September, 1974, through November, 1975. The millimeters of water in the 20 cm of soil surrounding each electrical resistance block were summed by site and depth over the sampling period. The summed value gave a representation of the total soil water environment surrounding each block over the year.

Browse utilization transects were evaluated four times per year: late February, May, August, and November. Four transects were located at distances of 0.5, 1.5, 3.0, and 5.0 km from the lake in each of two washes (Fig. 1). White bursage was selected for examination, since growth of the current growing season was easily recognizable, and it appeared to be a highly preferred and important browse species. Approximately 200 individual plants were examined in each transect. Degree of utilization was estimated by percentage of live stems that had been browsed. Estimates were tallied in utilization classes (0%, 1 to 5%, 6 to 25%, 26 to 50%, 51 to 75%, 76 to 95%, and 96 to 100%) to minimize error. Browse utilization data was evaluated from August, 1974, through November, 1975.

A tentative classification of perennial vegetation was developed following an intensive reconnaissance of the study area. Twenty-eight stands selected as representative of homogeneous community types were sampled by the point-center-quarter method. Eighty plants were sampled in each transect. Distance to nearest plant, species, average height, and average canopy diameter were recorded. Individual species canopy cover and density were calculated for each stand. The stands were classified using a diversity change index (Bonham and Brady 1973). In each community type thus classified, canopy cover and density were calculated for each species. Riparian communities were not sampled in this study.

Precipitation, soil moisture, and browse utilization data were analyzed by nonparametric statistical procedures (Zar 1974) to avoid the assumptions of parametric statistics (particularly those of normality and homoscedasticity). Precipitation at the two exclosures was compared by the Wilcoxon paired-sample test. Differences in soil texture (which could markedly influence soil moisture characteristics) were tested using Cochran's Q test for dichotomous nominal scale data in a randomized block analysis of variance. Blocks were soil depths; treatments were moisture block sites. Differences in total millimeters of water among the exclosures and paired plots were compared by the Kruskal-Wallis test, a single factor analysis of variance by ranks. Utilization differences between the two washes were compared by the Wilcoxon paired-sample test. Utilization differences at varying distances from the lake were teted using Friedman's two-way analysis of variance by ranks.

Results and Discussion

No significant differences ($\alpha = .20$) occurred in precipitation between the exclosures. The mean precipitation for the two exclosures over the 15-month period was 77.3 mm. The summer of 1975 was particularly dry. No significant differences ($\alpha = .10$) in soil texture occurred among sites. The sites could therefore be treated similarly in the analysis of their soil moisture regimes. Analysis of total water content of exclosures and the soils of the paired plots also indicated that no significant differences ($\alpha = .05$) occurred. Since soil moisture is the foremost limiting factor in desert ecosystems, this indicates that the site potential of the study plots is probably similar for each.

Table 1. Mean utilization (%) of live stems of white bursage in two washes (August 1974 to November 1975).

Distance from lake (km)	Red Rock Wash	East Red Rock Wash
5.0	1.1	2.8
3.0	7.7	6.1
1.5	64.2	56.6
0.5	69.0	63.5

Given the probable similarity in site potential, the secondary wash vegetation above and below Aubrey Hills would also be expected to be broadly similar in the absence of herbivory or other significant but unmeasured environmental parameters. The browse utilization transects were designed to provide objective data both on intensities of utilization and its spatial variation (Table 1). No significant differences ($\alpha = .20$) in utilization between the two washes occurred. Data from the two washes were therefore combined, and the mean values at each distance from the lake were tested with Friedman's two-way analysis of variance by ranks. Blocks were sampling dates, treatments were distance from the lake. Highly significant differences among distances from water ($\alpha = .001$) were found. Multiple comparisons of ranked data showed a highly significant difference ($\alpha = .01$) between 0.5 and 5.0 km from the lake and a significant difference ($\alpha = .05$) between 1.5 and 5.0 km from the lake. Transects 3.0 km from water were not significantly different from those at either greater or lesser distances. The

Table 2. Major vegetation community types of the Standard Wash study area.

Community type		Canopy cover (%)	Density (plants/ha)
Open Hills, *Larrea*	*Larrea tridentata*	1.03	165.5
	Opuntia echinocarpa	.09	19.2
	Ambrosia dumosa	.05	19.2
	Cercidium microphyllum	.04	1.1
	Opuntia basilaris and *O. ramosissima*	.01	8.0
	Total	1.22	204.0
Primary Wash, *Cercidium-Hymenoclea*	*Cercidium microphyllum*	3.01	34.7
	Larrea tridentata	2.52	53.7
	Hymenoclea salsola	1.59	179.0
	Lycium andersonii	.76	39.3
	Dalea spinosa	.16	10.7
	Acacia greggii	.15	3.1
	Opuntia echinocarpa	.06	6.4
	Bebbia juncea	.02	3.3
	Ambrosia dumosa	.02	14.6
	Encelia farinosa	.01	2.0
	Total	8.30	346.8
Secondary Wash, *Cercidium-Ambrosia*	*Cercidium microphyllum*	3.66	66.5
	Larrea tridentata	2.52	190.3
	Ambrosia dumosa	2.26	402.1
	Lycium andersonii	.12	11.9
	Krameria grayi	.05	12.9
	Opuntia spp.*	.03	37.0
	Total	8.64	720.7
Secondary Wash, *Cercidium-Larrea*	*Cercidium microphyllum*	1.25	29.7
	Larrea tridentata	1.20	95.6
	Lycium andersonii	.23	28.0
	Encelia farinosa	.07	27.7
	Ambrosia dumosa	.04	62.4
	Opuntia spp.*	.01	9.1
	Total	2.80	252.5

*Opuntia basilaris, O. echinocarpa, O. ramosissima.

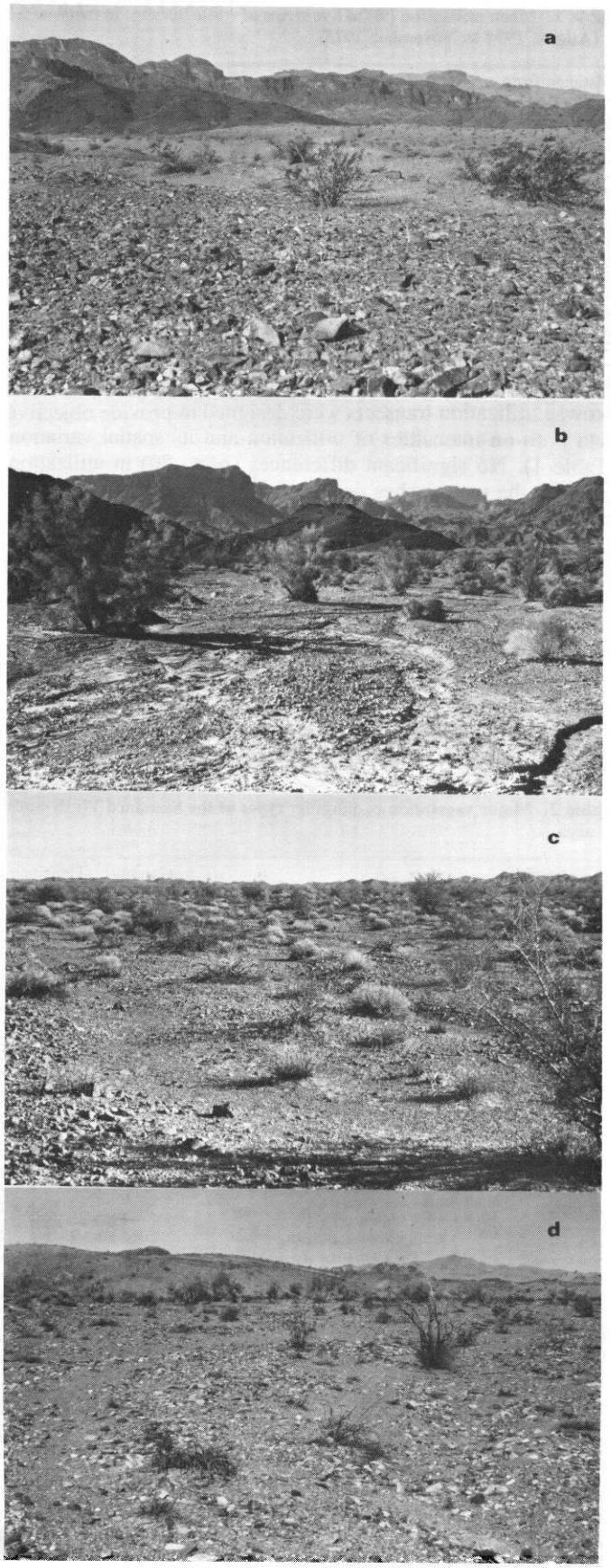


Fig. 2. *Major community types occurring in the Standard wash study area (a) Open Hills,* Larrea *community; (b) Primary Wash,* Cercidium-Hymenoclea *community; (c) Secondary Wash,* Cercidium-Ambrosia *community; (d) Secondary Wash,* Cercidium-Larrea *community.*

secondary wash areas below Aubrey Hills, in other words, were subjected to much higher levels of vegetation utilization than those areas above Aubrey Hills. Actual percent utilization (% of current year's growth removed by herbivory) quite likely exceeded 100% in several instances.

The results of this variation in utilization pressure was evident in terms of vegetation composition. Analysis of vegetative data resulted in the grouping of stands into four major vegetation community types (Table 2).

The "Open Hills, *Larrea*" community type (Fig. 2a) occurred on the dry interfluvial hills and was the most widespread community in the study area. It was composed almost entirely of creosotebush and had the lowest percent canopy cover and density of the community types.

The "Primary Wash, *Cercidium-Hymenoclea*" type (Fig. 2b) was restricted to the major drainage washes throughout the study area. The vegetation was dominated by relatively large foothills paloverde and creosotebush individuals and a great abundance of cheesebush. Smoke tree (*Dalea spinosa*) occurred only in this community type.

The "Secondary Wash, *Cercidium-Ambrosia*" type (Fig. 2c) was dominated by foothills paloverde, creosotebush, and white bursage. This community type was common in washes receiving lower utilization pressures and was restricted to the portion of the study area between Aubrey Hills and Arizona Highway 95. It had the greatest canopy cover and density of the four community types.

The "Secondary Wash, *Cercidium-Larrea*" type (Fig. 2d) occurred in topographic situations similar to the Secondary Wash, *Cercidium-Ambrosia* type, but was restricted to the portion of the study area between Lake Havasu and Aubrey Hills where utilization pressures were heaviest. The same species were dominant (with the exception of white bursage), but both canopy cover and density were only about one-third as great.

Burro impact on the study area was most pronounced in the secondary wash communities. The magnitude of impact can be evaluated by comparing cover and density values (Table 2) for the Secondary Wash, *Cercidium-Ambrosia* type (low utilization) and the Secondary Wash, *Cercidium-Larrea* type (heavy utilization). Over-utilization resulted in a great reduction in density and size of white bursage and a general reduction in density and canopy cover of nearly all species. There appeared to be no species acting as increasers or invaders under heavy burro utilization pressure.

That burros have had a substantial impact on the vegetation of this area is evident. However, assessment of the impact is complicated by the unavailability of data concerning the time required and the numbers of burros responsible for the differences observed in community structure. Information is also unavailable concerning the effects on other animal populations and the effects of interspecific competition for food resources. Browsing of white bursage, foothills paloverde, and creosotebush by hares was apparent (as evidenced by feces and stem gnawings) in both the exclosures and paired plots. Utilization by hares was greatest in the plots nearest Lake Havasu.

Woodward and Ohmart (1976) reported that burros grazed on interfluves mainly during the winter months, and washes were used primarily for travel to the Colorado River for water. Habitat use shifted to the washes with the greening of perennials in the spring. During the summer, burros were more restricted in their movements and primarily utilized the riparian habitat and washes within 3 km from the river. During the cooler months,

utilization was more widespread and at greater distances from water.

Grazing on the interfluves (Open Hills, *Larrea* community type) is largely consumption of wooly Indianwheat. Availability of this forage resource depends on favorable precipitation patterns in the winter. The secondary wash communities, on the other hand, provide both perennial and annual forage species during years of favorable precipitation. During years of poor precipitation, however, the forage provided by annuals in any location may be insignificant and the major source of forage will be perennial vegetation in the secondary washes.

Management, therefore, should be concerned primarily with carrying capacity of the secondary wash communities. They are the greatest forage resource, and consequently suffer the greatest feral burro impact.

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ECOSPHERE

Grazing intensity impacts soil carbon and nitrogen storage of continental steppe

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Abstract. Recent studies have underscored the importance of grasslands as potential carbon (C) sinks. We performed a grazing experiment with seven stocking rates (SR0, SR1.5, SR3.0, SR4.5, SR6.0, SR7.5, and SR9.0 for 0, 1.5, 3.0, 4.5, 6.0, 7.5, and 9.0 sheep ha^{-1}, respectively) to investigate the effect of increasing grazing pressure on soil C and nitrogen (N) storage in the temperate grasslands of northern China. The results revealed that C and N storage in both 0–10 cm and 10–30 cm soil layers decreased linearly with increasing stocking rates. Carbon storage in the 0–10 cm soil layer was significantly higher in lightly grazed grasslands than in heavily grazed grasslands after a 5-yr grazing treatment. Our findings suggest an underlying transformation from soil C sequestration under light grazing to C loss under heavy grazing, and that the threshold for this transformation is 4.5 sheep ha^{-1} (grazing period from June to September). Results confirmed that grasslands used for grazing in northern China have the capacity to sequester C in the soil under appropriate grazing pressure, but that they lose C under heavy grazing. Therefore, appropriate grazer densities will promote soil C sequestration in the grasslands of northern China.

Key words: carbon; carbon sequestration; carbon storage; grassland; grazing; nitrogen; soil fraction.

Received 10 August 2010; revised 29 November 2010; accepted 13 December 2010; **published** 19 January 2011. Corresponding Editor: S. Frey.

Citation: He, N. P., Y. H. Zhang, Q. Yu, Q. S. Chen, Q. M. Pan, G. M. Zhang, and X. G. Han. 2011. Grazing intensity impacts soil carbon and nitrogen storage of continental steppe. Ecosphere 2(1):art8. doi:10.1890/ES10-00017.1

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Introduction

Improving our understanding of the effects of land use changes on soil carbon (C) storage or sequestration in terrestrial ecosystems has become a recent topic of interest to researchers (IPCC 2007). Compared with croplands and improved pastures, natural rangelands exhibit relatively low soil C sequestration per unit area (Post and Kwon 2000, Conant et al. 2001, Jones and Donnelly 2004). However, the total amount of C sequestered in natural rangelands can be enormous because these lands occupy half of the earth's land area and contain approximately one-third of the global above- and belowground storage of C (Derner and Schuman 2007, Lal 2009).

Across rangelands, the effects of livestock grazing on soil C storage are variable and inconsistent; depending on the system, these herbivores may facilitate or depress C accretion rates (Milchunas and Lauenroth 1993, Schuman et al. 1999, Liebig et al. 2006, Derner and Schuman 2007, Ingram et al. 2008). The different effects of grazing on soil C storage or sequestration may reflect variations in climate, soil, landscape location, plant community type, and grazing management practices (Milchunas and

Lauenroth 1993, Reeder and Schuman 2002). Moreover, changes in soil C levels over time during biotic community development may be strongly linked with soil N levels (Knops and Tilman 2000). Thus, the influence of grazing on soil C storage in grasslands varies by region.

Researchers studying C storage or sequestration in soil have attempted to identify the fractions of soil organic matter (SOM) that respond more rapidly to land use changes than bulk SOM. These fractions could then serve as early indicators for the overall stock change (Christensen 2001, Olk and Gregorich 2006). Because the particle size fractions (sand, silt, and clay) of C pools are considered to be important factors that control SOM turnover, they are analyzed to evaluate the dynamics and turnover of SOM under various land use practices and climates (Leifeld and Kögel-Knabner 2005, Zinn et al. 2007, He et al. 2009).

Temperate grasslands in northern China cover approximately 110×10^6 ha. Because of their obvious ecological and economic importance, researchers have attempted to quantify their C storage and sequestration (Ni 2002, Fan et al. 2008, Lal 2009). Following the rapid expansion of the livestock industry after 1980, most temperate grasslands in China have undergone some degree of degradation or desertification (Tong et al. 2003). Measures to encourage grassland restoration were implemented in 2000 and are anticipated to increase soil C and N storage in northern Chinese grasslands. However, very few studies have addressed the effects of increasing stocking rates on soil C storage in temperate grasslands, even though such results are important for ecologists and grassland management decision-makers.

In the present study, we conducted a grazing experiment with seven sheep stocking rates in a temperate grassland of northern China to (1) evaluate the influence of different stocking rates on soil C and N storage, (2) explore the influence of grazing on the distribution of C and N in soil fractions, and (3) test the hypothesis that there exists an underlying transformation from C sequestration to C loss with an increase in stocking rates.

Materials and Methods

Study area

Field work was conducted in a typical steppe ecosystem on the Mongolian plateau in northern China (43°33′ N, 116°40′ E) which is administered by the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) of the Chinese Academy of Sciences. The climate is typical of a continental, semiarid climate. Mean annual temperature and precipitation (1982–2009) were 1°C and 334 mm, respectively. Soil is of the chestnut type, i.e., Calcic Kastanozems, equivalent to Calcic-orthic Aridisols in the U.S. soil classification system. The dominant vegetation consists of grassland plants, i.e., perennial rhizome grass (*Leymus chinensis* (Trin.) Tzvel) and perennial bunchgrass (*Stipa grandis* Smirn. and *Cleistogenes squarrosa* (Trin.) Keng) (Chen and Wang 2000).

Grazing experiment and sampling plots

Plots were established on grassland dominated by *L. chinensis* and *S. grandis* prior to the initiation of our experiment in 2004. The experimental area was historically used for raising sheep and goats, and grazing pressure was moderate. Considering the heterogeneity of the grassland, the study area was divided into two blocks; one block was situated on a flat area and the other block was situated on a moderately sloping area (Fig. 1). Seven sheep stocking rates, 0, 1.5, 3.0, 4.5, 6.0, 7.5, and 9.0 sheep ha^{-1} (hereafter designated SR0, SR1.5, SR3.0, SR4.5, SR6.0, SR7.5, and SR9.0, respectively), were set up in each block. The area of each fenced plot was 2 ha except for treatment SR1.5, in which the plot size was 4 ha. Beginning in 2005, sheep were transferred to plots in mid-June and were maintained there until mid-September. The same stocking treatments were applied to both blocks. The basic design of the grazing experiment is outlined in earlier works (Glindemann et al. 2009, Schönach et al. 2009). We also selected two grazing-free grasslands, designated as CK1 and CK2, outside of the fenced area of each block. In total, 16 sampling plots (14 grazing plots and two grazing-free grasslands) were established (Fig. 1).

Field sampling

At the end of the 5-yr grazing experiment (late September 2009), we established five sampling

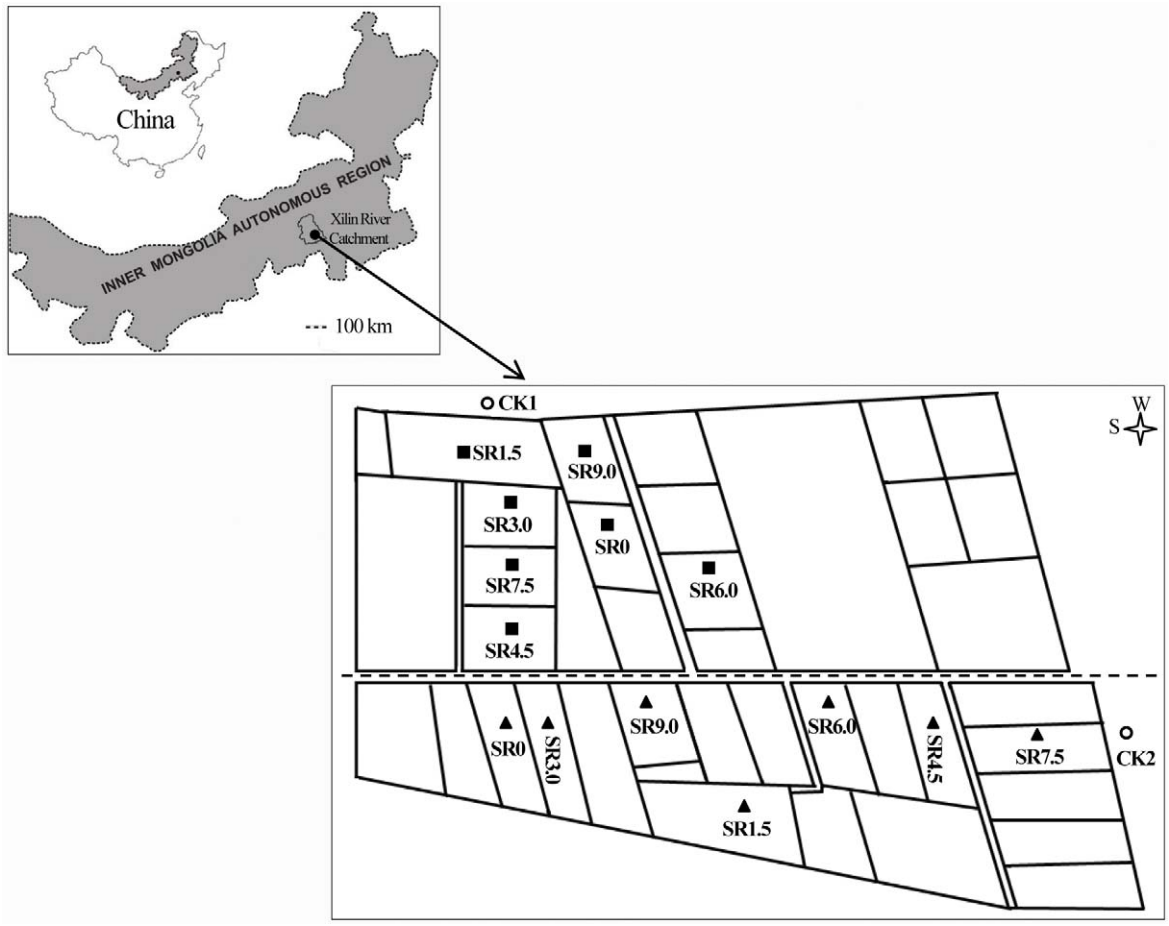


Fig. 1. Experimental sites and their relative positions. The experimental area was divided into two blocks. In each block, we set up seven stocking rates (namely, 0, 1.5, 3.0, 4.5, 6.0, 7.5, and 9.0 sheep / ha), designated as SR0, SR1.5, SR3.0, SR4.5, SR6.0, SR7.5, and SR9.0, respectively. In addition, we set up grazing-free plots outside of each fenced block as controls (CK1 and CK2).

points (a center point and four points each approximately 15 m from the corners) in each of the 16 plots. We established 1 quadrat (1 m × 1 m) at each sampling point and investigated plant community cover and height. Subsequently, aboveground biomass, with all of the plant species combined, was clipped at ground level.

Within each quadrat, three soil cores (2 m apart) were collected and combined from two layers at depths of 0–10 cm and 10–30 cm. A total of 10 soil samples were collected from each experimental plot. We measured soil bulk density at a depth of 0–30 cm at each point using the core method (100 cm^3 volume) (Blake and Hartage 1986); this allowed us to calculate the mass of C and N at each site.

Particle size fractionation and chemical analysis

We fractionated the soil samples into sand (50–2000 μm), silt (2–50 μm), and clay (<2 μm) fractions using ultrasonic energy to disrupt aggregates, following the methods of Roscoe et al. (2000). After manually removing visible root remnants, 50 g of soil (particles <2 mm) was dispersed in 250 ml of distilled water using a KS-600 probe-type ultrasonic cell disrupter system (Shanghai Precision and Scientific Instrument, Shanghai, China) operating for 32 min in continuous mode at 360 W. Under these conditions, the real power input was 56.02 W and the value of applied energy was 430 J ml^{-1} suspension, as calculated on the basis of equations from Roscoe et al. (2000). Sand (50–2000 μm) and

coarse silt (20–50 μm) were separated by wet sieving. To further separate fine silt (2–20 μm) and clay (<2 μm), the samples were centrifuged repeatedly at 150 × g for 5 min. The supernatants were collected in 250-ml centrifuge bottles and centrifuged at 3900 × g for 30 min; the precipitated fraction was referred to as clay. All of the fractions were dried at 50°C and ground for further chemical analysis.

Organic C content (%) of the samples was measured using the modified Mebius method (Nelson and Sommers 1982). For this procedure, 0.5 g of soil sample was digested with 5 ml of 1 N $K_2Cr_2O_7$ and 5 ml of concentrated H_2SO_4 at 180°C for 5 min, followed by titration of the digests with standardized $FeSO_4$. Total soil N (%) was analyzed using the modified Kjeldahl wet digestion procedure (Gallaher et al. 1976) and a 2300 Kjeltec Analyzer Unit (FOSS, Höganäs, Sweden).

Calculations

Soil organic C (SOC, Mg C ha^{-1}) and total soil N (TSN, Mg N ha^{-1}) were calculated on an area basis to a soil depth of 30 cm as follows:

$$\mathrm{SOC} = \sum D_i \times S \times B_i \times OM_i \div 100$$

$$\mathrm{TSN} = \sum D_i \times S_i \times B_i \times TN_i \div 100$$

where D_i, S, B_i, OM_i, and TN_i represent thickness of the soil layer (cm), cross-sectional area (ha), bulk density (g cm^{-3}), organic C content (%), and total N content (%), respectively; i = 1 and 2.

Similarly, C and N storage in soil fractions (sand, silt, and clay) (Mg C ha^{-1} and Mg N ha^{-1}) was calculated as follows:

$$\mathrm{C_{storage}(fraction_i)} = C_{con.}(fraction_i) \times F \times D \times S \times B \div 10^5$$

$$\mathrm{N_{storage}(fraction_i)} = N_{con.}(fraction_i) \times F \times D \times S \times B \div 10^5$$

where $C_{con.}(fraction_i)$ is the C content of the soil fraction (%), $N_{con.}(fraction_i)$ is the N content of the soil fraction (%), and F is the fraction content in soil (g fraction kg^{-1} soil).

Statistical analysis

Normality and homogeneity of variances were verified for all data using Kolmogorov–Smirnov and Levene tests, respectively. Then we used a two-way ANOVA to compare all means between the two blocks and seven sheep stocking rates. We found no significant interactions between stocking rates and topography (blocks). Therefore, the two blocks were treated directly as replicates, as we had anticipated initially. Then, a one-way ANOVA (with Duncan's test as the post-hoc test for multiple comparisons) was used to evaluate the effect of stocking rates on soil C and N. Regression analysis was used to explore the changing trends of soil C and N storage with increasing stocking rates. Data were represented as mean ± 1 SD (n = 10). All analyses were conducted using SPSS statistical software (ver. 11.0, SPSS, Chicago, IL, USA).

Results

Changes in aboveground plant biomass and soil bulk density

Aboveground plant biomass varied significantly from 163.5 ± 5.7 g m^{-2} in plot SR0 to 55.4 ± 9.3 g m^{-2} in plot SR9.0 ($F = 94.72$, $P < 0.01$), and decreased logarithmically with increasing stocking rates (Fig. 2A). Soil bulk density was significantly different among different stocking rates in the 0–10 cm soil layer ($F = 3.13$, $P < 0.01$), and the values were significantly lower in plots SR0 and SR1.5 than in plots SR6.0, SR7.5, and SR9.0 (Duncan multiple comparisons). Moreover, bulk density increased linearly with increasing stocking rates in both 0–10 cm and 10–30 cm soil layers (Fig. 2B).

Changes in soil C and N storage

The results revealed that, after the 5-yr grazing treatment, C storage in the 0–10 cm soil layer was significantly different among stocking rates ($F = 3.37$, $P < 0.01$), and C storage was higher in plots SR0 and SR1.5 than in plots SR7.5 and SR9.0. The influence of grazing on C storage was relatively small in the 10–30 cm and 0–30 cm soil layers. There were general decreasing trends for C storage with increasing stocking rates in the 0–10 cm, 10–30 cm, and 0–30 cm soil layers, which can be well simulated by linear equations (Fig. 3A).

Nitrogen storage was not significantly different in either the 0–10 cm or 10–30 cm soil layers

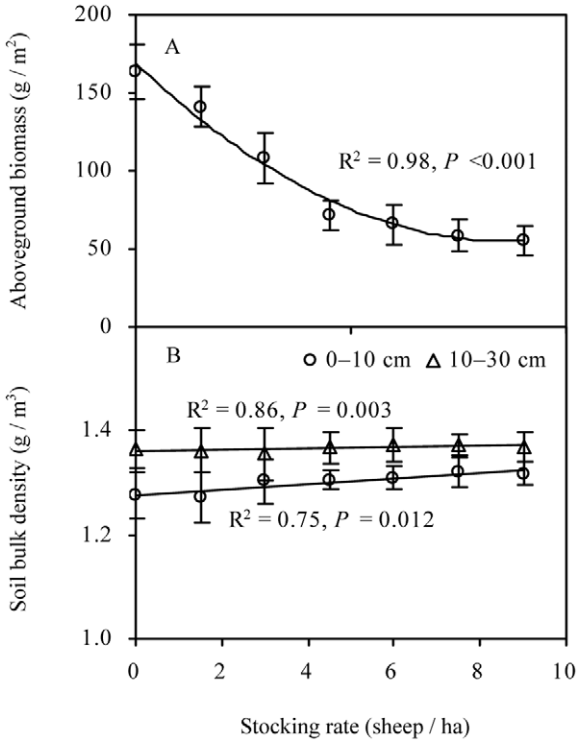


Fig. 2. Changes in aboveground plant biomass and soil bulk density with increasing stocking rates. For aboveground plant biomass, a logarithmic regression was used to determine the underlying relationship (A); bulk density increased linearly with increasing stocking rates (B).

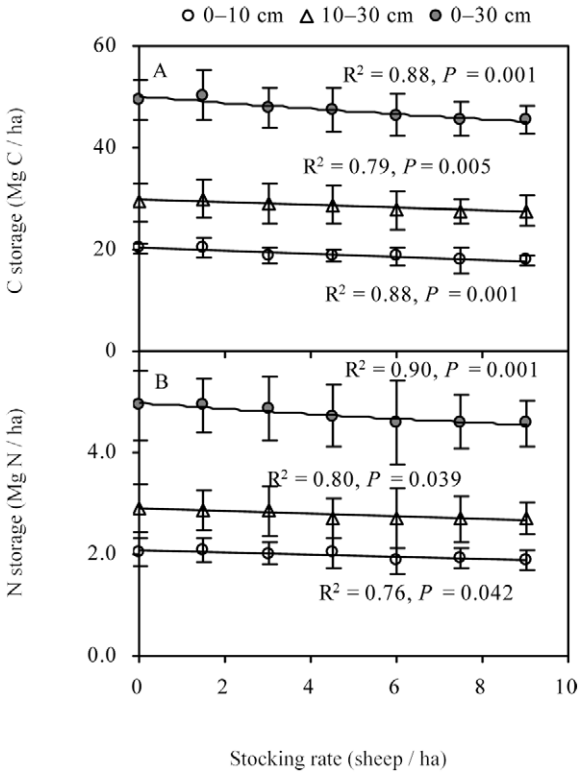


Fig. 3. Changes in soil C (A) and N (B) storage under different grazing rates. Data represented as means ± 1 SD (n = 10). For all corresponding variables, linear regression was used to determine the underlying relationships.

among various grazing levels, although the trend decreased linearly with increasing stocking rates (Fig. 3B). Moreover, the results revealed that the storage of C and N in the surface soil increased logarithmically with increasing aboveground plant biomass (Fig. 4).

Changes in C and N storage of soil fractions

Sand dominated the particle-size distribution across the 14 plots and comprised 67.1–70.6% of total soil weight in the 0–10 cm soil layer; silt comprised 26.5–29.8% of the total soil weight, and the clay content was relatively low (Fig. 5). Sand fractions increased significantly with increasing stocking rates ($F = 4.28$, $P < 0.01$ in the 0–10 cm soil layer; $F = 3.29$, $P < 0.01$ in the 10–30 cm soil layer), and the increasing trends can be well depicted quadratically (Fig. 5). Conversely, the silt fraction was decreased with increasing stocking rates. The influence of grazing on the clay fraction was small.

Carbon storage in the sand fraction (50–2000 μm) of the 0–10 cm soil layer was significantly different among stocking rates ($F = 3.36$, $P < 0.01$), and decreased quadratically with increasing stocking rates (Fig. 6A). Carbon storage in the silt and clay fractions in the 0–10 cm soil layer decreased with increasing stocking rates and showed strong quadratic relationships with stocking rates. Similarly, C stored in sand, silt, and clay in the 10–30 cm soil layer was not significantly different among grazing treatments, but showed quadratic relationships with increasing stocking rates (Fig. 6C).

Nitrogen storage in sand (50–2000 μm), silt (2–50 μm), and clay (<2 μm) in the 0–10 cm and 10–30 cm soil layers was not significantly different among stocking rates. However, N storage in

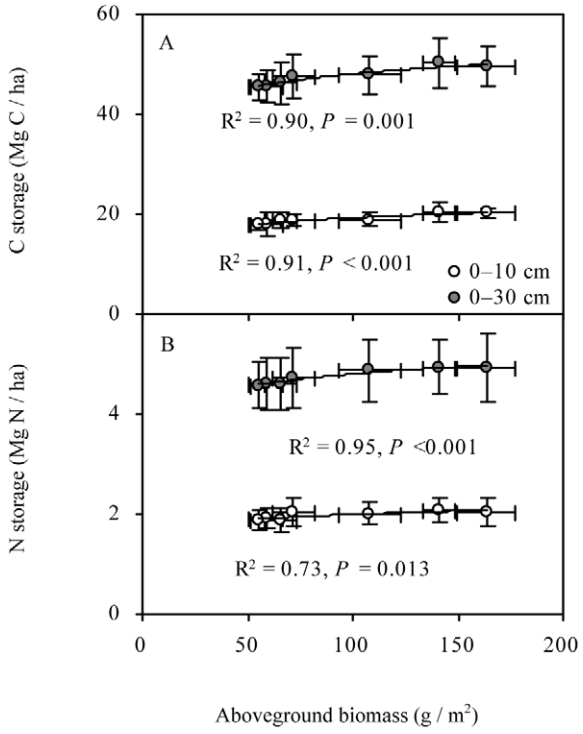


Fig. 4. Relationship between soil C and N storage with aboveground biomass in grazing grasslands. For all corresponding variables, logarithmic regression was used to determine the underlying relationships.

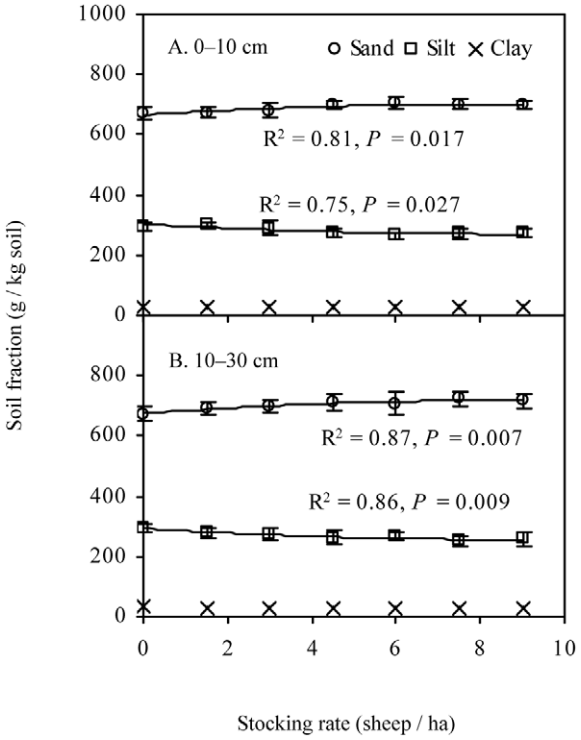


Fig. 5. Changes in the distribution of soil fractions with increasing stocking rates. For all corresponding variables, quadratic regression was used to determine the underlying relationships.

sand and silt in both the 0–10 cm and 10–30 cm soil layers decreased linearly with increasing stocking rates (Fig. 6B and D).

Discussion

Influence of grazing on soil C and N storage

In general, C and N storage in both the 0–10 cm and 10–30 cm soil layers decreased with increasing stocking rates in the Inner Mongolian grasslands. Wu et al. (2008) found that soil C and N storage (0–40 cm) increased logarithmically with the duration of grazing exclusion in Inner Mongolian grasslands. In the current study, soil C and N storage were slightly higher in plot SR1.5 compared to plot SR0 (Fig. 3). Possible explanations for soil C storage enhancement with light grazing include increases in production, elevated nutrient availabilities, and facilitation of vegetation regeneration (Frank and McNaughton 1993, Milchunas and Lauenroth 1993, Han et al. 2008). Another possible explanation is gains from dust deposition, which contribute considerably to increases in soil C and N. Hoffmann et al. (2008) estimated that the net deposition of C and N from dust in lightly grazed sites in the region reached 10.9 g C m^{-2} yr^{-1} and 1.0 g N m^{-2} yr^{-1} in 2005 and 2006; these rates were influenced by variations in vegetation height and coverage as a result of grazing activity. Our findings also suggest that the apparent increase in C and N storage in the sand and silt fractions of lightly grazed sites represented an important contribution to the new C and N accumulation of the entire soil. Moreover, the increases of C storage in silt and clay (<50 μm) also indicated that light grazing favors the accumulation of stable SOM (Christensen 2001).

Carbon and N storage declined in the heavily grazed grasslands, and soil acted as a C source. Declines in soil C and N storage under long-term heavy grazing have been reported previously (Cui et al. 2005, Elmore and Asner 2006, Han et

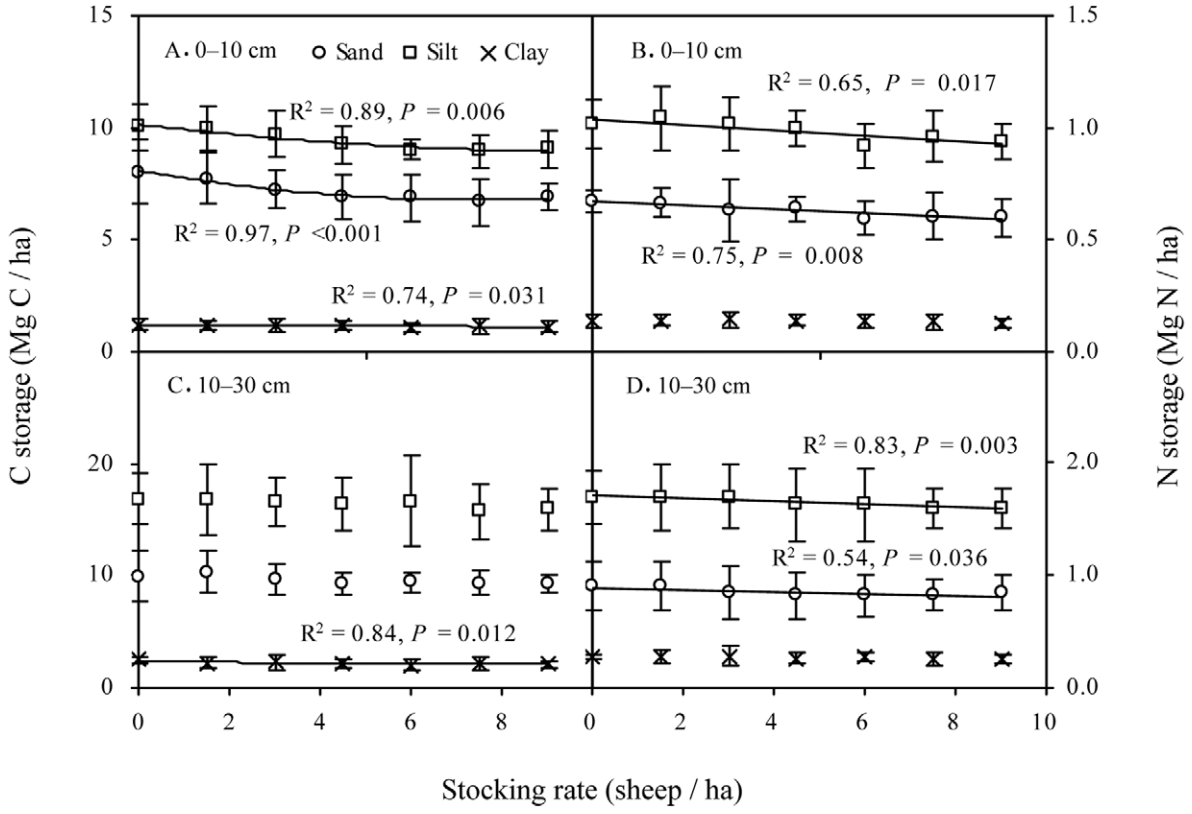


Fig. 6. Changes in C and N storage in soil fractions with increasing stocking rates. For C storage (A and C) and N storage, quadratic and linear regressions were used to determine the underlying relationships, respectively.

al. 2008, Steffens et al. 2008). Ingram et al. (2008) reported that heavy grazing resulted in a 30% loss in soil C storage (0–60 cm) in a mixed-grass ecosystem; losses were attributed mainly to plant community changes and the resultant accumulation of SOC closer to the soil surface, making it more vulnerable to loss. Several mechanisms have been proposed to explain decreases in soil C and N storage: (1) biomass removal by heavy grazing significantly decreases the input of organic matter from aboveground biomass and roots (Johnson and Matchett 2001), (2) heavy grazing may decrease productivity due to decreases in soil infiltrability and nutrient availability (Savadogo et al. 2007), and (3) disruption of the structure of soil aggregates and surface crust by livestock trampling enhances SOM decomposition and renders soil susceptible to water and wind erosion (Neff et al. 2005). Hoffmann et al. (2008) estimated average soil organic C and N losses in heavy grazing sites of 4.73 g C m^{-2} yr^{-1} and 0.44 g N m^{-2} yr^{-1} in the spring of 2005 and 2006. In contrast, some studies have reported that soil C storage is higher in heavy grazing sites, mainly because of increased root production in the surface soil that accompanies changes in species composition (Frank et al. 1995, Reeder and Schuman 2002, Liebig et al. 2006).

C and N sequestration under different stocking rates

We calculated the C and N sequestration rates in grassland soils under different stocking rates based on the differences between these grazing plots and CK plots (grazing-free grasslands). The results revealed that C sequestration rates (0–30 cm) were 59.6, 74.8, and 27.5 g C m^{-2} yr^{-1} in plots SR0, SR1.5, and SR3, respectively. In contrast, grasslands exhibited C and N loss under heavy grazing pressure. Overall, C and

N sequestration in the total soil and the silt plus clay fractions exhibited strong quadratic decreases with increasing stocking rates (data not shown). Our findings indicated that there was an underlying transformation from soil C and N sequestration under low grazing to C and N loss under heavy grazing, and the threshold for the transformation was 4.5 sheep ha^{-1}. As reported by Lal (2009), C sequestration rates ranged from 0–200 g C m^{-2} yr^{-1} in semiarid regions. Australian pastures can sequester 50–60 g C m^{-2} yr^{-1} (Gifford et al. 1992). By improving grassland management, soil C sequestration reached 59 g C m^{-2} yr^{-1} in North American study sites and 28 g C m^{-2} yr^{-1} in Australia (Conant et al. 2001). Conant et al. (2003) demonstrated that the soil C sequestration rate averaged 41 g C m^{-2} yr^{-1} in four managed intensive grazing sites in the southeastern U.S. Differences in the sampling depths and inadequate evaluation of C distribution in grazing ecosystems may have contributed to inconsistencies among the results (Schuman et al. 1999).

In general, we expected grazing exclusion to be a practical and important approach for achieving the soil C sequestration potential of temperate grasslands in northern China. Compared to the grazing-free grasslands (CK plots), grazing exclusion (SR0) annually enhanced C and N storage (0–30 cm) by 1.1% and 0.9%, respectively. In a meta-analysis by Conant et al. (2001), changes in grazing management and fertilization were demonstrated to lead to annual increases of 2.9% and 2.2% in C and N storage, respectively. Our results confirm the literature reports that C and N storage undergoes an initial rapid increase with the introduction of grazing exclusion in *L. chinensis* grasslands in northern China, where annual increase rates are 3.0% and 2.6% for C and N storage, respectively (He et al. 2008). Moreover, grazing exclusion enhances soil C storage in sand grassland in the Horqin region (Su et al. 2005) and in grassland of the agropastoral ecotone in Duolun County, China (Zhou et al. 2007). These increases were restricted mainly to the upper soil layer and were logarithmic throughout the duration of grazing exclusion (Wu et al. 2008). As mentioned in the first section of the discussion, dust deposition can partly contribute to this rapid increase (Hoffmann 2008). It is therefore certain that grazing exclusion can enhance soil C and N storage in temperate grasslands in northern China.

Trading C credits in the future opens new opportunities for promoting the use of terrestrial C sinks. The use of C sequestration programs would be of particular benefit to degraded or desertified grassland ecosystems in Asia, because the rehabilitation of these degraded lands is an urgent concern of global importance (Lal 2009). On the basis of our results, temperate grasslands in northern China have tremendous potential for increasing their C storage under low to moderate stocking rates. We also demonstrated that inappropriately heavy grazing would degrade soil C storage. Fortunately, deteriorating environmental conditions recently prompted the autonomous Inner Mongolian government to officially restrict or ban livestock grazing in the region after the year 2000. Therefore, an increase in soil C and N storage is anticipated in the grasslands of northern China as a result of the implementation of these measures aimed at encouraging grassland restoration.

In summary, soil C and N storage decreased with increasing stocking rates in Inner Mongolian grasslands. Compared with grazing-free grasslands, lightly grazing grasslands showed an apparent capacity to sequester C and N in soil, but heavily grazed grasslands exhibited a C and N loss. The grazing grasslands in northern China have the capacity to sequester C in soil under appropriate grazing pressure, but they exhibit C loss under heavy grazing. Our findings indicate that there exist a system transformation from soil C sequestration under low grazing to C and N loss under heavy grazing, and that the threshold for this transformation was 4.5 sheep ha^{-1} (grazing period from June to September). Our results are important for regional C budget considerations and for optimizing grassland management to improve SOM storage.

Acknowledgments

We thank the Inner Mongolia Grassland Ecosystem Research Station for their help with laboratory analysis. We also thank YF Bai, F Taube, A Susenbeth, and others for conducting the field experiment. Funding for this work came from the State Key Basic Research Development Program (2010CB833500), and from the projects of NSFC (31070431 and 40803024). NP He and YH Zhang contributed equally to this

work; two reviewers provided useful comments on earlier drafts of the manuscript.

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Grazing management on rangelands

By Carlton H. Herbel

RANGELANDS are a major life-support system for mankind. They provide forage for livestock and wildlife, habitat for wildlife, recreational opportunities, water, and aesthetic values. Today's growing numbers of people are putting more and more demands on rangeland productivity. Forage-based livestock production reduces grain requirements, conserves energy, and uses resources not readily usable by other means.

To meet forage-fed livestock needs and provide the other products and services that people expect from rangelands, these lands must be managed wisely. If rangelands are mismanaged to the extent that plant cover fails to provide sufficient soil cover, the species composition of the plant communities changes, reducing productivity and soil protection. Continued abuse can result in severe soil erosion. This does not imply that proper grazing is destructive. Some native plant communities evolved over thousands of years with grazing use by native animals. But native plant communities are not always the most productive under intensive livestock grazing. Production can be increased on some sites with the use of improved forage plants.

Grazing management concepts

Range management involves both range improvement and grazing management practices. Range improvement generally has greater potential than grazing management for increasing production. Such practices as brush management, revegetation, and fertilization can increase range forage yields up to 10 times. Manipulation of grazing time and intensity, on the other hand, usually results in relatively minor changes in range productivity (*3*). In some cases, rangeland productivity may even decline with grazing unless certain principles are adhered to.

Long-duration grazing refers to continuous grazing or grazing periods of several months to more than a year. The periods of deferment from grazing may also extend from several months to more than a year. Single herds or several herds of animals may be involved.

Conversely, short-duration grazing involves one or a few herds of animals that are moved to a new unit every 2 to 28 days (*11*). Deferment from grazing extends from 42 to 180 days. Both grazing and deferment periods are important.

Long-duration grazing often requires a minimum outlay of capital for fence and water developments. Management inputs are also relatively minor because decisions on livestock numbers and when to move the animals to another unit are not critical so long as the permanent range resources, plants and soils, are not irreversibly damaged.

Short-duration grazing, on the other hand, may require a larger outlay of capital for fence and water developments. Decisions on movement of livestock are critical because young plants should only be grazed once before receiving some deferment from grazing (*11*). Therefore, the risk and management requirements are both greater with the more intensive short-duration grazing. Higher management inputs, whether they involve a grazing system or an improvement practice, do not guarantee higher returns to the operator, however.

Some example systems

Continuous, yearlong grazing in the Southern Great Plains can be successful for a number of reasons (5): (a) Herbage production depends primarily upon summer rainfall, and monthly summer herbage production can vary from 23 to 672 kilograms per hectare (20-600 pounds/acre); (b) most species are grazed by cattle at one time or another; (c) many "increaser" species are excellent plants for grazing, and they may be productive under certain environmental conditions; (d) cattle compete with natural losses of forages and with other forage consumers, such as rabbits, rodents, and insects; (e) young forage and regrowth forage is more palatable and more nutritious than mature forage; (f) grazed plants save soil water for later green growth; and (g) favorable growing seasons, combined with proper grazing management, allow ranges to recover a desirable species composition.

Additional reasons for the success of yearlong continuous grazing in the southern Great Plains are that use is light during the growing season, and lighter stocking per unit area means less soil compaction by livestock when the soil is wet. Some of these same reasons could be attributed to rotational schemes also.

In a four-unit rotation system on the Edwards Plateau of Texas, each unit was grazed by livestock for 12 months, then deferred from grazing for 4 months (*6*). During a four-year cycle, therefore, each unit was deferred once during each of the four-month periods. Stocking included a combination of cattle, goats, and sheep. After 11 years, the stocking rate of the units in the deferred-rotation system was increased 33

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Reprinted from the Journal of Soil and Water Conservation
March-April 1982, Volume 37, Number 2
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percent (7). These units carried the increased livestock and showed greater improvements in range condition than did any of the units grazed continuously on a yearlong basis at three rates. An advantage of deferred rotation is the infrequency of livestock movement required. Under the system livestock must adjust to new forage and unit conditions only once every 12 months.

A rotation system using as many as 16 units, each grazed 2 weeks or less by one or two herds, has been studied in South Africa and Rhodesia (2, 9). Livestock are not moved at any set time, nor are the units necessarily stocked in sequence. When plants are growing rapidly, the livestock are moved frequently, perhaps as often as every 5 days, to prevent plant injury. When the plants are dormant, livestock movement is determined by the nutritional requirements of the animals.

An evaluation of grazing systems in South Africa produced these principles (9): (a) Slow rotation systems do not eliminate selective grazing; (b) in a 16-unit, high-intensity, low-frequency system, 12 units are grazed once for about a two-week period every six months, and the four other units can be used as reserve grazing in dry years or given a full year's rest in years of average precipitation; (c) high-intensity, low-frequency grazing is designed primarily to combine sufficient rest with efficient use to permit rapid restoration of denuded veld; there is less advantage to using this system on veld in good condition; (d) veld restoration may be retarded and greater abuse may occur if stocking intensity increases more rapidly than indicated by herbage production; (e) with variable precipitation, no system can eliminate selective grazing if set grazing periods and stocking rates are maintained, but high-intensity low-frequency grazing reduces selective grazing; and (f) high-intensity, low-frequency grazing, because it is an intensive system, may require more labor, fencing, and water development, but the relatively high capital investment required to implement this grazing may be justified by the increased carrying capacity.

Short-duration grazing or "cell" grazing (11) uses some of these same principles. Cell grazing, however, requires even shorter periods of livestock grazing when range plants are actively growing. This is a one-herd system with the units laid out somewhat like a wagon wheel. In the center are pens and watering devices. Movement of livestock to the next unit to be grazed is accomplished by opening the gate, which is located at the hub, and letting the livestock move themselves. Frequent movement among units prevents livestock from abusing individual plants.

Use of a grazing system may alter the species composition of a plant community. An increase in palatable plant species may permit increased use of the range resource. Nevertheless, the benefits obtained from improved grazing management practices are relatively small compared with those possible from manipulative range improvements.

Some additional principles

Manipulation of grazing livestock exemplifies the use of ecological principles in range management. The application of ecological principles to range science often means maintaining or improving native plant stands generally through grazing management. Many times range managers use a combination of extensive and intensive practices, for example, brush management combined with a grazing system, or revegetation and fertilization combined with a grazing system. A range manager can select the degree of intensity for a unit of rangeland depending upon potential for those sites within a unit of rangeland; economic, social, and political factors; and available technology. But no range manager should be bound by the use of terms. Rangelands can be managed for various objectives. Generally, range managers attempt to achieve a balance among management, social, economic, and environmental concerns.

Range managers must be flexible and innovative in planning operations on a range unit. Practices successful on one range unit may be less so on the next, or even unsuccessful on a unit nearby. No grazing scheme will eliminate the need for practicing all available, economic range management techniques. No practice will produce the desired results if the range manager does not understand and believe in the principles involved, keep records on the performance of units and animals, and adjust schedules and livestock numbers with changing conditions.

The following grazing management considerations exemplify the use of ecological principles in range management:

- *Proper utilization.* Desirable perennial plants produced on rangeland must be used moderately during the growing season. Thus, the old guideline, use half and leave half. Where additional soil protection is required, herbage utilization should not exceed 40 percent. Heavy use of perennial forage plants, followed by prolonged drought, can result in the death of many desirable plants. On the other hand, utilization greater than 50 percent is useful under some conditions. Ephemerals, often annual plants, generally are grazed by animals extensively when they are available. The forage crop may vary greatly from one time to another because of precipitation differences. It is not unusual for the annual forage crop on rangeland to vary from 50 to 150 percent of average.
- *Grazing intensity.* The animal unit month (AUM) quota is the livestock concentration multiplied by the proportion of time that a unit or portion of a unit is grazed (4). In a four-unit, rest-rotation scheme with one herd, the livestock con-

Revegetated rangeland in southern Utah reveals the productive impact of combining grazing management practices with range improvement practices.

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centration is 4.0 times and the AUM quota is 2.0 times as much as that that would occur if all units were grazed simultaneously throughout the grazing season. For the growing season, an AUM quota of 0.5 or less is considered a desirable stocking rate. There is no apparent justification for leaving a range unit ungrazed all year.

The primary purpose of range management is to eliminate excessive grazing. This is especially important during the growing season to increase the vigor and productivity of existing plants and, eventually, to improve species composition. An alternative to heavy grazing to obtain use of less desirable plants is to graze a unit during that time of year when less desirable species are more palatable than preferred plants. Another possibility is to use different kinds of livestock or wildlife to reduce the less desirable plants temporarily. In South Africa, it was found that the longer the period of grazing, the lower the carrying capacity and the more adverse the effect on the veld (*8*).

• *Stocking rate.* The main factor influencing animal production per unit area is stocking rate. But to achieve maximum production per unit area, live-weight gain per animal is reduced. Both high production per animal and per unit area can be achieved by varying the stocking rate during the grazing season. In a comparison of rotational grazing with continuous grazing at different stocking rates, significant increases in livestock performance were recorded from rotational grazing only when the stocking rate was at a high level (*1*).

• *Animal distribution.* For proper grazing use of forage plants, most situations call for an even distribution of livestock. In the large range units prevalent in most arid and semiarid areas, it is possible to find serious overgrazing near watering points and no use of forage in other portions of the unit. Animal distribution can be improved by (a) increasing the number of watering points, (b) establishing salting and supplemental feeding areas to 1 to 3 kilometers (0.6-1.8 miles) from watering points, (c) using more fencing (d) building trails, (e) fertilizing selectively, and (f) using a different class of livestock. Any practice that improves animal distribution will increase range productivity.

• *Proper plants.* Some major plant species in the Rocky Mountains and west of the Rocky Mountains did not evolve under grazing pressure as did species common to the Great Plains. Species that are not adapted climatically should not be considered important components of the range ecosystem. Plants must be adapted for grazing or browsing by animals and for soil protection. The value of all plants growing in an area must be considered. Even minor amounts of a few species may contribute much to animal performance in a brief but critical part of the year.

• *Reproductive potential.* In most range ecosystems, the desirable climax species are long-lived perennial plants. Often, these plants are poor seed producers and do not reproduce readily from seed. If these desirable species are depleted by overgrazing or drought, it is often difficult, if not impossible, to encourage their recovery by manipulating the grazing animal. Conversely, if seed production is important for reproduction, grazing use can be adjusted to encourage seed formation. Similarly, vegetative reproduction of certain species can be encouraged by manipulation of the grazing animal.

• *Flexibility.* Most grazing studies are established at a fixed stocking rate. Downward adjustments in livestock numbers are made only during severe drought. However, wide fluctuations in the forage crop, both amount present and plants that are prominent, occur frequently. When range operators adopt a grazing scheme, they often allow for flexibility in time of grazing and deferral from grazing as well as the number of livestock involved. This flexibility may be the difference between success or failure in the grazing scheme. Both plant and animal requirements must be considered. For example, some range units on a ranch may be manipulated to furnish highly nutritious forage during a period when livestock need greater nutrition. The critical growth stage of plants also varies over time because of weather conditions. Because of grazing history and weather conditions, it may be more important to defer grazing in some periods than in others. Range units should be grazed when the key plants are damaged least by grazing and when the forage best meets the nutritional requirements of the animals. This often means grazing in no set or predetermined sequence.

Grazing schemes should also be tailored to conform to a variety of vegetation types, soil types, physical facilities, and herd-management plans. There may be considerable variation in specific details for operating a certain grazing scheme among ranch operations. In some instances, it may be desirable to use a particular grazing system to attain a certain measure of improvement and then change to a different system for maximum net returns while maintaining the resource. South African research (*10*) suggests that the advantage of multi-unit schemes is the flexibility possible, which permits the range manager to alter the grazing scheme as the precipitation varies and as the specific requirements of each unit dictate.

• *Management plan.* When a grazing scheme is initiated, range improvements, such as brush management, revegetation, fencing, and water developments, are often not credited for improving rangeland productivity. The tendency instead is to credit the grazing scheme for improvements in range condition or animal performance. Any improvement that aids livestock distribution or increases forage yields will increase range productivity. Consideration of the overall management plan, including both range improvements and grazing scheme, is critical. All practices that are beneficial and economical should be integrated into the management plan.

Range units feature varying characteristics and must be managed accordingly. They may differ in their improvements, such as fencing and water developments; the proportion of various soils and types of vegetation; the numbers and kinds of livestock and wildlife supported; and the recreational opportunities they provide. Many times, cultural, economic, or political conditions determine the degree of management applied. As conditions change or technology improves, the range manager may decide to modify his or her objectives.

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Cheatgrass Invasion in Salt Desert Shrublands: Benefits of Postfire Reclamation

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Abstract

In 1998, fires burned more than 11 330 ha of rangeland on Dugway Proving Ground in Utah's west desert. Postfire revegetation was implemented in 2 affected salt desert shrub communities (greasewood; *Sarcobatus vermiculatus* Hook. and black sagebrush/shadscale; *Artemisia nova* A. Nels; *Atriplex confertifolia* Torr. & Frem.) to deter cheatgrass (*Bromus tectorum* L.) encroachment. We monitored cheatgrass densities for 3 years after the fire in burned drill seeded, burned not-seeded, and unburned plots to assess the rate of invasion and determine the impact on cheatgrass of drill seeding perennial species. Cheatgrass invaded quickly in both shrub sites following the fires. In the greasewood site, drill seeded species germinated but did not establish. This was likely due to a combination of soil salinity and extremely dry weather conditions during the second year of the study. Drill seeded species in the black sagebrush site germinated and established well, resulting in the establishment of 16.5 perennial grasses $\cdot$ m^{-2} and 1 356 shrubs $\cdot$ ha^{-1}. Cheatgrass densities were consistently lower in drill seeded versus not-seeded plots, although these were not always statistically different when Bonferroni comparisons were considered. The initial decrease in cheatgrass densities in drill seeded plots may have resulted from soil disturbance coupled with extremely low precipitation rather than competitive effects. Nevertheless, as seeded species mature and increase their competitive ability, we predict long-term suppression of cheatgrass in the absence of further disturbance.

Resumen

En 1998, el fuego quemó más de 11 330 ha de pastizal en Dugway Proving Ground en la región desértica oeste de Utah. Se implementaron acciones de revegetación posterior al fuego en dos comunidades arbustivas halófilas desérticas (''Greasewood''; *Sarcobatus vermiculatus* Hook. y ''Black sagebrush''/''Shadscale''; *Artemisia nova* A. Nels; *Atriplex confertifolia* Torr. & Frem.) para prevenir la invasión del ''Cheatgrass'' (*Bromus tectorum* L.). Monitoreamos las densidades de ''Cheatgrass'' durante tres años después del fuego en áreas: quemadas y sembradas mecánicamente, quemadas sin sembrar y áreas sin quemar, para evaluar la tasa de invasión y determinar el impacto de la siembra de especies perennes sobre el ''Cheatgrass.'' Después del fuego, el ''Cheatgrass'' invadió rápidamente ambos sitios de comunidades arbustivas. En el sitio ''Greasewood,'' las especies sembradas germinaron pero no se establecieron, esto probablemente debido a la combinación de la salinidad del suelo y las condiciones climáticas extremadamente secas que ocurrieron durante el segundo año del estudio. En el sitio ''Black sagebrush,'' las especies sembradas germinaron y se establecieron bien, estableciéndose 16.5 zacates perennes o m-2 y 1 356 arbustos o ha-2. Las densidades de ''Cheatgrass'' fueron consistentemente más bajas en las parcelas sembradas que en las no sembradas, aunque las diferencias no siempre fueron estadísticamente diferentes cuando se compararon con la prueba de Bonferroni. La disminución inicial de las densidades del ''Cheatgrass'' en las parcelas sembradas pudo haber resultado por el disturbio del suelo en conjunto con la precipitación extremadamente baja, mas que por efectos competitivos. No obstante, conforme las especies sembradas maduran e incrementan su capacidad competitiva, nosotros predijimos una supresión a largo plazo del ''Cheatgrass'' en ausencia de mas disturbio.

Key Words: black sagebrush, *Bromus tectorum*, drill seeding, greasewood, invasive, rehabilitation

INTRODUCTION

One of the greatest threats to ecosystems in semiarid regions of the western United States is the invasion of cheatgrass (*Bromus tectorum* L.). Once established, particularly in disturbed areas, cheatgrass can become a major obstacle preventing the recolonization and growth of more desirable native perennial species (Young et al. 1969; Young and Evans 1973, 1978). The rapid germination and early spring growth of cheatgrass allows it to utilize moisture and nutrients that are critical for native plant growth and survival (Melgoza et al. 1990; Smith and Nowak 1990). This preemptive use of resources puts native plants at a competitive disadvantage.

Cheatgrass also deters native perennial plant growth by altering natural fire regimes. Cheatgrass is extremely flammable and grows in dense stands in shrub interspaces, providing the accumulation of fine fuels necessary to carry fire to widely spaced woody plants (Young and Evans 1978; Whisenant 1990). The presence of a highly flammable continuous fuel load substantially increases the probability, frequency, and intensity of fire (Knapp 1996). Fire frequency in some cheatgrass infested rangelands has increased from 60 to 100 years to 3 to 5 years (Whisenant 1990). This increase in fire frequency combined with the propensity of cheatgrass to germinate quickly and produce large numbers of viable seeds perpetuates

Research was funded in part by US Department of Defense, Dugway Proving Ground, Utah. At the time of research, Jessop was a graduate student, Botany and Range Science, Brigham Young University, Provo, UT 84602.

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Manuscript received 14 February 2005; manuscript accepted 28 January 2007.

its growth and dominance by inciting "cyclic environmental degradation" that continually eliminates most native competitors (Young and Evans 1978).

The reclamation of cheatgrass-dominated lands has received much attention from ecologists and land managers throughout the Intermountain West, particularly in sagebrush (*Artemisia* spp.) steppe regions. Less consideration has been given to reclaiming cheatgrass-infested rangelands in other areas such as salt desert shrublands. This may be because these low-precipitation (< 200 mm annually), high-salinity, climatically harsh environments are inherently hard to reclaim following disturbance and historically have been impacted minimally by cheatgrass. Shrub die-off in the early 1980s (Dobrowolski and Ewing 1990) coupled with successive years (1983–1985) of extremely wet conditions has been linked to annual grass invasion and alteration of fire regimes in salt desert shrublands (West 1994). Increased fire occurrence and grazing pressure (Harper et al. 1996) continue to promote the expansion of cheatgrass into salt desert shrub communities.

For this study, we focused on the impact of drill seeding perennial species on cheatgrass encroachment following fire in depleted greasewood (*Sarcobatus vermiculatus* Hook.) and black sagebrush/shadscale (*Artemisia nova* A. Nels; *Atriplex confertifolia* Torr. & Frem.) sites in western Utah. Degraded native communities with even minimal amounts of cheatgrass present are particularly vulnerable to rapid invasion and dominance by cheatgrass following fire (Young et al. 1976). Following fire, there is a potential window of opportunity where drill seeding or other rehabilitation methods may be effectively implemented to slow cheatgrass invasion and reestablish a perennial community that could eventually displace cheatgrass.

Our objectives were to determine the rate of cheatgrass invasion into previously unburned, degraded salt desert shrub communities following fire; to assess the extent to which drill seeding perennial species deterred cheatgrass encroachment; and to determine if native residual species recovery in burned areas could impact cheatgrass. We tested the hypothesis that mechanical disturbance associated with drill seeding would depress cheatgrass production the first year. Subsequent cheatgrass suppression could occur from competition from seeded species that established in the first year.

METHODS

Study Area

The study sites were located at US Army Dugway Proving Ground (DPG), Tooele County, Utah. Based on vegetation maps provided by DPG, approximately 33 872 ha of training lands are dominated by cheatgrass, of which 11 307 ha (33%) are in the salt desert shrub zone. In addition to cheatgrass displacing native plants and decreasing faunal diversity, it also presents a potentially serious fire hazard. In order to minimize fire hazards and maintain the ecological integrity of training lands, efforts are being made to control cheatgrass at DPG. Large tracts of land dominated by cheatgrass make DPG ideal for cheatgrass research, particularly in relation to developing and testing methods to reclaim cheatgrass-dominated lands and minimize its spread into salt desert shrublands.

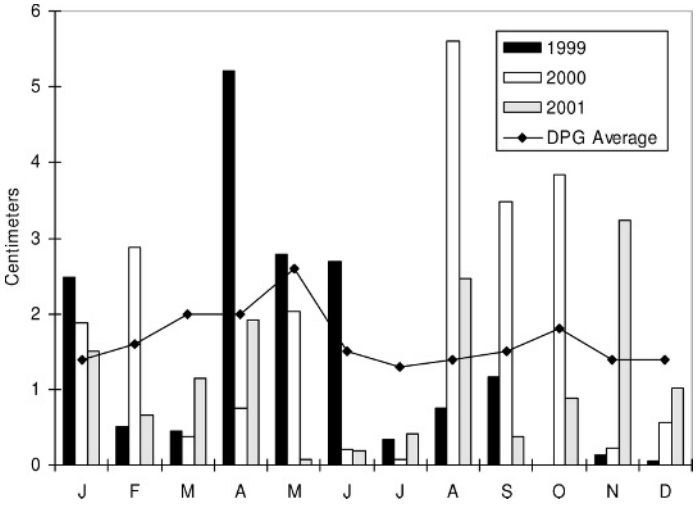


Figure 1. Monthly precipitation for 1999, 2000, and 2001, including the 36-year average for Dugway Proving Ground, Tooele Co, Utah. Total annual precipitation for 1999, 2000, and 2001 were 16.6, 21.9, and 13.9 cm, respectively, with the average total annual precipitation being 19.9 cm over 36 years.

During the summer of 1998, fires burned more than 11 330 ha of rangeland on DPG. Following the fires, 2 burned shrub communities were selected as study sites. One site was dominated by greasewood, the other by black sagebrush and shadscale. Both shrub communities are located on the southwest side of the Cedar Mountains. The greasewood community (UTM coordinates 3-28-133E, 44-60-942N) occurs at 1 332-m elevation and receives 150–200 mm of precipitation annually. Soils are Tooele fine sandy loam saline soils of the Tooele series of coarse-loamy, mixed (calcareous), mesic Typic Torriorthents (NRCS 1999). Currently, this site is occasionally used by mobile artillery units for live-fire training exercises. It has also been used as an impact zone for munitions. Prior to the fires of 1998, we observed that cheatgrass was present but not dominant in this community.

The black sagebrush and shadscale community (UTM coordinates 3-27-805E, 44-66-532N), hereafter referred to as the black sagebrush site, ranges from 1 494 m to 1 536 m in elevation and receives 250–300 mm of precipitation annually. Soils are Hiko Peak very stony loam soils of the Hiko Peak series of loamy-skeletal, mixed, mesic Xerollic Calciorthids (NRCS 1999). This site has not been actively used for military training exercises. Previous to the 1998 fire, we observed that cheatgrass encroachment was minimal, although high densities of small, single-stem plants were noted growing in patches underneath some shrubs. There is no record that either shrub community burned before the 1998 fires.

Temperatures on DPG range from −33°C to 43°C with an annual mean temperature of 11.2°C over the last 36 years. Precipitation occurs mainly during the spring months. Pronounced variations in precipitation amounts were observed during the 3 years (1999, 2000, 2001) of this study (Fig. 1).

Plot Layout and Data Collection

In each shrub community data were collected in 1-ha 1) burned not-seeded, 2) burned drill seeded, and 3) unburned plots. Each

Table 1. Seed mix composition and seeded species density for 2000 and 2001 following postfire revegetation at Dugway Proving Ground, Tooele Co, Utah. Seeded species density is shown only for the black sagebrush site since virtually no seeded species survived in the greasewood site.[1]

	Drill seed mix				2000		2001	
Origin	Species	Scientific name	% of mix	Site	Plants · m^{-2}	SE	Plants · m^{-2}	SE
I	Crested wheatgrass	*Agropyron cristatum*	36.8	S/G	22.8	± 2.19	15.8	± 1.86
N	Thickspike wheatgrass	*Elymus macrourus*	22.9	S/G	0.5	± 0.31	0.0	± 0.05
I	Russian wildrye	*Psathyrostachys juncea*	11.5	S/G	0.6	± 0.07	0.3	± 0.07
N	Great Basin wildrye	*Lymus cinereus*	11.5	S/G	0.6	± 0.05	0.3	± 0.07
N	Indian ricegrass	*Achnatherum hymenoides*	2.9	S/G	0.3	± 0.03	0.1	± 0.05
N	Blue flax	*Linum lewisii*	2.9	S/G	0.2	± 0.07	0.3	± 0.12
N	Fourwing saltbush	*Atriplex canescens*	11.5	S/G	0.0	± 0.03	0.1	± 0.03
	Broadcast seed mix				2000		2001	
Origin	Species	Scientific name	% of mix	Site	Plants · m^{-2}	SE	Plants · m^{-2}	SE
I	Dryland alfalfa	*Medicago sativa*	41.6	S	0.6	± 0.38	0.6	± 0.35
I	Yellow sweet clover	*Melilotus officinalis*	41.6	S	0.6	± 0.31	0.0	± 0.25
N	Wyoming big sagebrush	*Artemisia tridentata*	16.8	S	0.1	± 0.05	0.1	± 0.03

[1]N = native; I = introduced; S = sagebrush site; G = greasewood site.

plot type was replicated 3 times per community, giving a total of 9 plots (3 plot types × 3 replicates) per site. Drill seeding occurred over the entire burned area with the exception of burned not-seeded plots, which were centered within a burned area. Drill seeded plots were immediately adjacent to not-seeded plots. All plots within a community type were within 1 km of each other. Drill seeded plots were seeded with a rangeland drill at a bulk rate of 15.1 · kg · ha^{-1} with a perennial grass/forb/shrub seed mix. The seed mix was intended for general fire rehabilitation at DPG and was not specifically designed to be site or community specific. It consisted of both native and introduced species with the majority being crested wheatgrass (*Agropyron cristatum* L. Gaertner; Table 1; scientific nomenclature follows USDA NRCS [2005] for all species). At DPG, crested wheatgrass has been used extensively for revegetation projects because it establishes quickly, is resistant to spring wildfire, and has been shown to be effective at capturing sites from cheatgrass (D'antonio and Vitousek 1992). Additional species, including Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis* Beetle & Young, Welsh), dryland alfalfa (*Medicago sativa* L.), and yellow sweet clover (*Melilotus officinalis* L. Pallas.), were broadcast seeded following drilling at the black sagebrush site only. These species were considered inappropriate for the greasewood site because of higher soil salinity. Seeding of the black sagebrush site occurred during the second week of December 1998, while the greasewood site was seeded during the second week of March 1999.

A total of 40 samples were taken along four 100-m permanently fixed transects (10 samples per transect) within each plot. Cheatgrass density was recorded in order to assess the rate of encroachment and evaluate the effectiveness of the drill seeding treatment. We determined cheatgrass density by counting the number of plants (1 basal clump = 1 seedling, regardless of the number of stems) in a 16 × 25 cm quadrat. The density of drill seeded species was assessed using a 125 × 25 cm rectangular frame laid perpendicular to the drill rows so that 4 drill rows were covered with each placement. Each individual seedling counted was lumped into a grass, forb, or shrub category for the first year but afterward were separated by species.

To help clarify plant community response to fire and cheatgrass invasion, we recorded relative frequency (frequency per species/frequency for all species; Smith et al. 1987), canopy cover, and percent basal cover using a 0.25-m^2 nested frequency quadrat (NFQ) with 8 basal points. Frequency and canopy cover data were used to characterize community composition. For each species occurring in the NFQ, percent canopy cover was estimated ocularly using cover classes (< 1%, 1%–5%, 5%–25%, 25%–50%, 50%–75%, 75%–95%, >95%). Percent basal cover was used mainly to assess abiotic factors. Categories included in the basal cover estimate were litter, bare ground, pavement (2 mm to 2 cm), rock (>2 cm), and biological soil crusts.

Density, cover, and frequency values were pooled to get overall averages for plants in each of the experimental plots. To reduce potential edge effects, no sampling occurred within 5 m of plot borders. Data were gathered after the fire on the following dates: 3–23 June 1999, 5–7 June 2000, and 24–31 May 2001.

Three years after the fire, it was readily apparent that drill seeding had exerted a positive effect on native shrub recovery in the black sagebrush site. Obvious differences in shrub densities were observed between burned drill seeded and burned not-seeded plots. To quantify these differences, additional shrub density data were collected during August 2001 (shrub data were not collected in the greasewood site because there were very few shrubs in any treatment). The total number of shrubs were counted using circular transects. At each randomly selected starting point, a stake was pounded into the ground, a measuring tape attached to the stake was stretched to a predetermined length, and the researcher, while holding the tape, walked in a complete circle, counting all shrubs within the circle. Different radii lengths, reflecting various areas of circles, were used to facilitate ease and accuracy in counting shrubs. For example, shadscale in burned not-seeded plots was widely

dispersed. In order to get sufficient shrub density data on shadscale, it was necessary to use a large circle (17.8-m radius; 1 000 m^2). Because black sagebrush occurred in high densities in unburned plots, a smaller circle (4-m radius; 50 m^2) was used. Three samples were taken within each replicate of each plot type, giving a total of 9 samples. The mean number of shrubs was computed per treatment and converted to the number of plants · ha^{-1}. Only 4 shrub species were included in the density counts: black sagebrush, shadscale, and the 3 seeded species, four-wing saltbush and big sagebrush.

Statistical Analysis

Abiotic and temporal factors may influence the success of drill seeding at different sites. Therefore, comparisons of 2 inherently different communities may not be valid. Because of variations in soil types, soil chemistry, elevation, precipitation, and timing of seeding, we analyzed the greasewood and black sagebrush sites separately.

Data were analyzed as a completely randomized design with a 1-way treatment structure with repeated measures (years 1999, 2000, 2001). Repeated-measures analysis of variance (GLM model, SAS Institute 2002) was performed using relative frequency, percent relative cover, and mean densities of cheatgrass to determine significant differences in treatment effects. Factors analyzed in the design were year (1999 vs. 2000 vs. 2001), treatment (burned not-seeded, burned drill seeded, unburned), and year-by-treatment interactions. Where year-by-treatment interactions were significant, we analyzed each year separately using PROC GLM with a Bonferroni multiple comparisons test to determine specific differences in treatment effects. Treatment effects were considered to be significant at $P < 0.034$ (alpha = 0.1/3 replicates). We used the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. Because of nonnormal distribution, all data were square root transformed (variable + 0.50; Little and Hills 1978) prior to analysis. P values from both Shapiro–Wilk and Levene's test for homogeneity were not significant ($P > 0.05$), indicating that data were successfully normalized by the square root transformation and means were in fact homogeneous.

RESULTS

Greasewood Site

Emergence and Survival of Seeded Species. First-year emergence of seeded species at the greasewood site was very good. In 1999, seeded species emergence in burned drill seeded plots for grasses, forbs, and shrubs were 42.7, 2.4, and 0.24 plants · m^{-2}, respectively. One year later, virtually nothing had survived. No seeded species were noted in the quadrats in either 2000 or 2001. (In both 2000 and 2001, a few individuals of *Atriplex canescens* [Pursh] Nutt. were observed, however, in some of the drill-rows adjacent to our transects.)

Impact of Drill Seeding on Cheatgrass. There was a significant year-by-treatment interaction ($P < 0.05$) for cheatgrass density. In 1999, approximately 1 year after the fire, cheatgrass densities in burned drill seeded plots were 43% lower than burned not-seeded plots, 219.1 and 381.9 plants · m^{-2}, respectively, compared to 608.4 plants · m^{-2} in unburned plots ($P = 0.02$). From 1999 to 2000, cheatgrass densities in all plots dropped to < 3 plants · m^{-2}. By the summer of 2001, cheatgrass had rebounded in all treatments. Densities were lowest in the unburned plots (80.1 plants · m^{-2}) and higher in burned drill seeded (113.9 plants · m^{-2}) and burned not-seeded plots (139.1 plants · m^{-2}; $P = 0.03$; Fig. 2A). When pairwise Bonferroni comparisons were considered, only differences in cheatgrass densities between unburned and burned seeded plots in 1999 were significant ($P = 0.0249$).

There were no significant differences in cheatgrass frequency between treatments in the greasewood site ($P > 0.05$ for all years).

There was a significant year-by-treatment interaction ($P < 0.05$) for cheatgrass cover. In 1999, cheatgrass cover was not different between treatments (Bonferroni comparisons: unburned vs. burned not-seeded, $P = 0.068$; unburned vs. burned drill seeded, $P = 1.000$; burned not-seeded vs. burned drill seeded, $P = 0.1893$; Fig. 2C). The following year, cheatgrass cover was < 1% in all treatments. By 2001, cheatgrass cover was lowest in the unburned plots (4.2%) and highest in burned drill-seeded plots (9.2%). Pairwise Bonferroni comparisons showed that cheatgrass cover in unburned plots was significantly different than both burned seeded and burned not-seeded plots ($P = 0.0028$ and $P = 0.0080$ respectively; Fig. 2C), but differences in cheatgrass cover between burned seeded and burned not-seeded plots were not ($P = 0.9184$).

Response of Residual Native and Exotic Species. There was a conspicuous lack of native understory species in the greasewood site prior to burning. Following the fire, the site was quickly dominated by cheatgrass. The only native residual species noted after the fire was greasewood. Burning followed by drill seeding had a greater impact on greasewood cover than burning alone. Greasewood cover in unburned plots was 2.49% but decreased to 1.48% and 0.56% in burned not-seeded and burned drill-seeded plots, respectively ($P > 0.05$). Although we noticed that greasewood resprouted more readily in drill seeded plots, there was no apparent impact of its regrowth on cheatgrass.

Percent relative frequency of several exotic annual forbs changed substantially throughout the study. There were significant ($P < 0.05$) year-by-treatment interactions for halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.), bur buttercup (*Ranunculus testiculatus* [Crantz.] Bess.), Russian thistle (*Salsola iberica* L.), tumble mustard (*Sisymbrium altissimum* L.), and clasping pepperweed (*Lepidium perfoliatum* L.). Halogeton was not present in any treatment in 1999 but was found in all treatments in both 2000 and 2001 (mean frequency for all treatments = 2.3 and 3.4%, respectively). Bur buttercup, tumble mustard, and pepperweed were present in 1999 and 2001 (mean frequency for all treatments = 13.1% and 11.4%, respectively) but were virtually eliminated in 2000 (< 1%). Russian thistle frequency averaged across all treatments increased from 5% in 1999 to 85% in 2000 and then declined to 27% in 2001. Based on Bonferroni comparisons, in 2001, pepperweed, Russian thistle, and tumble mustard showed significant treatment effects ($P = 0.0173$, 0.0038,

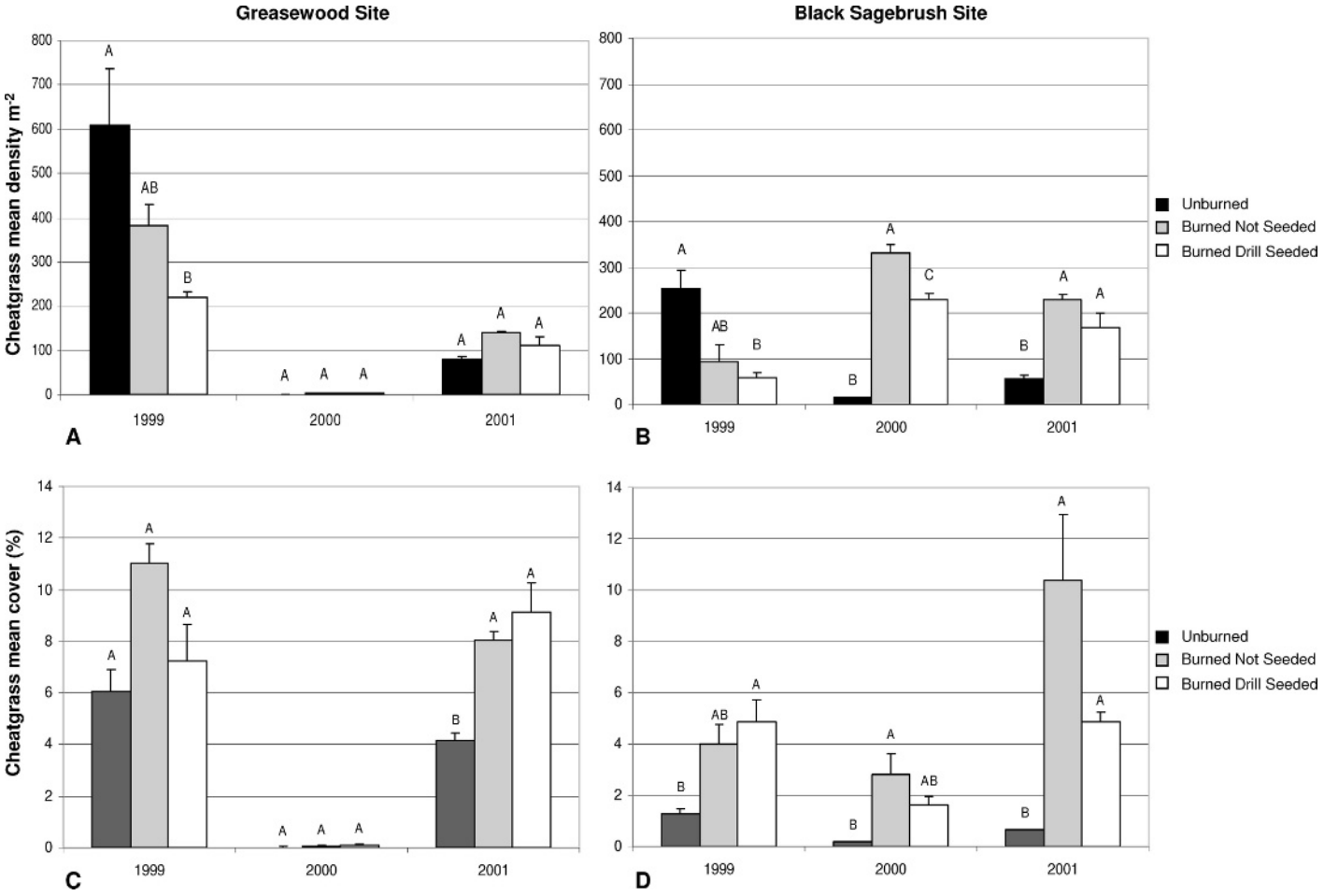


Figure 2. Cheatgrass densities (**A, B**) and mean relative % cover (**C, D**) compared in burned drill seeded, burned not-seeded, and unburned plots over 3 years in greasewood and black sagebrush sites at the Dugway Proving Ground, Tooele Co, Utah. For cheatgrass densities and cover, year × treatment = $P < 0.02$ for both sites; $n = 3$.

and 0.0205, respectively), but halogeton and bur buttercup did not ($P = 0.636$ and 0.0561, respectively). In 2001, cover for all exotic forbs combined was highest in unburned plots (5.7%) followed by drill seeded (3.9%) and not-seeded (2.2%) plots, although these differences were not significant ($P = 0.1606$).

Impact of Fire and Drill Seeding on Abiotic Factors. Fire and drill seeding had a considerable impact on the percent cover of litter, bare ground, and biological soil crusts. In 1999, litter decreased from 54.2% in unburned plots to 22.8% in burned not-seeded plots. Litter cover in burned drill seeded plots was 13.8%. This decrease in litter coincides with an increase in bare ground in disturbed sites (22.7% in unburned plots, 52.2% and 75.3% in burned not-seeded and burned drill seeded plots, respectively). In both 2000 and 2001 there was $< 4\%$ difference between unburned plots and burned not-seeded plots for litter and bare ground cover (litter cover year 2000 and 2001 = 59.4% ± 2% and 42.7% ± 2%, respectively; bare ground cover year 2000 and 2001 = 37.1% ± 2% and 46.4% ± 2%, respectively). In burned drill seeded plots, litter cover was 32% lower and bare ground cover $> 28\%$ higher than unburned and not-seeded plots in both 2000 and 2001. Biological soil crust cover decreased from 14.2% in unburned plots to 11.9% and 2.4% in burned not-seeded and burned drill seeded plots, respectively, for 1999. During 2000, biological soil crust cover was $< 3\%$ in any treatment. By 2001, biological soil crust cover was 7.6% in unburned plots compared to 5.1% and 1% in burned not-seeded and burned drill seeded plots, respectively.

Black Sagebrush Site

Emergence and Survival of Seeded Species. All species included in the seed mix emerged and established in burned drill seeded sites. Densities of seeded grasses, forbs, and shrubs in 1999 were 78.8, 15.8, and 0.35 plants · m^{-2}, respectively. While seeded species densities declined in 2000 by $> 85\%$, cheatgrass densities in burned drill seeded plots increased by 76% (Fig. 2B). By 2001, densities of seeded grasses, forbs, and shrubs were 16.5, 0.9, and 0.2 plants · m^{-2}, respectively (Table 1).

Following the fire, black sagebrush was completely eliminated from burned sites. However, after 3 years it was obvious that drill seeding successfully promoted the establishment and recovery of other native shrubs. Burned not-seeded plots were almost devoid of shrubs, while the surrounding drill seeded areas showed excellent establishment of four-wing saltbush and an increase in shadscale. Shrub density counts using the circular

transect method showed densities of 1 356 shrubs · ha^{-1} in burned drill seeded plots compared to 236 shrubs · ha^{-1} in burned not-seeded plots. Unburned plots averaged 11 711 shrubs · ha^{-1}. On average, shadscale decreased from 955 plants · ha^{-1} in unburned plots to 237 plants · ha^{-1} in burned not-seeded plots but increased to 522 plants · ha^{-1} in burned drill seeded sites even though it was not seeded.

Seeded grasses were second only to cheatgrass in mean relative frequency and cover. In burned drill seeded plots, cheatgrass frequency averaged 34.8% for all years combined, while seeded grasses had a mean frequency of 25.3%. Crested wheatgrass was highest in density, frequency, and cover among all seeded species. Seeded forbs accounted for 8.1% of all species encountered with alfalfa being most abundant followed by blue flax (Table 1).

Impact of Drill Seeding on Cheatgrass. Drill seeding perennial species in the black sagebrush site impacted cheatgrass density, frequency, and cover. There was a significant ($P < 0.05$) year-by-treatment interaction for both cheatgrass density and cover. When years were analyzed separately, cheatgrass densities were significantly different ($P < 0.05$) between treatments for all 3 years. Densities were consistently lower in burned drill seeded plots than in burned not-seeded plots for all years, but Bonferroni comparisons showed that these differences were significant only for 2000 ($P = 0.0107$; Fig. 2B). In 1999, cheatgrass densities averaged 253 plants · m^{-2} in unburned plots, 93 plants · m^{-2} in burned not-seeded plots and 53 plants · m^{-2} in burned drill seeded plots ($P < 0.05$; Bonferroni comparisons: unburned vs. burned not-seeded, $P = 0.0527$; unburned vs. burned drill seeded, $P = 0.0191$, burned not-seeded vs. burned drill seeded, $P = 1.000$). In 2000, cheatgrass densities in unburned plots were only 15 plants · m^{-2}, while burned not-seeded plots and burned drill seeded plots averaged 330 plants · m^{-2} and 230 plants · m^{-2}, respectively ($P < 0.05$; Bonferroni comparisons: unburned vs. burned not-seeded, $P = 0.0001$; unburned vs. burned seeded, $P = 0.0001$). In 2001, cheatgrass densities were lowest in unburned plots (55 plants · m^{-2}) and 27% lower in burned drill seeded plots (169 plants · m^{-2}) than in burned not-seeded plots (230 plants · m^{-2}; $P < 0.05$; Bonferroni comparisons: unburned vs. burned not-seeded, $P = 0.0014$; unburned vs. burned seeded, $P = 0.0083$; Fig. 2B).

In 1999 and 2000, cheatgrass cover was $< 5\%$ in any treatment. In 2001, cheatgrass cover increased to $> 10\%$ in burned not-seeded plots compared to 4.9% and $< 1\%$ in burned drill seeded and unburned plots, respectively ($P < 0.05$; Fig. 2D). Bonferroni comparisons showed that cheatgrass cover was significantly lower in unburned plots compared to burned not-seeded plots for 2000 ($P = 0.0082$) and 2001 ($P = 0.0014$), but differences between burned drill seeded and burned not-seeded plots were never significant.

Differences in relative frequency of cheatgrass between treatments were not significant ($P > 0.05$) for any year; however, the relative frequency of cheatgrass was 37%, 25%, and 9% lower in burned drill seeded plots than burned not-seeded plots for 1999, 2000, and 2001, respectively.

Response of Residual Native and Exotic Species. By 2001, percent cover of residual grasses and forbs in burned plots were not significantly different than unburned plots ($P > 0.05$) indicating natural recovery of many species following the fire (Fig. 3). Shrub cover declined severely in burned plots.

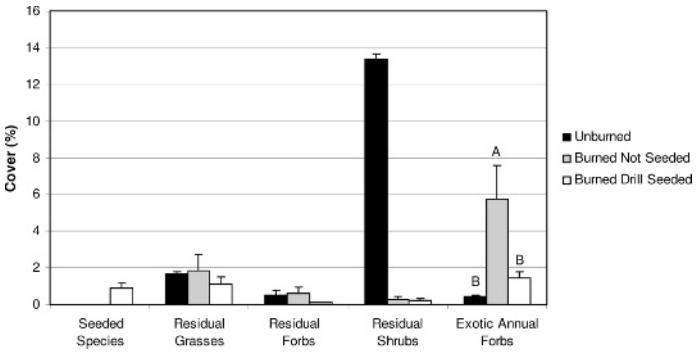


Figure 3. Percent canopy cover of seeded species, residual species, and exotic annual forbs in burned drill seeded, burned not-seeded, and unburned plots in a black sagebrush site 2 years following fire (2001). Residual shrubs = black sagebrush (*Artemisia nova* A. Nels.), winterfat (*Krascheninnikovia lanata* [Pursh] A. D. J. Meeuse & Smit), green rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), Ephedra (*Ephedra nevadensis* S. Wats.), broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby), shadscale (*Atriplex confertifolia* Torr. & Frem.), and horsebrush (*Tetradenia glabrata* Torr. & Gray). Residual forbs = hoary tansyaster (*Machaeranthera canescens* [Pursh] Gray), phlox (*Phlox hoodii* Richards.), and Munro's globemallow (*Sphaeralcea munroana* [Dougl. ex Lindl.] Spach ex Gray). Residual grasses = bluebunch wheatgrass (*Pseudoroegnaria spicata* [Pursh] A. Love), galletta (*Hilaria jamesii* Torr.), Sandberg's bluegrass (*Poa secunda* J. Presl), and bottle brush squirreltail (*Elymus hystrix* L.). Exotic forbs = tansymustard (*Descurainia sophia* L.), redstem storks bill (*Erodium cicutarium* L.), halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.), bur buttercup (*Ranunculus testiculatus* [Crantz] Bess.), Russian thistle (*Salsola iberica* L.), and tumble mustard (*Sisymbrium altissimum* L.). See Table 1 for seeded species.

By 2001, based on Bonferroni comparisons, cover of exotic annual forbs was significantly higher ($P = 0.0375$) in burned not-seeded plots (5.8%) than either burned drill seeded (1.5%) or unburned plots($< 1\%$; Fig. 3). The pattern was the same for exotic annual forb frequency (burned not-seeded plots = 44.5%; burned drill seeded plots = 22.4%; unburned plots = 13.2%; $P = 0.0348$). Halogeton, Russian thistle, and tumble mustard were not present on site in 1999 and 2000 but appeared in all plots in 2001. When lumped and averaged across years, relative frequency of exotic forbs was lowest in unburned plots (6.4%) and higher in burned drill seeded (15.6%) and burned not-seeded plots (30.2%).

Impact of Fire and Drill Seeding on Abiotic Factors. In 1999, cover for litter and bare ground in unburned plots was 21.3% and 23.1%, respectively. Fire decreased litter to $< 7\%$ and increased bare ground to $> 60\%$ in burned not-seeded and burned drill seeded plots. For 2000 and 2001, litter cover was consistent across all plots (mean = 28.3%; range = 25.8%–35.7%), while bare ground was 30.1% in unburned plots and 45.7% and 52% in burned not-seeded and burned drill seeded plots, respectively. Biological soil crust cover decreased from 19.9% in unburned plots to 4.1% and 2.3% in burned not-seeded and burned drill seeded plots, respectively, for 1999. During 2000 and 2001, biological soil crust cover averaged 13.3% in unburned plots but $< 1.2\%$ in the other treatments.

DISCUSSION

We observed general trends in both the greasewood and black sagebrush sites. In 1999, unburned plots in both sites had a higher density of cheatgrass compared to burned plots (Figs. 2A and 2B). This may give the impression that the unburned plots were dominated by cheatgrass. In reality, most of the cheatgrass in these areas were small, single-stemmed plants with few caryopses that were confined to dense patches under shrubs and dried Russian thistles. This is not uncommon because shrubs act as nurse plants ameliorating harsh environmental conditions and are often the foci of invasion for cheatgrass (Meyer et al. 2001). Few plants were noted in the shrub interspaces. In contrast, cheatgrass in burned areas was much more robust with multiple stems per plant, had many caryopses, and was distributed more evenly. In spite of the high density of cheatgrass in unburned plots, cover class estimates showed that cheatgrass cover was lowest in unburned plots in all 3 years in both shrub communities, suggesting that density does not always equate with dominance (Figs. 2C and 2D). Even though cheatgrass was a relatively minor component of both native shrub communities prior to burning, it quickly became dominant following the fire.

Following fire, there is a decrease in resource competition and an opening of available niches (Blank et al. 1994). The rapid germination and growth of cheatgrass enables it to fill these niches and persist (Melgoza et al. 1990). We predicted that occupation of available niches by seeded species and the resulting competition for moisture and nutrients would minimize cheatgrass encroachment and cause cheatgrass densities to decrease over time. Because almost no seeded species survived to compete with cheatgrass in the greasewood site and because cheatgrass densities were consistently lower in drill seeded versus not-seeded plots, we initially postulated that soil disturbance buried cheatgrass too deep to germinate. Soils in the greasewood site are soft and easily turned. However, within the same time period that our study was conducted, another study by Meyer et al. (2001) on DPG showed that during favorable moisture patterns, moderate soil disturbance significantly increased cheatgrass recruitment and seed production. Conversely, severe soil disturbance during dry periods either had no effect or significantly decreased cheatgrass recruitment. Results from Meyer et al. (2001) lead us to believe that the decrease of cheatgrass in drill seeded plots at the greasewood site was a combination of severe soil disturbance and extremely dry conditions. Meyer et al. (2001) concluded that cheatgrass invasion in salt desert shrublands may be more dependent on moisture than on disturbance. Evans et al. (1970), Davis et al. (2000), and Bates et al. (2005) observed pronounced variation in the growth and phenology of cheatgrass because of fluctuations in precipitation; our observations were similar. From 1999 to 2000, cheatgrass densities in unburned plots dropped from 608.4 to 0.64 plants $\cdot$ m^{-2} and across all plots frequency declined from 42% to 8%. This decrease in cheatgrass coincides with much lower precipitation during critical growth periods (Fig. 1).

Fire and drill seeding had a considerable impact on the percent cover of litter and bare ground. Bates et al. (2004) observed increased cheatgrass in areas with high litter. Evans and Young (1970, 1972) emphasized the importance of litter reduction as a means of minimizing the number safe sites for cheatgrass seed germination. Results of our study suggest that litter removal as a means of reducing safe sites is most effective when done with little or no soil disturbance. Even though litter was greatly reduced and cheatgrass densities were consistently lower in drill seeded plots (although not always statistically different based on Bonferroni comparisons), the creation of water catchments in the drill furrows and the increase in bare ground appeared to promote the growth of exotic annual forbs. Exotic annual forbs are common invaders in salt desert shrublands following disturbance. Bare ground cover increased substantially in both sites following disturbance by fire and drill seeding. This may have opened invasion niches for exotic forbs to fill. As with cheatgrass, some exotic forbs may be more dependent on moisture than disturbance during periods of drought. However, the same does not appear to be true for Russian thistle. In the greasewood site, bur buttercup, tumble mustard, and pepperweed were present in 1999 and 2001 (mean frequency for all treatments = 13.1% and 11.4%, respectively) but were virtually eliminated in 2000 (< 1% frequency) when spring and summer precipitation were well below average (Fig. 1). In contrast, across all plots Russian thistle frequency increased from 5% in 1999 to 85% in 2000. Although exotic forbs increased following disturbance in both sites, cheatgrass can outcompete many exotic forb species, including halogeton, tumble mustard, and Russian thistle, and will likely remain a dominant weedy species over time.

In both sites, fire and soil disturbance decreased cover of biological soil crusts. Biological soil crusts are important for maintaining soil stability and retaining soil moisture and nutrients and may influence the germination and establishment of vascular plants (Belnap 1994). Compared to unburned plots in our study, the combined impact of fire and drill seeding decreased biological soil crust cover by 86% in the greasewood site and by 93% in the black sagebrush site. On DPG, Burnham (2001) observed lesser amounts of cheatgrass where biological soil crusts were undisturbed. Similar observations were made in southern Utah by Evangelista et al. (2004). In these areas, crust disturbance was associated with higher amounts of cheatgrass, implying a resistance to invasion by cheatgrass. Crusts are slow to recover from severe disturbance, sometimes requiring 40 years or more to recolonize even small areas (Belnap 1994). Considering their ecological importance in semiarid ecosystems and their potential to resist cheatgrass invasion, the impact of soil-disruptive rehabilitation methods on biological soil crusts should be considered prior to implementation.

Seeded species in the greasewood site germinated but did not establish. This was likely due to low precipitation during critical growth periods (Fig. 1), drought conditions that persisted through summer months, and the saline soils characteristic of greasewood communities. Had there been more normal precipitation during the second year, we may have had increased seedling survival. Other seeding trials in similar greasewood sites in northern Utah have demonstrated that it is possible for seeded species to establish and persist (Britton et al. 1999).

In the black sagebrush site, seeded species densities decreased during the second year of the study while at the same time cheatgrass densities increased (Fig. 2B). This may have resulted partially from grazing pressure from feral horses. Feral horses

roam freely on DPG, and a band of horses occupies the study region year-round. Following drill seeding, the new growth of palatable plants attracted horses to the sites, and many of the seeded species were cropped nearly to the ground. Grazing combined with drought conditions may have reduced seeded species. We also observed that hoof prints from the horses acted as catchments for both cheatgrass seed and water, promoting higher cheatgrass densities. There was no indication that horses utilized the greasewood site.

By 2001, seeded species densities in the black sagebrush site increased substantially. Because data were collected from the same points in consecutive years, it may seem unusual that perennial plant densities would show a sharp decline in 2000 but then rebound in 2001. It is possible that there was less grazing pressure by the horses in 2001, that seedlings may have appeared to be dead in 2000 because of the dry conditions and were not counted even though they were still alive, or that densities of drill seeded species may have increased in 2001 because dormant seeds germinated.

We thought it unusual that shadscale densities increased in the black sagebrush site in burned drill seeded plots relative to burned not-seeded plots. Shadscale is not known to resprout after fire (West 1994) and was not included in our seed mix. However, the drill seeding process appeared to stimulate its recovery. This may have resulted from increased moisture in the drill rows or from soil churning that brought dormant seeds closer to the surface where more favorable environmental conditions promoted germination.

In a landscape scale fire rehabilitation study, Thompson et al. (2006) showed that even minimal establishment from seeded species following fire is enough to suppress annual weeds. In the black sagebrush site, drill seeded grasses averaged 16.5 plants $\cdot$ m^{-2}, while four-wing saltbush and shadscale combined averaged 1 356 plants $\cdot$ ha^{-1}. Drill seeded species cover was minimal because most plants were not mature (Fig. 3). Nevertheless, as drill seeded species mature and expand their root systems and become more competitive, we predict that cheatgrass and other annual weeds will continue to decline. Burned areas that were not drill seeded, however, will likely remain in a degraded state dominated by exotic annual weeds (Thompson et al. 2006). Residual species in burned areas that were not seeded may increase in abundance over time, but it is unlikely that they will recolonize to the point of dominance.

MANAGEMENT IMPLICATIONS

Our study showed that cheatgrass and other exotic annual weeds can quickly invade burned sites in salt desert shrublands. By the end of the study, cheatgrass density and cover were higher on burned plots, whether seeded or not. The emergence and survival of seeded species in the 2 sites was highly variable, yet there was still a trend of lower densities of cheatgrass in burned drill seeded plots versus burned not-seeded plots in both shrub communities, although these differences were not always statistically different based on Bonferroni comparisons. Additionally, cover of exotic annual forbs was lower on seeded plots than on unseeded plots and did not differ in cover from unburned plots. This emphasizes the importance of postfire intervention to reduce annual weed invasion.

Cheatgrass is still a relatively minor component of many salt desert shrublands in the Great Basin of North America, but its range continues to expand. As fires become more common in salt desert shrublands, attempts to restore sites before invasive species like cheatgrass become fully established may help curb the magnitude of invasion (Bakker and Wilson 2004) and increase the likelihood of maintaining a functional ecosystem. Thus, there is a need to identify reclamation techniques appropriate to these areas. Although germination and survival of drill seeded species varied between sites in this study, drill seeding following fire did suppress cheatgrass and help in reestablishing a perennial community in the black sagebrush site. Had there been more moisture during the second growing season, drill seeded species may have fared better all around but especially in the greasewood site. Even moderate success from drill seeding could suppress cheatgrass and other annual weeds in the long run.

ACKNOWLEDGMENTS

The authors would like to thank Duane Smith for operating the rangeland drill and the Dugway field crew for assisting in data collection. We thank Mark Evans, professor of statistics, Washington State University, and Bruce Roundy, professor of rangeland science, Brigham Young University, for statistical guidance. We appreciate the comments of multiple reviewers which greatly improved the manuscript.

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Organisms as Ecosystem Engineers

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Source: *Oikos*, Apr., 1994, Vol. 69, No. 3 (Apr., 1994), pp. 373-386

Published by: Wiley on behalf of Nordic Society Oikos

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OIKOS 69: 373–386. Copenhagen 1994

Organisms as ecosystem engineers

Clive G. Jones, John H. Lawton and Moshe Shachak

Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. – Oikos 69: 373–386.

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats. Autogenic engineers (e.g. corals, or trees) change the environment via their own physical structures (i.e. their living and dead tissues). Allogenic engineers (e.g. woodpeckers, beavers) change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means. The direct provision of resources to other species, in the form of living or dead tissues is not engineering. Organisms act as engineers when they modulate the supply of a resource or resources other than themselves. We recognise and define five types of engineering and provide examples. Humans are allogenic engineers par excellence, and also mimic the behaviour of autogenic engineers, for example by constructing glasshouses. We explore related concepts including the notions of extended phenotypes and keystone species. Some (but not all) products of ecosystem engineering are extended phenotypes. Many (perhaps most) impacts of keystone species include not only trophic effects, but also engineers and engineering. Engineers differ in their impacts. The biggest effects are attributable to species with large per capita impacts, living at high densities, over large areas for a long time, giving rise to structures that persist for millennia and that modulate many resource flows (e.g. mima mounds created by fossorial rodents). The ephemeral nests constructed by small, passerine birds lie at the opposite end of this continuum. We provide a tentative research agenda for an exploration of the phenomenon of organisms as ecosystem engineers, and suggest that all habitats on earth support, and are influenced by, ecosystem engineers.

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Interactions between organisms are a major determinant of the distribution and abundance of species. Ecology textbooks (e.g. Ricklefs 1984, Krebs 1985, Begon et al. 1990) summarise these important interactions as intra- and inter-specific competition for abiotic and biotic resources, predation, parasitism and mutualism. Conspicuously lacking from the list of key processes in most text books is the role that many organisms play in the creation, modification and maintenance of habitats. These activities do not involve direct trophic interactions between species, but they are nevertheless important and common. The ecological literature is rich in examples of habitat modification by organisms, some of which have been extensively studied (e.g. Thayer 1979, Naiman et al. 1988). However, in general, population and community ecology have neither defined nor systematically identified and studied the role of organisms in the creation and maintenance of habitats. There is not even a word, or words, in common use to describe the process. We will call the process *Ecosystem Engineering* and the organisms responsible *Ecosystem Engineers.*

Beaver (*Castor canadensis*) are familiar examples of

Accepted 21 September 1993

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organisms acting as ecosystem engineers. By cutting trees and using them to construct dams they alter hydrology, creating wetlands that may persist for centuries. "These activities retain sediments and organic matter in the channel, ... modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity" (Naiman et al. 1988).

However, beaver are by no means the only ecosystem engineers. As we will show, a vast array of species have effects that are fundamentally similar, albeit often on more modest spatial and temporal scales. Yet there is no common language to describe what ecosystem engineers do, no formal structure to model their effects, and no general theory round which to organise understanding of the process. Examples, which are developed more formally below (for others, see Table 1), include not only beaver and their dams but also gophers, ants and termites that move soil, woodpeckers that drill holes, alligators that make wallows, rock-eating snails, trees, corals, seagrass beds and *Sphagnum* blanket bogs.

The purposes of this article are fourfold: (i) to define and to give examples of ecosystem engineering by organisms; (ii) to develop a conceptual framework that explains and classifies its effects; (iii) to show how organismal engineering differs from related concepts (e.g. 'keystone species' Paine 1969, Krebs 1985); (iv) and to identify questions for further work on organisms as ecosystem engineers. First we define what we mean by an ecosystem engineer, before providing examples and a conceptual framework for what is, and is not, ecosystem engineering.

Definitions

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats.

The direct provision of resources by an organism to other species, in the form of living or dead tissues is not engineering. Rather, it is the stuff of most contemporary ecological research, for example plant-herbivore or predator-prey interactions, food web studies and decomposition processes.

Autogenic engineers change the environment via their own physical structures, i.e. their living and dead tissues. *Allogenic engineers* change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means.

Armed with these definitions we can now proceed to consider some detailed examples. We are not, at this juncture, concerned with the magnitude or scale of the impacts of engineers on communities and ecosystems. We are interested solely in discovering properties that all engineers have in common. We address the scale and magnitude of their effects later.

Classification of organisms as engineers

Table 1 summarises examples of organisms as ecosystem engineers. The table is illustrative, not exhaustive. Additional examples are discussed at greater length in the text.

All the examples of which we are aware can be assigned to one of five possible cases (Fig. 1), or to a combination of two or more of these cases. As in many other areas of ecology, the diversity of biological processes means that precise pigeon-holing is sometimes difficult. The boundaries between types of engineering are occasionally fuzzy and, in the real world, separating engineering from other ecological processes may also be difficult, simply because these non-trophic interactions always co-occur with trophic interactions. We discuss some difficult cases as we proceed. The majority of examples are, however, easy to classify. The legend to Fig. 1 explains the conventional notation used to describe them. For clarity, it is easiest to introduce the arguments using beaver and their dams.

Beaver conform to case 4 in Fig. 1. That is they are allogenic engineers, taking materials in the environment (in this case trees, but in the more general case it can be any living or non-living material), and turning them (engineering them) from physical state 1 (living trees) into physical state 2 (dead trees in a beaver dam). This act of engineering then creates a pond, and it is the pond which has profound effects on a whole series of resource-flows used by other organisms. The critical step in this process is the transformation of trees from state 1 (living) to state 2 (a dam). This transformation modulates the supply of other resources, particularly water, but also sediments, nutrients etc. A critical characteristic of ecosystem engineering is that it must change the availability (quality, quantity, distribution) of resources utilised by other taxa, excluding the biomass provided directly by the population of allogenic engineers. Engineering is not the direct provision of resources in the form of meat, fruits, leaves, or corpses. Beaver are not the direct providers of water, in the way that prey are a direct resource for predators, or leaves are food for caterpillars.

Now consider the autogenic equivalents of beaver (Fig. 1, case 3). Simple examples are the growth of a forest or a coral reef. Trees and corals are direct sources of food and living space for numerous organisms, but the production of branches, leaves or living coral tissue does not constitute engineering. Rather, it conforms to case 1 in Fig. 1 (the direct provision of resources). However, the development of the forest or the reef results in physical structures which do change the environment and modulate the distribution and abundance of other resources.

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Table 1. Examples of organisms acting as ecosystem engineers. Classification according to Fig. 1. Additional examples are discussed in the text.

Organism	Habitat	Activity	Impact	Refs.
Case 2 (allogenic)				
American alligators, *Alligator mississippiensis*	Everglades National Park	create wallows	retain water in droughts; provide refuges for fish, fisheating birds, etc.	Finlayson & Moser (1991)
Rabbits, *Oryctolagus cuniculus*, badgers, *Meles meles*	Europe	dig extensive burrows (rabbit warrens, badger setts)	burrows occupied by other species, e.g fox, *Vulpes vulpes,* and by many invertebrates	Southern (1964); Neal & Roper (1991)
Case 3 (autogenic)				
Marine phytoplankton	Gulf of Maine	blooms of phytoplankton particles scatter and absorb light in upper layers of water column	enhance warming of surface waters that may initiate development of thermocline	Townsend et al. (1992)
Microalgae in sea ice	Antarctica	scatter and absorb light within ice and underlying seawater; reduce strength of ice	enhance melting and break up of ice	Buynitskiy (1986); Arrigo et al. (1991)
Freshwater phytoplankton	Lake St. George, Ontario	intercept light in upper water column; small algal spp. more effective than large spp.	light interception leads to shallower mixing depth, lower metalimnetic temperatures and lower heat content of water column	Mazumder et al. (1990)
Cyanobacteria and other nonvascular plants	desert and semi-desert soils	exude mucilaginous organic compounds	glue the organisms, organic matter and soil particles together to form a microphytic crust; change infiltration, percolation, retention and evaporation of water; reduce soil erosion; affect seedling emergence	West (1990)
Bog moss, *Sphagnum* spp.	Northern and western Britain	build 'blanket' and 'raised' bogs via accumulated peat	major changes in hydrology, pH, and topography	Tansley (1949)
Submerged macrophytes	freshwater lakes, ponds and rivers	grow to create weed beds	attenuate light; steepen vertical temperature gradient; retard flow; enhance sedimentation; oxygenate rhizosphere	Carpenter & Lodge (1986)
Forest trees (broad-leaved and coniferous)	Hubbard Brook Experimental Forest, New Hampshire	shed branches and trunks into streams	create debris dams; alter morphology and stability of stream channels, storage and transport of dissolved organic matter and sediments; different tree species may create dams which differ in persistence	Likens & Bilby (1982); Hedin et al. (1988)
Higher plants	ubiquitous	dead leaves etc. accumulate as litter	alter microenvironment of soil; change surface structure, affecting drainage, and transfer of heat and gasses; act as physical barrier for seeds and seedlings; numerous impacts on structure and composition of plant communities	Facelli & Pickett (1991)
Terrestrial plants in 29 families, with >1,500 species	ubiquitous	grow structures (modified leaves, leaf axils etc.) that impound water	create small aquatic habitats, supporting a highly specialised insect fauna	Fish (1983)
Case 4 (allogenic)				
Marine meiofauna (protozoa and representatives of many invertebrate phyla)	ubiquitous	biodeposition, bioturbation, porewater circulation, and faecal pellet production	change physical, chemical and biological properties of sediments; change direction and magnitude of nutrient fluxes; increase oxygenation of sediments	Reichelt (1991)
Marine burrowing macrofauna	ubiquitous	burrow into and redistribute sediments; bioturbation; burrow ventilation	create dynamic sediment mosaics; actively transport solutes into burrows; increase oxygenation of sediments; stimulate microflora; increase decomposition rates	Anderson & Kristensen (1991); de Wilde (1991); Meadows & Meadows (1991b)

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Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Marine zooplankton	ubiquitous	fiter living, dead organic and inorganic (e.g. clay) particles, and concentrate into faecal pellets	sinking faecal pellets important in vertical transport and exchange of elements and organic compounds in oceans	Dunbar & Berger (1981); Wallace et al. (1981); Fowler & Knauer (1986)
Fiddler crab, *Uca pugnax*	New England salt marsh	dig burrows	increase soil drainage and oxidation-reduction potential; increase decomposition rates; increase primary production at intermediate tidal heights	Bertness (1985)
European periwinkle, *Littorina littorea*	New England rocky beach	bulldoze sediments from hard substrates	prevent sediment accumulation and hence growth and establishment of algal canopy; algae are case 3 engineers and further increase sedimentation rates; faunal composition markedly different with and without snails	Bertness (1984a)
Snails, *Euchondrus* spp.	Negev desert	eat endolithic lichens and the rock they grow in	increase rate of nitrogen cycling, soil formation and rock erosion	Shachak et al. (1987); Jones & Shachak (1990)
Bagworm caterpillars, ?*Penestoglossa* sp.	Golden Gate Highlands, South Africa	eat endolithic lichens and construct larval shelters ('bags') from quartz crystals	small increase in erosion rate, nutrient cycling and soil formation	Wessels & Wessels (1991)
Mound-building termites, Isoptera	widespread in tropics and subtropics	mound and subterranean gallery construction; redistribution of soil particles	change mineral and organic composition of soils; alter hydrology and drainage	Wood & Sands (1978); Lal (1991)
Ants, Formicidae	ubiquitous	nest and subterranean gallery construction; redistribution of soil particles	change local structure and composition of soils; alter 'above nest' vegetation; produce microsite enrichment	Elmes (1991)
Earthworms, Lumbricidae, Megascolecidae	ubiquitous	burrowing, mixing and casting	change mineral and organic composition of soils; affect nutrient cycling; alter hydrology and drainage; affect plant population dynamics and community composition	Lal (1991); Thompson et al. (1993)
Blind mole rats, *Spalax ehrenbergi*	Israel	digging and tunnelling	move large quantities of soil; increase aeration; create distinctive ecosystem	Heth (1991)
Mole rats, Bathyergidae (several genera)	South African lowland fynboss	digging and tunnelling	create impressive, cratered landscapes, with effects on soil formation, plant productivity and species composition	Richardson et al. (in press)
Prairie dogs, *Cynomys* spp.	North American short and mixed grass prairie	continual intense disruption by burrowing, creating soil mounds	change physical and chemical properties of soil persisting for 100–1000s of years	Whicker & Detling (1988)
Pocket gophers, *Geomys bursarius*	North American grasslands and arid shrublands	construct tunnels and move soil to surface mounds	alter patterns and rates of soil development, nutrient availability and microtopography; change plant demography, diversity and primary productivity; affect behaviour and abundance of other herbivores	Huntly & Inouye (1988); Moloney et al. (1992)
Indian crested porcupine, *Hystrix indica*	Negev desert	digging for food	dig up to 2–3 holes m^{-2}; diggings accumulate organic matter, runoff water; create favourable sites for seed germination	Yair & Rutin (1981); Gutterman (1982)
Elephants, *Loxodonta africana*	East African woodland and savannah	physical disturbance and destruction of trees and shrubs	widespread vegetation changes; alteration of fire regime; effects on food supply and population dynamics of other animals; ultimately changes in soil formation, riparian zones, and biogeochemical cycling	Naiman (1988)

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Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Case 5 (autogenic) and case 6 (allogenic) (examples combining elements of both)				
Crustose coralline algae, *Porolithon, Lithophyllum*	coral reefs	overgrow and cement together detritus on outer algal ridge of barrier reef	break force of water and protect corals against major wave action; effect via own bodies (case 5) and secretion of 'cement' (case 6)	Anderson (1992)
Ribbed mussels, *Geukensia demissa*	Rhode Island *Spartina* salt marsh	secrete byssal threads, and form dense mussel beds	on marsh edge, dense beds of mussels (case 5) and byssal threads (case 6) bind and protect sediments and prevent physical erosion and disturbance, e.g. by storms	Bertness (1984b)

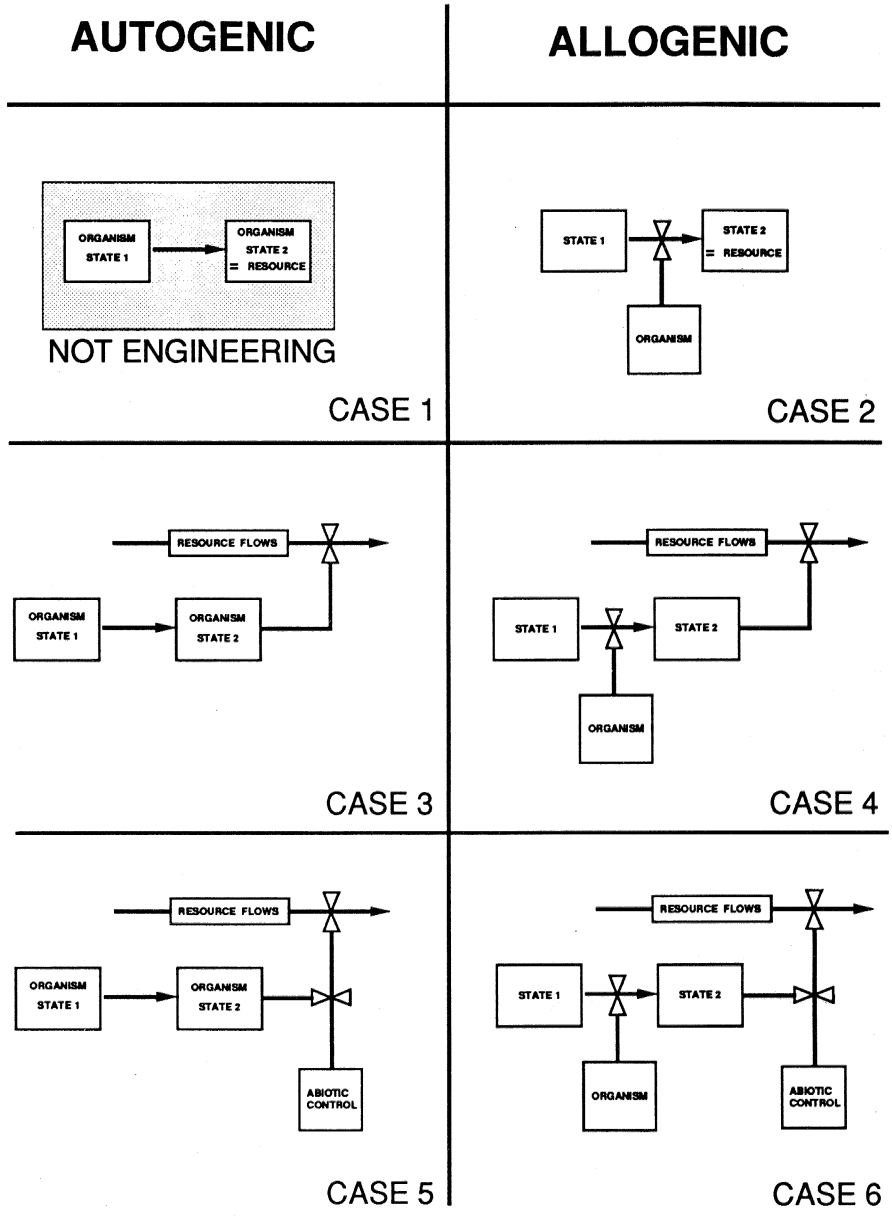


Fig. 1. Conceptual models of autogenic and allogenic engineering by organisms. For definitions and examples see text and Table 1. The symbol ⧖ defines points of modulation. For example, allogenic engineers transform living or non-living materials from state 1 (raw materials) to state 2 (engineered objects and materials), via mechanical or other means. The equivalent (state 2) products of autogenic engineering are the living and dead tissues of the engineer. These products of both autogenic and allogenic engineering then modulate the flow of one or more resources to other species (cases 2–4) or modulate a major abiotic controller (e.g. fire), which in turn modulates resource flows (cases 5–6). Case 1, the direct provision of resources by one species to another is not engineering, and involves no modulation of resource flows.

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This modulation constitutes autogenic engineering. Trees alter hydrology, nutrient cycles and soil stability, as well as humidity, temperature, windspeed and light levels (see Holling 1992); corals modulate current speeds, siltation rates and so on. It is obvious, but surprisingly rarely explicitly stated, that numerous inhabitants of the habitats so created are dependent upon the physical conditions modulated by the autogenic engineers, and upon resource flows which they influence but do not directly provide; without the engineers, most of these other organisms would disappear.

One further example may help to clarify the distinction between case 1 and case 3. The growth of seagrass beds modulates ocean currents, which in turn may alter sedimentation rates and hence food supplies for other organisms with substantial effects upon their performance (e.g growth and survival in the clam *Mercenaria mercenaria* (Irlandi and Peterson 1991)). The direct provision of food or living space by seagrasses (case 1) is not critical for *Mercenaria* but the clam's survival is nonetheless dependent upon these plants.

It could be argued that the growth of tree-trunks, branches, reefs or similar substantial biological structures (case 1, Fig. 1) itself constitutes ecosystem engineering. Inclusion or exclusion is a matter of choice. We have chosen to exclude it (whether it is the provision of food or of 'architecture' (Southwood et al. 1979 and Lawton 1983)) when the structures are considered solely and directly as resources, because this differs in kind from the remaining cases in Fig. 1. To qualify for our definition of an ecosystem engineer, an organism must modulate the supply of other resources for other species, rather than be the direct provider of resources. The growth of biological structures is thus a necessary but not a sufficient requirement for autogenic engineering.

We can illustrate our arguments further by considering the simplest kind of allogenic engineering (case 2, Fig. 1). Various organisms make holes in tree trunks and branches, some quickly (woodpeckers), others more slowly (rot fungi). They transform wood without holes into wood with holes, and indirectly provide resources for other creatures, nesting and roosting cavities for birds and bats for instance. The holes are the resource, not the organisms that make them. Notice that if some of the holes fill up with water (Kitching 1983), the little ponds so created are examples of case 4, and are conceptually identical to beaver dams.

Inevitably there are some grey areas in this classification and at the risk of being pedantic it is worthwhile considering just one. The natural hollows and cavities formed at branch junctions and root bases as the tree grows, and which may subsequently fill up with water ('pans' sensu Kitching (1983)) are not the same as rot- or woodpecker-holes and they do not belong in case 4; rather they conform to case 3 (trees are now autogenic engineers because their biomass gives rise to water-filled hollows). Numerous examples of these 'phytotelmata' are summarised by Fish (1983) (Table 1).

It is not universally the case that plants are allogenic and animals are autogenic engineers. Enhanced rates of physical and chemical weathering of rocks into soil by algae or higher plants (Bloom 1978) constitute allogenic engineering (case 4). Plants may act either as autogenic or as allogenic engineers, and provide some of the most complex cases of ecosystem engineering, to which we now turn.

Autogenic (case 5) and allogenic (case 6) engineering are at the extremes of continua that merge with cases 3 and 4 respectively. Cases 5 and 6 have the common property that autogenic or allogenic engineers interact with, and modulate powerful abiotic forces, for instance fires or hurricanes. Examples in cases 5 and 6 are distinguished from cases 3 and 4 by the extreme magnitude of the processes modulated by the engineers, and by the fact that these major abiotic forces are themselves fundamental modulators of the distribution and abundance of resources.

Fire provides a particularly interesting case. It is logical, albeit unconventional, to regard the production of combustible living and dead biomass as autogenic engineering (case 5). Different species of plants produce different qualities and quantities of living and dead fuel, modulating the magnitude, intensity and duration of fire and, in turn, profoundly altering the supply of resources for many other species (Christensen 1985). High grassland productivity in Serengeti-Mara in the 1960s markedly increased the incidence of fire, resulting in conversion of savannah woodland to an alternative state – grassland – which is now maintained by elephants (Dublin et al. 1990). The effects of elephants as allogenic engineers are summarised in Table 1.

Plants also act as allogenic engineers (case 6). In Puerto Rico *Dacryodes excelsa* trees are able to withstand hurricanes because their extensive roots and root grafts bind and stabilise bedrock and superficial rocks; this species therefore dominates tropical montain forests where hurricanes are common (Basnet et al. 1992).

Difficult cases: Pollinators, gall formers and cows

The richness of biological processes means that a completely satisfactory, comprehensive yet exclusive definition of ecosystem engineering may be impossible to achieve, although numerous examples are easy to classify (Table 1). Given the diversity of species interactions in nature, efforts to classify many other ecological phenomena suffer similar problems 'at the margin'.

Pollinators and gall-formers present an interesting challenge for our definition of engineering. Both have profound effects on the growth of plant tissue; in so doing, pollinators modulate the supply of resources for seed predators, and gall-formers create structures that are used not only by themselves for shelter and food, but also by inquilines (e.g. Askew 1975). Both types of interaction conform broadly to case 2 (Fig. 1). However, we do not find it helpful to regard pollinators as engineers, not least since self-pollination is case 1 and not engineering.

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But it is possible to regard gall-formers as engineers for inquilines; they physically modify plant-tissues, and create new habitats and resources for other organisms. The distinction between pollinators and gall-formers is, however, a fine one.

Our definition of engineering also embraces other, unexpected ecological phenomena, for example dung masses produced by large herbivores. Cows turn grass into cow pats, which are then colonised by a rich community of invertebrates, dependent upon the pats for food and shelter (Mohr 1943). The physical structure and environment provided by the droppings is at least as important to its inhabitants as the concentration of food resources (Elton 1966). It does not stretch the definition of engineering too far to regard cows as allogenic engineers, turning grass into cow pats (case 2). We would be the first to admit, however, that it is an unconventional perspective. Similar remarks apply to faecal pellet production by oceanic zooplankton (Table 1). For these and other borderline cases, the common sense way to view the issue is to ask whether understanding the ecological interactions is enhanced by recognising the engineering dimension.

Human analogues

The parallels between ecological and human engineers are, not surprisingly, very close. Humans are tool-using organisms that specialise in engineering. While human engineering often has intent or purpose, it is probably true to say that the major reason why humans have such adverse effects on the environment is because of the unintended consequences of our activities as engineers. Indeed people are now the primary agents of environmental change in most areas of the world (Naiman 1988, Likens 1992). Many human activities, from dam-building and skyscraper construction to forest clearance and the dredging and canalization of water courses, conform exactly to cases in Fig. 1, in which humans are allogenic engineers, altering the physical environment and modulating the flow of resources to other species.

Construction of nesting boxes for birds and hives for bees are examples of case 2. Ploughing by farmers and the construction of dams and reservoirs by water engineers provide examples of case 4. Building harbours and sea walls to reduce storm damage from waves are examples of case 6. Humans mimic autogenic effects, using tools to construct glasshouses and build air conditioning plants (mimicking case 3), and by bulldozing fire breaks to counteract fire (mimicking case 5). We classify human engineering activities as heavy or light, construction, civil, heating, plumbing, and air-conditioning to name but a few. Organisms do all these jobs, and from a functional perspective we see no fundamental difference between human and non-human engineering.

Related concepts

The idea that some organisms alter the physical structure of their environment, with impacts on their own and other populations is not new. But earlier work either focuses on particular species and habitats and lacks generality, or takes a more general view but fails clearly to define ecological engineering, or to distinguish it from other processes. For example, in an important set of reviews dealing with animal influences on ecosystem dynamics, co-ordinated by Naiman (1988), engineering and direct trophic effects are interwoven. Within this series of papers, Huntly and Inouye (1988) explicitly describe pocket gophers *Geomys bursarius* as "soil engineers" because of their role as earth-movers. Gophers are, indeed, excellent examples of allogenic (case 4) engineers (Table 1).

Ecologists in general have paid surprisingly little attention to how environments are created and maintained; most appear content to follow Andrewartha and Birch (1954) in recognising "a place to live" and "weather" as two of the four essential features of species' environments, without formally considering the role of engineering in habitat modification, creation and maintenance.

Bioturbators

In marine benthic environments the activities of large burrowing animals are known to play a dominant role in determining the physical structure of sediments, altering habitat suitability for other species (Rhoads and Young 1970, Thayer 1979, Lopez and Levinton 1987, Meadows and Meadows 1991a, see also Table 1). Rhoads and Young (1970) called the process 'trophic amensalism' when large deposit feeders create unstable sediments, restricting the presence of suspension feeders and attachment by sessile epifauna. The term amensalism is reasonable, because the effect is asymmetrical and is a form of competitive exclusion (Lawton and Hassell 1981), but the mechanism is not trophic and clearly differs from normal exploitation competition for food. 'Trophic amensalism' is actually another good example of case 4 allogenic engineering brought about by bioturbation of sediments.

Patch dynamics

Numerous studies recognise the importance of patches of bare or different substrates in otherwise closed communities (e.g. Dayton 1971, Wiens 1976, Paine 1979, Pickett and White 1985). Patches may be created by physical disturbance (waves, fire, landslips) or by the activities of organisms (grazing, predation or engineering), or by interactions between engineering, trophic and physical processes. For some applications of patch dynamic theory the way in which patches are created may be less important than their existence. In general, however, we believe that it is desirable to recognise engineering as one of several distinct ways in which patches are created and maintained, particularly since the factors that control patch formation by engineers are often different from those controlling patch formation by abiotic forces.

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Animal and plant artifacts

In their *Theory of Environment* Andrewartha and Birch (1984) define a framework for examining all the processes that impinge upon a single species population. This target species occupies the centrum of a web of directly and indirectly acting components, and Andrewartha and Birch point out that a link in the web may be another living organism or its artifact or residue. The Theory of Environment therefore clearly allows for engineering, without explicitly identifying it as a defined modifier in the web, or as a process worthy of study in its own right.

Meadows and Meadows (1991a) and Meadows (1991) review the environmental impacts of animal burrows and burrowing animals, and Hansell (1993) the ecological consequences of animal burrows and nests. Many of these artifacts (e.g. meiofaunal burrows, megapode nests, termite mounds and mole rat colonies) have landscape level effects, and serve to concentrate and redistribute resources for other species – that is they are classic examples of ecological engineering (Table 1).

Meadows (1991) points out that there are "underlying similarities between the impact of [burrowing] animals from different terrestrial and aquatic habitats on environmental change and modification." He provides a formal system to quantify the impacts of burrowing, distinguishing between animals with large per capita but geographically restricted effects (e.g. badgers) and those species with small per capita effects that nevertheless, because of their abundance and distribution, have impacts on entire landscapes (e.g. earthworms). Hansell (1993) recognises that the "services and substances of the builders create a new range of habitat niches which can be exploited by a wide variety of specialists" and suggests that "the presence of nest builders and burrowers can ... significantly contribute to species diversity in habitats." The examples provided by both authors all conform to either case 2 (other species use the nests and burrows) or case 4 (species respond to changes in distribution and abundance of resources). Their work therefore differs from ours only in its more restricted focus.

Extended phenotypes

The importance of animal artifacts is also recognised by Dawkins (1982), as an example of species' extended phenotypes. Dawkins writes (p.200): "A beaver dam is built close to the lodge, but the effect of the dam may be to flood an area thousands of square meters in extent. As to the advantage of the pond from the beaver's point of view, the best guess seems to be that it increases the distance the beaver can travel by water, which is safer than travelling by land, and easier for transporting wood. ... If this interpretation is right the lake may be regarded as a huge extended phenotype." Dawkins recognises other products of animal engineering as extensions of species' phenotypes and hence subject to natural selection, including caddis-fly cases, termite mounds and birds' nests.

He also points out that not every example of what we are now calling allogenic engineering can be regarded as an extended phenotype, because impacts on the environment are of no consequence to the engineer's fitness and hence are not subject to natural selection. A good example would be water-filled footprints made by an ungulate. The distinction between engineering that is subject to natural selection (because it is an extended phenotype) and engineering that is not ('accidental' engineering) appears to be unimportant in terms of its shorter-term ecological consequences; all types of engineering modify and modulate resource flows for other organisms. But there may be interesting longer-term differences, particularly in the nature of the feed-back loops that operate on 'extended phenotype' versus 'accidental' forms of engineered artifacts. We return to this point later.

Keystone species

Keystone species (Paine 1969, Krebs 1985, Daily et al. 1993) play a critical role in determining community structure. By definition, removal of keystone species causes massive changes in species composition and other ecosystem attributes. The critical links are usually regarded as trophic and therefore within the realm of traditional ecological thinking For example, removing top predators has a cascading effect throughout the foodweb, altering species composition and hence physical structure and nutrient cycling at lower levels (Estes and Palmisano 1974, Carpenter et al. 1987).

But critical effects frequently involve engineering, for example via disturbance (e.g. bioturbators (Thayer (1979), above; case 4). In the frequently cited example of sea-otters *Enhydra lutris*, removal of otters leads to an increase in sea urchins (*Strongylocentrotus* sp.) and hence to the disappearance of kelp beds, which in turn changes wave action and siltation rates, with profound consequences for other inshore flora and fauna (Estes and Palmisano 1974). Kelp are autogenic engineers (case 3); removal of kelp by urchins is, amongst other things, allogenic engineering (case 4). In other words, in this familiar example, the species traditionally regarded as the keystone (sea otter) has major effects because it changes the impact of one engineer (urchin) on another (kelp), with knock-on effects on other species in the web of interactions. The equally well known impact of kangaroo rats (*Dipodomys* spp.) on desert vegetation occurs because the rodents not only eat seeds but also cause considerable physical disturbance. By burrowing and moving large quantities of soil they create many shallow pits and little mounds, which facilitate decomposition and the establishment of annual plants (case 4 engineering) (Brown and Heske 1990).

Direct effects of keystone species via their role as engineers have recently been reported by Daily et al. (1993). Red-naped sapsuckers *Sphyrapicus nuchalis* (a type of woodpecker) act as keystone species in two ways in Colorado subalpine meadows. Their nesting holes

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drilled in aspens, *Populus tremuloides,* are essential nesting sites for two species of swallows (case 2); the swallows are missing from the community in the absence of sapsuckers. Feeding holes drilled by the sapsuckers in willows, *Salix* spp., also make sap flows available to several birds, mammals and insects (directly changing the distribution and abundance of this resource for other species – and therefore again conforming to case 2).

It is theoretically possible (though we think it will be uncommon in practice) for a keystone species to exert its effects entirely trophically, without also acting as an engineer, or without changing the engineering role of other species in the web. On the other hand, many engineers are keystone species even though they play relatively minor roles in community food webs.

Krebs concludes his textbook review of keystone species as follows: "Keystone species may be relatively rare in natural communities, *or they may be common but not recognised* (our emphasis). At present, few terrestrial communities are believed to be organised by keystone species, but in aquatic communities keystone species may be common". We believe that such views probably reflect a consensus among ecologists. They persist because we have failed to recognize the role of ecosystem engineers as keystone species. It is trite, but true, that a forest is a forest because it has trees, which not only provide food and living space but which also autogenically engineer the forest climate, and modulate the flows of many other resources to forest inhabitants, both above- and below-ground. Many single species of trees in temperate or boreal forests (with low tree-species richness) are both keystone species and significant ecosystem engineers.

Our views are very close to Holling's (1992) *Extended Keystone Hypothesis*, in which he argues that "all terrestrial ecosystems are controlled and organised by a small set of key plant, animal, and abiotic processes that structure the landscape at different scales." We would add two points. First a critical, but not exclusive controlling mechanism is some form of engineering; and second, we believe that keystone engineers occur in virtually all habitats on earth, not just terrestrial ones.

'Top down' vs 'bottom up', asymmetrical and indirect effects

Traditional population models focus on reciprocally coupled pairs of interactions, interspecific competition (-/-), enemy-victim (-/+) and so on (Williamson 1972). Highly asymmetrical competitive interactions (amensalism; 0/-) are common, possibly the norm, in some situations (Lawton and Hassell 1981). Enemy-victim interactions may also be asymmetrical (donor-controlled; 0/+), that is prey abundance controls predator abundance, but not vice versa (Lawton 1989, Hawkins 1992), with a growing debate in ecology about the relative importance of such 'bottom up' vs 'top down' effects (Hunter and Price 1992). Ecological engineering adds enormously to the catalogue of important, highly asymmetrical species interactions, because engineers impact upon many taxa (positively or negatively), but there may often be no direct, reciprocal effects of the impacted species upon the population of engineers.

One example will suffice. Beaver beneficially influence the abundances of aquatic biota, but not vice versa; that is they have massive 'bottom up' effects (o/+) that benefit numerous other aquatic organisms. Their activities are also detrimental to terrestrial species living upstream (and perhaps downstream) from the dam (o/-) just as bioturbators exclude sessile epifauna requiring stable substrates (see above). Generally we expect both the positive and negative effects of engineers to be highly asymmetrical.

This is not to say that there cannot be any feedbacks from organisms in the engineered habitat, back to the engineer. Undoubtedly there are, although feedback pathways are probably often rather long, indirect, and frequently slow. They remain virtually unstudied. For some engineers, it is difficult to imagine any reciprocal effects. For instance, the insect inhabitants of abandoned birds' nests (e.g. some tineid moths in the genus *Monopis* and staphylinid beetles in the genus *Microglotta* (Walsh and Dibb 1954, Emmet 1979)) probably never encounter the builder. Gophers, in contrast, engineer soil and change vegetation composition, biomass and productivity (Table 1); in turn, grasshopper populations become more abundant in the vicinity of gopher mounds (Huntly and Inouye 1988). Two feedbacks may operate on gophers. The first is reasonably well documented, positive and relatively direct, via plants that are food for gophers; soil disturbance favours the plant species that gophers prefer to eat. Second, it is at least conceivable, but untested, (D. Tilman, pers. comm.) that grasshoppers compete with gophers for food, providing a longer, negative feed-back loop on gopher numbers.

We predict that if feed-backs exist at all between engineers and the organisms they affect, they will characteristically be indirect, involving several intermediate processes and species.

Spatial and temporal scales

The impact of an ecological engineer depends upon the spatial and temporal scale of its actions. Water filled woodpecker holes and beaver dams may both be examples of case 4 engineering, but there is not much doubt about which is the more significant ecological phenomenon. Six factors scale the impact of engineers. They are:

(i) Life time per capita activity of individual organisms.
(ii) Population density.
(iii) The spatial distribution, both locally and regionally, of the population.

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(iv) The length of time the population has been present at a site.
(v) The durability of constructs, artifacts and impacts in the absence of the original engineer.
(vi) The number and types of resource flows that are modulated by the constructs and artifacts, and the number of other species dependent upon these flows.

Thus, the most obvious ecological engineering is attributable to species with large per capita effects, living at high densities, over large areas for a long time, giving rise to structures that persist for millennia and which affect many resource flows – for instance mima mounds created by fossorial rodents, including gophers (Cox and Gakahu 1985, 1986, Cox et al. 1987, Naiman 1988). Autogenic engineers may also have massive effects; as Holling (1992) succinctly states: "To a degree, ... the boreal forest 'makes its own weather' and the animals living therein are exposed to more moderate and slower variation in temperature and moisture than they would otherwise be." Boreal forest trees have large per capita effects on hydrology and climatic regimes, occur at high densities over large areas, and live for decades. But their impacts as autogenic engineers may have a relatively short memory if the forest is logged.

Organisms with small individual impacts can also have huge ecological effects, providing that they occur at sufficiently high densities over large areas, for sufficient periods of time. Burrowing meiofauna and bogforming *Sphagnum* mosses (Table 1) are good examples. Accumulated *Sphagnum* peat may persist for hundreds to thousands of years after the death of the living moss.

Ecological engineers may also enhance and speed up large scale physical processes, including geological erosion and weathering (Yair and Rutin 1981, Krumbein and Dyer 1985, Hoskin et al. 1986). Examples of rock-eating snails and caterpillars are listed in Table 1. Worldwide, but especially in the tropics, heavily undercut coastal cliffs of sedimentary rock are apparently being eroded by tides and storms. In fact the process is greatly accelerated by two groups of engineers, both with low per capita effects, but very abundant. Cyanobacteria (*Hyella* spp.) bore the rock and are food for chitons which rasp away the rock to reach them, apparently speeding up coastal erosion by an order of magnitude or more (Krumbein and Dyer 1985). Similarly, organisms whose shells, body parts and dead tissues help form sedimentary rocks, coal and soil (e.g. molluscs, diatoms and many higher plants) create structures whose effects on ecosystems persist for eons.

Engineering impacts are often greatest when the resource flows that are modulated are utilised by many other species, or when the engineer modulates abiotic forces that affect many other species. Not surprisingly, engineering that effects soils, sediments, rocks, hydrology, fire and hurricanes provides some of the most striking examples.

We know of very few field manipulation experiments designed to quantify the impact of ecosystem engineers by removing or adding species. Studies by Bertness (1984a,b, 1985) are excellent examples of manipulative experiments on both allogenic (cases 4 and 6) and autogenic (case 5) engineers (Table 1). A recent study by Hall et al. (1993) shows the potential power of field manipulations for disentangling per capita impacts from population impacts (although in the present context it is not ideal because predation and disturbance [case 4 engineering] effects are confounded). Edible crabs (*Cancer pagurus*) hunting for prey dig pits in shallow subtidal areas of the west coast of Scotland. The pits are conspicuous features of the seabed topography, yet exclusion of crabs from areas of the sea bed for twelve months failed to reveal any landscape-level effects of crab pits, either on substrate structure and composition (particle sizes, organic carbon etc.) or faunal diversity, composition and abundance. Crabs appear not to be abundant enough to significantly alter community structure, either by predation or by engineering, despite large and visually conspicuous individual impacts. This example contrasts markedly with the substantial effects of fiddler crabs (*Uca pugnax*) on productivity, decomposition, oxygenation and drainage in a New England salt marsh, revealed by experimental removal of crabs (Bertness 1985) (Table 1).

Another extremely poorly researched problem is the way in which the persistence of the products or effects of engineering influence population, community and ecosystem processes. If engineers make long-lived artifacts, then their effects will usually, also, be long lived. But ephemeral products can also have long-term impacts. For example, faecal pellets produced by marine zooplankton (Table 1) decompose relatively quickly, but not before they have sunk into the deep ocean, removing nutrients from surface waters for millenia.

A useful thought experiment is to consider taking the engineers away and imagining the consequences. In many cases their impacts are ephemeral, operating on timescales shorter than, or similar to, the lifetime of the organism itself (e.g. the nests of small passerine birds). But in other cases, the engineers leave monuments with impacts that extend many lifetimes beyond their own – mima mounds, termite nests, buffalo wallows, beaver dams, peat, sedimentary rocks and so on. These persistent effects must greatly slow down rates of ecological change, and impose considerable buffering and inertia on many ecological systems and processes. Rates of decay, the 'half-lives' of the products of ecological engineers, and their contributions to population, community and ecosystem stability, resistance and resilience (Pimm 1984) deserve much more attention from theoretical and experimental ecologists.

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Evolutionary effects

Earlier, we distinguished between engineered artifacts subject to natural selection as extended phenotypes, and 'the rest' – by-products of some other activity that are not themselves directly subject to selection; water-filled ungulate hoof prints were given as an example. Extended phenotype engineering, by definition, creates structures or effects that directly influence individual fitness (or colony fitness in social insects), for instance a beaver dam, woodpecker hole or termite mound. But the evolutionary effects of extended phenotype engineering, other 'accidental' engineering, and of organisms in the engineered habitat upon the engineer are far from straightforward, and generally unstudied. For example, the extended phenotype may be subject to selection from the physical environment, implying no biotic feedbacks. Or it may be subject to selection from polyphagous predators (e.g. nest-robbing snakes) that are in no way dependent upon the engineered habitat for their existence. On the other hand, engineering might generate habitats with species populations that, ultimately, feed back positively or negatively upon the engineers, via predation, disease, competition, or the invasion of additional species of engineers.

Some engineering undoubtedly has had evolutionary effects on other organisms. One of the best documented examples in the fossil record is a decline, from the Devonian onwards, in the diversity of immobile suspension feeders living on soft marine substrata, as mobile taxa diversified (Thayer 1979). Thayer attributes these major changes in the structure of marine benthic communities to the evolution of 'biological bulldozers' – bioturbators or engineers – that disturb sediments (see above), fouling, overturning and burying immobile suspension feeders, which are now largely confined to hard substrates. Thayer also speculates that by increasing the turnover rate of nutrients in sediments of continental shelves, bulldozers may have contributed to the Mesozoic diversification of phytoplankton (coccoliths, diatoms and dinoflagellates) and, via trophic linkage, to diversification of zooplankton (radiolaria and foraminifera).

An intriguing, but rarely considered problem is the degree to which engineering by other taxa might similarly have changed major patterns in the radiation and extinction of earth's biota. To the extent that engineers shape and modify most, possibly all, habitats on earth (see below), and given the trite but true observation that all organisms are adapted to their environment, engineering in some form or other must have driven, or contributed to, the evolution of myriads of species. But the extent to which major patterns of evolution might have been different if some types of ecological engineering had not evolved, or had taken a different form, is almost entirely unknown.

Questions

We finish with a haphazard list of open questions.

Are there any ecosystems on earth that have not been physically engineered by one or more organisms to a significant degree? A cautious, preliminary answer is no, there are not. We initially thought that it would be difficult to identify evidence of ecosystem engineering by biota in the open waters of oceans or large lakes, or in snow fields and ice packs, for instance. But the examples in Table 1 show that this prediction was wrong. We currently cannot identify any habitat on earth that is not engineered in some way by one or more species.

How many species (or what proportion of species) in various communities have a clearly defined and measurable impact as engineers? Is it 10%, 1% or 0.1%? What are the relative frequencies of the five classes of engineering identified in Fig. 1, say in terms of the numbers of species acting as engineers? Cases 5 and 6 are presumably rather rare; but how much rarer are they than the others types of engineering? Is the predominance of examples involving burrowing animals in case 4 real (we could easily have included still more examples) or is it because this form of engineering is particularly easy to see?

Are the most physically structured ecosystems (or subsystems, e.g. soil or sediments) the ones in which engineers are most important? How much of the structure have they created and modified?

How many other species are impacted by engineers in any ecosystem? What happens to species richness if we remove or add engineers? How much of the effects of keystone species are due to engineering versus trophic effects? Earlier, we speculated that few keystone effects are purely trophic; is this hypothesis correct? How do engineering and trophic relations interact?

Should conservationists and nature reserve managers pay more attention to the role of ecological engineers in maintaining ecosystem integrity, or do managers largely know which the important species are, without having put a name to the idea, or without having recognising the common themes identified in this paper?

How should we model engineering? The biological details in each case will be complicated, and there are at least five kinds of engineering; but there are also several sorts of interspecific competition, various ways of being a herbivore and a rich catalogue of enemy-victim interactions, none of which has stopped theoreticians from developing appropriate families of relatively simple models to understand and to predict the dynamics of such interactions. There is, in principle, no reason why we cannot write down the equation:

$$d\text{mayfly}/d\text{beaver} = F(x,y,z),$$

where mayfly populations respond to changes in beaver numbers on long time-scales, and where the response is influenced by various key variables, including feedbacks

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to beaver from other components in the engineered habitat. Interesting theoretical questions centre on the generation time of the engineer, the half-life of whatever it is that is engineered, the rate of restoration of non-engineered habitat, the generation times of impacted species, and their various interactions. There are intriguing problems of nested time-scales, delayed responses, donor-control, long chains of indirect interactions and so on, that might usefully be explored using relatively simple models.

Extending these arguments, there is no reason in principle why processes driven by engineering should not be coupled to the rich diversity of trophic linkages to create not simply descriptions and models of foodwebs (e.g. Pimm et al. 1991), but of *interaction webs*, that more accurately reflect interactions in communities and ecosystems. The conceptual framework brought together by Carpenter (1988) under the title of 'complex interactions' should clearly embrace engineering as one component.

Intriguingly, once the need to define and study interaction webs is recognised, it also becomes apparent that ecological engineering as we have defined it is only part of the picture. We have focused on physical state changes wrought on biotic and abiotic materials by organisms. But physical engineering is not the only form of ecosystem engineering that organisms carry out. Chemical and transport engineering are two obvious other forms that we consider will conceptually fit into the same general classification scheme. For brevity, we have not examined them here.

Last, but by no means least, what new insights will the concept of engineering bring to ecology? This review attempts to define and classify the phenomenon. But definition and classification are merely a small beginning, not an end. Are there major patterns in the distribution and abundance of organisms that might be explained, at least in part, by ecosystem engineering? What are they? What predictions might we make that would not have been made without the conceptual framework provided here, or something akin to it? We do not, currently, know the answers to these questions. But if the notion of organisms as ecosystem engineers results simply in an accumulation of 'just-so' stories, it will not have been particularly useful.

Acknowledgements – This work was supported by the Mary Flagler Cary Charitable Trust, the US–Israel Binational Science Foundation, and the NERC Centre for Population Biology, UK. Numerous colleagues have allowed us to sharpen and refine our ideas about engineering by discussing problems with them, and have generously provided us with examples and references; to all of them we express our sincere thanks. Contribution to the programme of the Institute of Ecosystem Studies. Publication 171 from the Mitrani Center.

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RALA-00153; No of Pages 8

Impacts of Wild Horses, Cattle, and Wildlife on Riparian Areas in Idaho

By **Molly M. Kaweck, John P. Severson, and Karen L. Launchbaugh**

On the Ground

- Our study confirms that grazing by cattle and horses can negatively impact riparian ecosystems if not properly managed.
- Population levels and grazing patterns of wild free-roaming horses limit management options, potentially leading to rangeland and riparian degradation.
- Grazing by wild free-roaming horses and cattle in riparian areas caused streambank disturbance and reductions in stubble height and herbaceous biomass.
- Both wild free-roaming horses and cattle affected riparian attributes while wildlife had little effect.
- Horses had a greater negative impact than did cattle when examined on an individual animal basis.
- Managers and ranchers in areas with wild free-roaming horses will need to consider potential impacts of unmanaged wild free-roaming horses in combination with livestock to mitigate the cumulative effects of multiple species of grazers on riparian condition.

Keywords: streambank alteration, stubble height, game camera, species interaction, grazing.

Rangelands xx(x):1–8
doi 10.1016/j.rala.2018.03.001
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Excessive and poorly timed grazing can negatively affect riparian ecosystems. Increasing populations and grazing habits of wild free-roaming horses make it difficult to manage their impacts on riparian areas. We empirically quantified effects of wild horses, cattle, and wildlife on riparian habitat characteristics using game cameras to monitor riparian use. We also examined riparian vegetation and streambank disturbance each month to compare with animal occurrences. We observed overall negative impacts of wild free-roaming horses and cattle on riparian attributes, but wildlife had little effect. In areas with wild horses, land managers should consider the combined use of unmanaged wild horses with livestock to address their cumulative effects in riparian areas.

Wild Horses, Cattle, and Riparian Areas

Wild free-roaming horses (*Equus caballus*) and burros (*E. asinus*) are surrounded by controversy in the western United States. As cultural icons of the West, they hold great emotional significance, often eliciting heated debates over how they should be managed. The horses and burros that are free-roaming across the western United States are biologically feral, but are hereafter termed "wild." Wild horses and burros roam public lands in 10 western states, with large and potentially unsustainable populations in several regions. Having few natural predators, wild horse and burro herds can increase by 15% to 20% each year and double every 4 years.[1,2] Estimates of wild horse and burro populations have risen from 30,000 individuals in 2005 to about 49,000 individuals in 2014,[3,4] although there is concern this number is underestimated due to limited detection of secretive individuals.[2] This prolific growth can result in populations exceeding appropriate management levels within their federally delineated herd management areas (HMAs; Table 1). Large populations of wild horses and burros in many areas can contribute to ecological damage and increase risk of rangeland degradation.[2]

The effects of wild horses on riparian areas are a concern for many land managers. Riparian areas are ecologically important zones around rivers, streams, and lakes. Although riparian areas comprise only about 2% of western lands, they are some of the most ecologically important habitats in rangelands[5] by providing important resources for many species of wild and domestic animals such as abundant forage, cover, and water.[2] Riparian areas are also important for trapping sediment, slowing runoff, and supporting ecologically functioning watersheds. Excessive animal grazing and trampling in riparian areas can decrease sediment capture, limit infiltration, and increase the energy of water flow.[6] These hydrogeomorphic impacts can magnify erosion and down-cutting which can lead to separation of the streambed from the flood plain and decrease riparian area size.[6]

Riparian areas attract wild and dometic grazing animals because of available water, cooler micro-climates, and more nutritious and abundant forage generally staying green longer into the summer than the surrounding upland vegetation.[7,8] The negative impacts of livestock grazing in riparian zones have been well documented for nearly half a century.[6] In

Table 1. Population estimates of wild horses and burros (total estimated number of individuals) in 10 western US states in 2014 as compared with the recommended high appropriate management level (AML) set by the Bureau of Land Management to maintain healthy rangeland and resources[4]

State	Total	High AML
Arizona	4,744	1,676
California	6,008	2,184
Colorado	1,205	812
Idaho	668	617
Montana	160	120
Nevada	25,035	12,796
New Mexico	146	83
Oregon	3,180	2,715
Utah	4,292	1,956
Wyoming	3,771	3,725
TOTAL	49,209	26,684

recent decades, research has also shown that wild horses can have detrimental impacts on riparian areas.[9,10,11,12]

Wild horses and domestic cattle (*Bos taurus*) are both implicated in degrading riparian areas (Fig. 1). However, horses may have a greater impact on riparian areas than cattle because horses often have year-round access to these areas, while cattle are generally removed for part of the year (Fig. 2).[9,13,14] Though free-roaming horses are generally smaller than modern rangeland cattle, they may have a greater than expected influence on riparian vegetation because horses have a digestive system that enables greater intake per unit of body weight than cattle.[13,15] In addition, because many breeds of wild horses can go longer without water than can cattle, they often spend less time per day within riparian zones than individual cows do.[1] Therefore, to truly understand the effects of horses compared with cattle, intensity of use should be assessed to account for both the number of animals and the time spent in the area rather than strictly the number of animals using the area.

Habitats used by wild horses are also used by wildlife and livestock species, making it difficult to determine which species has the greatest influence on riparian health.[9,16] Land managers often struggle to balance rangeland health and forage allocations for wild horses, livestock, and wildlife. These difficulties are compounded by the lack of empirical information about the compounding effects of grazing by different species of herbivores. In turn, maintaining wild horse populations while sustaining healthy plant communities requires a better understanding of their role in the rangeland ecosystems they inhabit.



Figure 1. Game camera picture of wild horses (foreground) and cattle (background) using a riparian area in southwestern Idaho.



Figure 2. Game camera picture of wild horses using a riparian area in central Idaho. Note grazing exclosure on left portion of photo.

We used a modeling approach to assess the effects of varying intensity of use by different herbivores on riparian condition. Our objective was to evaluate the relative effects of wild horses, cattle, and wildlife on riparian condition. Specifically, we aimed to 1) experimentally determine individual and combined impacts of observed animal groups each month on the change in measurements of riparian condition (streambank alterations, stubble height, and herbaceous biomass); and 2) assess how the presence of one animal species might affect the presence of other species.

Study Area

We monitored eight sites in Idaho (four in Owyhee County and four in Custer County; Fig. 3) for animal intensity of use and riparian habitat characteristics during 2015. Site selection was based on recommendations from local Bureau of Land Management (BLM) professionals and ranchers, accessibility for researchers, and known animal use. We controlled for potential effects of grazing at each site by establishing exclosures as experimental controls (described below). Riparian vegetation included overstories of willows

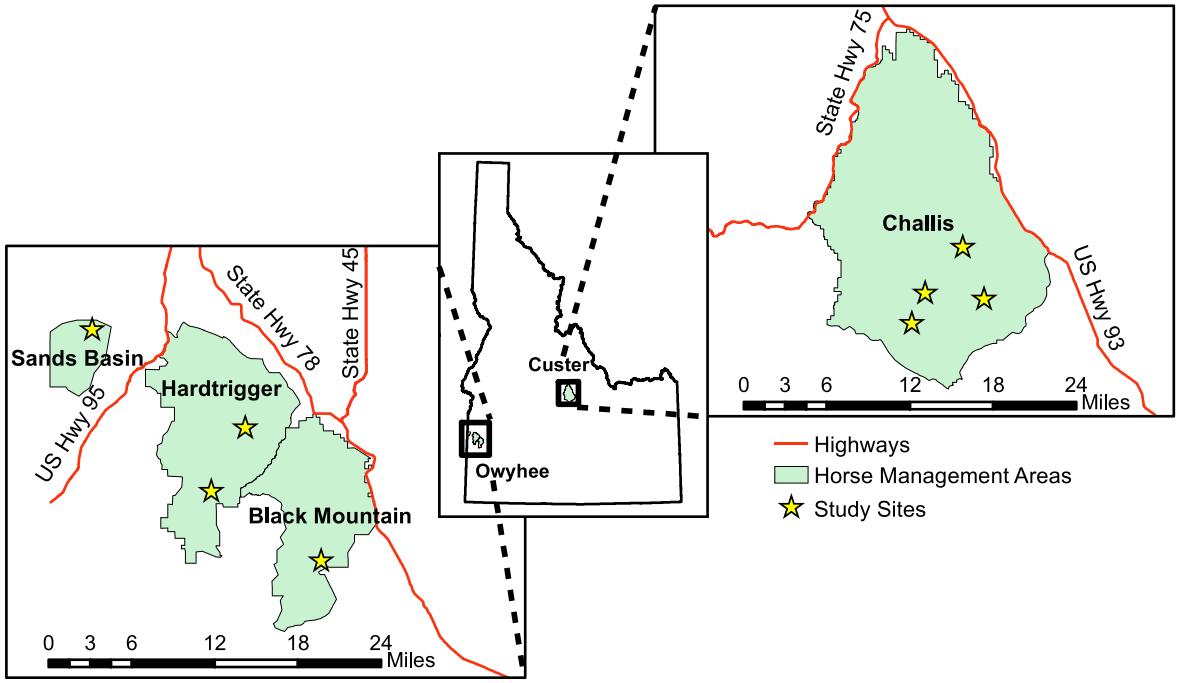


Figure 3. Study areas to assess effects of grazing ungulates on riparian areas in Idaho. Streams examined occurred in three herd management areas (HMA) in Owyhee County (i.e., Sand Basin, Hardtrigger, and Black Mountain) and the Challis HMA in Custer County.

(*Salix* spp.) and black cottonwood (*Populus balsamifera*), and understories of herbaceous plants including Nebraska sedge (*Carex nebrascensis*), beaked sedge (*C. utriculata*), Baltic rush (*Juncus balticus*), inland saltgrass (*Distichlis spicata*), and meadow barley (*Hordeum brachyantherum*).

The four study sites in Owyhee County were contained within three Herd Management Areas: Sands Basin, Hard-trigger, and Black Mountain, covering 130,500 acres with an estimated 276 horses. The streams we examined in the Owyhee area ranged from 2,100 to 6,600-feet above sea level. Precipitation at the Owyhee research sites during 2015 was 10.0 inches, occurring primarily during the winter and early spring. Only two of the four sites studied in the Owyhee area were grazed by cattle. These sites were grazed between April and July in 2015.

The four study sites in Custer County were within the Challis HMA, which covers 154,150 acres and had an estimated 218 horses. Elevations of stream reaches we studied ranged from 6,200 to 7,600 feet above sea level. The precipitation in Challis research sites in 2015 was 7.2 inches, occurring mostly between April and September. In 2015, cattle grazed on all study sites in the Challis HMA between June and September.

Animal Observations and Vegetation Monitoring

We monitored animal intensity of use and riparian habitat characteristics between April and October at each of the eight study sites. Exact monitoring times at each site varied due to weather and a wildfire that limited accessibility. Each of the eight study sites was located on BLM land and consisted of a 328-feet long stream reach, which was divided into five, 65-feet segments. Two segments along each stream reach were randomly selected for in-depth monitoring, yielding a total of 16 stream segments (two segments per study site).

We installed motion activated game cameras (Bushnell Trophy Cam HD 8MP Hybrid Night Vision Trail Cameras) to assess animal intensity of use at the study sites. We indexed intensity of use each month by counting the number of animal occurrences in each photo and categorizing the animals as wild horse, cattle, or wildlife. Wildlife species included ungulates such as elk (C*ervus elaphus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and moose (*Alces americanus*). We did not identify individual animals, but rather the total number of occurrences of each group resulting in an index of intensity of use rather than a population estimate.

We measured three characteristics of riparian habitat at each study site: streambank disturbance, vegetation/stubble height, and live herbaceous biomass. Streambank disturbance, or trampling, was estimated in 20 plots (7.8 × 19.6 inches) along each stream segment. Each plot contained five, 7.8-inch lines spaced evenly every 3.9 inches. We recorded the number of times one of the five lines intercepted a hoof print. Each line could only be counted once even if one line intercepted more than one hoof print. This methodology followed the protocol for streambank alterations in the Multiple Indicators Monitoring handbook.[17] To assess grazing effects on grasses, grass-like plants, and forbs, we selected nine plots (15.7 × 19.6 inches) in the floodplain of each stream reach. We then randomly selected three of the nine plots to be ungrazed control plots and constructed welded wire exclosures (20 × 24 inches) over these plots. The exclosures were slightly larger than the plot size and the welded wire panels were 5.5 feet tall, which we believe was enough to limit edge effects from animals reaching over the top or through the sides to graze the plot. The average vegetation height (including seed and flower stalks) was measured by gathering a 3-inch diameter area of grasses, grass-likes, and forbs, standing the leaves upright and determining the average height to the nearest centimeter.[17] Live herbaceous biomass was also visually estimated. For quality assurance, we conducted biomass calibrations at each stream reach and throughout the day for every sampling period. We achieved a 70% accuracy rate before ocular biomass estimates were recorded. Both riparian habitat characteristics, live herbaceous biomass and average vegetation height, were sampled in each plot to compare grazed and ungrazed vegetation.

To assess whether the presence of one species of animal (horses, cattle, or wildlife) was associated with riparian use by other animal species, we used Spearman's rank correlation to determine the strength, direction, and significance of the correlation between weekly observations of each species at each of the eight study sites.[18] We used mixed-effects linear regression to examine how different the intensity of use of each animal species each month affected stream bank disturbance and differences in biomass and stubble height between grazed and ungrazed plots. We modeled correlation structures of county, site, and repeated measures as random effects. We selected the model that best explained riparian changes, calculated the relative importance of each animal species, and estimated the change in riparian attributes for an increase of one individual occurrence of each animal species (i.e., the slope).

Animal Observations and Relationships

The game cameras captured 17,891 photos of animals from the end of April through October at our eight study sites, until access to the sites was prohibited by weather conditions, cameras were lost to theft, or a wildfire that occurred in Owyhee County in August 2015. Within those 17,891 photos, 44,408 animal occurrences were recorded. Of the 8,134 photos taken in the Challis area, 15,715 animal occurrences were documented, of which 15% were wild horses, 80% were cattle, and 5% were wildlife. In the Owyhee area, 9,757 photos recorded 28,693 animal occurrences, of which 35% were wild horses, 64% were cattle, and 1% was wildlife.

Due to grazing management practices, cattle were observed between April and July in the Owyhee study sites and had the most occurrences between the end of April and the beginning of May (Fig. 4). In Challis, cattle were observed between June and September, and had the most occurrences in mid-June

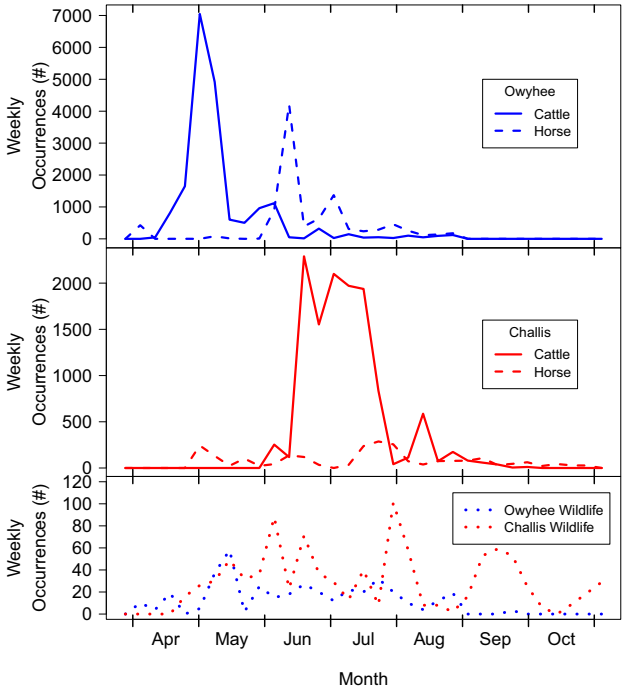


Figure 4. Animals observed on eight riparian areas managed by the Bureau of Land Management (BLM) in Owyhee and Custer Counties of Idaho. Weekly number of occurrences reflects the number animals counted in photos taken by two game cameras at each site. Cattle abundance was regulated by BLM grazing permits while horse and wildlife were not manipulated. Wildlife were observed in relatively low abundance, and were therefore split into a separate plot.

through the end of July (Fig. 4). Horses and wildlife had their highest use between mid-May and mid-September (Fig. 4). (See Fig. 5).

Our analysis did not show any evidence that use of riparian areas by one species of animal caused other species to avoid the area. In fact, there was a slightly positive relationship between horses and wildlife ($\rho = 0.24$, $P < 0.01$) and between horses and cattle ($\rho = 0.25$, $P < 0.01$), indicating that these species of animals were using riparian areas during similar times. This most likely reflects a pattern that animals were attracted to riparian areas for similar habitat features such as available water and green vegetation and that the presence of another species using the area during the month was inconsequential. We did not observe any relationship between cattle and wildlife use at our study sites ($\rho = -0.05$, $P = 0.60$).

Horse, Cattle, and Wildlife Impacts on Riparian Attributes

Overall Grazing Effects

The effects of cattle and wild horse grazing were evident in comparisons of grazed and ungrazed plots on the study sites (Fig. 5). Plant height in grazed plots was 55% lower than the paired ungrazed plots ($P < 0.001$, df = 389). Live herbaceous

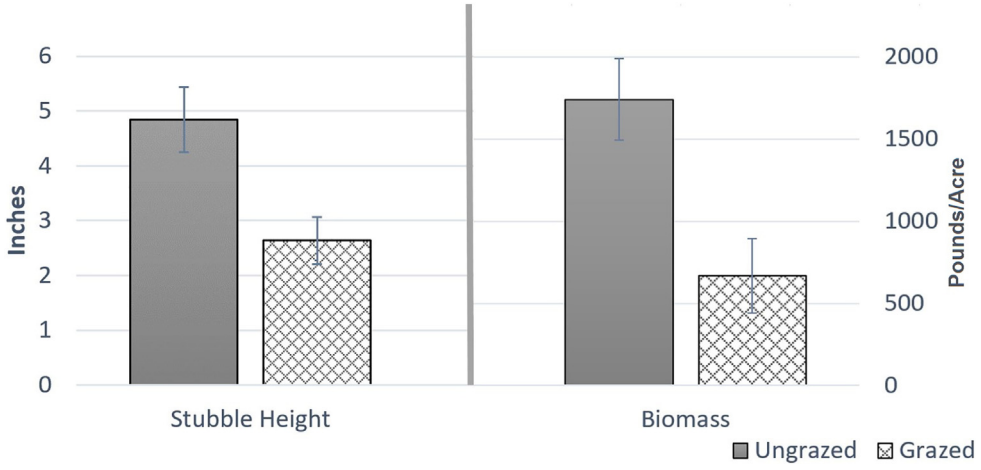


Figure 5. Comparison of vegetation stubble height and biomass in grazed and ungrazed paired plots along riparian areas in eight studies areas in Owyhee and Custer Counties of Idaho. Error bars represent 95% confidence intervals.

biomass was 2.13 oz/plot (2,693 lb/ac) lower in the grazed (1.32 oz/plot; 1,673 lb/ac) compared with ungrazed plots (3.45 oz/plot; 4,366 lb/ac), representing 62% utilization in the grazed riparian areas ($P < 0.001$, df = 389).

Streambank Disturbance

A combined effect of horses and cattle was selected as the best model affecting streambank disturbance (77% probability; Table 2). Horses were more influential than cattle, and both were much more important than wildlife relative to streambank disturbance, largely because of the greater abundance of horses and cattle compared with wildlife (Table 3). The effect of each additional individual animal occurrence, interpreted from model slopes, indicated that horses and cattle both increased streambank disturbance, but an individual horse occurrence (Slope ± 95% confidence interval [CI]; 0.016 ± 0.007) had about 4 times greater effect on streambank disturbance compared with an individual cow occurrence (Slope ± 95% CI; 0.004 ± 0.002), and an increase in 1,000 horse occurrences in 1 month could be expected to increase disturbance by 16.7%.

Table 2. Comparison of models with different sets of animal groups impacting three measures of riparian condition

Model	Probability
A) Streambank alterations ($n = 80$)	
Horse + cattle	0.773
Horse + cattle + wildlife	0.209
Horse	0.014
Horse + wildlife	0.004
Cattle	0.000
Cattle + wildlife	0.000
None	0.000
Wildlife	0.000
B) Vegetation height ($n = 228$)	
Horse + cattle	0.545
Cattle	0.203
Horse + cattle + wildlife	0.183
Cattle + wildlife	0.069
Horse	0.000
None	0.000
Horse + wildlife	0.000
Wildlife	0.000
C) Vegetation biomass ($n = 228$)	
Horse + cattle	0.507
Horse + cattle + wildlife	0.491
Horse + wildlife	0.001
Horse	0.001
Cattle	0.000
Cattle + wildlife	0.000
Wildlife	0.000
None	0.000

Note. Model probability is the relative probability of the model being the best in the set and is derived from AICc (corrected Akaikes Information Criterion) which is an index of support for a model. Models with horses and cattle consistently had the most support.

Table 3. Relative magnitude of wild horses, cattle, or wildlife on observed changes in riparian condition

	Variable Importance		
	Horse	Cattle	Wildlife
Streambank alterations	1.00	0.98	0.21
Vegetation height	0.73	1.00	0.25
Vegetation biomass	1.00	1.00	0.49

Note. Higher values mean more important effects with a maximum value of 1.00.

Vegetation Height

The combined effects of horses and cattle were also the best models describing changes in vegetation height (55% probability; Table 2). Cattle were more strongly related to stubble height reductions than were horses, and wildlife were relatively unimportant to explaining changes in stubble height (Table 3). Again, this is primarily because cattle occurred in greater numbers than horses and wildlife when there were observations of sharp reductions in stubble height. When considering the effect of an individual occurrence, horses and cattle both decreased vegetation height, but a horse occurrence (Slope ± 95% CI; -0.0009 ± 0.0008) had 1.4 times greater effect compared with a cow occurrence (Slope ± 95% CI; -0.0006 ± 0.0003), and an increase in 1,000 horse occurrences would be expected to decrease average vegetation height by 0.9 inches.

Herbaceous Plant Biomass

The combined effect of horses and cattle was also the best model to describe the effect of animal abundance on herbaceous biomass (51% probability; Table 2). Horses and cattle were the most important while wildlife were only moderately important (Table 3). Though cattle were observed at greater abundance, an individual horse occurrence (Slope ± 95% CI; -0.033 ± 0.013) had about 3 times greater impact on biomass than a cow occurrence (Slope ± 95% CI; -0.010 ±

0.005). An increase of 1,000 horse occurrences in an area over a month was estimated to decrease biomass by 32.7%.

Conclusions of Impacts to Riparian Areas

In our study, horses and cattle both affected riparian conditions, including streambank disturbance, stubble height, and herbaceous biomass. Our results complement a recent study of wild horse effects on riparian vegetation by Boyd and colleagues.[12] While they assessed grazed versus ungrazed, we were able to assess effects of intensity of use. We found that horses had a greater effect on these riparian attributes than did cattle on an individual basis. The larger effect of horses may have been caused by their greater individual forage consumption,[13,15] which has a subsequently greater impact on the vegetation. Increased forage consumption may also increase the amount of movement in riparian areas, thereby increasing disturbance from trampling.

Several studies have documented increased soil compaction and decreased water infiltration in response to use by wild horses,[16,19] which supports our observation of increased disturbance and trampling.

Our conclusions that wild horses are having the greatest effect per animal occurrence on change in herbaceous stubble height agrees with previous studies which showed that the presence of horses significantly reduced standing biomass, species richness, and plant cover.[9,11,14] Drastic responses have been observed at the Sheldon National Wildlife Refuge in Nevada, where stubble height of ungrazed plants was nearly 10 times greater than grazed plants after wild horses were removed and grazing pressures reduced.[14] Likewise, Beever and Bussard[9] compared plant heights in upland meadows grazed by only horses, by horses and cattle, or not grazed by either. Plant heights in areas grazed by horses only were 2.8 times lower than plant heights in areas with no grazing, while plant heights in areas grazed by both horses and cattle were 4.5 times lower than those in areas with no grazing.[9] A few studies have looked at the impacts made by wild horses separately from other ungulates and have found that when present, they negatively impacted plants and plant communities through biomass removal, reducing plant species richness and cover of grasses and forbs.[9,11,12,20] Although not selected as important in our models, when included, wildlife had a positive relationship with herbaceous biomass and height, possibly indicating that wildlife are attracted to high quality riparian areas and may potentially avoid degraded habitat, leading us to believe there may be indirect effects of wild horses on wildlife. While there is probably little dietary overlap, horses may affect habitat through trampling and other disturbance. More research assessing interactions between horses, wildlife, and their habitat is needed.

Management Implications

Large grazing ungulates, such as horses and cattle, can have significant detrimental effects on riparian areas at high population levels and stocking rates. It is well known that effective management of riparian areas can be accomplished by controlling season of grazing and levels of use. Riparian management is difficult in areas with wild horses because these animals generally have year-long access to riparian areas, and levels of use or population levels are difficult to restrict. The tough management reality is that in areas with both wild horses and cattle grazing, land managers and ranchers need to account for potential additive effects. To maintain riparian productivity and ecological integrity in riparian areas grazed by both species, cattle grazing and use by wild horses will need to be carefully managed. An alternative may involve fencing to limit access to riparian areas; this could improve riparian integrity, but would limit riparian benefits to cattle, horses, and some wildlife. Balancing the needs of livestock, wild horses, and wildlife is important but challenging, and maintaining ecologically important habitats such as riparian areas may be key to ensuring sustained multiple use of rangelands.

Acknowledgments

This work was made possible by the generous support of Idaho Bureau of Land Management Wild Horse and Burro Program, the Idaho Rangeland Resource Commission, Mountain Springs Ranch, Central Idaho Rangeland Network, and the University of Idaho Berkund Research Fellowship, Rangeland Center, and David Little Range Management Endowment. University of Idaho Berklund Research Fellowship, Rangeland Center and David Little Range Management Endowment.

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Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Potential Spread of Cheatgrass *(Bromus tectorum)* and Other Invasive Species by Feral Horses *(Equus ferus caballus)* in Western Colorado☆

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ARTICLE INFO

Article history:
Received 5 February 2018
Received in revised form 14 December 2018
Accepted 15 February 2019
Available online xxxx

Key Words:
cheatgrass
diet
equid
germination
invasive species

ABSTRACT

The invasive grass cheatgrass (*Bromus tectorum* L.) presents major challenges for land management and habitat conservation in the western United States. Feral horses *(Equus ferus caballus)* have become overabundant in some areas of the West and can impact fragile semiarid ecosystems. Amid ongoing efforts to control cheatgrass in the Great Basin, we conducted a study to determine if feral horses contribute to the spread of cheatgrass through distribution via their feces. We collected feral horse fecal samples from Little Book Cliffs Herd Management Area in western Colorado in 2014. Fecal samples were dried, and 20 from each of 3 collection sessions were cultivated to examine germination success. Six species germinated from 18 samples (30%; mostly one plant per sample where germination occurred), including cheatgrass from 8% of samples. In a separate study we examined the diet of this same horse population using fecal plant DNA barcoding. Plant species that germinated were rare in the diet and germinated from fewer samples than expected relative to their detection in the diet. Our results suggest that feral horses could be contributing to cheatgrass propagation. Native ungulates and domestic cattle also have this potential. Although management of all large ungulates is necessary to mitigate cheatgrass spread, control of feral horse numbers is particularly necessary.
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Introduction

The National Research Council recommended evaluating the potential contribution of feral horses *(Equus ferus caballus)* to the spread of cheatgrass (*Bromus tectorum* L.; NRC, 2013), as this plant has significantly modified grazing lands in the western United States (Anderson and Inouye, 2001). The Bureau of Land Management (BLM) in the US Department of Interior administers 247.3 million acres (100.1 million ha) of public land, including management of the feral horses that inhabit 31.7 million acres (12.8 million ha) of those lands in 177 herd management areas (HMAs) distributed among 10 western states. Understanding the ecosystem effects of feral horses is important for wildlife conservation and habitat management as ungulates are a potential vector for dispersal of invasive species (Bartuszevige and Endress, 2008) and because HMAs overlap with priority wildlife habitat management areas (e.g., for greater sage-grouse) and public lands affected by cheatgrass invasion.

Cheatgrass was introduced to North America more than 100 yr ago (Stewart and Hull, 1949; Mack, 1981) and in recent decades has been recognized as a critical threat to ecosystem and habitat management across the western United States (Mack, 1981; Mealor et al., 2013; Chambers et al., 2014a; Coates et al., 2016). The magnitude of the problem is highlighted by widespread distribution across sagebrush ecosystems, including vast areas of the Great Basin (Trowbridge et al., 2013; Schmelzer et al., 2014; Boyte et al. 2016) and Wyoming Basin (Mealor et al., 2013; Manier et al., 2014), with potential for additional expansion in the future (e.g., Bradley, 2009; Friggens et al., 2012). The spread of invasive species such as cheatgrass is driven by a combination of factors, including facilitation by human activities and land uses, and interactions with natural processes such as climate and fire (Stewart and Hull, 1949; Mack, 1981; Bradford et al. 2006; Mealor et al., 2013; Svejcar et al. 2017). Propagule pressure, a seed source in the case of cheatgrass and other annuals, and condition of the ecosystem and its ability to resist invasion are two critical biological factors affecting invasions (Davies and Johnson 2011), both of which may be affected by feral horses.

The spread and proliferation of cheatgrass is affected by several environmental factors. It is well suited to both shrub and grassland habitats ranging from 500 to 6 000 f. above sea level (150 − 1 800 m; Skinner et al., 2008) and areas with mean annual precipitation from 6

☆ This study was funded by the US Geological Survey Fort Collins Science Center (under CESU agreement G14AC00418) with support from the Bureau of Land Management Wild Horse and Burro Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

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https://doi.org/10.1016/j.rama.2019.02.006
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to 22 in (15 – 55 cm); thus it is adaptable to a wide range of semiarid and mesic habitat types. Cheatgrass is a winter annual, germinating late in the growing season and producing roots and a leaf rosette that persist through the winter. In spring it initiates growth rapidly with warming temperatures and produces seeds in 5 – 6 wk (Stewart and Hull, 1949). However, recent research has confirmed plastic phenology of some populations whereby plants in xeric environments complete flowering a week before mesic populations initiate flowering (Dyer et al 2012). Cheatgrass also has a strong positive response to fire and is highly flammable, leading to short-fire return intervals that reduce the vigor of perennial grasses, remove shrubs, and result in increasing dominance of cheatgrass over time (Stewart and Hull, 1949; Balch et al., 2013; Mealor et al., 2013; Chambers et al., 2014b). Although cheatgrass may be grazed by livestock and wildlife while green, this represents a short portion of the year; thus, the optimal forage period is quite narrow temporally (Stewart and Hull, 1949; Mealor et al., 2013).

Ungulates are a potential vector for dispersal of invasive species (Bartuszevige and Endress, 2008), as they can disperse plant species by consuming them in one area and depositing them in another via feces, as well as by transferring seeds in their pelage (Albert et al., 2015). Horses, cattle *(Bos taurus)*, and cervids can all excrete viable seeds in their feces (Cosyns et al., 2005; Bartuszevige and Endress, 2008). The effect of endozoochory (consumption of seeds) varies among plant species, depending on whether seeds can survive mastication, ingestion, and digestion and whether they are consumed at all (Malo and Suárez, 1996). In one study 5 – 22% of seeds fed to a horse were recovered from the feces, and of these 2 – 64% subsequently germinated (Harmon and Keim, 1934). Another study reported germination from 13% to 90% of seeds fed to horses (St John-Sweeting and Morris, 1990) and found smaller and harder seeds had higher survival after passing through the digestive tract.

On western public lands mule deer *(Odocoileus hemionus)* and elk *(Cervus elaphus)* tend to be nomadic or migratory across the landscape, and cattle are moved on and off the range seasonally. Yet feral horses are present in the same HMA year-round, imparting a different impact than other ungulates. Depending on the digestibility of forage and species of plant, it takes 18 – 48 hr for consumed seeds to be excreted by horses (Van Dyk and Neser, 2000). The highest transmission rate is 2 – 3 d after ingestion, and some seeds were excreted up to 10 d after consumption (St John-Sweeting and Morris, 1990). In 2 d a feral horse can travel many miles from where it consumed vegetation, having the potential to disseminate seeds across the landscape.

In studies examining semiferal horses in Europe, fecal seed content correlated positively with plant species abundance in the field and in the diet, with 21 – 27% of plant species found in the area germinating from horse fecal samples (Cosyns et al., 2005; Cosyns and Hoffmann, 2005). To understand what is likely to germinate from feces, it is important to know what an animal has consumed. Plant DNA barcoding is an emerging alternative to microhistology for diet analyses (Valentini et al., 2009). A previous study by King and Schoenecker (2019) indicated that plant DNA barcoding might be more accurate than microhistology at representing diet in horse feces. Building on these analyses, we conducted a germination study to determine viability of seeds in horse fecal samples and evaluate potential contribution of feral horses to the spread of invasive species, particularly cheatgrass. Specifically, we determined which plant species survived ingestion and germinated from horse fecal samples, as well as how the proportion of these species related to the diet of horses from the same study area.

Methods

Study Area

We collected feral horse fecal samples in the Little Book Cliffs Herd Management Area (HMA), near Grand Junction, Colorado (UTM 12 722588, 4342571) in spring (May), summer (August), and fall (October) of 2014. The area is semiarid with a mean precipitation of 2.3 cm (±2.16 standard deviation [SD]) and a mean temperature of 9.6°C (±8.5°C SD) over the previous 10 yr (RAWSWestern Regional Climate Center, n.d). Precipitation averaged 4.4 cm/mo during the study period, mostly in August and September (King et al., 2018; King and Schoenecker, 2019). The landscape consists of mesa tops dissected by deep canyons, with water sources located throughout the upland area in tanks provided for the horses.

There are four primary plant communities within the HMA; cheatgrass *(B. tectorum)* is found in all four types:

1. Piñon-juniper woodland: characterized by piñon pine (*Pinus edulis* Engelm.) and juniper (*Juniperus osteosperma* [Torr.] Little, and *J. monosperma* [Englem. Sarg.]) with varying amounts of herbaceous and shrub forage in the understory (West, 1988);
2. Mixed mountain shrub: a variable mixture of shrub species including Gambel oak (*Quercus gambelii* Nutt.), mountain mahogany (*Cercocarpus montanus* Raf.), snowberry (*Symphoricarpos* spp. Duham.), sumac (*Rhus trilobata* Nutt.), and big sagebrush (*Artemisia tridentata* Nutt.) with abundant grasses and a diversity of other herbaceous species (West, 1988, Landfire, 2016, p. 162);
3. Salt-desert shrub: shadscale and fourwing saltbush (*Atriplex confertifolia* [Torr. & Frem.] S. Watson and *A. canescens* [Pursh] Nutt., respectively), greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit) predominate with sparse cover of grasses and forbs that tolerate salinity and alkalinity (West, 1988);
4. Sagebrush-grassland: typically characterized by Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle & Young), but also basin big sage (*A. tridentata* ssp. *tridentata*), black sagebrush (*A. nova* A. Nelson), and rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird), codominant with grasses and a diverse mixture of other herbaceous species (West, 1988; Landfire, 2016).

Experimental Design and Data Collection

We subjectively divided the HMA into sampling areas using ArcGIS (version 10.30.1, ESRI) where each area could be sampled by ground observers in 1 d. Each area included sagebrush-grassland, woodland, and at least one type of shrub community and avoided areas inaccessible to horses or ground observers on foot. We developed a random sampling scheme of sampling areas to collect fecal samples for this and other studies from across the entire HMA. The order and choice of sampling areas to visit were randomized on each sampling occasion (May, August, and October), but coverage of the HMA remained consistent. To collect fecal samples we walked across a sampling area in a group of 3 – 6 people in parallel lines roughly 10 – 20 m apart, with each person covering a 3- to 4-m-wide belt transect, conducting as many sweeps as needed to cover the area. We collected samples from fecal piles that were visually assessed to be 0 – ≈6 mo old (most were estimated to be ≈2 – 3 mo old; King et al., 2018; King and Schoenecker, 2019). Samples were collected in a paper bag: two whole boli from the middle of a pile were placed in the same bag, using nitrile gloves or sterile tongue depressors to manipulate the fecal bolus. Paper bags containing samples were placed in large cotton bags to air dry under shelter during each sampling session. Subsequently, paper bags were placed in a drying oven at 40°C for 3 d and stored. The same methods were followed on each field sampling visit, resulting in collection of > 1 800 samples from across the HMA.

Germination Experimental Design

We used 60 samples (20 from each collection period) for the germination study. We randomly selected samples for inclusion but excluded samples that were moldy, part of a stud pile (a large dung pile marked

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by multiple stallions), or small, indicating they were probably deposited by a foal. We also excluded samples that had touched the ground in the field as these may have picked up seeds that were not consumed. The dried fecal samples were gently broken up by hand and planted one sample to a row in plastic trays of sterile composting soil. Each sample row was marked with a colored stake to identify it by sample name. Each tray also contained a control row ($n = 20$) consisting of sterile composting soil with no feces added. These seed trays were maintained in a greenhouse at Colorado State University (CSU) under ambient light and temperature conditions and watered daily. We conducted the germination experiment from 26 March, 2015 to 31 July, 2015, at which time there was no further evidence of germination. Plant species were identified by a CSU botanist (J. Hardin) from their leaves or seeds. We recorded the number of shoots (individual plants) and dry weight of aboveground plant material as a measure of biomass.

Proportion of Diet

To compare plant species in the diet to the proportion of germinated species, we sent 90 subsamples from the overall dataset (30 from each season) rehydrated in vials of alcohol to Jonah Ventures laboratory (https://jonahventures.com) for plant DNA barcoding analyses in order to examine horse diet. These were analyzed at the laboratory as described by King and Schoenecker, 2019). One sample did not produce enough amplifiable DNA, leaving 89 samples in the analyses. Results were presented as proportion of each sample made up by an operational taxonomic unit (OTU). Multiple OTUs of the same genus were combined for analyses. We summed the percentage of each genus OTU across all samples. Overall percentage component of the diet was formed from the sum across all samples as a percentage of the total.

Statistical Analyses

We explored which plant species germinated from fecal samples and described this qualitatively. We tested whether there was a difference in dry weight of germinated plants across sampling seasons with a Kruskal-Wallis test in the statistical software R (R Core Team, 2017). We used a nonparametric test due to lack of normality in our small sample size. We evaluated differences in detection of species that germinated and species in horse diets derived from plant DNA barcoding with a chi-squared test in *Microsoft Excel* using plant DNA data as an expected value.

Results

Germination of Fecal Samples

No plants germinated from controls. Of the 60 fecal samples that were cultivated in the greenhouse, 18 samples (30%) had plants germinate and survive. Fifty-five individuals representing six species germinated: desert madwort (*Alyssum desertorum* Stapf.), hedgemustard/tumblemustard (*Sisymbrium* spp.), spike dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), cheatgrass (*B. tectorum*), bluegrass (*Poa* spp.), and sixweeks fescue (*Vulpia octoflora* [Walter] Rydb.; formerly *Festuca octoflora* Walter). *Alyssum desertorum, Sisymbrium* spp., and *B. tectorum* are non-native, invasive species (native status of *Poa* spp. depends on the species). When germination occurred, there was only one species per sample, except for one instance in which two species germinated from the same sample (*A. desertorum* and *Poa* spp.). Fewer species germinated from fecal piles deposited in spring (two species) compared with summer (five species) and fall (four species). The greatest dry weight biomass was from summer fecal piles: most dry weight consisted of *A. desertorum* (46.5 g), followed by *B. tectorum* (17.9 g; Kruskal-Wallis K = 7.1928, df = 2, $P = 0.02742$; Fig. 1). *B. tectorum* made up 22% of the total dry weight and germinated from 5 (8%) of the 60 fecal samples, all collected during summer or fall (see Figs. 1 and 2).

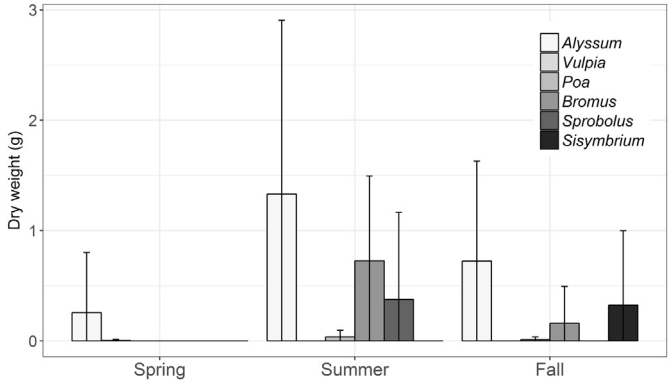


Figure 1. Mean dry weight (± 95% confidence intervals) of plant species that germinated from feral horse fecal samples collected from Little Book Cliffs Wild Horse Herd Management Area, Colorado in three different seasons in 2014.

Comparison with Diet Analyses

Results of plant DNA barcoding indicated 42 genera or plant groups made up > 20% of horse diet when summed across all samples (King and Schoenecker, 2019). Although forbs made up 19.24% of the diet, the forb species that germinated from the fecal samples were detected only in trace amounts (*Alyssum* spp. not detected *Sisymbrium* spp. = 0.01% of diet). Graminoids made up 68.76% of the diet, of which *Poa* spp. made up 14.81%. *Bromus* spp. accounted for 8.86% of the diet, although only 1.80% of that was *B. tectorum*. *Sporobolus* spp. made up a trace amount of the diet (0.05%). *Vulpia* spp. were not detected by plant DNA barcoding, although fescues (*Festuca* spp.) made up 0.10% of the diet; because *Vulpia* spp. were formerly recognized as *Festuca* spp. (USDA Plants, 2018), these data are presented together here. The grass species that germinated corresponded to grass genera that were evident in almost all samples, whereas the forbs that germinated were rare in diet analyses (see Fig. 2). All species germinated less than would be expected from their presence in fecal samples, except for *A. desertorum* ($X^2 = 270.3967$, df = 4, $P = < 0.0001$; see Fig. 2).

Discussion

We had low germination rates from our fecal samples, compared with studies on domestic and feral horses in more mesic habitats (Cosyns et al., 2005; Cosyns and Hoffmann, 2005; Quinn et al., 2008) and compared with the detection of these species in horse diets from the same area (King and Schoenecker, 2019). Only 6 species germinated from horse feces in our study, whereas in a European study 21 − 27% of plant species present germinated and 8 − 27 species germinated from

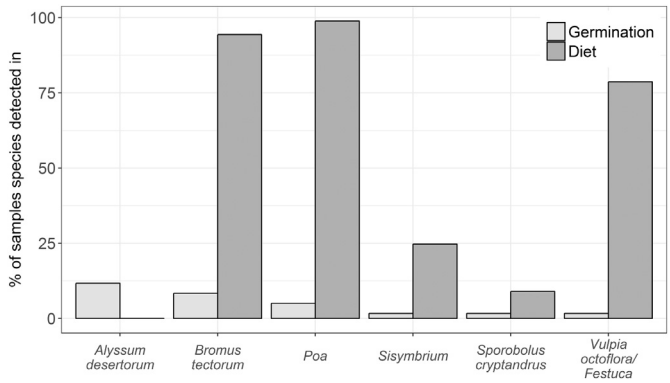


Figure 2. Difference in detection of plant species that germinated from feral horse fecal samples collected in Little Book Cliffs Wild Horse Herd Management Area, Colorado in samples collected for the germination experiment (60 samples) and those collected for plant DNA barcoding analyses (90 samples).

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samples collected in California and Colorado (Cosyns et al., 2005; Cosyns and Hoffmann, 2005; Wells and Lauenroth, 2007; Quinn et al., 2008). This may be attributed to seeds being compromised when we dried our samples but may also be the result of low productivity (low number of seeds) or low gut-survival rate of forage species seeds from this semiarid area. The latter two possibilities are more likely as fecal samples were dried at approximately the maximum environmental temperature in the study area. The greatest germination rate was from samples collected later in the year, which correlates with availability of viable seeds in this ecosystem.

The low proportion of the diet made up by the species that germinated was unexpected, although the grasses were almost ubiquitous in diet samples. Plant DNA barcoding detects plant species by amplifying chloroplast trnL (Valentini et al., 2009). The relative abundance of chloroplasts is a representation of the relative protein content of that plant, rather than the biomass. Lack of, or low, detection in the diet could be due to low relative abundance of chloroplasts from these species or be indicative of low protein content. We expected to see a similar proportion of species consumed to those that germinated; other studies have found the proportion of germinating seeds correlates with local abundance (Couvreur et al., 2005). Unfortunately, we did not have data on plant species abundance in the study area.

Importantly, the diet analyses showed that horses consume cheatgrass (King and Schoenecker, 2019) and the germination experiment showed that horses can distribute viable seeds in their feces. Although germination may be reduced by digestion (Blackshaw and Rode 1991), our work shows that desert alyssum, hedgemustard, and cheatgrass seeds can remain viable after passing through the digestive tract of a horse. The principal dispersal mechanism of cheatgrass is physical attachment to the pelage of animals via small stiff hairs on the glumes and the awn attached to each lemma (Stewart and Hull, 1949; Mealor et al., 2013). Thus, although it may not be a primary mechanism of dispersal, the potential for long distance movement and introduction of cheatgrass into new habitats is additionally created by transport within the digestive system of horses. The potential for cheatgrass spread from horse feces could be across a substantial area. For example, maximum distances traveled by feral horses in Australia were 5–17.5 miles per day (Hampson et al. 2010). This maximum equates to the distance from one side to the other of an average western HMA. Plant DNA barcoding analyses indicated that cheatgrass made up only 1.8% of horse diet but was found in horse diets across all three seasons we sampled. It germinated in 8% of fecal samples, all of which were collected in August and October, but even this small amount may be sufficient to have an effect on invasive plant distributions when multiplied by many horses over a period of years. While these results have important ramifications for management, it should be noted that horses are not the only grazers on the landscape that may consume and spread invasive plant species (Bartuszevige and Endress, 2008). Further research would be worthwhile to examine the contribution of domestic livestock, wildlife species, *and* feral horses to dispersal of cheatgrass and other invasive plants in arid and semiarid landscapes, especially those that include important rangeland habitats and conservation areas.

Implications

Across the Great Basin, detrimental effects of cheatgrass through shortened intervals between fires and conversion of native grass and sagebrush habitats to cheatgrass dominance create considerable management challenges (Knapp, 1996; Cox and Anderson, 2009). Feral horse herds roam across sagebrush and grassland habitats, including priority habitats in and around wild horse and burro HMAs in the western United States that are also challenged by cheatgrass invasion. We have demonstrated that feral horses consume cheatgrass and excrete viable seeds, confirming their potential to contribute to cheatgrass range expansion and distribution within these important rangeland ecosystems. Whereas horses can directly contribute to the propagation of cheatgrass through their feces, they may also be contributing to its persistence through the effects of overgrazing (Knapp, 1996; Davies et al., 2014). More than half of the on-range feral horse population on public lands is found in Nevada, and the population continues to grow. Together with climate change and frequent fires, overgrazing and other land uses can stress arid and semiarid ecosystems, making them less resilient to invasive species (Chambers et al., 2007; Chambers and Wisdom, 2009; Chambers et al., 2014a, 2014b). While livestock are moved seasonally on the range, horses are present in HMAs year round. Where horses are at high densities, this can lead to degradation of the rangeland, decreasing ecosystem resistance. Managing cheatgrass therefore requires management of all grazers on public lands, including better control of feral horse numbers.

Acknowledgments

We would like to thank Jim Dollerschell, Rangeland Management Specialist at the Bureau of Land Management, and the members of the Friends of the Mustangs volunteer group for their assistance with this study. We appreciated fieldwork assistance provided by fecal sampling volunteers. The CSU greenhouse staff, Janet Hardin, and Katie Cleary were instrumental to the germination experiment.

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Please cite this article as: S.R.B. King, K.A. Schoenecker and D.J. Manier, Potential Spread of Cheatgrass *(Bromus tectorum)* and Other Invasive Species by Feral Horses *(Equus ferus caballus)* in Western Colorado, Rangeland Ecology & Management, https://doi.org/10.1016/j.rama.2019.02.006

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Please cite this article as: S.R.B. King, K.A. Schoenecker and D.J. Manier, Potential Spread of Cheatgrass *(Bromus tectorum)* and Other Invasive Species by Feral Horses *(Equus ferus caballus)* in Western Colorado, Rangeland Ecology & Management, https://doi.org/10.1016/j.rama.2019.02.006

Plant Ecol (2009) 201:471–480
DOI 10.1007/s11258-008-9468-0

Feral horses dung piles as potential invasion windows for alien plant species in natural grasslands

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Received: 3 December 2007 / Accepted: 14 July 2008 / Published online: 1 August 2008
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Abstract Small scale disturbances could act as patches that provide sites for the colonization of competitively inferior species, promoting the establishment of non-native species in some cases. We analyzed the vegetation associated with feral horse dung piles in montane pampas grasslands in Mid-East Argentina and described the changes following their abandonment, evaluating whether dung piles act as invasion windows, allowing the entrance of alien plant species. We estimated the portion of the study area directly covered by horse manure and dung height was used to estimate the time elapsed after the abandonment of each pile. Vegetation replacement on dung piles of different ages was assessed and compared with grassland controls using discriminant analysis. We used regression analysis to look for changes in vegetation cover, species richness, species diversity and evenness in response to height (age) of the dung piles, and principal component analyses (PCA) to identify groups of plants associated with different successional stages. We compared cover of alien plant species on dung piles with grassland controls using one-way ANOVA. On average, 2.5% of the study area was covered by horse dung. Total vegetation cover, species richness, diversity and evenness increased after the piles were abandoned. Characteristic plant groups were associated with initial, middle and last phases of the studied succession. Vegetation on the dung piles significantly differed from that in grassland controls and two species were consistently associated with dung piles: the invasive Red Star Thistle, *Centaurea calcitrapa*, and a native grazing-intolerant grass, *Nassella clarazii*. Non-native species cover was also higher in dung piles than in control plots. Dung piles cover a significant portion of grassland area in our study site, produce significant changes in the vegetation and are associated with some invasive alien plants that could eventually colonize more pristine areas in the vicinity. On the other hand, they might represent refuges for palatable species, since horses seem to avoid them for grazing.

Keywords Conservation · Invasive alien species · Natural grasslands · Refuges · Stud pile · Manure

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Introduction

Invasive alien species usually modify the disturbance regime of invaded ecosystems changing patterns of succession and promoting colonization by pioneer or

ruderal species, which results in the modification of natural communities (Vitousek et al. 1996; Mack et al. 2000). The presence of a non-native species quite often favours the introduction of others through a process called "invasion meltdown" (Parker et al. 1999; Grosholz 2005; Facon et al. 2006), as has been cited in several cases when the arrival of plant species was associated with the presence of large alien herbivores (Parker et al. 2006). The introduction of domestic and feral livestock results in degradation of the native flora affecting the whole landscape, decreasing the cover of the herbaceous layer and favouring the dominance of plants that are less susceptible to grazing, such as unpalatable (Huntly 1991; Vázquez 2002; Tood 2006), spiny or rosette species (Fernández-Alès et al. 1993), and of medium to low height species (Lavorel et al. 1999), increasing the richness and diversity of non-native plants in many cases (Chaneton et al. 2002; Vázquez 2002; Parker et al. 2006).

The introduction of herbivores results in higher impacts when introduced animals are functionally different from those already present, or thrive in greater densities in respect to those found naturally in the native community (Hobbs and Huenneke 1992). Large alien ungulates have produced smaller changes in the savannas of Africa and North America, possibly because large, hoofed, congregating grazing mammals already existed in the evolutionary history of these habitats, resulting in the evolution of grasses tolerant to heavy grazing—including both tussock and rhizomatous or turf grasses. The situation is different on the large South American plains where herbivores of this kind were not previously present and so dominant tussock grasses are intolerant to heavy grazing (Mack 1989). Similarly, the grazing intensity by domestic herbivores in southern South America is thought to be about ten times more than it was before their introduction (Oesterheld et al. 1992).

Grazing and trampling are the best known agents of change associated with the presence of introduced herbivores (Trimble and Mendel 1995; Vázquez 2002; Rook et al. 2004), whereas, in comparison, much less is known, about the impact of the accumulation of manure, which is a conspicuous effect of ungulate activity. Feral horses and other ungulates, e.g. vicuñas, guanacos, llamas and Przewalski horses (Bouman 1986; Vilá 1994; Dalmasso et al. 1999; Beever and Brussard 2000; King and Gurnell 2007), behave in a particular way: herds or family groups deposit their dung at special sites, forming conspicuous mounds, called *dung piles* or *stud piles* (King and Gurnell 2007). It is thought that these accumulations mark the territory occupied by a male and they also serve as a signal for reproduction, letting a male know when females in his territory are on heat (Bouman 1986; Vilá 1994). Manure in dung piles increases the availability of soil nutrients, especially nitrogen and phosphorus (Nielsen 1997; Dai 2000; Aarons et al. 2004) and favours the conservation of humidity. This might contribute to the development of special patches of vegetation growing directly on manure and in its surroundings (Shiyomi et al. 1998; Dai 2000). In many ecosystems, the invasion of non-native plant species is dependent on this type of disturbance that creates appropriate microhabitats for their establishment, especially if the disturbance results in an increase in water and nutrients (Lake and Leishman 2004). These microhabitats can act as "invasion windows" fostering the establishment and potential dispersal of invasive alien species. Moreover, many species are transported in manure, which also contributes to their establishment (Dobbie et al. 1993; Malo and Suárez 1995a, b; Campbell and Gibson 2001; Wells and Lauenroth, 2007). Previous studies are concerned with analysis of the effects of manure of domestic livestock (Shiyomi et al. 1998; Dai 2000; Loucougaray et al. 2004), but no evaluation of the impact of wild herbivore dung piles has been undertaken, especially feral horses on natural ecosystems.

Horses have been present in the Argentine plains since the beginning of European colonization (Vázquez 2002) and they form feral populations in several natural and semi-natural grasslands and shrublands across the country (INBIAR, Database on Biological Invasions in Argentina 2007). A population of feral horses inhabits the Ernesto Tornquist Provincial Park (ETPP), one of the last few relicts in a relatively good state of conservation in the Pampas Phytogeographic Province (Scorolli 1999). The ETPP has provided a favourable habitat for the growth of this population which started with a nucleus of a stallion and four mares that were introduced in 1942 (Scorolli 1999), reaching a current density of 25 horses per km^2 (A. Scorolli, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, pers. comm.). The presence and activity of feral horses in the area results in a highly altered matrix of low

grassland from which small areas of taller tussock grasses (*Paspalum quadrifarium*) emerge, in association with low, wet sites. It is known that grazing in the reserve results in a reduction of vegetation cover and height and increases the abundance of shrub species and unpalatable grasses (A.E. de Villalobos and S.M. Zalba pers. comm.), as well as the cover of alien species (Frangi and Bottino 1995; Long and Grassini 1997). However, the impact of dung piles on vegetation communities in the reserve had not been previously analyzed.

In this study, we assess the area directly affected by feral horse manure in the ETPP. We evaluate differences in plant communities growing on dung piles compared with control plots without manure, and describe the successional changes in dung pile vegetation over time and also discuss the possible role of dung piles in the introduction and dispersal of invasive plants in the reserve.

Methods

Study area

The study was carried out in the Ernesto Tornquist Provincial Park (ETPP), which has an area of approximately 6,700 ha in the Ventania mountains, between 38°00′–38°10′ S and 61°45′–62°08′ W, and includes mountains of around 1,000 m a.s.l. Climate is temperate, with an average annual temperature of 14°C (Burgos 1968). The average precipitation is 800 mm, with occasional snow in the winter.

The study area in the reserve consists of 2,000 ha of piedmont valleys with 5 –11% slopes, shallow soils and occasional rocky outcrops. In the absence of intensive grazing the grass canopy is 50–60 cm tall, dominated by *Piptochaetium hackelii*, *P. napostaense*, *Nassella melanosperma* and *Chascolytrum subaristatum* among others (Frangi and Bottino 1995). Tussock paspalum (*Paspalum quadrifarium*) is dominant on stream edges and in areas where the soil is saturated with water during rainy periods (Frangi and Bottino 1995).

Sampling design and statistical analysis

The sampling was carried out in January and February 2004 over an area where horses were active (Scorolli 1999). Fifteen linear transects 50-m long were placed at random, in order to determine the percentage of the study area was directly covered by manure.

Fifteen dung piles >1 m in diameter were selected in order to avoid biases due to very small dung piles or isolated dung (i.e. dung not grouped in piles). The area of dung piles was calculated assigning each pile to either a circular or oval shape. The height of each pile was calculated as the average from five measurements taken in the centre of the pile and in the middle of their largest and smallest radiuses. Mean height was used to estimate how much time had passed since abandonment by the animals (age of the dung pile). Loss of humidity, decomposition of organic material and physical factors such as wind and rain, result in hardening and then disintegration and fragmentation of the manure over time and also in the loss of the boundaries of the lumps (Dai 2000). These changes in turn cause a decrease in the height of the pile and a concomitant increase in its area. Therefore, it can be assumed that dung height shows a negative correlation with time after abandonment of the pile and so it can be used as an indicator of its age. Alternatively, differences in dung height might respond to an original variation in the size of the pile; if dung height reduces with time, we would expect to find a negative correlation between both variables. Actually, the area of dung piles (2.80 ± 0.324 m^2, mean $\pm$ SE) and their height were negatively correlated ($R = -0.679$, $P < 0.01$, $n = 15$), supporting the idea of reductions in dung height and increases in size over time.

We determined the percentages of plant species cover and of bare manure by visual estimation for each dung pile. Plant species were collected and identified in the laboratory according to Zuloaga and Morrone (2007).

Plant species richness and Shannon's diversity index and evenness (Begon et al. 1996) were calculated for the vegetation on the dung piles. A linear regression analysis was undertaken between the height of the dung (as an indicator of the time passed since abandonment of the pile) and the total percentage of vegetation cover, species richness, Shannon's diversity index as well as the evenness in the whole dung pile.

A principal components analysis (PCA) was carried out using the correlation matrix between the percentage cover for each species in order to search for patterns in the floristic composition of the dung

piles. Occasional species (i.e. species present on only one dung pile with a percentage cover <1%) were excluded. As the first principal component explained a meaningful part of the total variation according to Kaiser–Guttman criterion (Legendre and Legendre 1998), we correlated it with dung pile height in order to describe plant species replacement with time.

Twenty 1-m^2 grassland controls placed at least at 10 m from the nearest dung pile were randomly selected. Species composition on these plots was assessed and compared with dung piles using stepwise discriminant analysis. A canonical variate analysis was used to determine which variables were more important in separating dung piles from grassland controls. We also compared non-native species cover per square meter between control plots and dung piles by Kruskal–Wallis non-parametric analysis of variance.

Results

Manure cover at the study site was 254 ± 52 m^2 ha^{-1}, representing 2.5% of the total surface area. About 78 species were found growing directly on the dung piles, among which 35 (45%) were considered occasional. About 61 species were detected in control plots of which nine (15%) were considered occasional. The percentage of uncovered substrate (i.e. non-vegetated substrate covered only by manure) increased with the height of the dung pile, i.e. greater percentages of bare manure were associated with more recent dung piles

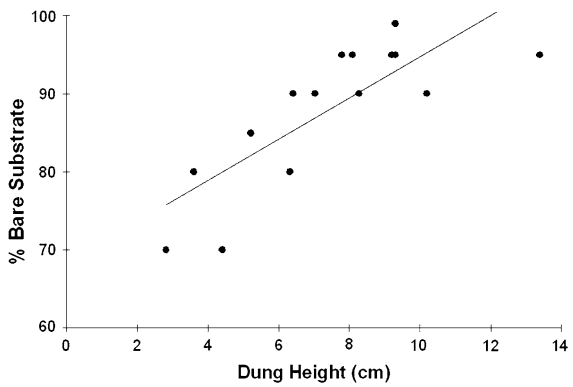


Fig. 1 Linear regression between the percentage of bare substrate and dung height. The height of the dung is used as a proxy inversely related to the time passed since the abandonment of the dung pile. $R^2 = 0.64$, $n = 15$, $P < 0.01$

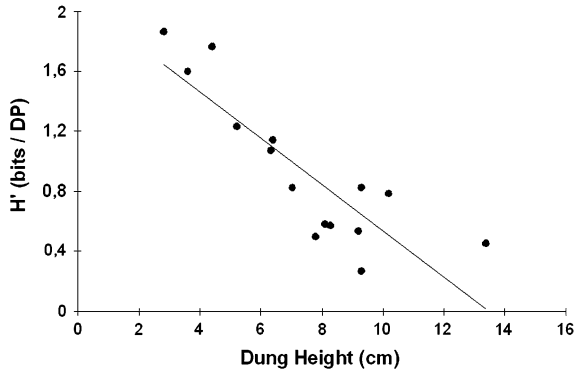


Fig. 2 Linear regression between Shannon's diversity (H′) and height of the dung piles. $R^2 = 0.725$, $n = 15$, $P < 0.01$. DP: Dung pile

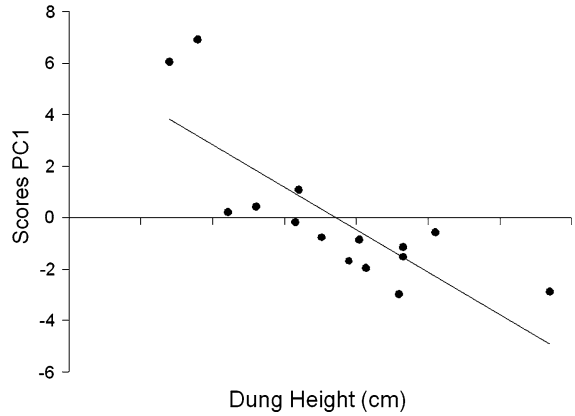


Fig. 3 Linear regression between dung piles scores on the first principal component (PC1) and the height of each pile

($R^2 = 0.640$) (Fig. 1). Shannon's diversity index increased significantly with reductions in height of the dung pile ($R^2 = 0.725$) (Fig. 2). The same occurred with species richness and evenness ($R^2 = 0.461$ and $R^2 = 0.701$, respectively). The first principal component of the PCA obtained from the data of species cover in the dung piles explained 18% of the total variance, while the second component explained 13%. No clearly defined groups of dung piles were detected by their ordination on these first two axes.

The height of the dung pile was negatively correlated with the position of the dung piles on the first principal component (correlation coefficient = −0.798; $P < 0.01$) (Fig. 3). The ordering of dung piles on the first principal component reveals changes in the abundance of different species in association with the age of the dung pile, according to species loads in

Table 1 Correlation coefficients (*R*) between species cover and the coordinates of dung piles on the first principal component (PC1). Only species with correlation coefficients, equal to or greater than half the highest value obtained are shown

Species	*R* PC1
Nassella clarazii	0.9350
Evolvulus sericeus	0.8444
Chaptalia exscapa	0.7924
Cyperus aggregatus	0.6770
Paronychia spp.	0.6622
Pfaffia gnaphaloides	0.6468
Centaurea calcitrapa	0.5720
Conyza monorchis	0.5642
Piptochaetium medium	0.5275
Acmella decumbens	0.5181
Helenium radiatum	0.4879
Margyricarpus pinnatus	−0.2537
Hedeoma medium	−0.3438
Berroa gnaphalioides	−0.3499
Baccharis rufescens	−0.4058
Chevreulia sarmentosa	−0.4551

the first PCA axis (Table 1). Some species, e.g. *Eragrostis lugens, Eryngium nudicaule, Margyricarpus pinnatus* and *Pavonia cymbalaria,* were present in most of the dung piles and some of them, e.g. *Aristida spegazzinii*, *Pfaffia gnaphaloides* and *Piptochaetium stipoides,* showed greater cover in the oldest dung piles. Another group of plants including *Baccharis rufescens*, *Chevreulia sarmentosa*, *Hedeoma medium*, *Piptochaetium montevidense* and *Plantago myosuros* appeared in recent and middle aged dung piles. Other plants associated with dung piles of middle age continued to be present in the oldest ones, e.g. *Centaurea calcitrapa, Chaptalia exscapa, Cyperus aggregatus, Eleusine tristachya*, *Evolvulus sericeus, Nassella clarazii, Piptochaetium medium* and *Sporobolus indicus* (Table 2).

The best stepwise discriminating model obtained when comparing vegetation on the dung piles and in the control selected thirteen species from a total of 67 (Table 3). *Centaurea calcitrapa* and *Nassella clarazii* only appeared growing on the dung piles, while *Baccharis rufescens*, *Helenium radianum* and *Pfaffia gnaphaloides* showed higher cover on them. Alternatively, *Aristida spegazzinii*, *Baccharis stenophylla*, *Chaptalia exscapa*, *Eragrostis lugens*, *Juncus tenuis*, *Mimosa rocae* and *Piptochaetium stipoides* were consistently associated with the control plots. The discriminant function discriminates significantly between both vegetation groups (Wilk's-Lambda = 0.008, df = 13, $P < 0.001$) with a 100% of the samples correctly allocated.

Table 2 Species cover on dung piles and mean cover in control plots. Cover: **1**. 0–1%; **2**. 1–5%; **3**. 5–25%, **4**. 25–50%, **5**. 50–75%, **6**. 75–100%. Species were selected considering changes in abundance in association with piles of different height

Species	Dung Pile height (cm)															Control Plots
	13.4	10.2	9.3	9.3	9.2	8.3	8.1	7.8	7.0	6.4	6.3	5.2	4.4	3.6	2.8	
Piptochaetium stipoides	1	0	1	1	1	0	1	1	2	1	1	2	1	1	2	5
Margirucarpus pinnatus	1	1	1	0	1	1	0	1	1	1	0	1	1	0	1	2
Eragrostis lugens	1	1	1	0	1	0	0	0	1	1	1	0	1	1	1	3
Aristida spegazzini	1	1	1	0	1	0	1	1	0	1	0	0	2	1	0	2
Pavonia cymbalaria	1	1	1	0	1	0	0	0	1	2	0	1	1	1	0	2
Pfaffia gnaphalioides	1	1	1	0	0	0	0	0	1	1	1	0	1	1	2	1
Eryngium nudicaule	1	1	0	0	1	1	0	1	1	0	1	0	1	1	0	1
Baccharis rufescens	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Hedeoma medium	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1
Chevreulia sarmentosa	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1
Piptochaetium haeckelii	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Plantago myosurus	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Piptochaetium medium	0	0	0	0	0	1	1	0	0	0	1	2	1	1	2	2
Eleusine tristachya	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1
Cyperus aggregatus	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Sporobolus indicus	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
Nassella clarazii	0	0	0	0	0	0	0	0	0	1	0	0	0	2	2	0
Evolvulus sericeus	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1
Centaurea calcitrapa	0	0	0	0	0	0	0	0	0	0	2	2	3	0	3	0
Chaptalia exscapa	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1

Table 3 Standardized canonical discriminant function coefficients (*C*) from canonical variate analysis on plant species cover between dung piles and grassland controls

Species	*C*
Centaurea calcitrapa	−2.021
Nassella clarazii	−1.360
Helenium radianum	−1.244
Juncus tenuis	−1.202
Baccharis crispa	−0.958
Baccharis rufescens	−0.624
Pfaffia gnaphalioides	0.870
Aristida spegazzinii	1.025
Eragrostis lugens	1.912
Mimosa rocae	1.199
Baccharis stenophylla	2.404
Chaptalia exscapa	3.047
Piptochaetium stipoides	3.435
Functions at group centroids	
Dung piles	−12.273
Grassland controls	9.205

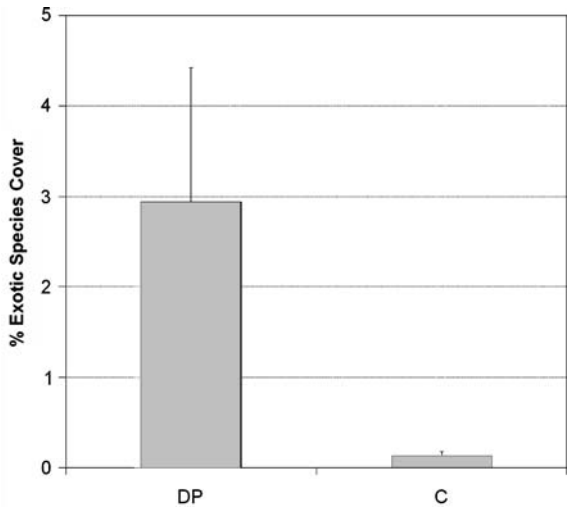


Fig. 4 Alien species cover per square meter in dung piles (DP) and control plots (C). The bars represent standard deviation

Non-native species cover was higher in dung piles than in grassland control plots ($H = 4.69$, $P < 0.05$) (Fig. 4). Only one alien species, *Geranium dissectum*, was found growing in control plots with a mean cover of <0.15%. However, nine alien species were associated with dung piles with *Centaurea calcitrapa* being the most abundant species in some of the piles (Table 4).

Table 4 Alien plant species frequency (Freq.) and mean cover (M.C.) on dung piles and control plots

Species	Dung Pile ($n = 15$)		Control plots ($n = 20$)	
	Freq.	M.C. (%)	Freq.	M.C. (%)
Bromus hordeaceus	1	0.03	0	0
Centaurea calcitrapa	4	2.40	0	0
Echium plantagineum	1	0.20	0	0
Geranium dissectum	3	0.10	5	0.13
Petrorhagia nanteulli	2	0.07	0	0
Plantago lanceolata	1	0.03	0	0
Polycarpon tetraphyllum	1	0.03	0	0
Scleranthus annuus	1	0.03	0	0
Taraxacum officinale	1	0.03	0	0

Discussion

Despite the widespread presence of feral ungulates in grassland ecosystems, this is the first effort to assess the effect of feral horse dung piles on plant communities. The area covered by manure in the ETPP (ca. 2.5%) is greater than the results obtained for cattle dung by other authors in other ecosystems of the world. Dai (2000) found around 1% cover of cattle manure in a field on the island of Öland, in the south of Sweden. Omaliko (1981) reports that the percentage of surface covered by cattle manure reached 0.38% in a savanna area in Nigeria. Malo and Suárez (1995c), working in a Mediterranean pasture in Spain, found that the cover of cattle manure reached 0.5% of the area, varying during the year, and locally reaching 2%.

In our study, the percentage of bare substrate decreases with the age of the dung piles whereas species richness, diversity and evenness increase. It is possible that the initial impact of the accumulation of manure restricts the colonization of the site to a reduced group of species capable of tolerating the high concentration of salts that comes from the dung and urine of the horses. With the passage of time, environmental conditions may become less extreme, allowing the establishment of other species. The coexistence of both groups could explain the increase in total vegetation cover, richness, diversity and evenness that follows. This conclusion has to be taken with caution, as there is a risk of confounding

the effect of time with the concomitant increase in area that occurs as dung piles disintegrate. However, plant cover (shown as the complement of bare substrate in Fig. 1) increases more rapidly than dung piles area: since the area of the dung piles augments in a factor of 5 times (ca. 1 m^2 to ca. 5 m^2), the percentage plant cover changes from ca. 1% to ca. 30% in the studied dung piles. On the other hand, the recorded increases in plant species richness and diversity greatly exceed those expected only by an increase in area, considering that minimal sampling area in this grasslands is about 1 m^2 (Zalba 1994).

A process of successional replacement of the vegetation becomes evident when the variation in the specific composition of dung piles over time is analyzed. The presence of a particular species would depend on its relative capacity to arrive at the site, germinate and become established, as well as to resist competitive replacement by new species. A group of plants (e.g. *Aristida spegazzinii, Piptochaetium stipoides, Pfaffia gnaphalioides*) that commonly appear in the plots sampled in the surrounding grassland matrix was also present on dung piles of different ages, showing greater cover in the older ones. It is possible that at least some of these species were present before the site was covered by dung and were capable of resisting the impact of manure, resprouting from underground structures, such as rhizomes, stolons, root suckers or bulbs, after the abandonment of the dung piles. Another group of species might initially respond in the same way, but then not be able to tolerate the environmental conditions in the dung piles in successive stages, or the competition from opportunistic species that take advantage of this habitat, and eventually disappearing. This group of plants appeared in young dung piles, but was not found in the oldest ones (e.g. *Hedeoma medium, Baccharis rufescens*). Finally, a third group of species was only associated with the lowest dung piles, indicating that they appeared after a certain time had passed after the abandonment of the dung pile (e.g. *Centaurea calcitrapa, Chaptalia exscapa, Nassella clarazii*).

Dung piles represent a sudden and significant disturbance due to the accumulation of a large amount of manure, with the consequent decrease in the cover of the underlying vegetation and the enrichment of nutrients and humidity. According to the Grime′s triangular model for representing plant strategies (CSR theory) (Grime 1977, 2001) plant competition is not important in recently disturbed areas with great availability of resources and rapid colonization. So, the initial stages of plant establishment on a dung pile would be determined by the survival of tolerant species that are already present in the site, plus pioneer species present in the soil seed bank, in seed rain or transported in the dung. Seeds of species of some genera recorded on dung piles in ETPP, e.g. *Carex*, *Conyza*, *Cyperus*, *Daucus*, *Eleusine*, *Erodium*, *Geranium*, *Juncus*, *Oxalis* and *Plantago*, among others, are able to survive the passage through the digestive tract of horses and other ungulates and are effectively dispersed by them (Malo and Suárez 1995b; Campbell and Gibson 2001; Cosyns and Hoffmann 2005; Mouissie et al. 2005). As time passes, the conditions in the dung piles would become more moderate, allowing the arrival of other species. Competition might then become the factor that structures the communities.

Changes in vegetation growing on dung piles respect to grassland controls should be taken with care considering that manure covers an important portion of the area and it is possible that control plots could have been covered by dung in the past. To have a real knowledge of the effect of manure, plots historically free of dung should be used, what is actually not possible due to the extensive use of the area for cattle ranching. Nevertheless, an effort has been made to select controls that were free of dung evidences and we think that the described restriction does not preclude drawing conclusions about the effect of dung piles.

The association of alien species with dung piles is of particular interest. In particular *Centaurea calcitrapa,* the most abundant non-native species found in the dung piles, is relatively uncommon in natural grasslands at the study area, but very frequent on road edges and other disturbed places (Long and Grassini 1997). During this study, *C. calcitrapa* was not recorded in grassland habitats away from the dung piles, but it was very frequent in old dung piles, exceeding percentage covers of 5%. The species was seen flowering on the piles, supporting the idea that it can complete its life cycle before the complete disintegration of the pile and so producing seeds that can disperse from there. Dung piles in which the species is present might therefore function as a source from where the species could colonize grassland

habitats in the future, provided that certain ecological, genetic and/or demographic changes occur, constituting a potential centre of dispersion of propagules over the area.

The case of *Nassella clarazii* is also interesting as it was only found in the oldest dung piles and the specimens found were more than 25-cm tall (A. Loydi, pers. observ.). *N. clarazii* is very palatable and sensitive to grazing (Rúgolo de Agrasar et al. 2005), and so it is not common in this intensively grazed ecosystem and in fact it was not found in the grassland control plots. Abundance of sensitive species to grazing seems to depend on refuge availability in both terrestrial and aquatic ecosystems (Quenga Kerr and Paul 1995; Lavorel et al. 1999; Callaway et al. 2000; Milchunas and Noy-Meir 2002; Oesterheld and Oyarzábal 2004; Callaway et al. 2005; Rebollo et al. 2005; Baraza et al. 2006; Graff et al. 2007). These refuges allow threatened organisms to escape from the effect of herbivores, avoiding local extinction in areas that are heavily grazed (Callaway et al. 2000). The presence of ungrazed specimens of *N. clarazii* associated with dung piles might be because of feral horses avoid grazing there and therefore these areas might act as refuges that favour palatable species. The tendency of domestic horses to avoid grazing in latrine areas has been reported by numerous authors (Nielsen 1997; Shiyomi et al. 1998; Loucougaray et al. 2004), however, Beever and Brussard (2000) and Lamoot et al. (2004) did not record this behaviour when analyzing populations of feral and free-ranging horses. Alternatively, the presence of the species might be related to the particular ecological conditions at dung piles and this could be further tested by experimental manipulation with exclosures.

It can be concluded that dung piles cause local changes in vegetation communities of Pampas grassland that may scale up both their spatial and temporal boundaries. These might still affect plant communities after the disintegration of the manure, the virtual disappearance of the piles and even after the eventual removal of the population of the invasive herbivore, mainly due to their role as facilitators of invasion processes. Dung piles in some cases may act as invasion windows and sources of propagules for invasive alien species, leading to potentially irreversible changes in the grassland. On the other hand, the presence of grazing-sensitive species on the dung piles is indicative of the effect of grazing outside their boundaries and also of the potential for recuperation of grassland by managing the stocking rate of non-native herbivores.

Acknowledgements This work was funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina) and Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur. The authors also wish to thank Dolores Rodríguez Rey and José Luis Vidal for field assistance and two anonymous reviewers for their valuable comments.

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ECOSYSTEM ENGINEERS

Equids engineer desert water availability

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Megafauna play important roles in the biosphere, yet little is known about how they shape dryland ecosystems. We report on an overlooked form of ecosystem engineering by donkeys and horses. In the deserts of North America, digging of ≤2-meter wells to groundwater by feral equids increased the density of water features, reduced distances between waters, and, at times, provided the only water present. Vertebrate richness and activity were higher at equid wells than at adjacent dry sites, and, by mimicking flood disturbance, equid wells became nurseries for riparian trees. Our results suggest that equids, even those that are introduced or feral, are able to buffer water availability, which may increase resilience to ongoing human-caused aridification.

Terrestrial large herbivores (henceforth megafauna) have undergone extensive extinctions and range contractions beginning during the late Pleistocene (100,000 to 12,000 years before the present) and continuing today (*1*, *2*). Although climate change at the end of the last glacial maxima may have played a contributing role (*3*), emerging consensus indicates that most prehistoric losses were driven by human activity (*1*, *2*). In tropical and temperate ecosystems, megafauna declines are linked to the formation of closed woodlands, increased wildfire, and reduced dispersal of large-seeded plants (*4*). Less is known, however, about how megafauna may have shaped dryland ecosystems, which comprise a third of Earth's surface (*5*).

Water is the main limiting resource in dryland ecosystems. It determines species composition, food web structure, and vegetation dynamics (*6*, *7*). Yet, the capacity for animals to enhance water availability by exposing subsurface water has received little attention. Wild donkeys (*Equus africanus asinus*) and horses (*E. ferus caballus*), as well as most other equids and all elephant species, regularly dig wells of up to 2 m in depth (Fig. 1, A to D; see table S1 for review). We evaluated well digging and its associated ecosystem effects in a North American system where equids have established feral populations.

We surveyed four Sonoran Desert groundwater-fed streams every 2 to 4 weeks over three summers (table S2). At each site we mapped "background" (e.g., already present) and "equid well" water [data S1 and (*8*)]. Streams were 7 to 32 km apart and were ~300 to 1800 m long (table S2). Like many desert streams, site hydrology was highly variable, as was the relative contribution of equid wells. Equid wells were particularly important to provisioning water in midsummer as temperatures increased and water tables receded (Fig. 1E). At one fully intermittent stream that lost all background water, equid wells provided 100% of surface water. Even at sites which remained perennial (background water retained at headwater springs), wells provided up to 74% of surface water by accessing the water table in dry reaches (Fig. 1E). Likewise, equid wells increased water density relative to background water by an average of 332% (SD = 416%) and by as much as 1450% (Fig. 1F).

Isolated water features can be areas of heightened antagonistic interactions among wildlife, including predation, disease transmission, competition, and herbivory (*9*–*11*). Equid wells strongly reduced the isolation of water features, reducing average nearest-neighbor distances between water features by an average of 65% (an 843-m reduction, SD = 798 m) and by as much as 99% (a 2.3-km reduction) (Fig. 1G). Thus, in addition to increasing the total amount of water available (Fig. 1E), we argue that equid wells may relax the potential for strong antagonistic interactions and reduce the distances that animals must travel to reach water.

To understand whether equid wells have value for other species, we deployed camera traps at five sites in the Sonoran and Mojave Deserts, sampling over 3258 trap nights (table S2). We calculated daily species richness and the duration and frequency of visits as measures of vertebrate activity, which we compared between equid wells, background waters, and adjacent dry controls. We excluded the equids themselves and species <100 g to control for poor detection probabilities for small animals.

Overall, we detected 59 vertebrate species at equid wells, of which 57 were recorded drinking [Fig. 2, A to D; table S3; data S2; and (*8*)]. Daily species richness was 64 and 51% higher on average at equid wells and background waters, respectively, than at dry controls (post hoc test: t ratio = −7.6 and −10.3, $p < 0.0001$; Fig. 2E). Likewise, visit duration was 274 and 620% longer at equid wells and background waters than at dry controls (t ratio = −7.8 and −9.7, $p < 0.0001$; Fig. 2F), and visit frequency was 91 and 60% higher on average (t ratio = −11.3 and −16.32, $p < 0.0001$; Fig. 2G). These effects increased with temperature at both water types (Fig. 2G; see table S4 for omnibus test results). There was no difference between equid wells and background waters in terms of richness (post hoc test: t ratio = −1.6, $p = 0.25$) or duration (t ratio = 1.9, $p = 0.14$), but background waters had higher visit frequencies than equid well waters (t ratio = −3.4, $p = 0.002$).

Responses were similar across vertebrate body sizes (fig. S1), and species composition did not vary between resource types [permutational multivariate analysis of variance (PERMANOVA): $F = 0.9$, $p = 0.7$; fig. S2]. Domestic cattle activity showed a similar pattern but was analyzed separately, because cattle densities were determined by humans and fluctuated during the study period (fig. S3 and table S4).

Some of the species detected drinking from equid wells are free-water dependent, such as mule deer (*Odocoileus hemionus*), whose summer distribution is shaped by surface water [table S3 and (*12*)]. Other desert species, such as javelina (*Pecari tajacu*), are capable of extracting sufficient water from food and thus can be free-water independent (table S3). However, this requires increased food consumption rates, especially at high temperatures (*13*). By maintaining water availability, equid wells may both enable the persistence of free-water–dependent species and prevent transitions from "food web" to "water web," thereby reducing the potential for oscillatory population dynamics (*14*).

Well digging also influences vegetation. On a dammed perennial Sonoran Desert river, abandoned equid wells host numerous riparian trees (primarily *Populus fremontii* and *Salix gooddingii*; Fig. 3A), members of a small-seeded, fast-growing, flood-adapted functional group whose germination requires moist substrate without competing vegetation and whose conservation is considered a regional and global priority (*7*, *15*, *16*). We collected data on germination and establishment of these trees across available habitats and found higher seedling density in equid wells than in adjacent moist riverbank zones (89% of seedlings, Wilcoxon signed rank test: $W = 109$, $p = 0.007$; Fig. 3B), a difference which persisted after typical summer mortalities [generalized linear mixed-effect model: $\chi^2 = 54.6$, $p < 0.0001$; Fig. 3B, data S2, and (*8*)].

Although riverbanks provided the moist substrate necessary for germination, they were

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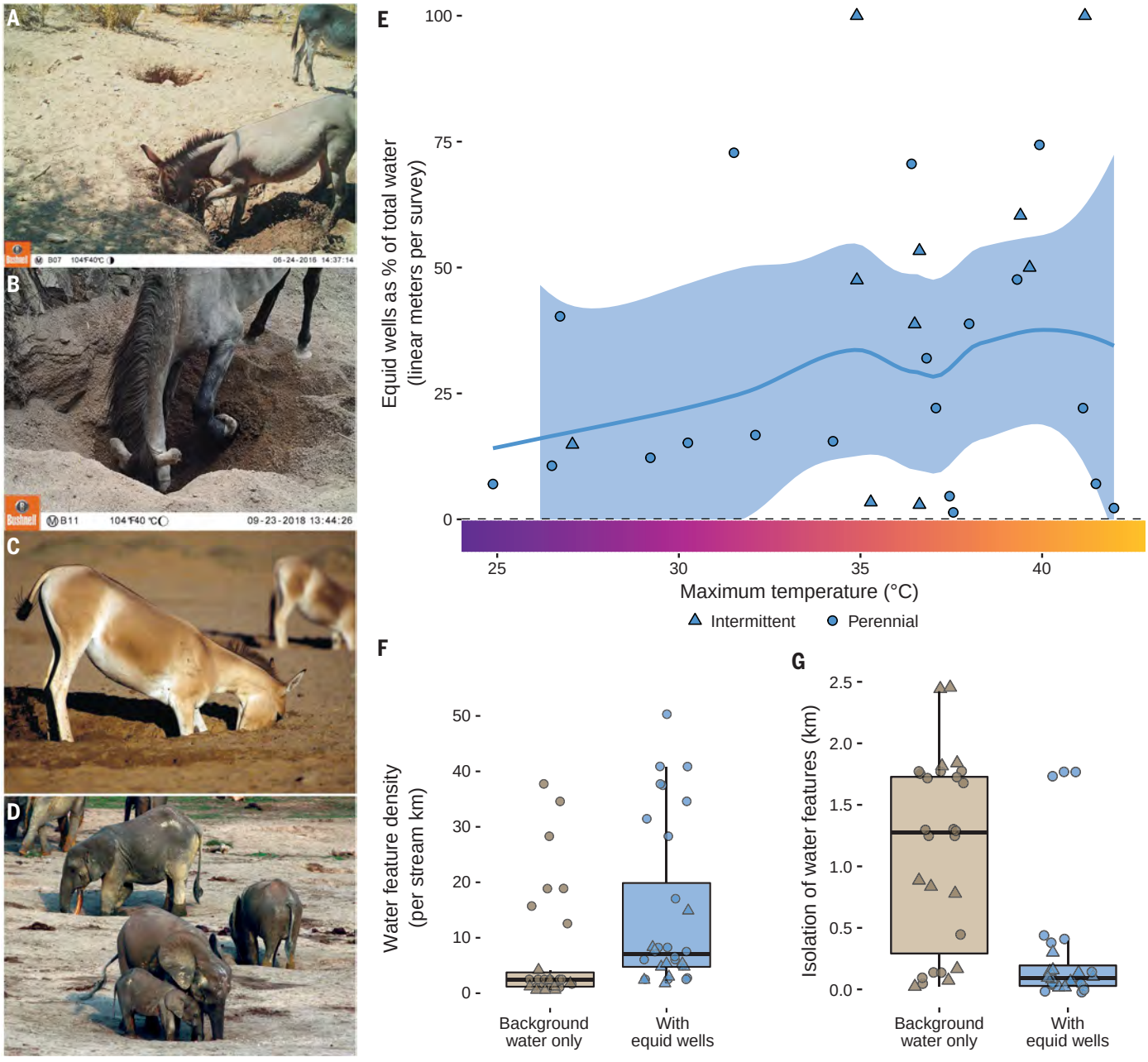


Fig. 1. Well digging increases water availability in desert streams. (**A** to **D**) Well digging by (A) wild donkeys (*E. africanus asinus*) and (B) wild horses (*E. ferus caballus*) in the Sonoran Desert, USA; (C) khulan (*Equus hemionus*) in Mongolia; and (D) African elephants (*Loxodonta africana*). (**E**) The contribution of equid wells increases with temperature. Each point shows the percentage of total water provided by equid wells at each survey and site, measured in meters parallel to the direction of stream flow. Line and fill show loess regression and confidence intervals. Maximum daily temperatures were obtained from PRISM (*23*). (**F**) Equid wells increase the density of water features (per km). (**G**) Equid wells reduce the isolation of water features, measured as average nearest-neighbor distances between waters. For (F) and (G), boxplots indicate median (central line), interquartile range (bottom and top of box), and minimum and maximum values excluding outliers (lines). [Photo credits: E.J.L. [(A) and (B)], P. Kaczensky (C), and R. Ruggiero (D)]

significantly more herbaceous ($p < 0.0001$; fig. S4A), and seedling density showed a strong negative relationship to herbaceous cover ($p < 0.0001$; fig. S4B). This suggests that riverbanks are less competitively suitable for these small-seeded pioneer trees, a relationship shown in previous work (*7*, *16*). Thus, by exposing moist substrate free of competing herbaceous vegetation, we argue that equid wells can serve as flood-mimicking nurseries. The importance of megafauna for the dispersal of large-seeded, high–wood density functional groups is well known (*4*), yet facilitation of pioneer trees through megafauna disturbance is less recognized. Further research is necessary to understand how these nurseries may contribute to long-term riparian forest dynamics.

Equid well digging was limited by water-table depth, with equids unlikely to dig deeper than 2 m (table S1). Well digging was also constrained by substrate, primarily occurring in flood-disturbed systems of loose sand and gravel ($p < 0.0001$; fig. S5). The ecological relevance of this behavior also appears to be shaped by the availability of alternative water sources in the broader landscape and by

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stream intermittency. Intermittent streams, the most common stream type across nearly half of Earth (*17*), were where equid wells had the strongest effects on water availability. Stream intermittency is projected to increase as currently perennial streams lose yearlong flows (*18*) and as drylands expand [Fig. 4 and (*19*)] as result of groundwater mining, agriculture, and climate change (*17*). These reductions in water availability, coupled with rising temperatures, are projected to have strong effects on biodiversity and ecosystem function

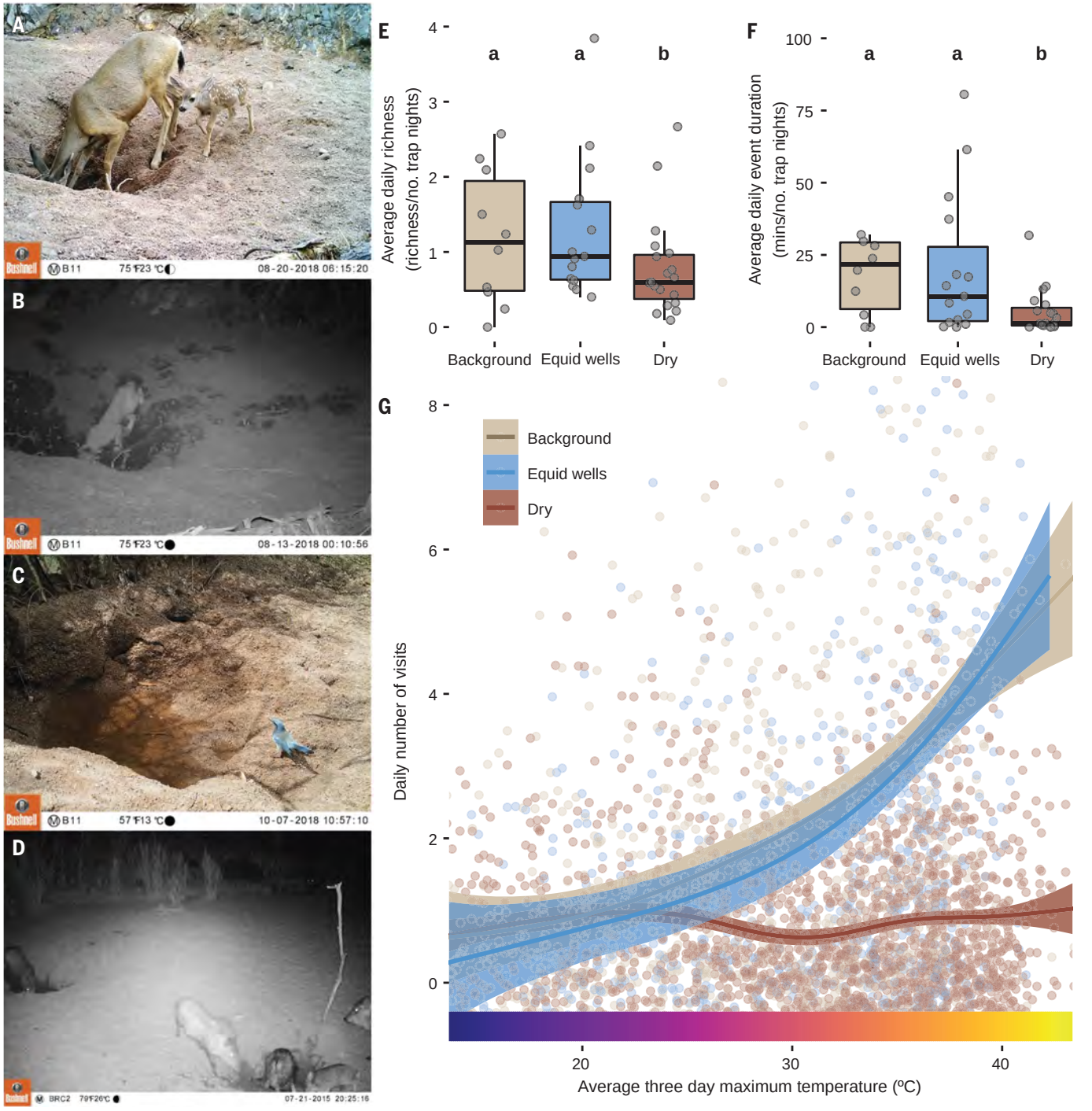


Fig. 2. Use of equid wells by vertebrates. (**A** to **D**) Use of equid wells by select species: (A) mule deer (*O. hemionus*), (B) bobcat (*Lynx rufus*), (C) Woodhouse's scrub-jay (*Aphelocoma woodhouseii*), and (D) javelina (*P. tajacu*). (**E** and **F**) (E) Average daily species richness and (F) daily visit duration, by camera station, relativized by number of trap nights. Letters (a and b) indicate significance groupings ($p < 0.001$). Boxplots indicate median (central line), interquartile range (bottom and top of box), and minimum and maximum values excluding outliers (lines). (**G**) Daily visit frequency by average 3-day maximum temperature (°C). Points indicate days. Line and fill illustrate generalized linear model of relationship between temperature and visit frequency. Equids and vertebrates <100 g (e.g., small passerines and mice) were excluded from analyses, the latter because of poor detection probabilities for small species. Domestic cattle were analyzed separately because of high, but inconsistent, stocking rates throughout the season (fig. S1). [Photo credits: E.J.L. [(A) to (D)]

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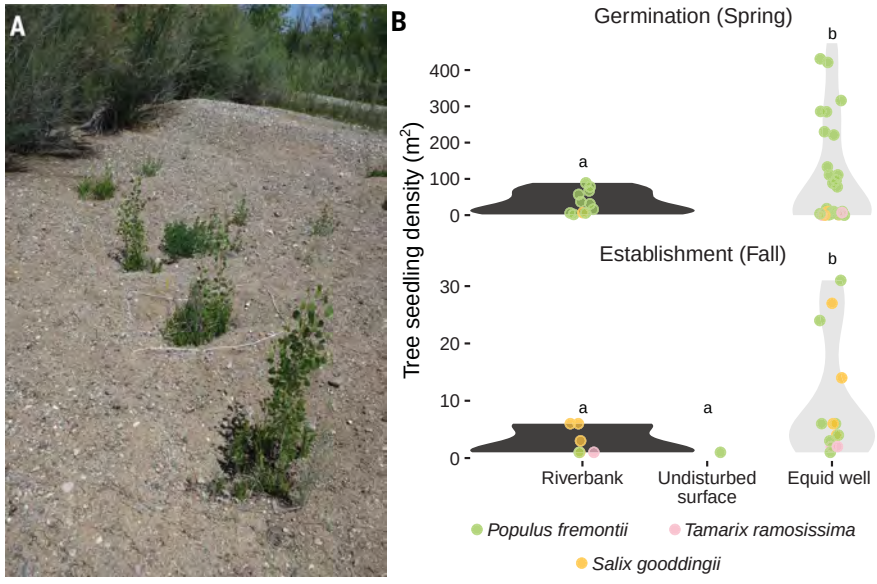


Fig. 3. Equid wells function as germination nurseries for riparian pioneer trees. (**A**) Fremont cottonwood (*P. fremontii*) in a series of abandoned equid wells. (**B**) Seedling density between riverbank germination zones, undisturbed surfaces, and equid wells. Filled intervals behind points indicate density distribution of seedlings. Letters (a and b) indicate significance groupings ($p < 0.01$). [Photo credit: E.J.L.]

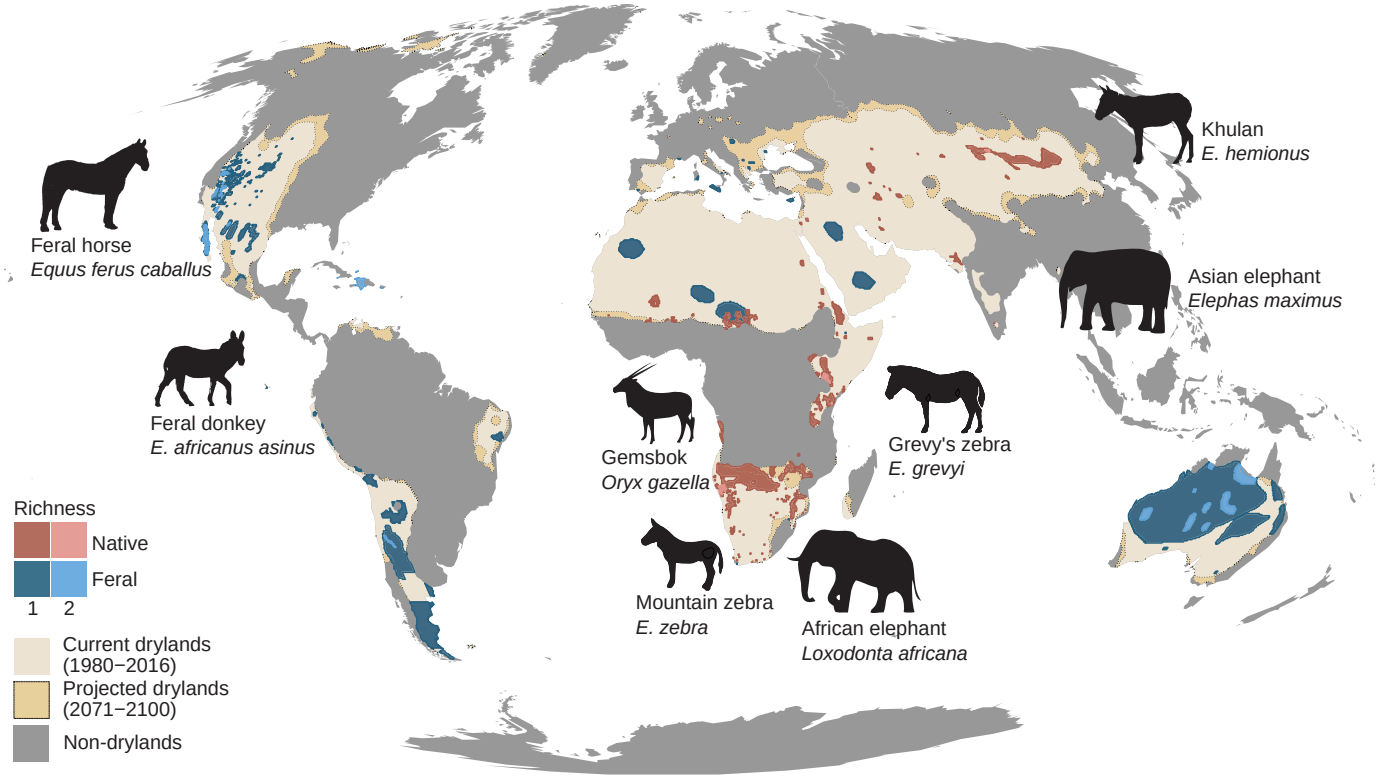


Fig. 4. Well-digging megafauna contribute the capacity to buffer water availability across many drylands. Species richness (number of species) of native and introduced megafauna known to regularly dig wells ≥0.5 m in depth overlaid on current (beige) and projected (yellow ochre) global drylands [semi-arid plus arid Köppen-Geiger climate zones (*19*)]. Gray fill indicates non-drylands. Feral equids (blue) have been documented regularly digging wells in suitable terrain in North America and Australia [table S1; ranges from (*24*, *25*)]. Projected dryland expansion is based on business-as-usual emissions [Representative Concentration Pathway (RCP) 8.5].

(*6*). Our results suggest that equids and other well-digging megafauna have the potential to mitigate these changes, whether native or introduced (Fig. 4).

Recent and ancient extinctions and range contractions of megafauna, and the loss of their distinct ecological functions, has led to highly modified modern landscapes (*4*). Although introduced megafauna have primarily been studied as threats to conservation goals (*20*), growing evidence suggests that they present a countercurrent to ancient losses (*21*) and may replace lost ecological functions (*22*). Specifically, we show that feral equids can increase water availability in drylands, with associated effects on a variety of species and ecosystem processes. We suggest that well digging by feral equids may replace a function lost with the extinctions of large vertebrates across the world's drylands.

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ACKNOWLEDGMENTS

This work is dedicated to the memory of co-author Nathan C. Nieto, a dear friend and mentor. We thank M. Schlaepfer, M. Davis, P. B. Shafroth, D. C. Allen, H. Greene, and five anonymous reviewers for their constructive feedback. We thank M. Lundgren, C. Lundgren, A. Willis, R. O'Leary, C. Alexander, A. Varela, J. Givens, M. Thuan Nhut Cao, M. Riffle, M. Clyne, A. Riley, and E. Anderson for their assistance with fieldwork. **Funding:** This work was supported through crowdfunding and two Arizona State University fieldwork grants. **Author contributions:** All authors conceptualized and designed the research. E.J.L. collected and analyzed the data. All authors contributed to the interpretation of the data and writing of the manuscript. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data and scripts used for analyses are available on Figshare (*8*).

SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S5
Tables S1 to S4
References (*26*–*74*)
Data S1 and S2

5 July 2020; resubmitted 27 October 2020
Accepted 25 March 2021
10.1126/science.abd6775

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Materials and Methods

Well digging by feral equids has been documented in North America and Australia, but has never been formally studied. On the Flinders River in northern Queensland, Australia, wild horses (*Equus ferus caballus*) have been described digging wells deeper than their own height (~2m, *26*). We have also documented well digging by wild donkeys in southern Australia, in the Painted Desert. Well digging has been documented in mesic ecosystems as well, where surface water availability may be limited by edaphic or geologic factors even with abundant precipitation. In particular, wild horses on Sable Island, Novia Scotia, Canada, have been reported digging wells to groundwater on the dry side of the island (*27*).

We conducted our study in the Sonoran and Mojave Deserts, North America, where feral donkeys and one band of feral horses were both observed digging wells. In our study sites, equid wells reached just over one meter in depth, though in one ephemeral, rainwater-fed system wild donkeys were observed digging wells deeper than their own height (~1.5-2 m deep) to water captured in sediment-filled stone basins. Equid wells were common in ephemeral rainwater-fed desert drainages and stone water catchments, and in groundwater-fed systems, including in the channels of intermittent streams and on the floodplains of perennial rivers, where they created water access points outside the density of streamside vegetation. Equid wells generally occurred in clusters of 3-30 wells, in open, unvegetated areas up to 3 km^2, and were observed year-round.

Effect of well digging on water availability

We selected four groundwater-fed streams to survey the effect of well digging on water availability. All sites were in separate drainages, 7-32 km apart (average 14.7 km), and 1-8 km (average 3 km) from other unmonitored streams. Sites were 0.3-1.8 km long (average 1 km) (see Table S2 for site descriptions, Fig. S5). All four sites had the potential to become intermittent (e.g. losing surface water as the water table becomes subsurface), however, like many dryland groundwater-fed springs, flow variability led to three of the four sites retaining perennial headwater springs during the survey periods. All sites had extensive downstream intermittent reaches, containing surface water only seasonally.

The full length of each site was surveyed every 2-4 weeks during the summers of 2015, 2016 and 2018 (Table S2). We followed water mapping protocols of The Nature Conservancy (*28*). This consisted of georeferencing and measuring the length each water feature parallel to the direction of stream flow. From this, we were able to calculate the total linear meters and spatial distribution of ‘background’ (e.g. already present without well digging) and ‘equid well’ water features (Data S1).

The spatial pattern and density of distinct water features affects the distances animals must travel to drink, and the types and intensity of interactions that occur (e.g. *11, 29, 30*). We therefore calculated how equid wells increased the density of water features (per survey km) and the isolation of water features using the R package ‘sf’ (v0.8-0). Isolation was calculated by averaging nearest neighbor distances (i.e. the distance of each water feature to only its nearest neighbor) with equid wells included and excluded. To avoid inflating isolation metrics we only included features >10 m apart from any other (thus only counting equid wells if >10 m from background water, and counting equid wells <10 m apart as a single feature). Metrics were calculated using the R package ‘geosphere’ v1.5-10. Since these metrics could not be calculated on surveys where background water was absent, the nearest two perennial water sources to each site, outside the survey area, were included in each calculation.

Equid wells as vertebrate resource points

To understand the value of equid wells to other vertebrate species we installed camera traps (Bushnell Trail Cam Pro) >100 m apart, at the same four Sonoran Desert water availability survey sites, and at an additional site in the Mojave Desert (Mojave National Preserve, permit MOJA-2018-SCI-0050, Table S2). At each site we monitored three resource types: equid wells, background waters, and dry controls. Dry controls were established randomly in similar vegetation, at least 100 m away from any water source. Overall, trail cameras recorded 446,817 images of vertebrate species, sampling a total of 957 trap nights at background water sources, 686 at equid wells, and 1,749 at dry controls (Data S2).

We visually identified all vertebrates to the best of our ability, using field guides as necessary (*31, 32*). Five taxa could only be identified to genus and one only to family. We excluded species <100 g from statistical analyses, due to inconsistent detection probabilities and because of uncertainty identifying mice and small passerines during low light conditions in camera trap images. We excluded wild equids as we were interested in the utilization of equid wells by other species. Cattle were analyzed separately because high but variable stocking rates would influence patterns of resource use across the study period.

We classified images into 'visits' based on contiguous activity by the same species, with no more than a fifteen-minute interval between images. We then quantified vertebrate activity patterns in terms of daily visit frequency, total daily visit duration, and daily species richness (number of unique species per day). Given that the importance of surface water is shaped by precipitation and temperature, we collected an ensemble of climate variables from PRISM, an interpolated 4 x 4 km climate dataset for North America (*23*). Variables included daily maximum temperature, daily mean temperature, and daily precipitation. Since organismal responses to temperature and precipitation often exhibit lag periods (e.g. responding to conditions over prior days) (*33*) we derived eight lag variables: days since any precipitation ≥1 mm; days since precipitation ≥1 cm, total cumulative precipitation over the prior 3, 7, and 14 days; and average maximum temperature over the prior 3, 7, and 14 days.

We then used generalized linear mixed effect models in the R package 'glmmTMB' v1.0.1 to analyze how resource types (i.e. equid wells, background waters, and dry controls) and environmental variables influenced vertebrate activity. We chose distributions appropriate for each response variable and nested date within site as a random effect. We employed multi-model inference techniques to eliminate spurious and correlated environmental variables (*34*). Across all analyses, omnibus tests were conducted with the 'Anova' function in R package 'car' v3.0-8 (*35*), while post-hoc tests were conducted using the 'emmeans' package v1.4.7 (*36*).

To understand if resource use patterns differed by vertebrate body size, we compared the same response variables (daily richness, duration, and event frequency) by three body size classes, consisting of <1 kg, 1 kg – 10 kg, and ≥10 kg. Furthermore, we conducted a PERMANOVA on a Bray-Curtis dissimilarity matrix to test if species composition was significantly different between resource types. We visualized the dissimilarity in species composition between camera stations with a Principal Coordinates Analysis (PCoA). The PERMANOVA was conducted in the R package 'vegan' v2.5-6 (*37*) while the PCoA was performed in the R package 'ape' v5.4 (*38*).

Equid wells as vegetation nurseries

The recruitment of riparian trees in abandoned equid wells was observed on the Bill Williams River in the Sonoran Desert of Arizona. Unlike the partially or fully intermittent study sites

above, the Bill Williams River is a dammed perennial desert river characterized by a stable, flow regulated water table, multiple channels and extensive beaver ponds. Riverbanks are densely vegetated with cattails (*Typha* spp.) and other herbaceous plants.

Fremont cottonwood and Goodding's willow (*Salix gooddingii*) are important riparian, groundwater-dependent plants of the Bill Williams River and many other dryland rivers. These trees possess adaptations reflective of many global ecologically important, early succession riparian tree species (henceforth 'pioneer' trees) including copious production of small seeds released in concurrence with seasonal flood events and low wood density and thus fast growth rates (*39-41*). These traits are adapted for scouring floods which remove competing vegetation and deposit germination beds of bare moist mineral substrate (*16*). In the absence of floods, germination is limited to the moist soil of riverbanks: zones densely vegetated with herbaceous plants in the absence of flood disturbance. As the Bill Williams River is a dammed system, it receives managed floods released to stimulate the germination of cottonwoods and willows if there is sufficient water in the upstream reservoir. At the time of the study, the last flood pulse had been released the year prior (2014) (gage #09426000, *42*).

Based on observations of cottonwood recruitment in abandoned equid wells, we investigated whether these features provided a substitute for flood disturbance by creating access to bare moist mineral substrate and removing competing vegetation. We randomly selected five well clusters for spring germination surveys and follow-up fall establishment surveys. At each cluster, 10-15 $1m^2$ plots were randomly distributed among 3 potential germination zones: abandoned equid wells, undisturbed surfaces, and the nearest riverbank. Riverbank zones and undisturbed surfaces differ in their combinations of key variables important to pioneer tree germination and establishment. Riverbank zones have moist substrate but are densely vegetated, while undisturbed surfaces lack herbaceous vegetation but are dry. Undisturbed surfaces were not sampled during the spring germination survey, as they lacked seedlings, but were added in the fall establishment survey. Riverbank zone plots were 10-50 m from well clusters while undisturbed surface plots were placed randomly on the same geomorphic surface (e.g. sandbar) as the equid well cluster. All woody seedlings were counted and the percent cover of each herbaceous plant species was recorded (Data S2).

We compared spring germination rates between riverbank (n=24) and equid well (n=24) plots with non-parametric, paired Wilcoxon signed rank tests. To analyze fall survivorship data, we used zero-inflated Poisson mixed effect models, with site as a random effect. To understand the relationship between herbaceous cover and habitat type and between woody seedlings and herbaceous cover, we used zero-inflated mixed effect models with season nested within site as a random effect, modelled with a Gamma distribution. All analyses were conducted in R with the package 'glmmTMB' v1.0.1 (*43*). Omnibus tests were performed by the 'Anova' function in the 'car' package (*35*) while post-hoc tests were conducted with the package 'emmeans' v1.4.7 (*36*).

Constraints on equid well digging

We surveyed for equid wells in the Southwestern USA and in Northwestern Mexico from 2015-19 by searching Google Earth for riparian vegetation, which is indicative of a water table within 1.5-2 m of surface (*44*). To understand the constraints of well digging, we classified riparian systems based on substrate and general topographic position: (1) steep, mountainous cobble-dominated systems; (2) flood-prone systems with loose unconsolidated gravel and sand substrates; (3) silt and clay dominated systems; and (4) systems with compacted, mixed soil types with low flood disturbance (as indicated by lack of debris-wrecks and high organic matter

in soils). We then conducted a mixed effect logistic regression using the R package ‘lme4’ v1.1-23, to understand how substrate type influenced the probability of well digging.

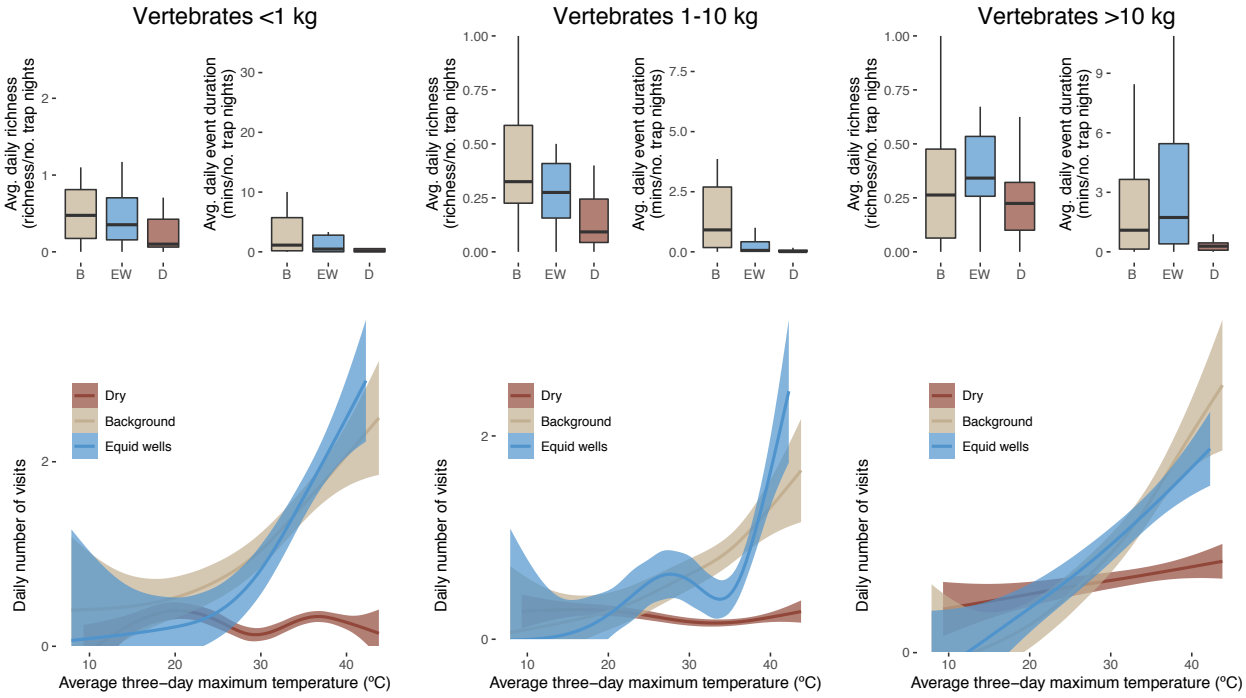


Fig. S1.

Patterns of resource use were similar across vertebrate body size classes. Vertebrates <100 g were excluded from the smallest body size class. B=background water, EW=equid well water, D=dry controls.

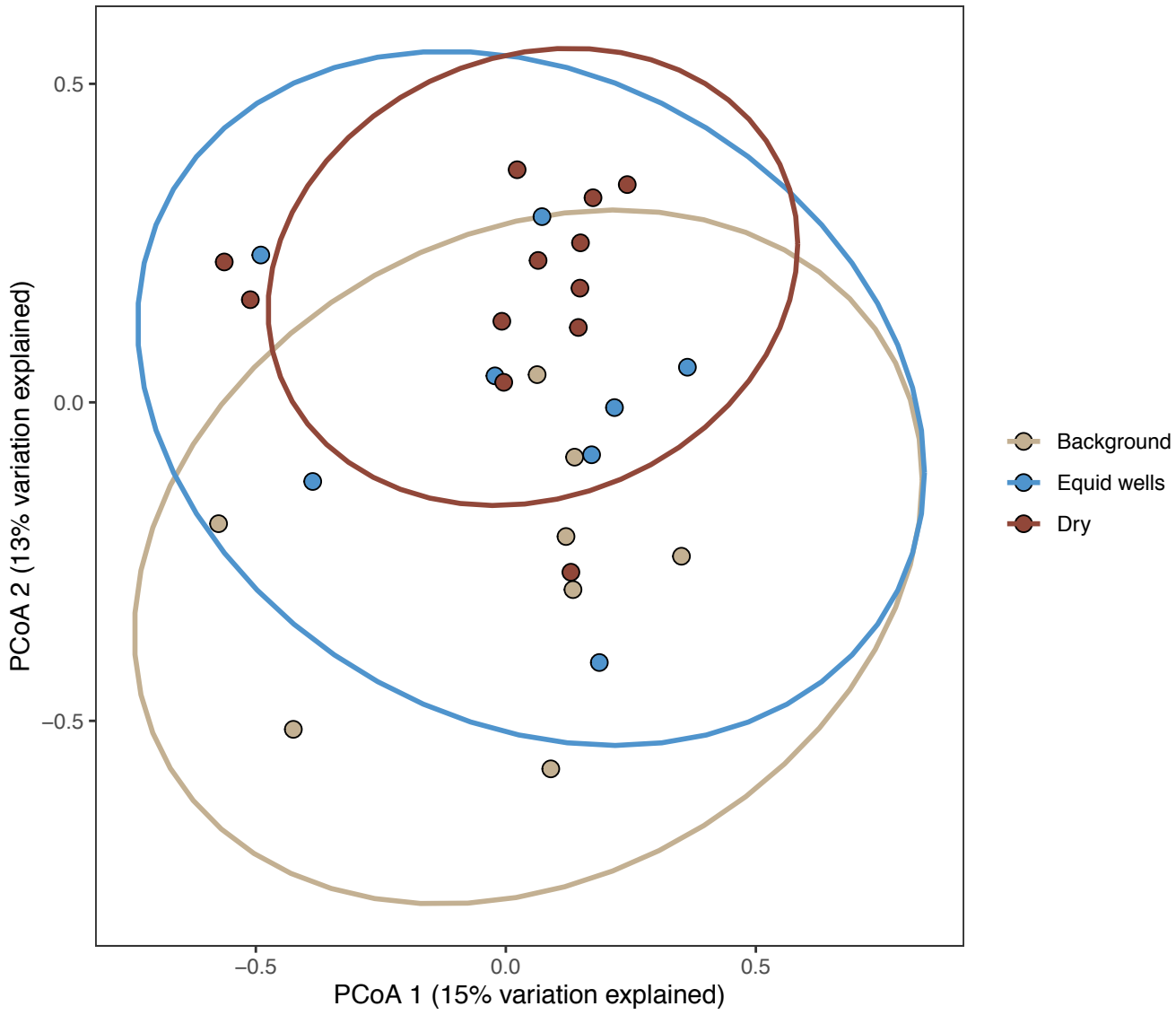


Fig. S2.

First two axes of a Principal Coordinates Analysis (PCoA) describing differences in species composition between camera stations. Points are individual camera stations, colored by resource type. There was no significant difference in species composition based on water type (PERMANOVA: F=0.9, p=0.7).

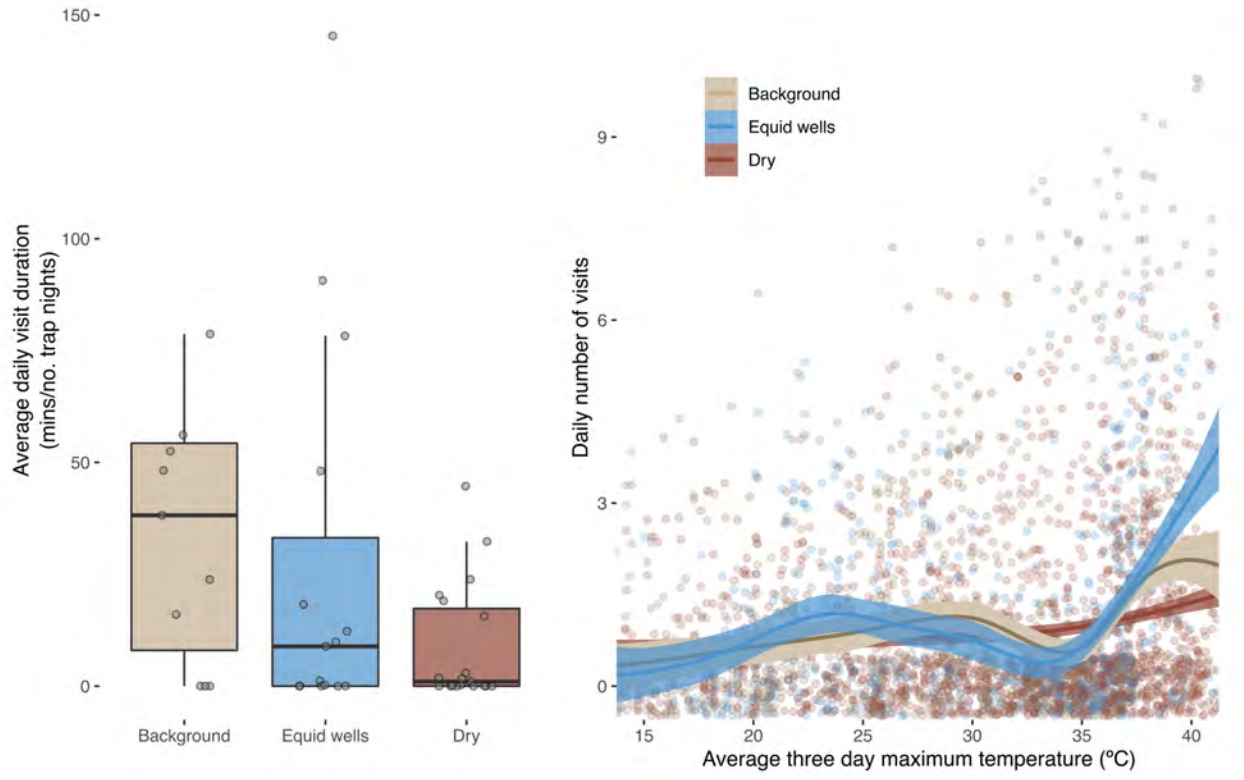


Fig. S3.

The response of domestic cattle to background waters, equid wells, and dry controls. Cattle stocking densities were variable during the season, reflecting local husbandry practices.

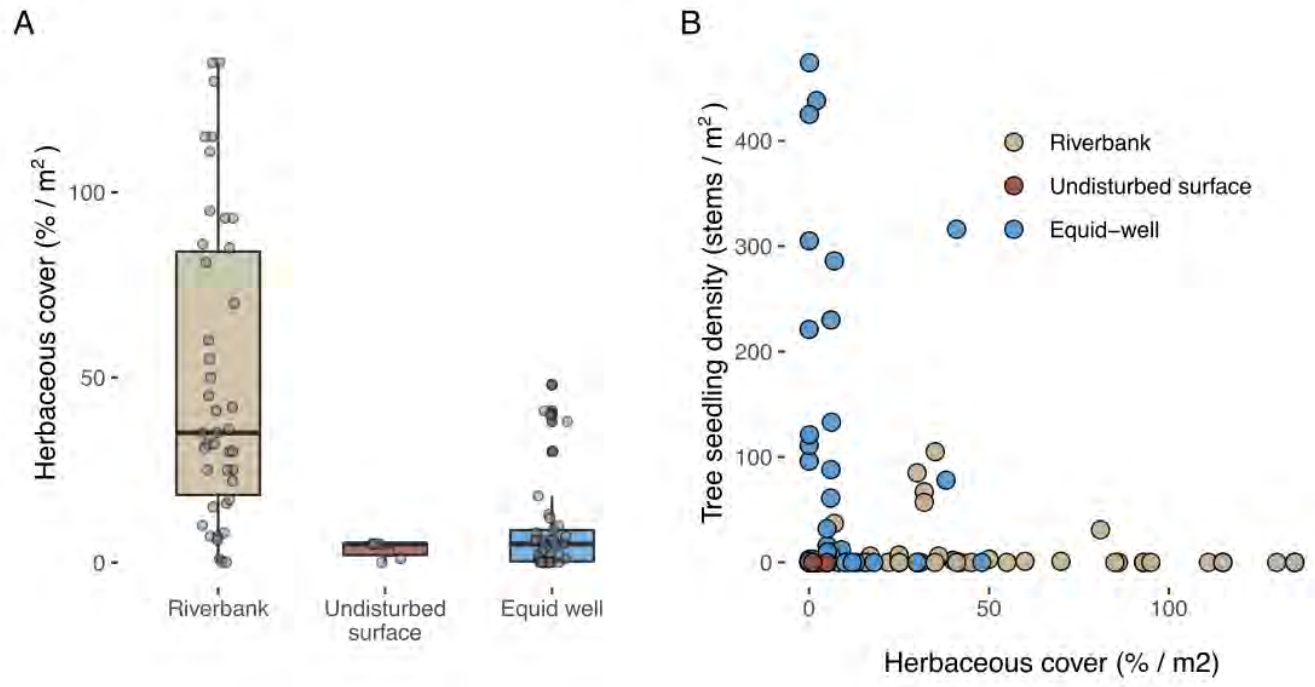


Fig. S4.

Relationship of herbaceous cover to germination zones and tree germination. **A**. Herbaceous cover was significantly higher on moist riverbank zones than on undisturbed surfaces or equid wells (zero-inflated mixed effect model: $\chi^2 = 14.1$, $p < 0.0009$, post-hoc $p < 0.0042$) and was not significantly influenced by season (e.g., spring or fall, $\chi^2 = 0.08$, $p = 0.8$). **B**. A strong negative relationship existed between tree germination and establishment and herbaceous cover (zero-inflated negative binomial mixed effect model: $\chi^2 = 16.9$, $p < 0.0001$).

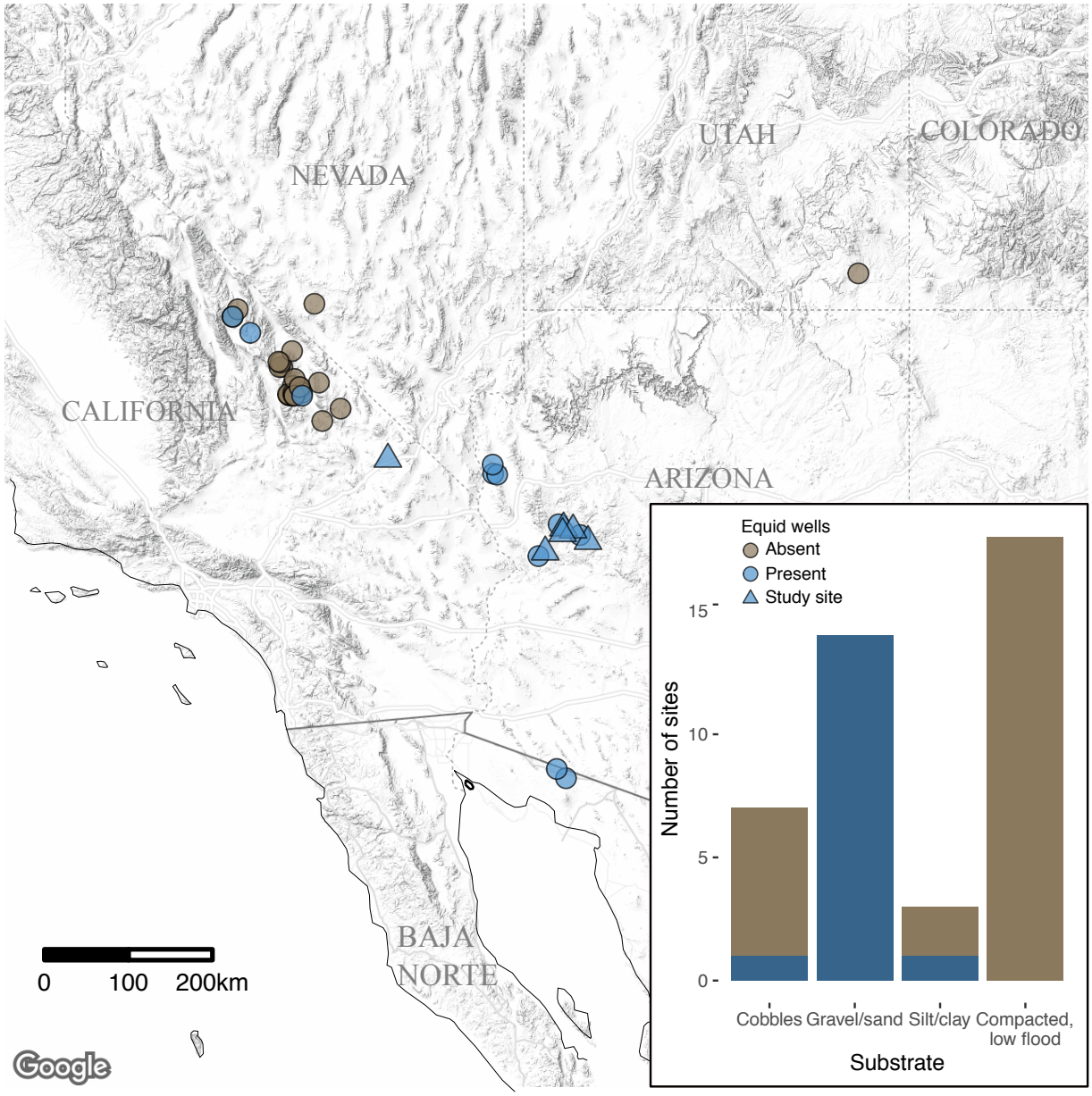


Fig. S5.

Distribution of equid well digging locations across the Southwestern United States and Northern Mexico (this study). Color indicates the presence or absence of wells. Triangles indicate study sites. The absence of wells at certain sites is explained by substrate (logistic regression: χ^2=27.7, p<.00001), indicated in the inset. Equid wells were largely absent in systems with coarse cobble substrates over bedrock and in low-flood systems with compacted substrates of mixed materials. Equid wells were likewise absent from all but one silt and clay dominated system, such as found in the beds of ephemeral lakes.

Table S1.

Species known to dig wells to groundwater, with sources, depth, and notes. As a largely overlooked behavior, we here review all current published knowledge about well digging among extant vertebrates. Well digging, particularly to depths significant for maintaining water availability in drylands, appears to primarily be a megafauna function. Smaller bodied animals, also listed below, appear to dig less regularly and to shallower depths, thus limiting their ability to maintain access to subsurface water.

Species	**Source**	**Depth**	**Description**
African elephant (*Loxodonta africana)*	Payne 1999 (*45*); Haynes 2012 (*46*); Ramey et al. 2013 (*47*)	1.5 m. Maximum depth unknown	African elephants dig large clusters of wells, of 0.5-1.5 m in depth, but are likely capable of digging deeper. Forest elephant wells sustained water presence during the summer dry season and were used by numerous animals (*45*). Elephant-well water has reduced bacterial loads, suggesting a reason for digging even when background water is present (*47*).
Asian elephant (*Elephas maximus*)	Joshi 2009 (*48*)	Unknown	Joshi 2009 (*48*) reported well digging by Asian elephants during the dry season. These elephant wells were reported in use by spotted deer (*Axis axis*), sambar (*Rusa unicolor*), mongoose (species unreported), Bengal foxes (*Vulpes bengalensis*), jackals (*Canis aureus*), boar (*Sus scrofa*), and various birds.
Feral horse (*Equus ferus caballus*)	This study; Rolls 1969 (*26*); Rozen-Rechels 2015 (*27*)	Observed (this study) up to 1.5 m. Reported up to ~2 m (*26*)	In the Flinders River in northern Queensland, Australia, wild horses have been reported digging wells deeper than their own height (~2 m, Rolls 1969). On Sable Island, Canada, wild horses create the only sources of surface water on one half of the island (*27*).
Feral donkey (*Equus africanus asinus*)	This study; McKnight 1958 (*49*)	Observed up to 1.2 m (this study). Reported up to ~1.5-2 m	McKnight 1958 (*49*) mentions wild donkeys digging ≥5 feet (~1.5 m) to groundwater in North America, location undisclosed. We have also documented well digging by wild donkeys in ephemeral washes in the Painted Desert of Southern Australia.
Khulan (*Equus hemionus kulan*)	Feh et al. 2002 (*50*); Payne et al. 2020 (*51*)	0.5 m, maximum depth unknown	Khulan regularly dig wells, generally ~0.5 m in depth, though likely capable of reaching similar maximum depths as donkeys and horses. Khulan wells are used by domestic and wild animals, including the endangered Gobi Desert Grizzly Bear (*Ursus arctos gobiensis*) (*52*) and argali (*Ovis ammon*) (*53*).
Grévy's zebra (*Equus grevyii*)	Klingel 1974 (*54*)	0.5 m, maximum depth unknown.	Grévy's zebras regularly dig wells in dry sandy streambeds during the dry season, which have been documented in use by Grant's Gazelles (*Nanger granti*),

			giraffes (*Giraffa campelopardalis*), and elephants (*Loxodonta africana*) (*54*).
Mountain zebra (*Equus zebra*)	Klingel 1968 (*55*)	0.5 m, maximum depth unknown.	Klingel 1968 (*55*) reported on mountain zebras digging wells of 0.5 m in depth, which were subsequently utilized by giraffes (*Giraffa campelopardalis*), kudus (Tragelaphus strepsiceros), gemsbok (*Oryx* gazella), hyena (*Crocuta* crocuta), elephants (*Loxodonta africana*), springbok (*Antidorcas marsupialis*), plains zebra (*Equus quagga*), lions (*Panthera leo*), and cheetahs (*Acinonyx jubatus*).
Gemsbok (*Oryx gazella*) & chacma baboons (*Papio ursinus*)	Hamilton et al. 1977 (*56*)	~ 1 m	Gemsbok and chacma baboons were described regularly digging wells in the Namib Desert. Wells reached just over a meter in depth in the peak of the dry season. It appears that gemsbok initiated well digging, digging to 0.5 m in depth. While inefficient at digging through dry sand, baboons would then deepen the gemsbok-dug wells once they had hit wet sand (*56*).
Coyote (*Canis latrans*)	This study	~0.20 m	We observed a single shallow, 20 cm deep well in thick drying clay in the Sonoran Desert, USA. Not observed elsewhere. The coyote origin was verified with trail cameras.
Common wombat (*Vombatus ursinus*)	Millington 2020 (*57*)	2-4 m	In what appears to be a single case, a pair of wombats dug a 2-4 m deep well, which was used by other species during severe drought. This well was morphologically distinct from a burrow, as it descended vertically and was located at the base of a large gradual depression, described as a 'crater'. This behavior has not been observed elsewhere. Given widespread range contractions among wombats, particularly for dryland-inhabiting wombat species, wombat wells may have once been common on the landscape (*25*).
Agile wallaby (*Macropus agilis*)	Doody et al. 2007 (*58*)	0.15 m	Agile wallabies dig clusters of 1-7 15 cm deep drinking 'holes.' Doody et al. 2007 (*58*) indicates that these holes were likely dug to avoid crocodile predation at the riverbank.
Common wallaroo (*Osphranter robustus*)	Wilson and Mittermeier 2015 (*59*)	Unknown, published image suggests ~0.2 m	Common wallaroos are reported digging wells in dry creek beds, despite the fact that they are mostly free-water independent, irregularly drinking water even when temperatures >43ºC. Photograph in Wilson and Mittermeier

			(2015) appears to be ~0.2 m in depth (*59*).

Table S2.

Site and survey details for sites where water availability and camera trap analyses were conducted. Cane Springs was not surveyed for water availability and thus possesses NA values for survey length, distance to nearest water, and number of water availability surveys.

Lat	Long	Site, Desert, (elev. m)	Stream length (m)	Distance to nearest external water (m)	Number of water availability surveys (years)	Number of camera trap nights (years)
-113.3857	34.46983	Black Canyon, Sonoran Desert (813)	1,817	8,308	8 (2)	386 (2)
-113.5269	34.43563	Cattail Spring, Sonoran Desert (784)	318	1,904	7 (1)	1,234 (1)
-113.5151	34.49495	Greenwood Spring, Sonoran Desert (894)	400	1,368	7 (2)	1,021 (2)
-113.2009	34.35265	Hackberry Wash, Sonoran Desert (540)	1,680	1,628	10 (2)	482 (2)
-115.7977	35.23301	Cane Springs, Sonoran Desert (983)	NA	NA	NA	545 (1)

Table S3.

Vertebrate species documented during trail camera monitoring. * denotes species definitively recorded drinking from equid wells. Column 'H_2O' indicates species known to be free-water independent ('I') or dependent ('D'), with reference. Species that are mostly free-water independent, but require it during periods of their life history (e.g. lactating), during extreme heat, or in the absence of succulent forage, are denoted with 'I/D'. Given that most species have not been studied, presumed water-independent arid-adapted species, frequently observed in regions without surface water, are marked with 'PI' (presumed independent). Species that have been observed drinking regularly and are associated with more mesic habitats are marked as 'PD' (presumed dependent). The number of recorded visits are listed by resource type ('Dry', 'Equid-wells', 'Background'). Only species ≥100 g were included in statistical analyses to control for bias in detection probability.

Species	Common name	Class	Order	Mass (g)	H_2O	Dry	Equid-wells	Background
Accipiter cooperii *	Cooper's Hawk	Aves	Accipitriformes	526.64	PD	0	1	19
Ammospermophilus harrisii *	Ground Squirrel	Mammalia	Rodentia	126	I (*60*)	38	89	54
Amphispiza bilineata *	Black-throated Sparrow	Aves	Passeriformes	13.5	I/D (*61*)	1	9	60
Aphelocoma woodhouseii *	Woodhouse's Scrub-Jay	Aves	Passeriformes	90	PD	4	74	34
Artemisiospiza nevadensis	Sagebrush Sparrow	Aves	Passeriformes	18.5	D (*62*)	0	0	7
Baeolophus ridgwayi *	Juniper Titmouse	Aves	Passeriformes	16	PD	0	1	0
Bassariscus astutus *	Ringtail	Mammalia	Carnivora	1015	I (*63*)	2	3	3
Bos taurus *	Cattle	Mammalia	Cetartiodactyla	750000	D (*64*)	1976	905	1191
Bubo virginianus *	Great-horned Owl	Aves	Strigiformes	1191.2	PD	0	10	27
Buteo albonotatus	Zone-tailed Hawk	Aves	Accipitriformes	822.5	PD	0	0	18
Buteo jamaicensis *	Red-tailed Hawk	Aves	Accipitriformes	1362	PD	2	4	22
Callipepla gambelii *	Gambel's Quail	Aves	Galliformes	166	I/D (*65*)	213	268	326
Campylorhynchus brunneicapillus	Cactus Wren	Aves	Passeriformes	38.9	PI	1	0	2
Canis latrans *	Coyote	Mammalia	Carnivora	13250	I/D (*63*)	181	99	39
Caprimulgidae spp *	Nightjar Spp.	Aves	Caprimulgiformes	63	PI	5	29	26
Cardellina pusilla	Wilson's Warbler	Aves	Passeriformes	7	D (*66*)	0	0	3
Cardinalis cardinalis	Northern Cardinal	Aves	Passeriformes	42.6	PD	1	1	4
Cathartes aura *	Turkey Vulture	Aves	Cathartiformes	2200	PI	0	3	53
Catharus guttatus *	Hermit Thrush	Aves	Passeriformes	27.8	PD	0	2	12
Chamaea fasciata	Wrentit	Aves	Passeriformes	14.7	PI/D	0	0	1
Colaptes auratus	Northern Flicker	Aves	Piciformes	120	PD	0	2	0
Colaptes chrysoides *	Gilded Flicker	Aves	Piciformes	110.5	PI (*67*)	2	6	8
Corvus corax *	Common Raven	Aves	Passeriformes	1041.2	PI	4	116	304
Crotalus atrox	Western Diamond-backed Rattlesnake	Reptilia	Squamata	1965	D (*68*)	0	0	6
Dipodomys spp *	Kangaroo Rat	Mammalia	Rodentia	120	I (*69*)	2	1	2
Dryobates scalaris	Ladder-backed Woodpecker	Aves	Piciformes	34.5	PI (*67*)	5	0	1
Empidonax spp	Empidonax Flycatcher	Aves	Passeriformes	13.5	PD	0	0	2
Equus asinus *	Donkey	Mammalia	Perissodactyla	164998	D (*64*)	1104	969	956

Equus caballus *	Horse	Mammalia	Perissodactyla	3.00E+05	D (*64*)	527	220	358
Erethizon dorsatum	North American Porcupine	Mammalia	Rodentia	10750	PD	0	0	1
Geococcyx californianus *	Greater Roadrunner	Aves	Cuculiformes	376	PI	7	8	8
Geothlypis tolmiei	MacGillivray's Warbler	Aves	Passeriformes	10.4	PD	0	0	8
Geothlypis trichas	Common Yellowthroat	Aves	Passeriformes	9.5	PD	0	0	4
Haemorhous mexicanus *	House Finch	Aves	Passeriformes	21.4	D (*66*)	6	95	77
Icterus cucullatus *	Hooded Oriole	Aves	Passeriformes	24.3	PD	2	16	11
Icterus parisorum *	Scott's Oriole	Aves	Passeriformes	36.2	PI/D	0	10	4
Incilius alvarius *	Colorado River Toad	Amphibia	Anura	130	D (*70*)	4	93	7
Junco hyemalis	Dark-eyed Junco	Aves	Passeriformes	19	PD	0	0	20
Lanius ludovicianus	Loggerhead Shrike	Aves	Passeriformes	46	PI	0	0	2
Leiothlypis celata *	Orange-crowned Warbler	Aves	Passeriformes	9	PD	0	1	0
Lepus californicus	Black-tailed Jackrabbit	Mammalia	Lagomorpha	4175	I/D (*71*)	70	19	4
Lynx rufus *	Bobcat	Mammalia	Carnivora	8600	PD	21	28	26
Megascops kennicottii	Western Screech-Owl	Aves	Strigiformes	205	PD (*67*)	1	45	34
Melanerpes uropygialis *	Gila Woodpecker	Aves	Piciformes	65	I/D (*67*)	3	71	54
Melospiza lincolnii	Lincoln's Sparrow	Aves	Passeriformes	17.35	PD	0	0	4
Melospiza melodia	Song Sparrow	Aves	Passeriformes	22.7	PD	0	0	28
Melozone aberti	Abert's Towhee	Aves	Passeriformes	48.7	PD	0	3	8
Melozone fusca	Canyon Towhee	Aves	Passeriformes	44.4	PD	1	1	2
Mephitis mephitis *	Striped Skunk	Mammalia	Carnivora	3500	D (*72*)	18	6	2
Micrathene whitneyi *	Elf Owl	Aves	Strigiformes	41	PI (*67*)	1	6	1
Mimus polyglottos	Northern Mockingbird	Aves	Passeriformes	53	I/D (*67*)	1	2	104
Myadestes townsendi *	Townsend's Solitaire	Aves	Passeriformes	32.5	PD	0	7	13
Myiarchus spp *	Myiarchus Flycatcher	Aves	Passeriformes	29.5	PI/D	2	9	29
Neotoma spp *	Woodrat	Mammalia	Rodentia	236	I (*73*)	14	2	163
Odocoileus hemionus *	Mule Deer	Mammalia	Cetartiodactyla	57000	D (*65*)	268	136	267
Otospermophilus variegatus *	Rock Squirrel	Mammalia	Rodentia	663	PD	5	36	50
Ovis canadensis *	Bighorn Sheep	Mammalia	Cetartiodactyla	70275	I/D (*65*)	3	3	39
Pecari tajacu *	Javelina	Mammalia	Cetartiodactyla	20200	I/D (*74*)	155	137	100
Peromyscus spp *	Deer mouse	Mammalia	Rodentia	20.5	I (*60*)	0	1	79
Phainopepla nitens *	Phainopepla	Aves	Passeriformes	28	I/D (*67*)	1	1	1
Pheucticus melanocephalus *	Black-headed Grosbeak	Aves	Passeriformes	42	PD	0	4	1
Pipilo maculatus	Spotted Towhee	Aves	Passeriformes	40.4	PD	0	0	17
Piranga ludoviciana	Western Tanager	Aves	Passeriformes	30	PD	0	0	3
Pituophis catenifer	Gopher Snake	Reptilia	Squamata	1360.5	PI/D	0	0	1
Procyon lotor *	Northern Raccoon	Mammalia	Carnivora	6000	PD	2	1	0
Puma concolor *	Mountain Lion	Mammalia	Carnivora	63000	PI/D	37	9	37

Regulus calendula	Ruby-crowned Kinglet	Aves	Passeriformes	6.75	PD	1	2	16
Salpinctes obsoletus	Rock Wren	Aves	Passeriformes	16.5	I/D (*61*)	0	0	11
Sayornis saya	Say's Phoebe	Aves	Passeriformes	21.8	PD	2	0	2
Setophaga coronata	Yellow-rumped Warbler	Aves	Passeriformes	12	PD	0	1	9
Sialia mexicana	Western Bluebird	Aves	Passeriformes	26.5	PD	0	0	1
Sphyrapicus nuchalis	Red-naped Sapsucker	Aves	Piciformes	48.5	PD	0	0	1
Spilogale gracilis *	Spotted Skunk	Mammalia	Carnivora	600	PD	4	5	4
Spinus psaltria	Lesser Goldfinch	Aves	Passeriformes	9.23	D (*67*)	0	0	10
Sylvilagus audubonii *	Cottontail Rabbit	Mammalia	Lagomorpha	900	PD	122	31	9
Taxidea taxus *	American Badger	Mammalia	Carnivora	8000	PI/D	3	13	3
Toxostoma crissale	Crissal Thrasher	Aves	Passeriformes	62.7	PI	2	0	0
Toxostoma curvirostre *	Curve-billed Thrasher	Aves	Passeriformes	80.65	PI/D	10	19	14
Turdus migratorius	American Robin	Aves	Passeriformes	75.5	PD	0	0	7
Tyto alba	Barn Owl	Aves	Strigiformes	580	PI	0	0	1
Urocyon cinereoargenteus *	Gray Fox	Mammalia	Carnivora	4750	PD	227	186	191
Ursus americanus *	Black Bear	Mammalia	Carnivora	154250	PD	0	1	0
Zenaida asiatica *	White-winged Dove	Aves	Columbiformes	140	D (*65*)	19	127	133
Zenaida macroura *	Mourning Dove	Aves	Columbiformes	119	D (*65*)	18	65	205
Zonotrichia leucophrys *	White-crowned Sparrow	Aves	Passeriformes	25.82	PD	2	3	24

Table S4.

Vertebrate use of water sources model results. The relationship between daily vertebrate activity patterns (measured as visit frequency and visit duration) and daily richness at equid wells, background waters and dry controls and as influenced by temperature and precipitation. Day was nested within site as a random effect. All analyses were conducted in R with the package 'glmmTMB' version 1.0.1 7 (*43*). Omnibus test results were calculated using the function 'Anova' in the 'car' library (*35*).

Response variable	**Final included variables**	**Test results**
Equids and cattle excluded, including only species ≥250 g.		
Visit frequency (*zero-inflated negative binomial distribution*)	Resource type	χ^2=411.5, p < 0.0001
	Avg. three-day maximum temperature	χ^2 =114.1, p < 0.0001
	Cumulative three-day precipitation	χ^2 = 0.06, p = 0.80
	Resource type * Avg. three-day maximum temperature	χ^2 = 98.5, p < 0.0001
	Resource type * Cumulative three-day precipitation	χ^2 = 3.1, p = 0.21
Species richness (*zero-inflated Poisson distribution*)	Resource type	χ^2 = 153.4, p < 0.0001
	Max daily temperature	χ^2 = 62.1, p < 0.0001
	Cumulative three-day precipitation	χ^2 = 0.13, p = 0.71
	Resource type * Max daily temperature	χ^2 = 40.9, p < 0.0001
	Resource type * Cumulative three-day precipitation	χ^2 = 2.7, p = 0.25
Visit duration (*zero-inflated negative binomial distribution*)	Resource type	χ^2 = 310.6, p < 0.0001
	Avg. three-day maximum temperature	χ^2 = 92.5, p < 0.0001
	Cumulative three-day precipitation	χ^2 = 0.3, p = 0.56
	Resource type * Avg. three-day maximum temperature	χ^2 = 8.03, p = 0.02
	Resource type * Cumulative three-day precipitation	χ^2 = 2.5, p = 0.29
Cattle only		
Visit frequency (*zero-inflated negative binomial distribution*)	Resource type	χ^2= 53.5, p < 0.0001
	Avg. three-day maximum temperature	χ^2 = 82.7, p < 0.0001

	Cumulative three-day precipitation	$\chi^2 = 0.0001$, $p = 0.99$
	Resource type * Avg. three-day maximum temperature	$\chi^2 = 15.29$, $p = 0.0004$
	Resource type * Cumulative three-day precipitation	$\chi^2 = 2.7$, $p = 0.25$
Visit duration (*zero-inflated negative binomial distribution*)	Resource type	$\chi^2 = 210.1$, $p < 0.0001$
	Avg. three-day maximum temperature	$\chi^2 = 21.4$, $p < 0.0001$
	Cumulative three-day precipitation	$\chi^2 = 0.32$, $p = 0.57$
	Resource type * Avg. three-day maximum temperature	$\chi^2 = 22.5$, $p < 0.0001$
	Resource type * Cumulative three-day precipitation	$\chi^2 = 2.5$, $p = 0.29$

Data S1. (Data_S1_Water_Pattern.gpkg)

Geospatial data of water feature locations per survey. Dataset thus contains site, date of survey, length of each water feature, and origin of each water feature (background water or equid well). See metadata description in Data S2's 'Metadata' tab. Dataset and all relevant code is available on figshare (*8*, figshare doi: 10.6084/m9.figshare.13668794).

Data S2. (Data_S2_Community_Responses.xlsx)

This excel workbook contains the data required to analyze vertebrate utilization of equid wells and vegetation responses to equid wells. The workbook contains four sheets, including a metadata sheet describing all columns in all datasets (including Data S1). All relevant code is available on figshare and is described in metadata (*8*, figshare doi: 10.6084/m9.figshare.13668794).

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Check for updates

Received: 10 October 2021 | Accepted: 8 June 2022

DOI: 10.1111/1365-2656.13766

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

A novel trophic cascade between cougars and feral donkeys shapes desert wetlands

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Funding information
Australian Research Council, Grant/Award Number: DP180100272; University of Technology Sydney

Handling Editor: Rafael Raimundo

Abstract

1. Introduced large herbivores have partly filled ecological gaps formed in the late Pleistocene, when many of the Earth's megafauna were driven extinct. However, extant predators are generally considered incapable of exerting top-down influences on introduced megafauna, leading to unusually strong disturbance and herbivory relative to native herbivores.
2. We report on the first documented predation of juvenile feral donkeys *Equus africanus asinus* by cougars *Puma concolor* in the Mojave and Sonoran Deserts of North America. We then investigated how cougar predation corresponds with differences in feral donkey behaviour and associated effects on desert wetlands.
3. Focusing on a feral donkey population in the Death Valley National Park, we used camera traps and vegetation surveys to compare donkey activity patterns and impacts between wetlands with and without cougar predation.
4. Donkeys were primarily diurnal at wetlands with cougar predation, thereby avoiding cougars. However, donkeys were active throughout the day and night at sites without predation. Donkeys were ~87% less active (measured as hours of activity a day) at wetlands with predation ($p < 0.0001$). Sites with predation had reduced donkey disturbance and herbivory, including ~46% fewer access trails, 43% less trampled bare ground and 192% more canopy cover (PERMANOVA, $R^2 = 0.22$, $p = 0.0003$).
5. Our study is the first to reveal a trophic cascade involving cougars, feral equids and vegetation. Cougar predation appears to rewire an ancient food web, with diverse implications for modern ecosystems. Our results suggest that protecting apex predators could have important implications for the ecological effects of introduced megafauna.

KEYWORDS
burros, feral equids, invasive species, megafauna, mountain lions, predation, rewilding, trophic cascades

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1 | INTRODUCTION

Many of the world's large herbivores and predators were lost in the late Pleistocene, most likely due to human impacts (Sandom et al., 2014; Smith et al., 2018). A second wave of decline is ongoing, as the majority of surviving large herbivore species (henceforth megafauna) are now threatened with extinction (Ripple et al., 2015). Conversely, several megafauna species have established thriving populations following introductions, restoring lost species richness and some important ecological traits (Lundgren et al., 2018, 2020). However, many apex predator species, especially the largest, did not survive the late Pleistocene extinctions and those that remain are often persecuted by humans (Middleton et al., 2020; Ripple et al., 2014). This begs the question: can extant apex predators exert top-down influences on introduced megafauna, given that many introduced megafauna are larger than co-occurring native herbivores?

We report on a novel trophic cascade (Wallach et al., 2015) between cougars *Puma concolor*, feral donkeys *Equus africanus asinus* and vegetation in North America. Cougars co-occurred with a diversity of equid species for more than a million years until the North and South American late Pleistocene extinctions ~9–12,000 years ago (Williams et al., 2018). The little paleoecological evidence that exists, however, suggests that cougar–equid interactions may have been uncommon, with equids mainly preyed upon by larger or pack-hunting now-extinct predators (Figure 1a,b, DeSantis & Haupt, 2014). While research on cougar predation of feral horses is increasing (Andreasen et al., 2021), most policy and ecological literature continues to ignore or explicitly deny the possibility that feral equids experience ecologically significant predation, with oft-repeated claims that they 'have no natural predators' (Bureau of Land Management, 2018; Death Valley National Park, 2018). In contrast, we recorded the first documented predation of feral donkeys by cougars, including a yearling (Figure 2a,b) and foal (Figure 2c,d), and mapped widespread predation of juvenile donkeys in the Mojave Desert (Figure S1).

Predation can control herbivore populations through direct killing. Indeed, cougar predation on juvenile introduced feral horses can reduce or prevent population growth rates in some circumstances (Greger & Romney, 1999; Turner et al., 1992). However, predation also influences prey indirectly, by driving predator-avoidance

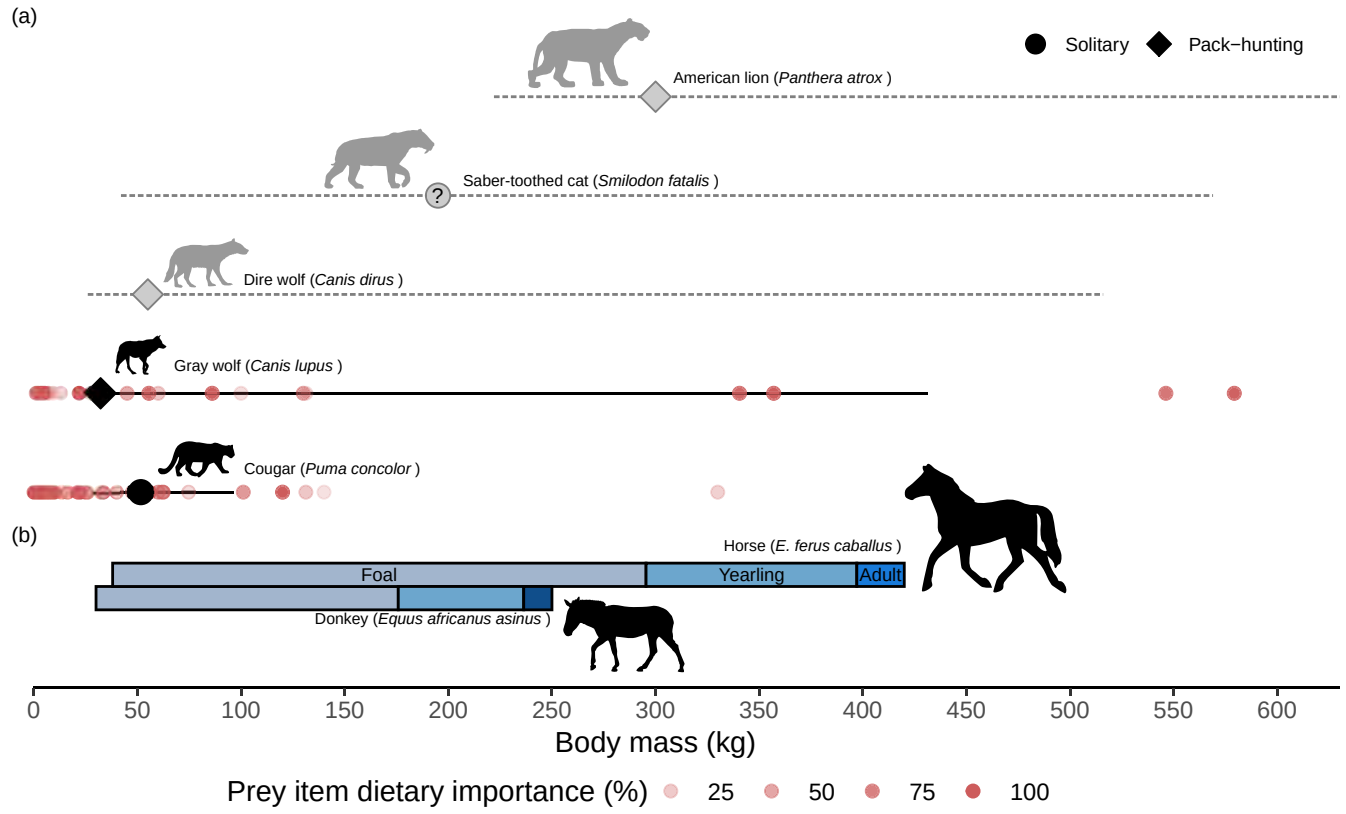


FIGURE 1 Body size and hunting style determine predator–prey interactions and may constrain the ability of extant predators to influence introduced megafauna. *X*-axis (body mass) is shared across all subplots. (a) North American apex predators before and after the late Pleistocene extinctions. Horizontal lines indicate theoretical optimum prey body mass range of extant (black) and extinct (dashed) predators (from Van Valkenburgh et al., 2016). Points indicate average predator body mass and hunting style, which remains uncertain for *Smilodon fatalis* (denoted with question mark). Red points indicate published prey items by body mass, with transparency denoting the importance of prey in diet (data from CarniDIET, Middleton et al., 2021). Of extant North American predators, only the cougar *Puma concolor* substantially overlaps in geographic distribution with feral equids (IUCN Red List, 2018; Wallach et al., 2020). (b) Estimated body mass ranges for equid age classes.

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FIGURE 2 First photographic evidence of cougar predation on feral donkeys, captured with camera traps. (a, b). Successful predation of a yearling donkey in the Sonoran Desert, Arizona. The cougar is looking up from the ground. Arrow in inset points to the cougar's left eye. (c, d). Predation of a foal in the Death Valley National Park, in the Mojave Desert of California. Donkey ages were determined from tooth eruption sequences of carcasses. Images (a) and (c) were tonally adjusted for visibility (see Figure S2 for original versions).

behaviours that can modify their effects on the environment (Fortin et al., 2005; Laundré et al., 2010). These include increased vigilance, reduced consumption rates, shifts in activity rates and temporal patterns, and longer movement distances (Cunningham et al., 2019; Fortin et al., 2005; Laundré et al., 2010; van Beeck Calkoen et al., 2021). These changes can emerge even after recent exposure to predators. For example, moose mothers *Alces alces* rapidly changed their behaviour after experiencing the first predation of a calf by range-expanding grey wolves *Canis lupus* (Berger et al., 2001).

Feral donkeys and horses can have strong effects on ecosystems through herbivory and trampling (Baur et al., 2018) and by competitively displacing other species from limiting resources (Hall et al., 2016). For these reasons, many feral equid populations in the United States have been targeted for complete removal and most experience strict population control. However, it remains unknown whether the effects of feral equids could be shaped by predation. If so, this would have implications for policies towards feral equids and their predators and would contextualize how we understand the effects of feral equids and other introduced megafauna.

We utilized a 'natural comparisons' approach at desert wetlands with and without cougar predation of feral donkeys to investigate how cougars influenced donkey temporal activity patterns and rates, and how predation was associated with the disturbance and herbivory related effects of donkeys on desert wetlands.

2 | MATERIALS AND METHODS

2.1 | Study area

This research focused on the Southern Panamint mountains of the Death Valley National Park (Figure 3, permit: DEVA-2018-SCI-0036). This ~150 km^2 landscape is highly connected by donkey trails, and we regularly witnessed bands of donkeys travelling

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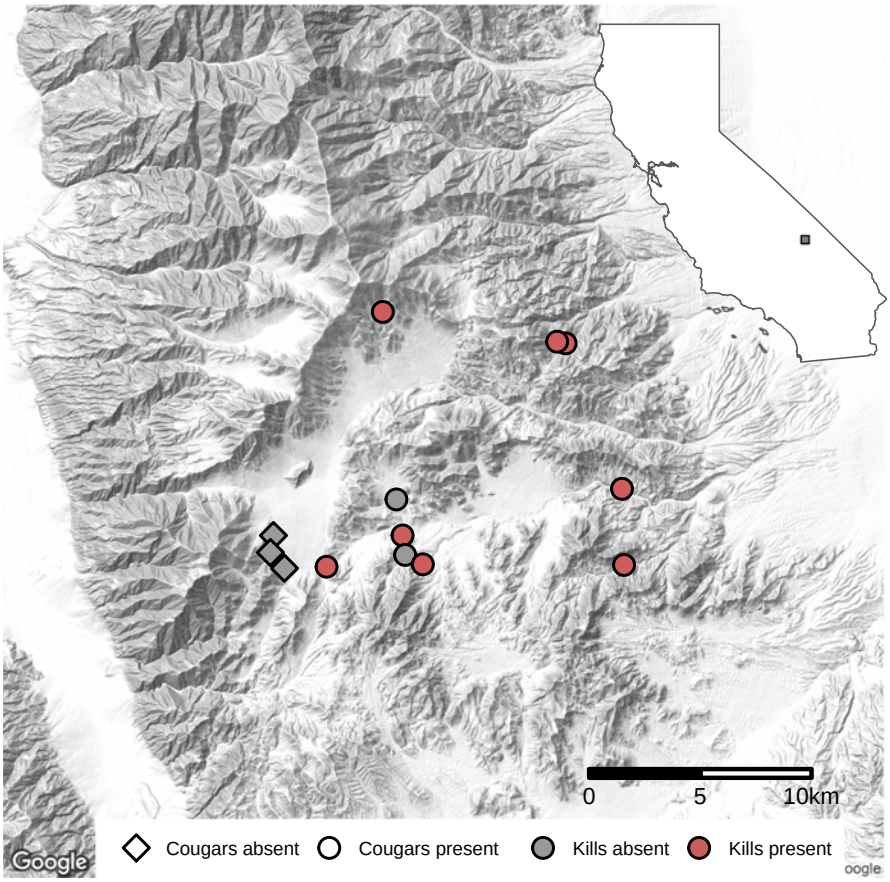


FIGURE 3 Primary study area in the Southern Panamint Mountains of the Death Valley National Park. Points indicate monitored wetlands, which varied by the presence of cougars and kills. The three wetlands where cougars were absent were proximate to campsites. Inset indicates location in the state of California. See Table S1 for camera trap nights per station. See Figure S1 for distribution of kills and the additional study sites used to corroborate donkey temporal activity responses to cougars.

between wetlands within this study region, suggesting that this can be considered a single population of donkeys. Unlike many areas with feral equids, cougars in the Death Valley National Park are strongly protected from hunting. We monitored every known wetland in this region (n = 17) but excluded three because of camera malfunctions. All work was non-manipulative and did not require the Institutional Animal Care and Use Committee approval in the USA but received animal ethics approval at the University of Technology Sydney, Australia (ETH16-0237).

The wetlands in this region varied in relation to predation risk. There were eight wetlands (2,530 trap nights) where cougar predation on donkeys was detected, two wetlands where cougars were detected but donkey kills were absent (436 trap nights), and three wetlands without any cougar detections (312 trap nights). These latter wetlands were at campsites. Unfortunately, this led to a discrepancy in trap nights between these treatment levels due to camera thefts at these wetlands. While the mixed effect models we employed (specified below) are robust to differences in sample size (Pinheiro, 2014), all other analyses used resampling methods to ensure that our results were robust to unbalanced sample sizes.

Evidence of predation was determined by surveying for cached carcasses on cougar trails at each wetland (see the Supporting Information) as well as from direct photographic evidence of kills (i.e. Figure 2). Although it is possible that the cached donkey carcasses were the result of non-predation related mortality events and had been scavenged by cougars, the inverse relationship between the total number of donkey carcasses and feral equid activity rates supports that these carcasses were not caused by some underlying density-dependent process, such as disease (z = −3.5, p = 0.0005, see Supplementary material and Figure S3).

2.2 | Temporal activity patterns of donkeys and cougars

Temporal activity patterns were calculated with the 'overlap' (v0.3.3) and 'circular' packages (v0.4-93) in R v4.0.0 (Agostinelli & Lund, 2017; Meredith & Ridout, 2014; R Core Team, 2020). Sampling effort (i.e. number of trap nights) and the number of donkey detections varied between sites with and without cougar predation, which would bias pooled estimates. We therefore resampled our data over 1,000 iterations, sampling equally between sites with and without predation (see Supplementary material for resampling details). From these resampled activity distributions, we calculated 95% confidence intervals (CIs) to test if there was a significant difference in activity between sites with predation and without, based on the overlap or non-overlap of CIs.

Half of the sites (three of six) without kills were at campsites, which could also drive nocturnality if donkeys were avoiding human activity. We therefore compiled data from additional study regions from earlier research efforts to corroborate our results (Lundgren, Ramp, Stromberg, et al., 2021). However, since we did not have

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ground survey data of local predation events in this broader region, we conducted this analysis based on whether cougars were locally detected or not (Figure S1; Data S1).

2.3 | The influence of cougar predation on the activity duration of feral donkeys

Desert wetlands can become foci of activity for water-dependent animals such as donkeys, particularly at high temperatures, leading to intense herbivory, disturbance and competition (Baur et al., 2018; Hall et al., 2016). Daily donkey activity rates at each wetland were summarized per day as the total duration of 'events'. Events were defined as any donkey detection within 30 min of any other. We chose to evaluate event duration instead of the number of events, given that some wetlands were occupied continuously for nearly 12 hr a day in singular events, while others were occupied for <30 min a day but in several short-duration events.

First, we used a Wilcoxon signed rank test to analyse whether the total duration of activity (henceforth 'activity rate') over 100 trap nights varied between sites with and without cached donkey kills. We then analysed how the presence of cached donkey kills, daily maximum temperature and their interaction, affected daily donkey activity rates in the Southern Panamints of Death Valley. We used negative binomial mixed effect models in the R package GLMMTMB v1.0.2.1 (Brooks et al., 2017), nesting camera station within site, crossed with date, as random effects. We treated the presence of local donkey kills, daily maximum temperature, and their interactions, as fixed effects. Daily maximum temperatures were extracted from the PRISM Climate Group (2020).

Following Brooks et al. (2017), we used the R package DHARMa (Hartig, 2022) to test for over or under dispersion and zero inflation, of which the latter was significant. To address this, we used the DHARMa function 'testZeroInflation' to evaluate different formulations of zero inflation terms and chose the model with the least evidence of zero-inflation ($p = 0.088$). This model included the presence of kills in its zero-inflation component, thus testing whether there was a higher probability of days with zero donkey activity at sites with kills. To test whether the unexplained variation in this model was related to spatial distribution of sites, we used the function 'Moran.I' in the R package APE v5.4 to test for spatial autocorrelation on the scaled residuals, which we extracted with the function simulateResiduals (DHARMa).

2.4 | Effects of feral donkeys on wetlands

To understand if cougars influenced the effects of donkeys on wetlands, we collected data from 14 desert wetlands in the Southern Panamints of Death Valley National Park. We excluded wetlands that experienced flood disturbance, as this would confound the effects of donkeys themselves. We focused on pools where donkeys accessed water and measured the percentage of surface water vegetated by emergent vegetation (e.g. rooted in aquatic substrate), the percent of the water surface covered by canopy foliage, the number of access trails per pool and the percent of the pool's perimeter occupied by vegetation ≥0.5 m in height.

To quantify the degree of disturbance extending upland from these water access points, we set 3 parallel 30-m long belt transects 10 m apart, with the central transect centered on the spring access point. Every 10 m along each transect, we estimated percent trampled ground, percent undisturbed ground, percent herbaceous cover, and percent woody cover in 1-m^2 quadrats (9 total per access point). Although we collected data on plant cover by type and species, we did not include these in subsequent analyses because it was confounded by elevation and edaphic differences across sites, and thus did not directly capture the effects of donkeys.

To characterize wetland structure, we analysed these data by calculating the Gower distance between sites based on all seven response variables, which we analysed with a PERMANOVA test in the R package VEGAN v 2.5-6, with the presence of kills, the presence of cougars, elevation, and terrain complexity as independent variables. Terrain complexity was calculated from a 1/3 arc-second digital elevation model (USGS National Geospatial Program, 2019), which synthesized terrain roughness, terrain ruggedness and slope with a principal components analysis (PCA). PC1 explained 92.5% of total variation and was subsequently used as a synthetic terrain complexity variable (Figure S4). We visualized this data with a Principal Coordinates Analysis (PCoA) on the Gower distance matrix. The first two axes (PCoA 1 and PCoA 2) explained 47.5% of total variation between sites (28.3% and 19.1% respectively).

To test if these differences could have been driven by other underlying spatial gradients, we calculated a geographic distance matrix with the R package GEOSPHERE v1.5-10. We then conducted a Multiple Regression on Distances Matrices analysis with the function 'MRM' in the R package ECODIST v2.0.7 with 1,000 iterations, which tested whether the dissimilarity between wetlands was explained by their spatial distribution.

3 | RESULTS

Donkey temporal activity differed between wetlands depending on the presence of cougars and donkey kills. Donkeys were active throughout the day and night at sites where cougars were absent. However, donkeys were almost exclusively diurnal at sites with cougars, particularly where there was also evidence of cougar predation, thereby avoiding peaks of cougar activity (Figure 4a). Data from additional sites in the Mojave and Sonoran Deserts (Figure S1) corroborated this pattern, showing a transition from nocturnal to diurnal activity in the presence of cougars (Figure S5).

Donkeys were less active overall (hours over 100 trap nights) at wetlands with cougar predation (Wilcoxon signed rank test: $W = 45$, $p = 0.03$). Daily donkey activity rates also differed between sites with and without cougar predation: while daily activity rates increased with maximum daily temperature at all sites ($z = 11.96$,

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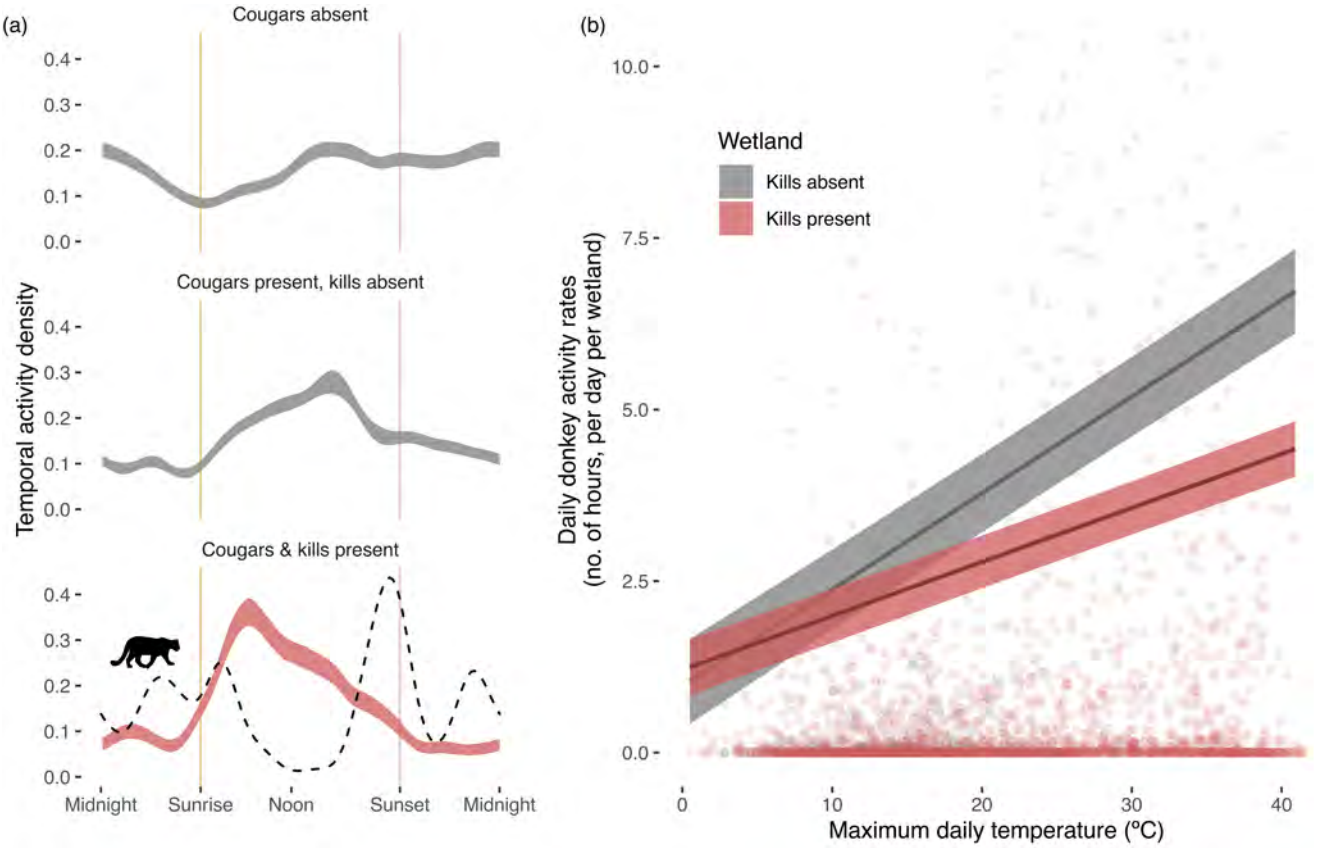


FIGURE 4 Cougars shape donkey activity at desert wetlands. (a) Donkey temporal activity under different levels of predation risk. *X*-axis indicates time of day. Ribbon indicates 95% confidence intervals from bootstrapped detections. Dashed line indicates cougar activity pattern. Cougar detection frequencies were insufficient at sites without kills to calculate their activity pattern (3 events). Data from additional sites in the Mojave and Sonoran Deserts (Figure S1) corroborated this pattern (Figure S5). (b) Relationship between maximum daily temperature and the daily activity rates of donkeys at wetlands (hours/day/site) for sites with and without predation. Regression lines are extracted from negative binomial model with error estimates indicating standard error of model prediction.

$p < 0.0001$, Figure 4b; Table S2; Data S1–S2), this response was reduced at sites with kills (interaction term: $z = -4.91$, $p < 0.0001$, Figure 4b; Table S2). At wetlands without kills, activity increased to an average of 5.5 hr/day on days ≥35°C ($SD = \pm 4.4$, max = 16.5 hr, see Figure 4b for model predictions, Table S2); while at sites with kills, activity remained low and relatively stable, averaging 0.7 hr/day on days ≥35°C (±1.7, max = 12.6 hr, Figure 4b; Table S2). Sites with kills also had more donkey-free days (zero-inflated model component: $z = 3.4$, $p = 0.0007$, Table S2). There was no evidence of spatial autocorrelation in the responses of donkeys to temperature and predation (Moran's *I* on scaled residuals: $p = 0.22$).

Cougar predation on donkeys was associated with reduced herbivory and disturbance-related effects on wetlands (PERMANOVA: $R^2 = 0.22$, $F = 3.34$, $p = 0.0003$, Figure 5a–c; Data S3). Wetlands with kills had 192% more canopy cover (41.5% ± 33.7 compared to 14.2% ± 16% without kills, mean ± *SD*), 102% more vegetation around water perimeter (60.29% ± 18 to 29.75% ± 24.13 without kills), 46% fewer trails (1.6 ± 0.74 to 3.0 ± 1.8 without kills), and 43% less trampled bare ground (from 50.2 ± 16.5% to 88.8 ± 12.9% without kills, see Figure S6 for responses of individual variables). These differences were not explained by the presence of cougars (independent of kills), terrain complexity, elevation ($p = 0.25$–0.36, Table S3), nor geographic distances between sites (multiple regression on distance matrices, $R^2 = 0.02$, $F = 1.35$, $p = 0.35$).

4 | DISCUSSION

Cougar predation on feral donkeys was associated with altered donkey activity patterns and rates and with reduced herbivory and disturbance-related effects on desert wetlands. This adds to growing evidence that ecologically important predator–prey interactions can emerge rapidly in novel ecosystems, with implications for modern ecosystem functioning (Cattau et al., 2017; Wallach et al., 2015; Zavaleta et al., 2001). These results also suggest that removals or eradications of introduced equids and prevailing policies of predator persecution may have unintended consequences.

Feral donkeys and cougars appear to be linked in an emerging ecological network. Donkeys were the primary recorded prey of cougars at our study sites (24 of 29 cached carcasses). In addition to shaping donkey ecology, cougar predation on donkeys may drive novel evolutionary trajectories in cougars (Cattau et al., 2017) and

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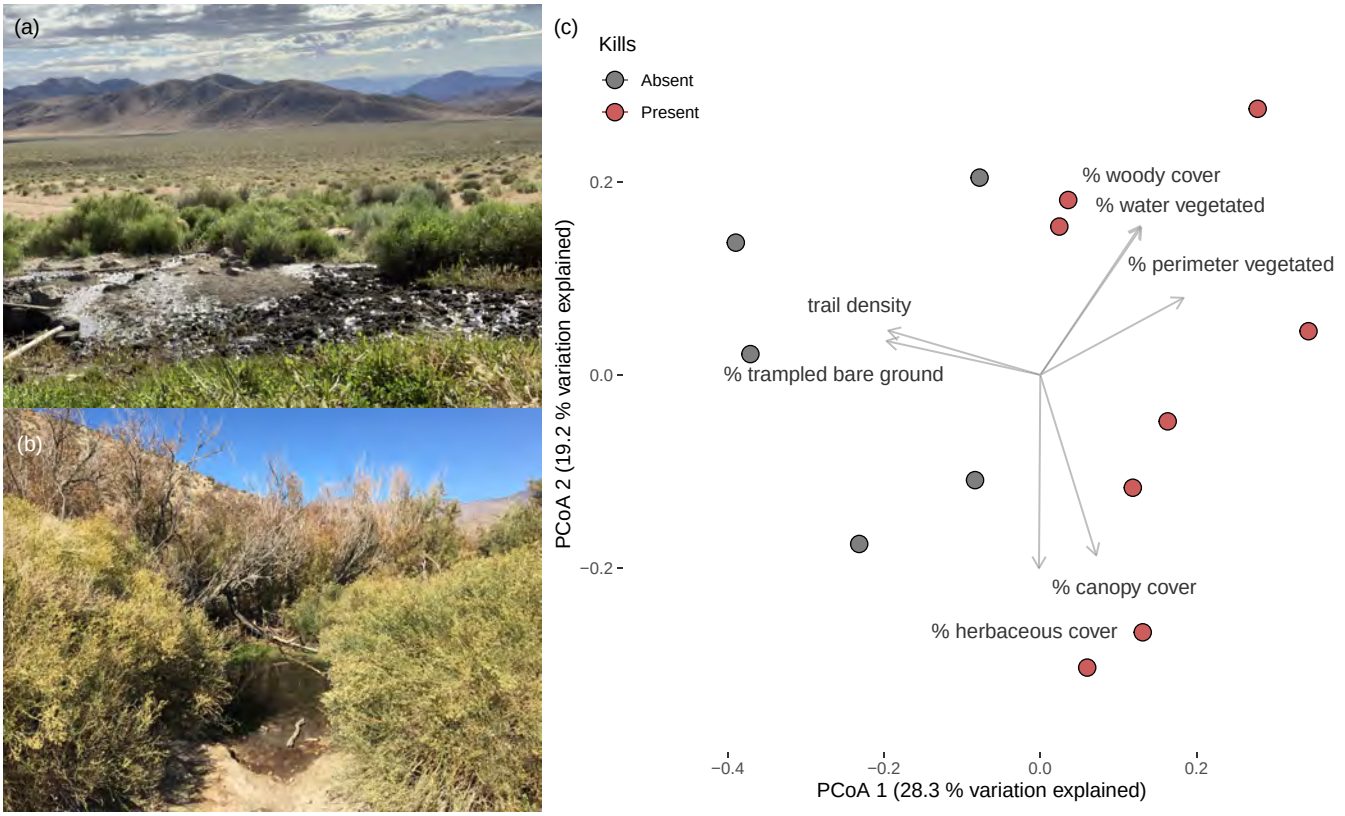


FIGURE 5 Cougar predation is associated with reduced herbivory and disturbance-related influences on desert wetlands. (a) A representative wetland lacking both cougars and kills compared to a similar sized wetland nearby (~6 km apart) (b) where cougars and kills were present (site of the kill in Figure 1c,d). Photos were taken at a similar distance from water's edge, by EJL (a) and OSM (b). (c). Principal coordinates analysis (PCoA) showing differences in wetlands (points) with and without cougar predation on donkeys (PERMANOVA: $F = 3.5$, $p < 0.001$). Relationship between response variables and PCoA axes are indicated by overlaid arrows and text. See Figure S6 for response of individual variables.

reduce predation pressure on their other prey. While we did not conduct exhaustive analysis of cougar diets, the importance of donkeys in cougar caches, and of horses as prey elsewhere (Andreasen et al., 2021), suggests that removals of feral equids could have consequences both for cougars and for their alternative prey (e.g. bighorn sheep) due to prey switching.

Cougars, like most apex predators, are persecuted in service of the meat industry and to increase populations of their prey for sport hunting and conservation (Arizona Department of Game and Fish, 2016; Ripple et al., 2014). As with other apex predators, persecution can reduce the ability of cougar populations to hunt larger and more challenging prey by removing older individuals from the population and by disrupting the transmission of hunting techniques from mother to young (Peebles et al., 2013). Even moderate persecution may thus reduce the potential for ecologically relevant trophic cascades between cougars and feral equids. Policy responses to feral equid populations may benefit from attending to pervasive policies of predator persecution (Phillips, 2018).

Our study took advantage of a natural experiment, comparing sites with cougar predation to sites without. The absence of kills at certain springs appears to have been driven both by the presence of campsites and by terrain complexity (Figure S7). We did not detect any cougars, or kills, at springs close to campsites (i.e. human shielding, Ripple & Beschta, 2006; Suraci et al., 2019). Likewise, as expected given the ambush cover requirements of cougars (Dickson & Beier, 2006), springs in topographically flat terrain lacked kills and had few cougar detections (Figure S7). Collectively, these sites had the highest donkey activity rates yet few or no cougars, suggesting that cougars were not simply tracking prey availability but were driving the observed differences in donkey behaviour (Smith et al., 2019). Human recreation and terrain differences could have had independent effects on donkey activity rates and wetland vegetation. However, donkeys did not appear disturbed by the presence of campers, nor was there evidence to suggest intrinsic differences in the potential vegetation between sites. Regardless, further research is necessary to strengthen these inferences.

Donkeys, like the majority of extant megafauna, are threatened in their native range (Lundgren et al., 2018; Ripple et al., 2015). This has led to calls for more inclusive conservation approaches to protect species both in their native and introduced ranges (Wallach et al., 2020). Promoting protections for introduced megafauna can find productive common ground with other conservation goals, such as increasing protection and tolerance for apex predators.

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Expanding protections for apex predators may further influence the ecologies of feral donkeys and feral horses. For instance, the reestablishment of other documented equid predators (Table S4), such as wolves *Canis lupus* (Webb et al., 2009), could increase predation risk in low ambush terrain, further shaping how these animals influence ecosystems.

For more than a million years, cougars cooccurred with several species of equid across North and South America (Williams et al., 2018). However, much of conservation remains rooted in recent history, with little recognition of the prehistoric and historic legacies of human-caused extinctions and range contractions (Galetti et al., 2017; Monsarrat et al., 2019; Sandom et al., 2014; Smith et al., 2018). As such, the apparently novel effects of feral equids on desert wetlands are cited as the primary reason for their eradication and removal (Death Valley National Park, 2018). However, megafauna influences on wetlands were likely ubiquitous from the early Cenozoic (40–30 million ybp) until the late Pleistocene extinctions (Kodric-Brown & Brown, 2007; Lundgren, Ramp, Stromberg, et al., 2021; Naiman & Rogers, 1997). Indeed, previous donkey removals in the Death Valley region led to the extinction of several endangered and endemic fish populations due to the loss of donkey-maintained open water habitat (Kodric-Brown & Brown, 2007). Despite this, the feral donkeys of Death Valley and surrounding lands are currently being targeted for complete removal (Death Valley National Park, 2018).

If we had studied feral donkeys as 'invaders', without paying attention to predation, our data would contain a great degree of inexplicable noise. Instead, by studying these animals as any other wildlife, we find echoes of the late Pleistocene in a novel trophic cascade. Studying these interactions in light of Earth's history can yield insight into the structure and function of both modern and prehistoric ecological communities (Lundgren, Ramp, Wu, et al., 2021). The introduction of equids after their ~12,000 year hiatus—and predation upon them by cougars—suggests that global patterns of inadvertent rewilding can not only increase biodiversity and restore lost ecological functions (Lundgren et al., 2020; Wallach et al., 2018) but also can rewire ancient food webs (Pires, 2017). Our results suggest that the conservation community should prioritize the protection of apex predators and the world's remaining megafauna, regardless of their nativeness.

AUTHORS' CONTRIBUTIONS

E.J.L. made the initial observations; E.J.L., E.I.F.W., O.S.M., W.J.R., D.R. and A.D.W. designed and conducted fieldwork; E.J.L., E.K., C.D.H., O.S.M. and E.I.F.W. conducted statistical analyses; all authors contributed to conceptualization and writing.

FUNDING STATEMENT

Open access publishing facilitated by University of Technology Sydney, as part of the Wiley - University of Technology Sydney agreement via the Council of Australian University Librarians.WOA Institution: University of Technology SydneyConsortia Name: CAUL 2022

ACKNOWLEDGEMENTS

We thank the Death Valley National Park staff, particularly Alison Ainsworth and Mike Reynolds. We thank Mark Meyers of Peaceful Valley Donkey Rescue–tasked with the non-lethal removals of feral donkeys from Death Valley–for assistance with field work logistics, equipment donations and site information. We thank Melanie Tietje and Sophie Monsarrat for statistical insight and Mark Davis, Martin Schlaepfer, Justin Suraci and two anonymous reviewers for helpful feedback on the manuscript. Work was supported by the Australian Research Council (grant number DP180100272) and crowdfunding. Open access publishing facilitated by University of Technology Sydney, as part of the Wiley - University of Technology Sydney agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and custom scripts available from the Dryad Digital Repository https://doi.org/10.5061/dryad.bvq83bkbk (Lundgren et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lundgren, E. J., Ramp, D., Middleton, O. S., Wooster, E. I. F., Kusch, E., Balisi, M., Ripple, W. J., Hasselerharm, C. D., Sanchez, J. N., Mills, M., & Wallach, A. D. (2022). A novel trophic cascade between cougars and feral donkeys shapes desert wetlands. *Journal of Animal Ecology*, *91*, 2348–2357. https://doi.org/10.1111/1365-2656.13766

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from 12 patients with recessive dystrophic epidermolysis bullosa. They show convincingly that susceptibility to developing invasive SCC, both clinically and experimentally, depends strictly on the retention of part of the collagen VII protein. Keratinocytes from patients carrying mutations that abrogate the deposition of collagen VII do not develop into invasive SCC, whereas those from patients with mutations that result in deposition of a crucial fragment of collagen VII do become cancerous.

Collagen VII is produced primarily by keratinocytes, with perhaps a small contribution from dermal fibroblasts. The collagen VII molecule has a characteristic central glycine-rich, triple-helical collagenous domain, with noncollagenous domains at its amino and carboxyl ends. Keratinocytes from patients with mutations that specifically leave intact the amino-terminal noncollagenous domain (NC1) of collagen VII, and more specifically the fibronectin III–like repeats within the NC1 domain (FNC1) that bind to laminin 5, developed into invasive SCC. Furthermore, introduction of either the NC1 or FNC1 domains into patient keratinocytes deficient in collagen VII restored a predisposition to tumorigenesis, whereas introduction of NC1 without the fibronectin repeats did not. Interestingly, antibodies that specifically recognized the FNC1 domain of collagen VII either prevented tumor development or suppressed tumor invasion when administered to mice with SCC tumors caused by Ras/IκB-transformed keratinocytes from normal individuals. Invasion studies in vitro confirmed the in vivo findings and further revealed that interaction of FNC1 with laminin 5 was required for the invasive phenotype to develop.

What do these results tell us about epidermolysis bullosa and SCC? First, they suggest an explanation for why chronic wounds seldom develop into SCC in patients with mutations in adhesion complex proteins that are closer to the epidermis (for example, laminin 5, hemidesmosomal proteins, and intermediate filament proteins). Keratinocytes harboring such mutations lack an intact adhesion complex between the NC1 domain of collagen VII and laminin 5 and the hemidesmosomes. Hence, these keratinocytes are not tethered to the dermis and may not receive the stromal signals that they would need to migrate to and invade the dermal layer. Laminin 5 is the ligand for $\alpha_6\beta_4$ integrin, a signaling receptor on the surface of basal keratinocytes. Hence, interactions between collagen VII and laminin 5 may be the conduit for stromal signals that direct the migratory and invasive behaviors of epidermal tumors (*6*).

Ortiz-Urda *et al*. also show that boosting production of NC1 enhances the invasiveness of transformed keratinocytes from normal individuals, and of keratinocytes from patients with other skin diseases. A central regulator of collagen VII expression is transforming growth factor–β (TGF-β) (*7*), which enhances invasion and metastasis of established squamous cell tumors and other epithelial neoplasms (*8*). The new work suggests that the relationship between collagen VII and TGF-β is worth exploring further. There are also two possible clinical applications of the current study. Attempts to restore collagen VII locally using gene therapy in patients with dystrophic epidermolysis bullosa are under active investigation (*9*). The authors caution that for certain patients, restoration of collagen VII containing the NC1 domain could increase their risk of developing SCC, particularly in those who lack production of collagen VII. On the other hand, the good news is that the NC1 domain could be a therapeutic target for treating invasive SCC and other cancers. However, a therapeutic molecule that binds to the NC1 domain must block the molecular interactions required for tumor invasion while leaving intact those required for anchoring the epidermis to the dermis. We are faced with a possible Pyrrhic victory as we contemplate the epithelial-stromal interface: perhaps winning the battle against SCC but losing the battle against the disfiguring skin defects of dystrophic epidermolysis bullosa.

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10.1126/science.1110346

EVOLUTION

Fossil Horses—Evidence for Evolution

Bruce J. MacFadden

Thomas Huxley, an early advocate of Darwinian evolution, visited the United States in 1876 on a lecture tour. Huxley had planned to talk about evidence for evolution based on a fragmentary sequence of fossil horses from Europe. One of Huxley's first stops was at Yale, where he studied the fossil horse collection assembled by the paleontologist O. C. Marsh during expeditions to the western territories. Huxley was so taken with the definitive evidence provided by Marsh's fossil horse collection that he used this evolutionary sequence as the focal point for his subsequent talk to the New York Academy of Sciences (*1*).

Since the late 19th century, the 55-million-year (My) phylogeny of horses (Family Equidae)—particularly from North America—has been cited as definitive evidence of long-term "quantum" evolution (*2*), now called macroevolution. Macroevolution is the study of higher level (species, genera, and above) evolutionary patterns that occur on time scales ranging from thousands to millions of years. The speciation, diversification, adaptations, rates of change, trends, and extinction evidenced by fossil horses exemplify macroevolution.

The sequence from the Eocene "dawn horse" eohippus to modern-day *Equus* has been depicted in innumerable textbooks and natural history museum exhibits. In Marsh's time, horse phylogeny was thought to be linear (orthogenetic), implying a teleological destiny for descendant species to progressively improve, culminating in modern-day *Equus*. Since the early 20th century, however, paleontologists have understood that the pattern of horse evolution is a more complex tree with numerous "side branches," some leading to extinct species and others leading to species closely related to *Equus*. This branched family tree (see the figure) is no longer explained in terms of predestined improvements, but rather in terms of random genomic variations, natural selection, and long-term phenotypic changes (*3*).

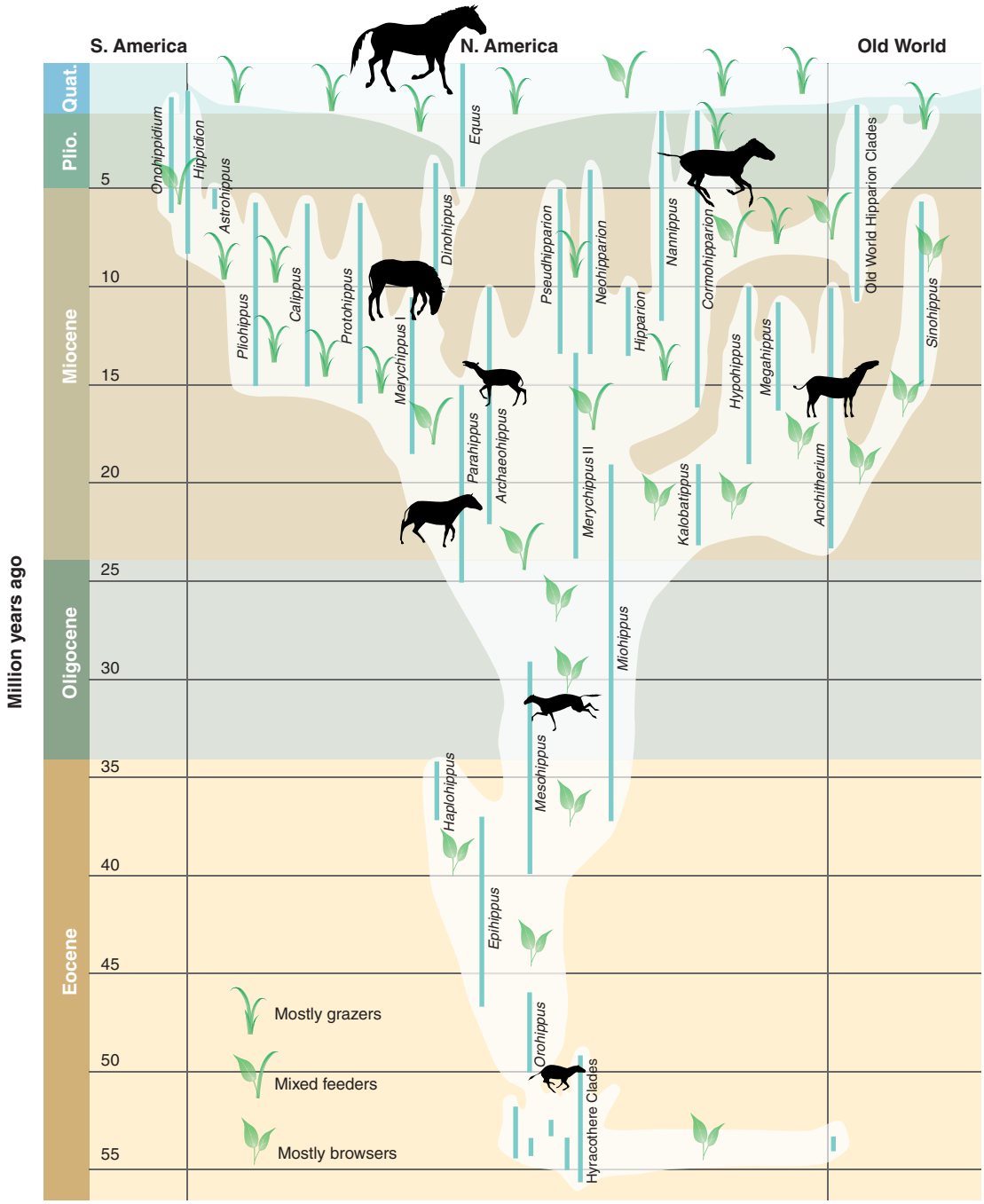
The Equidae, a family within the odd-toed ungulate Order Perissodactyla (which includes rhinoceroses, tapirs, and other closely related extinct groups), consists of the single extant genus *Equus*. Depending upon interpretation, it also includes several subgenera, 8 to 10 species, and numerous subspecies (*4*). On the basis of morphological differences, *Equus* is separated into two or

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three deep clades within the genus. These include caballines (domesticated horse, *E. caballus*); zebras (three species recognized); and asses, donkeys, and related species. Recent studies of mitochondrial DNA indicate two deep clades within *Equus*, namely, the caballines and the zebras/asses (*5*). These deep clades split ~3 million years ago (Ma) in North America and subsequently dispersed into the Old World. *Equus* became extinct in the New World ~10,000 years ago, probably as a result of multiple factors including climate change and hunting by early humans. In the Old World, although its range contracted, *Equus* persisted and was then domesticated in central Asia about 6000 years ago from a stock similar to Przewalski's wild horse, *E. caballus* (sometimes considered its own species, *E. przewalskii*) (*4*).

The single modern genus *Equus* stands in marked contrast to a highly diverse adaptive radiation of the Family Equidae over the past 55 My that resulted in some three dozen extinct genera and a few hundred extinct species (*3*). Although the overall branched pattern of horse phylogeny (see the figure) has remained similar for almost a century, new discoveries and reinterpretation of existing museum fossil horse collections have added to the known diversity of extinct forms. Recent work reveals that Eocene "hyracothere" horses, previously known as "eohippus" or *Hyracotherium*, include an early diversification of a half-dozen genera that existed between 55 and 52 Ma in North America and Europe (*6*). New genera have recently been proposed for the complex middle Miocene radiation (*7*), although the validity of these genera is still debated.



Adaptive radiation of a beloved icon. Phylogeny, geographic distribution, diet, and body sizes of the Family Equidae over the past 55 My. The vertical lines represent the actual time ranges of equid genera or clades. The first ~35 My (Eocene to early Miocene) of horse phylogeny are characterized by browsing species of relatively small body size. The remaining ~20 My (middle Miocene until the present day) are characterized by genera that are either primarily browsing/grazing or are mixed feeders, exhibiting a large diversification in body size. Horses became extinct in North America about 10,000 years ago, and were subsequently reintroduced by humans during the 16th century. Yet the principal diversification of this family occurred in North America. Although the phylogenetic tree of the Equidae has retained its "bushy" form since the 19th century [for example, see (*2*, *3*)], advances in knowledge from fossils have refined the taxonomy, phylogenetic interrelationships, chronology, and interpretations of the ancient ecology of fossil horses.

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Horse teeth frequently preserve as fossils and are readily identifiable taxonomically. They serve as objective evidence of the macroevolution of the Equidae. Horse teeth have undergone considerable changes over the past 55 My. The tempo of this morphological evolution has sometimes been slow and at other times rapid (*2*, *3*). Primitive Eocene through early Miocene (between 55 and 20 My) horses had short-crowned teeth adapted for browsing on soft, leafy vegetation. During the later Miocene (between 20 and 15 Ma), horses underwent explosive adaptive diversification in tooth morphology. Shorter crowned browsers,

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which inhabited forests and open-country woodlands, declined in diversity during this time (*8*). In contrast, many other clades of horses evolved high-crowned teeth adapted for grazing on the extensive grasslands of more open-country biomes, which spread during the Miocene (25 to 15 Ma). Once high-crowned teeth evolved, some clades underwent a secondary adaptation, that is, they went from being grazers to being mixed feeders with diets consisting of grass and some leafy plants (*9*). Studies of carbon isotopes preserved in fossil horse teeth indicate that before ~7 Ma, early tropical and temperate grasslands of the world consisted primarily of grasses that used the C_3 photosynthetic pathway, whereas today these grasslands consist mostly of C_4 grasses (*10*).

In many fossil groups, the trend toward larger body size in ancestral-descendent sequences has been termed "Cope's rule." Early Eocene hyracothere horses classically have been compared in size to a small dog (~10 to 20 kg), although house-cat–sized species have been discovered more recently. At the other end of the evolutionary spectrum, wild modern *Equus* attains a body size of ~500 kg (*3*, *4*). Although the 55-My-old fossil horse sequence has been used as a classic example of Cope's rule, this notion is now known to be incorrect. Rather than a linear progression toward larger body size, fossil horse macroevolution is characterized by two distinctly different phases. From 55 to 20 Ma, primitive horses had estimated body sizes between ~10 and 50 kg. In contrast, from 20 Ma until the present, fossil horses were more diverse in their body sizes. Some clades became larger (like those that gave rise to *Equus*), others remained relatively static in body size, and others became smaller over time (*3*).

Fossil horses have held the limelight as evidence for evolution for several reasons. First, the familiar modern *Equus* is a beloved icon that provides a model for understanding its extinct relatives. Second, horses are represented by a relatively continuous and widespread 55-My evolutionary sequence. And third, important fossils continue to be discovered and new techniques developed that advance our knowledge of the Family Equidae. The fossil horse sequence is likely to remain a popular example of a phylogenetic pattern resulting from the evolutionary process.

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PHYSICS

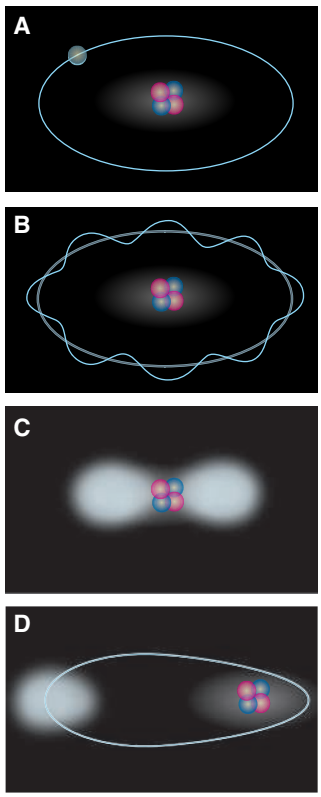
Toward Creating a Rutherford Atom

David M. Villeneuve

The early 20th century saw a rapid evolution in the concept of the atom (see the first figure). In 1911, Ernest Rutherford proposed that the atom resembled a tiny solar system, with most of the mass concentrated in a nucleus, and electrons revolving around it in planetary orbits (see the first figure, panel A). Although his model has been supplanted by quantum mechanics, Maeda *et al.* show on page 1757 of this issue (*1*) that it is possible to make Rutherford atoms in the laboratory.

Doubts about the Rutherford model were raised soon after he proposed it. The emission spectrum of hydrogen was known to have a regular progression of lines, and Johannes Rydberg had shown in 1888 that these lines could be fit to a simple algebraic formula. The Rutherford model could not explain this behavior.

In 1913, Niels Bohr postulated that the angular momentum of the electrons must be quantized. This quantization led to discrete orbits (see the first figure, panel B), which were labeled by an integer quantum number and explained Rydberg's formula. When Bohr's model was supplanted by quantum mechanics as we know it today, the concept of the electron as a planet was replaced by a mathematical wave function that was not directly observable. The electron orbits became fuzzy clouds (see the first figure, panel C).



Evolution of the concept of atomic structure. (**A**) In the Rutherford model, an electron orbits a massive nucleus in a planetary orbit. (**B**) In the Bohr model, the electron is partly a wave that can only go in discrete orbits. (**C**) In the quantum mechanical picture, the electron is spread out within an orbital. (**D**) In the Rydberg atom, the electron is localized into a small volume and follows an almost classical orbit, as demonstrated by Maeda *et al.* (*1*).

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Quantum mechanics has been highly successful in predicting the structure of atoms and molecules, giving birth to notions such as quantum teleportation and quantum computing. It is so precise that experiments have been proposed to look for tiny changes in the fundamental constants as the universe ages over a period of years (*2*). Yet we know that objects in the macroscopic world that we inhabit are not fuzzy clouds. Electrons are real particles that travel through wires and form images on television screens. So where does the quantum world end and our everyday classical world begin?

This question is being addressed by scientists who try to construct atoms that resemble classical objects. Maeda *et al.* (*1*) show that this approach can yield atoms that behave like Rutherford's miniature solar system.

To make a Rutherford atom, one must first localize the electron cloud, that is, confine it to a small volume. In quantum mechanics, this is achieved by creating a coherent superposition of states, called a wave packet (see the second figure). For example, a femtosecond laser pulse is a superposition of many sine waves that add constructively only in

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Rangeland soil carbon and nitrogen responses to grazing

Manley, J T; Schuman, G E; Reeder, J D; Hart, R H . Journal of Soil and Water Conservation ; Ankeny Vol. 50, Iss. 3, (May 1995): 294.

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ABSTRACT (ABSTRACT)

Land managers, livestock producers and the public are concerned about the effects of grazing on soil quality and sustainability of rangeland resources. Manley et al discuss the results of an 11-year comparative study of the effects of heavy stocking, light grazing and livestock enclosures on soil quality.

FULL TEXT

Research on grazing lands has historically focused on the effects of various management practices on forage production and animal response; little attention has been given to the impact of grazing on the nutrient dynamics of soils. Recent interest in "soil health" or "soil quality" has directed attention to grazing impacts on soil parameters that make up soil health/quality. Few studies have evaluated the effects of grazing on soil organic matter and its relationship to water and nutrient cycling, and related plant productivity. In general, the available data do not indicate any single or consistent response of soil organic carbon (C) and nitrogen (N) to grazing. Some research has reported increases in both soil organic C and N (Dormaar et al, 1990; Dormaar and Willms 1990a; Ruess and McNaughton), while other studies have found no response in soil organic C and N to grazing (Kieft; Mathews et al.; Milchunas and Laurenroth). Smoliak et al. reported that increased grazing pressure on mixed prairie resulted in decreases in needleandthread (Stipa comata) and an increase in blue gram (Bouteloua gracilis), which has a greater shallow root mass; hence, soil organic carbon increased. Bauer et al. found that grazing reduced soil organic C and increased soil organic N. These inconsistent findings demonstrate the complex interaction between grazing and soil organic matter.

Many factors determine the response of soil organic matter to livestock grazing. Floate summarized these factors as (a) the initial status of vegetation and soil, (b) environmental factors, especially moisture and temperature, and (c) grazing history (intensity, frequency, duration, and type of animal). Soils with inherently low soil organic C are more prone to change in response to grazing (Dormaar et al. 1977) than soils high in organic C. Precipitation and temperature limit above-ground biomass production and soil organic matter (Parton et al.), and influence rates of litter decomposition and nutrient cycling (Charley). Year-to-year fluctuations of environmental conditions may affect differences in biomass production as much as grazing (Ashby et al.; Milchunas and Laurenroth).

Grazing intensity, frequency, and duration all affect the plant community and the magnitude and direction of change in soil organic C and N. Light grazing can result in greater species diversity and production compared to areas where livestock grazing is excluded (Johnston). On the other hand, high intensity and/or early season grazing have been found to have a greater negative impact on litter and live plant biomass than light intensity and/or late season grazing of mixed prairie pastures in Canada (Naeth et al.). Moderate grazing of mixed grass prairie in North Dakota resulted in greater litter decomposition and soil N mineralization than either heavy or no grazing (Shariff et al.).

Most research on this subject has compared soil C and N concentrations in the surface soil of grazed pastures and nongrazed exclosures. However, animal grazing has been reported to increase soil bulk density (Bauer et al.; Dormaar and Willms 1390b; Pluhar et al.) and increases in soil bulk density will greatly affect the results if soil C and N concentrations, not total mass, are reported, greatly over-stating the response to grazing treatments (Simpson et al.). Soil organic C and N should therefore be reported based on mass. However, not everyone agrees how to best express and evaluate management effects on C and N changes in soil. Skene suggests that the use of soil bulk density to normalize data may lead to misinterpretation. He and other researchers presently assessing soil C and N dynamics are suggesting chat soil volume be considered and that comparisons be made on equal soil volumes even though soil depth may vary because of bulk density. Additionally, since root biomass and distribution affect soil organic matter content and distribution, soil profiles should be sampled sufficiently deep to ensure that a majority of the rooting depth is included in the assessment.

The objective of our research was to evaluate the effects of several grazing management strategies on soil organic C and N after 11 years on a semi-arid mixed grass prairie. Grazing management strategies evaluated included zero, light, and heavy grazing intensities and season-long, rotationally-deferred, and short-duration rotation grazing.

STUDY SITES AND METHODS

Study sites. The research was conducted at the High Plains Grasslands Research Station near Cheyenne, Wyoming. The native rangeland is a mixed-grass prairie, with rolling topography and elevations ranging from 1910 to 1950 m (6266 to 6397 ft). The climate is semi-arid with an annual frost-free period of 127 days and mean (1871-1986) annual precipitation of 338 mm (13.3 in), of which 70% occurs from April 1 through September 30. Dominant soil series are Ascalon and Altvan sandy loams [mixed, mesic, Aridic Argiustoll (Stevenson et al.)].

Dominant cool-season grasses are western wheatgrass (Pascopyrum smithii) and needleandthread and the dominant warm-season grass is blue grama. A survey of the plant community prior to initiating the grazing study indicated the range sites of the area were in good condition.

Prior to establishment of the grazing management phase of the research in 1982, the area had not been grazed by domestic livestock for about 40 years. Grazing strategies, grazing intensities, and pasture design are shown in Figure 1. (Figure 1 omitted) Soils were sampled where grazing management was continuous season-long at a light stocking rate (22 steer-days/ha), and rotationally deferred, short-duration rotation, and continuous season-long, all at a heavy stocking rate (67 steer-days/ha). The heavy stocking rate resulted in slightly less than 50% utilization of the annual production. Further details of the grazing strategies are given in Hart et al. Before the grazing research started, permanent 50-m (160 ft) line transects were located on near-level (0-6%) sites in each pasture on the Ascalon soil series. The experimental design of the grazing study is a randomized block design with two replicate blocks (Hart et al.).

Soil sampling, In July 1993, soil samples were collected from the continuous season-long, light stocking rate (CL); continuous season-long heavy stocking rate (CH); short-duration rotation, heavy stocking rate (SH); rotationally deferred, heavy stocking rate (RH) pastures, and the exclosure (EX). Soil sample sites were established at 10 m (32 ft) intervals along the permanent 50 m (160 ft) line transects that had been established for evaluating plant community response to the grazing treatments. Five cores were taken on each transect to a depth of 30 cm (12 in) and separated into 0-3.8, 3.8-7.6, 7.6-15, and 15-30 cm (0-1.5, 1.5-3, 3-6, and 6-12 in) increments. Surface plant litter was carefully removed from the area where soil samples were taken. Cores were taken with a hydraulic soil sampling machine with a soil tube diameter of 4.G cm (2 in). Because of soil moisture limitations, the deeper soil

cores [30-91 cm (12-36 in)] were not taken until May 1994. Soil cores were taken to the 91 cm depth, the surface 30 cm increments removed, and samples collected for the 30-46, 46-61 and 61-91 cm (12-18, 18-24, 24-36 in) depths. The individual soil sample increments were placed in sealed plastic bags in coolers and transported to a constant temperature room [5deg C (41deg F)] until analysis. Upon return to he laboratory the samples were broken up by hand and plant crowns and visible roots removed. Duplicate soil cores were collected at the second and fourth sampling locations on each of the transects for determining bulk density (Blake and Hartge) (Table 1). (Table 1 omitted)

Sample analysis, The soil samples were dried in forced air ovens at 60deg C (140deg F) to a constant weight. The dried samples were ground to pass a 2-mm (0.08 in) screen. Soil organic N was determined on a subsample by the micro-Kjeldahl method described by Schuman et al. The digest was analyzed for ammonia by continuous flow colorimetric analysis (Technicon TRAACS 800). Soil organic C was determined utilizing a modification of the Walkley-Black procedure (Nelson and Sommers). The modification was a conversion from a colorimetric endpoint to a millivolt endpoint (Raveh and Avnimelech). Soil organic C was determined on a subsample of the soil ground to 0.50 mm (0.02 in).

Data analysis. Soil organic C and N concentration, for each transect and by depth increment, were converted to a mass basis (kg/ha) using the mean bulk density of the two soil cores obtained from each line transect. The bulk density data in Table 1 are presented for assessing C and N changes on a concentration basis because of the debate surrounding data presentation on a mass basis. Analysis of variance was used to evaluate treatment effects on soil organic C and N and least-significant-difference (LSD) procedures were used for mean separation (Steel and Torrie). All statistical analyses were evaluated at P <=0.10.

RESULTS AND DISCUSSION

Soil organic C and N in the surface 7.6 cm (3 in) of soil were significantly lower in the exclosure compared to all of the grazing management strategies (Figures 2 and 3). (Figures 2 and 3 omitted) No differences existed between any of the grazing strategies, except that in the 3.8-7.6 cm (1.5-3 in) soil depth the organic C was significantly lower under the continuous-light grazing strategy than under any heavily grazed management, but was still significantly greater than in the exclosure. In the 7.6-30 cm (3-12 in) soil depth, differences in soil organic C and N contents among grazing strategies were more varied, but C and N contents in the exclosure remained lower than, or at best comparable to, C and N under the various grazing treatments. These data exhibit the importance of the surface few centimeters of soil as it relates to C and dynamics under a grassland. Seventy to 90% of the root biomass is present in the surface 30 cm (12 in) of the soil in this type of grassland system (Dormaar et al. 1984); therefore, nutrient availability in this zone is very important. In the 30-31 cm (12-36 in) depth, soil organic C and N contents were not significantly different among ungrazed and grazed treatments (Figure 4). Soil organic C and N concentrations were quite low and variable at this depth in the soil. Only a small percentage of the root system is present in this soil depth increment; therefore, it is not surprising that grazing for 11 years had no affect on the lower portion of the soil profile.

The higher levels of soil organic C and N in the surface soil of the grazed rangeland may be due in part to the effects of grazing on litter and standing dead component-s of the above-ground biomass. Although grass roots are the primary source of organic matter in rangeland soils, above-ground litter provides a secondary source (Aandahl). The grazing treatments essentially eliminated the standing dead component and greatly reduced the surface litter component. Animal traffic may be enhancing physical breakdown and soil incorporation of this residual plant material. In comparison, 70% of the aboveground phytomass in the exclosures was in the form of litter and standing dead plant material. We estimate that this large component of recalcitrant material immobilized

about 35 kg N/ha (31 lb N/ac) and 1550 kg C/ha (1,383 lb C/ac) aboveground in the exclosures(1). Species composition shifts within a plant community can also result in C changes as discussed earlier (Smoliak et al.). However, our research did not show an increase in blue grama (Hart et al.) nor did it show a significant below-ground biomass response to grazing(2).

In general, defoliation is thought to stimulate an increase in allocation of C and N to regrowing leaves and a decrease in allocation of C to roots (Detling et al.), resulting in reduced root biomass (Dormaar et al. 1990; Johnston) and reduced root exudate contributions to soil organic matter. Thus researchers have predicted losses rather than gains, of soil organic C and N with grazing (Holland et al.). However, multiple harvests (simulated grazing) taken throughout the growing season have been shown to result in greater plant production than a single estimate obtained at peak standing crop (Mutz and Drawe). Dodd and Hopkins found that clipping blue grama five times gave greater production than clipping three or four times, indicating that this species would respond to grazing defoliation and produce greater aboveground biomass. Grazing also stimulates tillering (Floate) and rhizome production (Schuman et al. 1973). Thus, if plant growth is stimulated by grazing, then greater CO sub 2 sequestration would occur, which could result in greater C allocation to below-ground portions of the system. Dyer and Bokhari (Dyer and Bokhari) inferred that blue grama responded to defoliation by rapidly translocating material to the crowns and roots and by increasing root respiration and/or root exudation rates. Ruess and McNaughton (Ruess and McNaughton) suggested that grazing accelerates the rate of nutrient cycling by stimulating primary production and net nutrient flux, thereby increasing the percentage of the system's nutrients that are available and which cycle rapidly near the soil surface.

The results of this study indicate that responsible grazing strategies implemented 11 years earlier did not detrimentally affect soil organic C and N levels in the active and important upper 30 cm (12 in) of the soil profile under native mixed-grass rangeland. In fact, the data indicate that grazing enhanced the overall soil quality as assessed by these parameters, and that plant production should be sustainable.

(FOOTNOTES)

1 G.E. Schuman, 1994, unpublished data

2 R.H. Hart, 1994, unpublished data.

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DETAILS

Subject:	Soils; Research; Nitrogen; Livestock; Land; Carbon
Publication title:	Journal of Soil and Water Conservation; Ankeny
Volume:	50
Issue:	3
Pages:	294
Publication year:	1995
Publication date:	May 1995
Publisher:	Soil and Water Conservation Society
Place of publication:	Ankeny
Country of publication:	United States, Ankeny
Publication subject:	Water Resources, Agriculture--Crop Production And Soil
ISSN:	00224561
e-ISSN:	19413300
CODEN:	JSWCA3
Source type:	Scholarly Journals
Language of publication:	English
Document type:	Feature
Accession number:	02413796

ProQuest document ID:	220961735
Document URL:	https://unr.idm.oclc.org/login?url=https://www.proquest.com/scholarly-journals/rangeland-soil-carbon-nitrogen-responses-grazing/docview/220961735/se-2?accountid=452
Copyright:	Copyright Soil and Water Conservation Society May 1995
Last updated:	2017-11-09
Database:	SciTech Premium Collection

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Interactions Between Pronghorn Antelope and Feral Horses in Northwestern Nevada

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Management

by

Jo O. Meeker

May 1979

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ACKNOWLEDGEMENTS

I am grateful to the members of the Renewable Natural Resources Department, University of Nevada, Reno, for their encouragement and assistance in the conduct of this study. Special thanks go to the members of my graduate committee: Dr. Donald A. Klebenow (Chairman) and Dr. J. Wayne Burkhardt of the Renewable Natural Resources Department and Dr. Stephen H. Jenkins of the Biology Department. They were all willing to listen to me at any time and generally allowed me to convince myself of a course of action on the subject of that particular discussion. Thanks are especially due to Dr. Robert C. Beall, formerly of the Renewable Natural Resources Department, who served as my major advisor and director of research prior to his departure from the University. My many discussions with Dr. Beall led to my research project, and his standard comment, "Ain't research fun?" helped in maintaining my enthusiasm during the less enthralling portions of my field research. Thanks also go to the U.S. Fish and Wildlife Service personnel of the Charles Sheldon Antelope Range for their assistance and adjustment of schedules to fit my research needs.

Last, but definitely not least, I want to thank my family: my wife, Pat, for her willingness to become a "research widow" and for her assistance in research and preparation of this paper; my daughter, Amanda, for her assistance in laboratory work; and my son, David, for his two summers with me in the field, where he became a "mini-biologist" and a friend of animals.

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ABSTRACT

A study of interactions between pronghorn antelope *(Antilocapra americana)* and feral horses *(Equus caballus)* was conducted during two summers at the Sheldon Antelope Range in northwestern Nevada. Visual observations were used to determine watering and foraging interactions and fecal analysis was performed to determine diet overlap. A total of 142 measurable instances of watering were recorded and analyzed to determine if the juxtaposition of horses affected antelope drinking and loafing times. Numerous grazing and meeting situations between the two species were observed to determine if either interfered with the activities of the other. Results indicated a lack of interference competition between antelope and horses at water or under grazing or moving situations. No acts of aggression were observed between the species. There was some evidence of a degree of symbiotic relationship existing between them. Fecal analysis indicated dietary overlap of approximately 12.8 percent, with phlox *(Phlox hoodii)*, the second most abundant forb in the study area, being the only plant species to contribute over five percent to each species' diet.

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INTRODUCTION

The ever-increasing human population of the United States has, without doubt, had a detrimental effect on wildlife populations. Humans have appropriated for their own use that land which they desired. These actions have resulted in decreased quantity and quality of natural habitat for wildlife, especially the larger or less human-tolerant species.

The pronghorn antelope *(Antilocapra americana)* is one species whose population has been greatly affected by human expansion. Nelson (1925) estimated that there were 35 million pronghorn in North America in 1805. During the next century, this population decreased to some 13,000 (Hoover et al. 1959). From that low point, the population increased to an estimated 385,500 by 1964 (Yoakum 1972).

Proper management of this remnant herd of a once enormous population is necessary if the antelope is to remain an important large game animal. The resource manager must have all available information concerning the ecology of the pronghorn, including its interactions with other ungulates, in order to accomplish this required management. It is the intent of this paper to report the results of a study of interactions between pronghorn antelope and feral horses *(Equus caballus)* during the summer months in a sagebrush-bunchgrass community in northwestern Nevada.

The term "feral" is used in preference to the term "wild" because the wild horse became extinct in North America by the end of the Pleistocene epoch and did not appear again until reintroduced by early Spanish colonists (Hickman and Hickman 1972). From this reintroduction, the population of feral horses has grown to numbers in excess of 60,000,

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primarily in the western United States (Monroe 1977). This growing population of horses is a factor that must be considered by western rangeland managers (Cook 1975).

It is, therefore, my desire that this study will contribute to our knowledge of both pronghorn and horses and their interactions. Should this be the case, it will serve as a management tool for those resource managers operating in the intermountain sagebrush-bunchgrass biome.

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LITERATURE REVIEW

The food habits of pronghorn have been well documented for the sagebrush-bunchgrass vegetative community. Ferrel and Leach (1950 and 1952) analyzed stomach contents of 83 antelope taken in California during spring, fall, and winter. They reported that browse, principally big sagebrush *(Artemisia tridentata)*, made up the bulk of the spring and winter diet, while forbs comprised over half of the fall diet. Mason (1952), in studying the Hart Mountain, Oregon antelope, found the most important year-round food source to be sagebrush with forbs contributing heavily to the diet during the summer months. In their study of food preference of penned antelope in Wyoming's Red Desert, Severson and May (1967) found the most important summer foods to be Douglas rabbitbrush *(Chrysothamnus viscidiflorus)* and big sagebrush. Olsen and Hansen (1977) found that sagebrush was the most important food source for pronghorn and that diet diversity increased during the summer. The Olsen and Hansen study provides the only available reference to diet overlap between antelope and feral horses in the sagebrush-bunchgrass community. They reported an extremely small similarity (4 ± 4%) in the diets of these two species. This observation is supported by a study in the cold desert region of eastern Nevada, where the Bureau of Land Management found the summer diet of feral horses was composed of 92 percent grasses, while the pronghorn's diet was 95 percent shrubs and forbs (G. W. Cropper, pers. comm.). It appears that little overlap of diets is to be expected in areas with plentiful resources, but in areas with a limited food supply, this overlap might be considerable. Hansen (1976) reported that the most important food plant for feral horses in southern New Mexico was

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Russian thistle *(Salsala kali)*. This testifies to the survivability of the feral horse. His New Mexico study also showed the lowest percentage (50%) of grasses and grass-like plants that he had observed in horse diets from six states. On the other hand, only two studies could be located which reported grasses in excess of five percent of an antelope's diet (Hjersman and Yoakum 1959, Mitchell and Smoliak 1971). This, too, would indicate a lack of serious diet overlap under conditions of forage plentitude. Daily forage requirements for antelope and horses have been reported as 3.1 and 2.5 percent of total body weight respectively (Stoddard and Smith 1955, Thomas 1974). Average weights were estimated at 410 kg for horses (G. Cropper, pers. comm.) and 45 kg for antelope (Pyshora 1977). Based on these estimates, the daily forage requirements were 10.25 kg for horses and 1.395 kg for antelope.

Little has been reported on water requirements of either antelope or feral horses. Beale and Smith (1970) found that the pronghorn of western Utah did not use free water when the moisture content of abundant forbs exceeded 75 percent. However, during the hot, dry summer, the daily requirements averaged 2.8 liters per animal. In a similar study in Wyoming, Sundstrom (1968) reported daily water requirements varied from 0.3 liters per day in May to 4.5 liters per day in August. However, neither study reported on drinking frequency. Water requirements of a domestic 454 kg horse vary from 15 to 57 liters per day depending on ambient temperature, activity, and reproductive condition (Evans et al. 1977). It was also recommended that horses be watered frequently during the day. Pellegrini (1971) reported that feral horses in Mineral County, Nevada watered every other night and remained at the water hole all night.

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However, the U.S. Forest Service was able to inventory feral horses in eastern Nevada by time-lapse photography of water holes during the day (Baxter 1977). This was an indication that these animals also water during daylight hours. A thorough literature search failed to reveal any information on interactions between antelope and feral horses in either grazing or watering situations.

The primary aim of this paper is to report any competition that exists between antelope and feral horses in the Charles Sheldon Antelope Range. The definition of interspecific competition preferred by this author is that used by Miller (1967:6): "Biological competition is the active demand by members of two or more species at the same trophic level for a common resource or requirement that is actually or potentially limiting." This definition has been expanded to include, in part, that of Krebs (1972:211) who stated that ". . . if the resources are not in short supply, competition occurs when the organisms seeking the resource nevertheless harm one or other in the process." Competition which exists for a limited resource is termed exploitation competition, and an interference component exists when organisms harm one another in seeking a needed resource, regardless of its availability (Krebs 1972).

The exploitation component of competition for food resources can be determined, with reservations, by comparing dietary overlap of sympatric species to the availability of the relevant foodstuffs. Hansen and Ueckert (1970:640) stated, "The contribution of individual plant species to the diets of sympatric herbivores and the availability of these plants are essential criteria for determining if dietary competition exists." Cody (1974) stated that the mere analysis of stomach contents can give an

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extremely biased picture of the ecological overlap between species. This could be true were stomach contents used for analyzing the overlap of diets between two species with different feeding habits or areas. This would mean that each was obtaining food not available to the other and, regardless of the degree of overlap, competition would not exist. This should not be the case where the two species under consideration were large terrestrial herbivores feeding in the same general area, and where samples used were composited from 15 or more fecal subsamples.

Several methods are available for collecting data for determination of an herbivore's diet: direct observation, fistulation of either esophagus or stomach, stomach removal, and feces collection. When dealing with a free-roaming large herbivore population, fecal analysis may be the most feasible method.

Direct observation would require the ability to observe from extremely close ranges, or an estimation of how much of a certain plant was removed by an animal and which animal took it, should more than one species be present. Fistulation would require excessive handling of wild animals to the point that the animal would be tame rather than wild. Analysis of stomach contents would be destructive sampling that would require the sacrifice of animals. These drawbacks would be eliminated through the use of fecal analysis, a method that requires nothing more than that material the animal no longer needs.

A microscopic technique for identifying plants eaten by herbivores was developed by Baumgartner and Martin (1939). This technique has been refined and used to study food habits of domestic sheep (Croker 1969), quokkas (Storr 1960), ground squirrels, crickets and grasshoppers

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(Hansen and Ueckert 1970), bighorn sheep (Todd and Hansen 1973), meadow voles (Neal et al. 1973), deer (Anthony and Smith 1974), free-roaming horses (Hansen 1976), free-roaming horses, cattle, elk, sheep and pronghorns (Olsen and Hansen 1977), and snowshoe hares (Wolff 1978). Numerous verification studies of the accuracy of fecal analysis have been performed (Sparks and Malechek 1968, Free et al. 1970, Anthony and Smith 1974, Dearden et. al. 1975, Vavra et al. 1978, Havstad and Donart 1978). These studies have reported that the microscopic analysis of feces provides an accurate representation of herbivore diet. Westoby et al. (1976) reported on three problems identified in their study of the accuracy of quantifying artificially compounded mixtures of vegetative material. These problems were: (1) wrong name applied to all fragments of one material, (2) attempt and failure to name material which was not reliably identifiable, (3) miss material altogether. These problems cannot be eliminated but their effect could be reduced. Collecting reference material during the same time period that fecal samples were collected would reduce errors due to phenological stage. Constant referral to photomicrographs and reference slides would reduce misidentification. Rare plants may be missed during analysis, but this should not negate the results since their contribution to either diet would be negligible.

Schroder and Rosenzweig (1975:16) stated, "The only necessary and sufficient means of demonstrating the existence of competition between two species is to observe the numerical responses of the presumed competitiors to perturbation of one or both species." Although perturbation analysis should show competition, it is felt that the

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inclusion of the word *only* is excessively restrictive. The interference component could be ascertained, although possibly not quantified, by observation of the interaction between two species for a limited resource, i.e., food or water. Dietary overlap for a limited food item should indicate the exploitation component of competition. Additionally, perturbation analysis would be difficult, if not impossible, for studying competition between large, long-lived mammals existing on public domain.

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STUDY AREA

The Charles Sheldon Antelope Range (Fig. 1) was established in 1939 for the purpose of preserving, studying and managing pronghorn antelope and other wildlife species (U.S. Dept. of the Interior 1969). This range contains over one-half million acres and supports a stable pronghorn population of approximately 800 animals (B. Wiseman, pers. comm.).

The study area was located in the northwestern portion of the Sheldon Antelope Range, approximately 270 km north of Reno, Nevada. There were an estimated 100 antelope and 115 horses in this area during 1977. The 1978 populations were estimated at 85 antelope and 195 horses. The study area consisted of approximately 40 square kilometers of North Rock Springs Table, known as Horse Heaven (Fig. 1). It was rolling country broken by an occasional valley. Elevations ranged from 1,890 m in the northwest to 2,010 m at the summit of a north-south ridge which bisected the area.

Average temperatures during the summer months of 1977 and 1978 (Table 1) were characterized by high daytime and low nighttime readings.

Table 1. Average temperatures (C) in the study area.

	1977		1978	
	High	Low	High	Low
June	25.1	4.0	21.6	-0.3
July	27.2	3.4	27.4	2.9
August	26.1	3.4	25.8	2.3

The differential between highs and lows exceeded 20 C for each of the six summer months monitored. The average annual precipitation for the past

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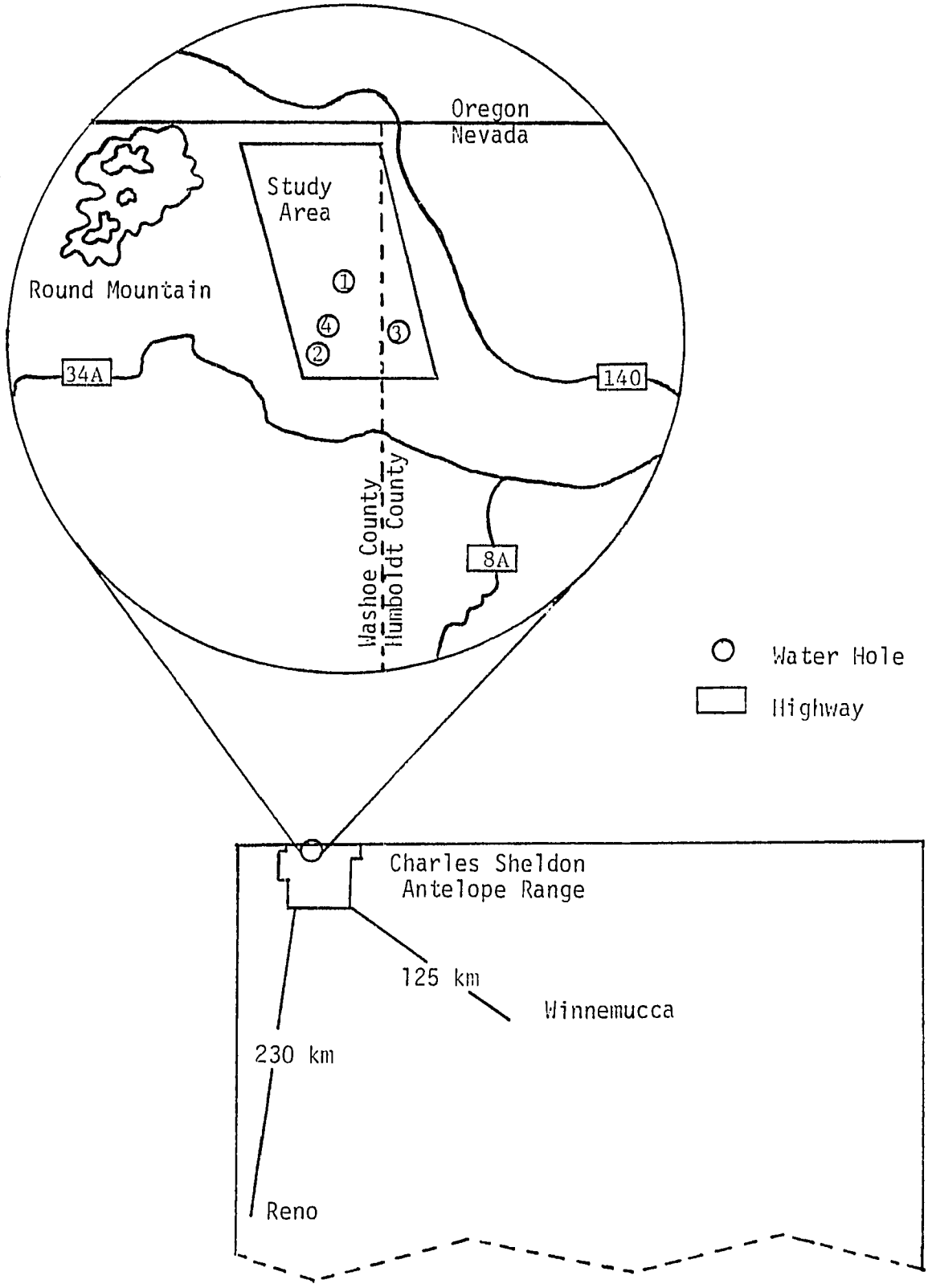


Fig. 1. Location of study area.

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ten years has been 19.5 cm, varying from 14.3 to 30.9 cm per year. Total precipitation was 15.9 cm during 1977 and 27.6 cm for 1978.

The study area was located within the sagebrush and bunchgrass major plant community of North America (Kuchler 1964). Yoakum (1972) estimated that 27 percent of North America's pronghorn antelope occupy this vegetative type. The dominant vegetation consisted of low sagebrush *(Artemisia arbuscula)* and Sandberg bluegrass *(Poa sandbergii)*. Numerous patches of big sagebrush occurred throughout the study area. Forbs were plentiful but tended to be patchy in distribution and some species failed to set seed during the summer of 1977.

The soil of the study area was of the order Aridisols, suborder argids. The parent material was predominantly basalt residuum with some admixture of tuffaceous alluvium (Soil Conservation Service 1970). Scattered throughout Horse Heaven were small areas of mollisols. Recent deposits of rhyolite or basalt were laid over old lake sediments. The surface was rock covered and water runoff was rapid.

The water situation in the study area was adequate to provide for the needs of the resident wildlife population. All water was collected from runoff in either natural or man-improved cachments. Fig. 1 portrays the relative location of the four watering places that existed during a good water year. Water hole number 1 was the preferred water hole and received heavy use by both feral horses and antelope until it dried up (July 6, 1977 and August 1, 1978). This was a natural cachment and was the most distant from roads and human activity. Water hole number 2 consisted of one man-improved and two natural cachments. These water holes received little antelope and no horse activity until water hole

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number 1 dried up and the horses moved to the west in late summer. These water holes dried up in mid-July, 1977, and contained water all summer, 1978. Water hole number 3 was a man-improved cachment and received little activity before number 2 dried up, but the bulk of horse and antelope activity, after this. This water hole held sufficient water to meet the needs throughout both summers. Water hole number 4 was a small natural cachment that contained no water in 1977 but had water until mid-July 1978. Some antelope used this water, but no evidence of horse use could be found.

Other ungulates that used this area were mule deer *(Odocoileus hemionus)* and domestic cattle *(Bos taurus)*. Deer used the area frequently for water and less so for browsing along the bluff edges. Suitable deer habitat, but with less water, existed to the east and south of the study area. Livestock grazing was not permitted during 1977, but approximately 250 cattle were in the study area during portions of the summer of 1978.

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METHODS AND MATERIALS

Based on available information on location of feral horse and antelope usage, six agronomy cages were positioned on May 29 and 30, 1977. Four cages were located on Round Mountain and two in Horse Heaven. These cages, each 2.5 by 4 m, were used in an attempt to predict forage production within the study area. At the end of the growing season for each forage type, ground cover was determined for each plant which was totally within the exclosure and current year's growth was removed. Plant diameter was determined by measuring the longest and shortest diameter of the plant and averaging these values. Crown diameter was determined for shrub and forb species and basal diameter for grasses. Vegetative clippings were placed in paper bags and allowed to air dry for a minimum of two months prior to weighing. Current year's growth was weighed to the nearest one-tenth gram. Covariance and regression analysis were used to determine whether plant diameters could be used to predict production. This type of analysis was deemed appropriate because the parameter measured was affected little by grazing activity.

Vegetative data for the study area was obtained from 50 systematically located 0.5 by 20 m strip transects during July 1977. Transects were located without regard to vegetative type. The only areas excluded from sampling were bluff faces. In the two cases where this affected sampling, the plot was displaced to the nearest location that eliminated the obstacle. All plants whose measured component fell totally or partially within a transect were included in the survey. Crown diameter and the estimated percentage of the crown within the plot were recorded for all shrubs and forbs by species. Basal diameter and the percentage within

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the plot were recorded for all grass species. A computer program, SHELM1, was written and used to obtain percent cover and density for all species of vegetation within each study plot.

Fecal samples for diet comparison were collected during the latter phases of vegetative sampling. These samples were collected in the vicinity of the only water hole within the study area that still contained water. Antelope feces were collected from animals observed defecating, to preclude the possibility of including feces from mule deer that frequented the area. Subsamples weighing about 4 g each were collected from separate fecal groups until 20 subsamples were obtained for each species. The subsamples were then combined by species to form the sample for analysis. Anthony and Smith (1974) reported that subsamples from 15 pellet groups were adequate to describe deer diets in Arizona. Samples were placed in airtight plastic bags and kept frozen until final preparation for analysis.

Specimens of all known plant species in the study area were collected for identification and preparation of reference slides. Plants were identified by the use of Munz (1968) and Hitchcock et al. (1955-69) and verified, where possible, by comparison with known specimens in the Nevada Agricultural Experiment Station Herbarium. Detailed instructions for reference slide preparation are outlined in Appendix A. These reference slides were studied in detail for approximately two weeks and black-and-white photomicrographs were made of diagnostic characteristics. This detailed study was followed by the preparation of a dichotomous key based on characteristics of the leaf portion of the plants (Appendix B). The leaves of grasses were found by Davies (1959) to have the greatest

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diagnostic value, due to leaf cell structure not being greatly affected by phenological stage of the plant. The lack of a key for all plant parts did require additional effort when analyzing feces, but the time spent was less than that required for the preparation of additional keys.

The next step in the learning process was the quantification of unknown mixtures of plants from the study area. A fellow graduate student prepared these mixtures in quantity. Continued work with test mixtures increased the writer's knowledge of the plants involved until test mixtures were repeatedly analyzed within five percent accuracy. This accuracy is considered sufficient by the Colorado State University Composition Analysis Laboratory (R. M. Hansen, pers. comm.).

Microscope slides of fecal material were prepared as outlined in Appendix A. Fecal analysis was performed by noting species occurrence in 20 systematically located fields on each of five slides for a total of 100 fields. One hundred fields have been reported as adequate to describe an herbivore's diet (Martin 1955, Sparks and Malechek 1968, Free et al. 1970, Todd and Hansen 1973). The contribution of each plant species to an herbivore's diet was determined using the frequency conversion technique developed by Sparks and Malechek (1968). In this technique, the presence of a species in a microscope field is noted, but the number of such fragments is disregarded. This frequency is then converted to relative density using the tables developed by Fracker and Brischle (1944). Sparks and Malechek (1968) reported no loss in accuracy using this method, as compared with counting all fragments of all species appearing in each field.

Correction factors for any over- or under-estimation of species

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contained in hand-compounded mixtures have been developed (Dearden et al. (1975). Such correction factors were not applied in this study because Hansen (R. M. Hansen, pers. comm.) stated that the increased work load does not justify the slight increase in accuracy.

Data concerning antelope-horse interaction at water holes was collected by observation through a 15X-45X spotting scope. Each observation of antelope watering was recorded by time of day, number of antelope, drinking time, loafing time, number of horses and their distance from the water. Antelope were identified as male, female, or kid. Drinking time was determined by timing, with a 0.1-second stop watch, the amount of time that an antelope remained in a drinking posture at the water. Drinking posture was defined as head over the water and body perpendicular to the water's edge. Small periods of surveillance by the animal were not deducted from drinking time. Loafing time consisted of all time the antelope remained in the vicinity of the water, less drinking time, prior to obvious departure behavior. When actually departing the vicinity of the water hole, an antelope usually acted as though it had a destination in mind, that is, it moved off without hesitation or loitering. This procedure was modified for a period during the summer of 1978 to include cattle when they were present in the study area. This data was analyzed using analysis of covariance and regression to determine if horse proximity had an effect on antelope use of water.

A second method of data collection on water hole interactions was attempted. This method entailed the use of a Minolta movie camera with time-lapse capability, similar to that used by the U.S. Forest Service in

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eastern Nevada (Baxter 1977). This camera was implaced in the vicinity of the water hole and adjusted to expose one frame per minute. The desire was to photograph all animals watering during daylight so that a customer list could be developed. Also, any interactions would be recorded on film as verification for visual observation. This method did work as expected for horses and in many cases, allowed for band identification. Due however to the small size and coloration of antelope and the physical layout of the water holes, the system photographed far too few antelope (many less than visually observed) to be of any value. Since this method of data collection was considered a failure, it will not be further discussed in this paper.

During the early phases of this study, all observations of horse-antelope interactions during grazing or movement were recorded as to number of antelope, number of horses and a description of the interaction. After 30 such observations, with the results never varying, it was decided to define a normal behavior pattern and record only those incidents that appeared unusual. The normal was considered to be that the antelope would give way to horses, usually keeping a distance of approximately ten m between the two species. One exception to this was in the case of a stud fight, when all animals, horse and antelope alike, scattered. This portion of the study will be discussed qualitatively rather than quantitatively later in this paper.

Standard statistical procedures were used to analyze all data (Snedecor and Cochran 1976). Statistical significance was accepted at the 95 percent level of assurance unless otherwise noted.

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RESULTS AND DISCUSSION

The agronomy cages failed to produce the desired results. They had been positioned, by necessity, prior to summer dispersion of feral horses. The horses were concentrated in one large herd on the flat area between Round Mountain and Horse Heaven. Antelope were scattered throughout the study area. When the horses did disperse, they all moved east to Horse Heaven and remained there during the summer. As a result of this movement, this study was concentrated on Horse Heaven and consequently, only two agronomy cages were in the actual study area. Despite this, all six cages were treated as projected and material clipped and weighed.

Fifteen plant species were identified within the agronomy cages while a total of 54 species of vegetation were found within the study area as a whole (Table 2). Only five species were found in numbers sufficient for further analysis. An analysis of covariance performed on available data showed that a significant difference existed in the diameter to production relationship between cages for low sagebrush and Thurber's needlegrass *(Stipa thurberiana)*. Sandberg bluegrass, squirreltail *(Sitanion hystrix)*, and sand wort *(Arenaria spp.)* were essentially uniform throughout, but were of little value because they played an insignificant role in diet overlap, as determined by fecal analysis. The agronomy cages failed to reveal the true species diversity of the study area due to inadequate sampling. This fact points out the necessity that production sampling methods closely parallel or be an integral part of other vegetative sampling procedures.

Vegetative sampling by transect was designed to be used with the data collected from the agronomy cages to predict forage production.

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Table 2. Vegetational characteristics of the study area.

Common Name (*Scientific Name*)	[a]Freq.	[b]Cover		Density	
		Percent	[c]C.I.	Plant/m^2	C.I.
Shrubs					
Low sagebrush (*Artemisia arbuscula*)	98	21.2	±2.43	3.28	±0.433
Big sagebrush (*A. tridentata*)	14	3.6	±3.11	0.07	±0.022
Mountain mahogany (*Cercocarpus ledifolius*)	d				
Twistleaf rabbitbrush (*Chrysothamnus viscidiflorus*)	64	2.9	±1.07	0.69	±0.263
Bitterbrush (*Purshia tridentata*)	10	1.6	±2.34	0.01	±0.015
Snowberry (*Symphoricarpos parishii*)	4	0.1	±0.25	0.002	±0.004
Grey horsebrush (*Tetradymia canescens*)	8	0.1	±0.15	0.01	±0.015
Totals		29.5	±4.11	4.06	±0.465
Forbs					
Western yarrow (*Achillea millefolium*)	d				
Mountain dandelion (*Agoseris spp.*)	2	e	--	0.01	±0.024
Wild onion (*Allium spp.*)	d				
Pussytoes (*Antennaria spp.*)	d				

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Table 3. Continued.

Common Name *(Scientific Name)*	[a]Freq.	[b]Cover Percent	[c]C.I.	Density Plant/m^2	C.I.
Rock cress *(Arabis spp.)*	50	e	--	0.10	±0.047
Sand wort *(Arenaria spp.)*	60	0.4	±0.15	1.81	±0.735
Aster *(Aster scopulorum)*	42	0.2	±0.12	0.76	±0.445
Woolypod locoweed *(Astragalus purshii)*	22	e	--	0.14	±0.157
Locoweed *(A. spp.)*	24	0.1	±0.07	0.18	±0.119
Balsamroot *(Balsamorhiza spp.)*	70	0.8	±0.31	0.82	±0.330
Paint brush *(Castilleja spp.)*	6	e	--	0.01	±0.007
Goosefoot *(Chenopodium rubrum)*	d				
Tansey mustard *(Descurainia pinnata)*	d				
Austin's daisy *(Erigeron austinae)*	6	e	--	0.02	±0.040
Fleabane *(E. bloomeri)*	66	0.1	±0.06	0.89	±0.449
Wild buckwheat *(Eriogonum latens)*	60	0.3	±0.13	0.27	±0.106
Wild buckwheat *(E. microthecum)*	22	0.2	±0.12	0.10	±0.084
Wild buckwheat *(E. spp.)*	8	0.1	±0.20	0.02	±0.021

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Table 3. Continued

Common Name (*Scientific Name*)	[a]Freq.	[b]Cover Percent	[c]C.I.	Density Plant/m^2	C.I.
Green gentian (*Frasera spp.*)	6	e	--	0.02	±0.028
Stemless goldenweed (*Haplopappus acaulis*)	24	0.2	±0.11	0.16	±0.098
Iris (*Iris missouriensis*)	d				
Peppergrass (*Lepidium perfoliatum*)	d				
Prickley gilia (*Leptodactylon pungens*)	14	0.2	±0.19	0.11	±0.112
Lupine (*Lupinus spp.*)	20	0.6	±0.52	0.50	±0.483
Evening primrose (*Oenothera tanacetifolia*)	d				
Hounds-tongue (*Penstemon speciosus*)	d				
Beard-tongue (*P. spp.*)	6	e	--	0.19	±0.268
Phlox (*Phlox hoodii*)	70	0.6	±0.25	1.04	±0.535
Cinquefoil (*Potentilla spp.*)	d				
Dock (*Rumex spp.*)	d				
Dandelion (*Taraxacum officinale*)	d				
Clover (*Trifolium macrocepholum*)	2	e	--	0.06	±0.129

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Table 3. Continued.

Common Name (*Scientific Name*)	[a] Freq.	[b] Cover Percent	[c] C.I.	Density Plant/m^2	C.I.
Death camus (*Zigadenus spp.*)	d				
[f] Unknown forbs	4	e	--	0.01	±0.017
Totals		3.8	±0.65	7.23	±1.794
Grass and Grass-Like					
Bluebunch wheatgrass (*Agropyron spicatum*)	16	0.1	±0.08	0.07	±0.064
Cheatgrass (*Bromus tectorum*)	4	e	--	--	--
Sedge (*Carex spp.*)	d				
Great Basin wildrye (*Elymus cinereus*)	d				
Idaho fescue (*Festuca idahoensis*)	d				
Meadow barley (*Hordeum brachyantherum*)	d				
Foxtail barley (*H. jubatum*)	24	0.1	±0.08	0.38	±0.341
Wiregrass (*Juncus spp.*)	d				
Junegrass (*Koeleria cristata*)	2	e	--	0.02	--
Mat muhly (*Muhlenbergia richardsonis*)	d				

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Table 3. Continued

Common Name *(Scientific Name)*	[a]Freq.	[b]Cover Percent	[c]C.I.	Density Plant/m^2	C.I.
Sandberg bluegrass *(Poa sandbergii)*	98	1.7	±0.33	6.20	±0.957
Squirreltail *(Sitanion hystrix)*	90	0.3	±0.09	1.39	±0.374
Thurbers needlegrass *(Stipa thurberiana)*	28	0.2	±0.13	0.22	±0.159
[f]Unknown grass	58	0.2	±0.08	1.01	±0.491
Totals		2.5	±0.38	9.29	±1.237
Grand Totals		35.8	±4.32	20.58	±2.310

[a]Plot size: 10 m^2 (0.5 x 20 m).
[b]Crown cover for shrubs and forbs, basal cover for grasses.
[c]Confidence Interval ($P < .05$).
[d]Species was not recorded in sample plot.
[e]Cover less than 0.05 percent.
[f]Unknown plants either grazed too low or were too weathered for identification.

The sampling process was laborious and time-consuming and, with the failure of the cages to produce usable results, did not produce the desired estimates of forage production. It did, however, allow for the estimation of percent cover and density (Table 2).

The total vegetative cover (basal for grass plus crown for shrubs and forbs) was estimated to be 35.8 ± 4.32 percent with the bulk of this coming from low sagebrush at 21.2 ± 2.43 percent. Other shrubs contributed lesser amounts for a total shrub crown cover of 29.5 ± 4.11 percent and a density of 4.06 ± 0.465 plants per square meter. Total forb crown cover was 3.8 ± 0.65 percent with no species contributing in excess of one percent. The forb density was much higher than shrubs at 7.23 ± 1.794 plants per square meter with sand wort and phlox *(Phlox hoodii)* being the two major contributors. Grasses provided less ground cover (2.5 ± 0.38%) than the other plant groups but grass density was greatest with a 9.29 ± 1.237 plants per square meter. By far the most common plant in the study area was Sandberg bluegrass with over six plants per square meter. This was the only plant, other than sagebrush and rabbitbrush, that contributed ground cover in excess of one percent. This grass, however, receives little if any, summer use due to its early maturation. As can be seen from the species list (Table 2), the study area produced a highly diverse and relatively dense (20.58 ± 2.310 plants per square meter) vegetative community.

The patchy nature of the vegetation is evident when examining the frequency of plant appearance. Three species were recorded in only one plot, while only nine species appeared in over one-half of the plots. The number of individual plants appearing in the 10 square meter plots

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varied from 100 to 458. Those plots with few plants were generally in the more fertile areas with larger plants, while the high density plots were usually those with poor soil and an abundance of small desert adapted plants such as bluegrass, sand wort, and phlox.

There were plant specimens collected in the study area that did not appear in a plot and would, therefore, be considered rare. Some of these rare plants were used by horses or antelope, as subsequent fecal analysis indicated. This fact illustrated the difficulty of obtaining complete information while working with populations of free-roaming animals covering a relatively large area. It was evident that pockets of certain types of vegetation were missed during the sampling process. The study area was selected based on use during daylight hours; therefore, it is quite possible that the study animals grazed outside the designated study area during the hours of darkness. It is felt that this does not invalidate the study because none of these rare plants contributed significantly (over 5%) to either herbivore's diet.

Fecal analysis indicated a wide range of plant species taken by both feral horses and pronghorn antelope (Table 3). Each herbivore species, however, appeared to have certain plant species that it preferred. In the case of the pronghorn, the combination of western yarrow *(Achillea millefolium)*, Austin's daisy *(Erigeron austinae)*, and cinquefoil *(Potentilla spp.)* made up 17.3 ± 9.27 percent of diet, while only a trace (less than 0.05% cover) of these species were found in the vegetative sampling. This indicated that these plants were highly preferred during July, 1977. Bluebunch wheatgrass *(Agropyron spicatum)* and Thurber's needlegrass made up 37.8 ± 10.32 percent of the feral horse diet, while

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Table 3. Botanical composition of feral horse and pronghorn antelope diets in northwestern Nevada, July, 1977.

Species	Diet Composition (Percent ± Confidence Interval) Antelope	Horse
Shrubs		
Artemisia spp.	18.0 ± 6.01	0 ---
Chrysothamnus viscidiflorus	14.0 ± 3.71	1.3 ± 1.18
Purshia tridentata	11.0 ± 3.71	0.2 ± 0.61
Symphoricarpos parishii	0.8 ± 1.53	0 ---
Totals	43.7 ± 5.23	1.5 ± 1.26
Forbs		
Achillea millefolium	3.7 ± 2.10	0 ---
Arenaria spp.	0.5 ± 0.92	3.1 ± 2.28
Aster scopulorum	0 ---	1.6 ± 2.36
Astragalus spp.	3.6 ± 1.43	0 ---
Balsamorhiza spp.	0.3 ± 0.72	0.6 ± 1.14
Castilleja spp.	0 ---	0.2 ± 0.61
Chenopodium rubrum	1.7 ± 1.54	0 ---
Erigeron austinae	7.7 ± 3.69	1.5 ± 1.41
E. bloomeri	2.2 ± 0.90	0 ---
Eriogonum spp.	12.2 ± 4.38	0 ---
Iris missouriensis	0.3 ± 0.72	0 ---
Leptodactylon pungens	2.7 ± 3.87	1.2 ± 1.77
Lupinus spp.	0 ---	5.7 ± 3.42
Oenothera tanacetifolia	1.1 ± 1.44	0 ---
Penstemon spp.	4.9 ± 2.46	0.9 ± 1.04
Phlox hoodii	5.0 ± 3.88	7.5 ± 3.20
Potentilla spp.	5.9 ± 3.48	0.4 ± 0.65
Taraxacum officinale	0.3 ± 0.78	0 ---
Unknown forb	1.6 ± 0.82	0.3 ± 0.67
Totals	53.5 ± 6.15	23.0 ± 4.37
Grass and Grass-Like		
Agropyron spicatum	0 ---	7.8 ± 2.21
Bromus tectorum	1.3 ± 1.10	0 ---
Elymus cinereus	0 ---	0.2 ± 0.55
Hordeum brachyantherum	0 ---	1.6 ± 1.70
H. jubatum	0 ---	12.8 ± 5.25
Koeleria cristata	0 ---	7.2 ± 1.55
Muhlenbergia richardsonis	0 ---	0.5 ± 1.38
Poa sandbergii	0 ---	0.9 ± 1.23
Sitanion hystrix	0.3 ± 0.78	13.3 ± 1.59
Stipa thurberiana	0.9 ± 1.60	30.0 ± 8.11
Carex spp.	0.3 ± 0.72	0 ---
Juncus spp.	0 ---	0.8 ± 1.05
Unknown grass	0 ---	0.4 ± 0.68
Totals	2.5 ± 2.63	75.6 ± 4.42

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the total cover of the two species was only 0.3 ± 0.21 percent. This again indicated highly preferred forage species. During vegetative sampling, it was difficult to find needlegrass that had not been grazed except where protected by other vegetation. This latter observation indicated to this author that horses may be reluctant to force their way into sagebrush plants to obtain grass when other forage is more readily available.

There were 23 different plant species identified in antelope feces and 22 species in horse feces. A comparison of plant growth forms utilized by the two herbivores displayed the divergent preferences. Shrubs contributed 43.7 ± 5.23 percent to the antelope diet while only 1.5 ± 1.23 percent to that of the horse. Grasses were just the opposite, with the horse diet being 75.6 ± 4.42 percent grass, while the antelope used only 2.5 ± 2.63 percent grass. Forbs contributed significantly to both diets, comprising 53.5 ± 6.15 percent of antelope and 23.0 ± 4.37 percent of horse diets.

Fecal analysis revealed that 12 plant species were taken to some degree by both horses and antelope (Table 3). It must be noted, however, that of these 12, only phlox contributed significantly (5% or more) to both herbivore diets. This plant was the second most abundant forb available (1.04 ± 0.535 plants per square meter) within the study area and was in full bloom during the period that the fecal samples were collected. Three other plant species contributed over one percent to the diet of both herbivore species. Rabbitbrush use by antelope (14.0 ± 3.71%) was an expected result, but the horse use (1.3 ± 1.18%) of this shrub was not confirmed by visual observation. Antelope were frequently observed

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grazing on rabbitbrush but horses were never observed using this shrub. The other two species under discussion here, Austin's daisy and prickley gilia *(Leptodactylon pungens)*, are both low growing plants making direct observation of grazing virtually impossible. The fact that antelope and horses used Austin's daisy, when it was rare, indicated that it was an actively sought after plant by both species. This was an indication of potential competition, but should not be weighed too heavily since the slight use by horses is not exceptionally precise. Prickley gilia was more common and did not contribute significantly to either species' diet and should therefore not be considered as a source of serious competition.

The two diets were compared by two statistical methods, Spearman's rank correlation coefficient (r_s) (Snedecor and Cochran 1976) and Kulcyzenski's similarity index (SI) (Oosting 1956). The results of neither of these methods should be taken as absolute values. Rather, these values are indicators of diet similarity or dissimilarity and as such should be mutually supportive in nature.

Spearman's r_s is computed using the formula:

$$r_s = 1 - \frac{6 \sum d^2}{n(n^2 - 1)}$$

where d is the difference in ranks between the paired observations and n is the number of paired observations. The rank correlation can range from +1 to -1, complete concordance to complete discordance. This is the most widely used measure of diet overlap. Its use in this case may therefore enable this experiment to be compared with like studies and lend support to later findings.

The result of the computation in this study is $r_s = -0.327$. This indicates some degree of discordance. The diets are statistically

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different ($P < .10$) which is consistent with the relatively small diet overlap discussed above and quantified below.

Kulcyzenski's similarity index (SI) was used to compute the amount of overlap that existed between the diets of horses and antelope. It is computed using the formula:

$$SI = \frac{\sum 2W}{\sum (a + b)} \times 100$$

where W is the lesser percentage of a food species in the diets being compared and a + b is the sum of the percentages of that species in both diets. The results of this analysis showed that there was a 12.78 percent overlap between feral horses and pronghorn antelope in the study area during July 1977. The subject species shared that percentage of the total forage selected. This index is, of course, valid only for the location and conditions that existed at the time the sample was taken.

An extension of Kulcyzenski's index which may be used as a management tool is that developed by Sazama (1975), which estimates forage made available to a herbivore by removal of another herbivore from the range. This procedure uses the formula:

$$DU_A = \frac{DMI_R \times SI}{DMI_A}$$

where DU_A is the increased days-use of forage made available to herbivore species A, DMI_R is the daily dry matter intake rate of herbivore species R removed from the range, DMI_A is the daily dry matter intake rate of herbivore A, and SI is Kulcyzenski's similarity index. Average weights were estimated at 410 kg for horses and 45 kg for antelope. Computations based on the above assumptions indicate that the removal of one horse would make additional forage available sufficient for 0.939 or

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approximately one antelope.

This information would be valid only for the location and conditions that existed during the summer of 1977. Because this conversion number is site specific, it would be of considerable value to resource managers to have like conversions available to them for various sites and conditions under their control. A more common practice is to transform antelope numbers into Animal Unit Months and apply this calculation to vast areas under all conditions (Hjersman and Yoakum 1959). This latter practice could prove detrimental to both the wildlife concerned and to their habitat. Based solely on weight, one horse consumes approximately the same amount of dry forage as seven antelope. However, when considering dietary overlap, the replacement ratio is approximately one to one. Replacement stocking levels established on a weight basis could place excessive pressure on the overlap vegetation and cause its elimination from the habitat. This loss would require the affected herbivores to switch diet or to migrate to new feeding areas.

The factors controlling the population sizes of the *potentially* competing species and the role of the food items used in common must be known in order to assess the significance of dietary overlap. If both populations were limited by factors other than food resources, e.g., predation or social behavior, dietary overlap may be of no consequence and should not be considered as competition. The additional food made available to one species by a reduction in numbers of the other species concerned would not be utilized. There would be no numerical response by one species to removal of the other. An exception must be made for food items that are actively sought after and taken whenever found. Such food

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items are always in danger of local extinction due to their desirability. Management of the area should not be based on the preservation of highly desirable species, unless the inclusion of this item in the diet was essential to at least one of the species concerned. In this study, Austin's daisy might be considered a highly desirable species. It was a rare plant (Table 2) and was found in both antelope (7.7 ± 3.7%) and horse (1.5 ± 1.4%) diets. Further research on the role of Austin's daisy is required before the competition for this plant can be assessed.

The feral horse population at the Sheldon Antelope Range is controlled by trapping and removal. The factors limiting the antelope population are not known at this time. If it were assumed that this population is limited by food resources, the overlap vegetation takes on a much different role. Under this assumption, a reduction in horse numbers would make more forage available to antelope and the antelope population should increase by a number equal to the number of horses removed. The manager should be aware of this one to one replacement rather than to expect each horse to be replaced by seven antelope, as would be expected considering only forage requirements based on animal weight.

The resource manager must consider wildlife food requirements when determining stocking levels of exotic animals, e.g., seasonal livestock grazing. The diet overlap and the role of the overlap vegetation should be known. He must also know the population limiting factors of the wildlife concerned. Where the wildlife population is limited by food resources, the manager must determine the role of the overlap vegetation. If a plant within the overlap is a limiting factor, the manager must not

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permit the stocking of additional herbivores or he may be faced with a reduction in the resident population. Where overlap food items are not limiting factors, the manager may act as discussed below. Where the wildlife population is limited by factors other than food, the manager must consider the role of any overlap vegetation. In the event that overlap vegetation is essential to wildlife, the manager must stock exotics at the rate based on the demonstrated diet overlap and the availability of the plant species. Should the overlap vegetation be plentiful, or highly preferred plants, the manager should be able to stock at a rate based on daily dry forage requirements of the exotic species without affecting wildlife populations.

It must be noted that stocking levels based on dietary overlap could result in under-utilization of those plants used exclusively by one herbivore. This could, in turn, allow these unused plants to out-compete and displace those plants used by the resident herbivore. This reduction of preferred plants would lead to the deterioration of the habitat in terms of the resident population.

The results of the investigation into water hole interactions between horses and antelope indicate a lack of competition for water. Worthy of note, but not statistically valid, was the observation that antelope continue to utilize a water hole three to four days after horses have deserted it due to poor water quality. Water hole number 2 (Fig. 2) dried up both summers while experiencing extensive use by both species. On both occasions, the horses transferred their attention to water hole number 3 (Fig. 2) when the water in hole number 2 reached some unacceptable level. Antelope continued to use water hole number 2 even though the sediment

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load was such that cracks would be evident on the surface when the water was not roiled. This would indicate that antelope are adapted to utilize a poorer quality of water than horses. Because of this, it would appear that the antelope could out-compete horses during a drought year. This should not be taken as conclusive, since a badly lamed horse was observed to survive for four days by ingesting mud for water. This was a strayed domestic horse which was subsequently picked up by its owner and recovered fully. This indicated that horses will use poor quality water if necessary, but do not if better water is available.

During the summer of 1978, a total of 142 measurable observations were made of antelope watering. The observations were partitioned into four categories:

I. Horses within 800 m of the water (N = 51).

II. Horses (or cattle) over 800 m from, but in sight of, the water (N = 27).

III. Horses (or cattle) out of sight of the water (N = 43).

IV. Cattle within 800 m of the water (N = 21).

Additionally, there were 35 usable observations of antelope watering made during the procedures test in the summer of 1977. These observations all fell into Category I.

An analysis of covariance was performed to determine if the 1977 observations could be combined with the 1978 data. This test compared the number of antelope and watering times of each set of data. The results of this analysis indicated that these relationships were significantly different for the two years, with antelope drinking longer during a dry year (1977) than during a wet year (1978). This difference

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cannot be explained by temperatures because the average highs were comparable during both periods (Table 1). Wind data were not available, but higher wind velocities in 1977 could have caused increased water loss due to evaporation which would, in turn, require increased intake. The 1977 data will not be further discussed in this paper.

An analysis of variance was used to ascertain if any differences existed in the sizes of the watering antelope herds between the four categories. The results of this analysis failed to reveal any significant difference between the four categories. Since all antelope herds were considered to be from one population, comparative statistical analysis could be performed.

Analysis of covariance comparing drinking times, adjusted for antelope numbers, between the four categories indicated no significant difference existed. Like tests conducted by adjusting drinking times with previous night's low temperature, current day's high temperature, and horse numbers and distance from water produced the same results. It is evident from this that antelope are not particularly concerned with the presence of other herbivores when they are drinking. Antelope and horses were observed on numerous occasions drinking together within an estimated five m of one another. Antelope also drank concurrently with cattle, although not as frequently as with horses. When drinking with horses, antelope tend to dash from the water when horses paw the water or cross the water hole directly toward them. This same reaction was observed when only antelope were watering and a dominant male splashed water. Therefore, it is believed to be a reaction to the unexpected rather than actual fear of a horse. Antelope appeared to have favored

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watering places at the water hole and would wait if horses occupied the places rather than water elsewhere. Antelope would generally move directly to their seemingly preferred places when horses occupied other parts of the water hole edge. In the case of water hole number 2 (Fig. 2), preferred entries were at the east and west ends. Little antelope watering took place elsewhere. These areas were the flattest approach to the water hole and afforded good visibility of the water hole from a distance. When watering at water hole number 3 (Fig. 2), the preferred places were at the extreme eastern end for small groups or singles. This area was the flattest approach to the water with good visibility. Large herds would water at the west end where a man-made cachment had resulted in a relatively high earthen dam and reduced visibility. This indicated that antelope prefer watering places with the best possible visibility but will forego this preference when in large herds. This indication was supported by a comparison of the natural versus the man-improved portion of water hole number 2 (Fig. 2). Analysis of covariance indicated that antelope spent more time ($P < .10$) drinking at a natural as opposed to a man-improved water hole. This is probably due to two factors: reduced visibility caused by the dam; and the extreme posterior-high position required for reaching water in a bulldozer-dug cachment. Resource managers should be aware of this preference and construct cachments as naturally as possible.

Testing for loafing time differences was performed through analysis of covariance, adjusting for the same factors as were used for drinking times. This analysis indicated that a significant difference existed between the loafing times of antelope among the four categories. The

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Duncun's Multiple Range test showed that antelope spent a significantly longer time loafing when horses were in sight of, but over 800 m from, the water hole. Multiple Regression performed on this treatment yielded an r^2 value of less than 0.01, indicating a total lack of correlation between the numbers of antelope in a herd and the loafing time. Further examination of the data revealed that it was marked by severe extremes, ranging from a doe herd of 11 animals loafing for 0.6 minutes to a 3-buck herd that bedded for 88.5 minutes. When these observations and two other extremes, 2-buck herds that loafed for 59.3 and 39.1 minutes each, were removed, the analysis of covariance indicated that there was no significant difference between the categories. This, like the analysis of drinking times, indicated that the antelope in the study area were unaffected in their loafing habits by the presence or absence of other large herbivores.

The observation of horse-antelope interactions under feeding or movement situations produced similar, though not quantifiable, results as did that of water hole interactions. In over 1,000 hours of observation, not one single act of aggression was noted between the two study species. Antelope normally gave way to moving horses, but did so with little disruption of their activities. The usual avoidance maneuver was that of walking perpendicular to the direction the horse was moving for 10 to 15 m and then resuming the former activity. This is probably just respect for a larger animal rather than a response triggered by former ill treatment. Exceptions to this rule usually resulted when the antelope appeared to be startled by the sudden appearance of the horse. Antelope would then run for a greater distance than when they walked. This latter

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behavior was also noted to occur on the sudden appearance of coyote *(Canis latrans)*, raven *(Corvus corax)* and sage grouse *(Centrocercus urophasianus)*, all of which are common in the study area. This is even a departure from the usual, in the case of coyotes, since the normal antelope reaction is one of curiosity followed by aggressive behavior.

One observation of a horse touching an antelope was observed. A territorial male antelope was standing in a horse trail observing a coyote at a distance when he was approached, from the rear, by a small band of horses. The lead mare of the band stopped at a distance of less than a meter. After a pause of a few seconds, and when the antelope did not move, the mare placed her nose between his back legs and lifted that part of him off the trail. The reaction of the antelope was swift and decisive--he rapidly departed the area. But after running approximately 100 m, he stopped and resumed his inspection of the coyote. This action was not considered agressive in nature, because the horse gave the antelope ample time to move prior to taking any action.

Observations were made which could indicate that some degree of symbiosis may exist between feral horses and pronghorn antelope. On numerous occasions, antelope, startled by human activity, were observed running toward bands of horses. In some cases, the initial stimulus was strong enough to cause the antelope to continue to run beyond the horses. In these cases, the antelope herd would run in one of two patterns, either on a relatively straight course or in an exaggerated zigzag fashion. It was noted that when the antelope ran straight past the horses, the only reaction of the horses would be one of curiosity. However, on all four occasions that the antelope ran the zigzag pattern, the horses would

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also run off in the same direction preceding the antelope. Three of these occasions were human evoked while the fourth was instigated by several coyotes feeding on a horse carcass.

On three separate occasions, it was observed that herds of antelope, upon approaching a water hole, ceased movement and waited some distance from the water with all members looking intently into the water hole. On two of these occasions, the antelope waited until horses entered the water hole and then proceeded to the water hole and drank simultaneously with the horses. In the third case, the antelope watered only after a raven flew onto the edge of the water hole. This may indicate that, when unsure of conditions, an antelope will use other organisms as a guide. These actions indicated that a symbiotic relationship may exist between antelope and other species, including feral horses.

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CONCLUSION

This study indicated that there was little competition existing between pronghorn antelope and feral horses in Horse Heaven during the summers of 1977 and 1978. The two species water and forage together freely, with antelope giving ground only when directly approached by horses. No aggressive action was observed by either species toward the other species.

The only area where a minor degree of competition may exist is in diet. The results of Kulcyzenski's and Sazama's formulas applied to the fecal analysis data indicated that horses and antelope share approximately 12 percent of their diets and, therefore, antelope and horse may exist in the area on a 1:1 replacement ratio.

Additional work is needed on a more comprehensive dietary overlap study at Sheldon Antelope Range and other areas to determine if more severe competition may exist at other times of the year.

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APPENDIX A

DETAILED INSTRUCTIONS FOR THE PREPARATION OF REFERENCE AND FECAL MATERIAL MICROSCOPE SLIDES

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These instructions follow, in part, those received from the Colorado State University Composition Analysis Laboratory (R. M. Hansen, pers. comm.).

Reference Slide Preparation:

1. Plants to be used were separated by plant parts: leaves, stems, and reproductive parts.

2. Material was oven dried for 24 h at 100 C to remove moisture.

3. Material was ground in a Wiley mill through a 20-mesh screen (1 mm openings).

4. Ground material was washed in hot water over a 200-mesh screen (0.074 mm openings) to remove extraneous solubles and extremely small nondiagnostic particles.

5. Material was soaked in household bleach (Clorox) to remove pigments. The time was variable according to how pale the material appeared to the naked eye. Maximum time used was approximately 15 minutes.

6. Material was rewashed in hot water over the 200-mesh screen to remove bleach and impurities caused by the bleaching action.

7. A small quantity of material was transferred to a glass slide mounting.

   Note: As practice for fecal slide preparation, where the amount of material must be approximately the same for all slides, a template was fabricated to result in three identifiable fragments per microscope field at 125 power. This template was fashioned from a 0.8 mm thick eave gutter-hanger by drilling 5 mm diameter holes at 2.5 cm intervals for a total of 5 holes. This allowed preparation of five slides at a time with the proper amount of material when using 22x22 mm cover slips.

8. Three drops of Hoyer's mounting medium were applied to and thoroughly mixed with the material on the slide. Hoyer's mounting medium is made by combining 200 g chloral hydrate crystals with 20 cc glycerine and adding 30 g photopurified gum arabic and 50 cc water.

9. A clean dissecting probe was used to distribute the material evenly over an area approximately the size of the cover slip.

10. A cover slip was placed over the material and the slide heated over an alcohol burner until all material was boiling evenly.

    Note: A comparison was made between the use of plastic and glass

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cover slips. Plastic cover slips produced the best results due to their ability to conform to the outline of plant fragments, thereby producing a thinner slide.

11. The slide was removed from the flame and immediately placed on a wet sponge to remove air bubbles.

12. The slide was then dried and transferred to the microscope for examination.

13. When microscopic examination revealed that material was sufficiently bleached to make identification possible, the four remaining slides of the same species were prepared in the same manner.

14. When microscopic examination revealed that the material had not been sufficiently bleached, a sub-routine was inserted between steps 7 and 8 above.

    7a. Two to three drops of Hertwig's clearing solution were added to and thoroughly mixed with material on the slide. Hertwig's clearing solution is made by combining 270 g of chloral hydrate crystals with 19 cc of 1 normal hydrochloric acid and adding 60 cc glycerine.

    7b. The slide was heated over the alcohol burner until solution was evaporated.

        Note: Some practice of step 7b is required to prevent burning of the plant material.

15. Slides were placed in an oven and baked at 55 C for 24 h minimum. This heating sets the mounting medium and renders a permanent slide.

Fecal Material Slide Preparation

1. Fecal material was removed from the freezer and emptied into beakers.

2. Beakers were covered with paper towels to preclude accidental contamination while allowing moisture to escape.

3. Material was oven dried at 100 C for 24 h to remove any moisture.

4. Material was ground in a Wiley mill through a 20-mesh screen.

5. Material was placed in a large clean jar with a sealing lid and agitated for 15 minutes to thoroughly mix the subsamples.

6. Ground material was washed in hot water over a 200-mesh screen to remove endogenous solubles and small particles.

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7. The remainder of the procedure is as outlined in Steps 5 through 15 for reference material. Test slides made indicated that, in all samples of animal feces collected, bleaching with Clorox was sufficient and produced better results than the use of Hertwig's solution.

   Note: The reason for making the fecal material slides permanent was to preclude movement of fragments during microscopic examination.

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APPENDIX B

A DICHOTOMOUS KEY TO AID IN THE IDENTIFICATION OF EPIDERMAL FRAGMENTS OF SELECTED FLORA IN THE CHARLES SHELDON ANTELOPE RANGE, NORTHWESTERN NEVADA WITH ILLUSTRATIVE PHOTOMICROGRAPHS

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1. The following key was designed as a tool, to be used in conjunction with photomicrographs, to aid in the determination of plant species that are components of the feces of large herbivores feeding in northwestern Nevada. It was not designed for absolute determination of all plant species.

2. The key is based on characteristics of leaf components of the species collected from the study area (Table 3). Like species growing under different conditions may vary slightly and may not fit this key.

3. Identification characteristics can usually be seen at 125X magnification, but it was learned that 250X magnification increases confidence of positive identification.

4. Microhistological terms used in this key follow those used by Metcalfe and Clarke (1950), Metcalfe (1960), and Cutler (1969).

5. Small fragments of plant material seldom contain multiple diagnostic characteristics after passing through a herbivore's digestive tract. Therefore, all clues must be consolidated to identify some species. Trichomes seldom remain attached to the epidermal fragments but serve as valuable clues as to the presence of certain species within the sample. There must be some degree of transfer of clues from one fragment to another in order to validate a characteristic that does not appear in the key.

6. Fragments from individual species may, and normally do, key to more than one couplet.

7. Numbers in parentheses refer to photomicrograph plates in this appendix. Photomicrographs were taken at 250X unless otherwise noted.

A.	Cells primarily linear in arrangement	B
A.	Cells usually not linear in arrangement	C
B.	Two sizes of cells present - long cells and two types of short cells (suberose and silica)	Key No. 1
B.	Not as above	Key No. 2
C.	Cell outline irregular, lobed (jigsaw puzzle)	Key No. 3
C.	Not as above	D
D.	Cells somewhat regular in outline, Triangular through polygon to round	Key No. 4
D.	Cells irregular, not as above	Key No. 5

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KEY NUMBER 1

1.	Microhair present (1a)	*Muhlenbergia richardsonis*
1.	Microhair absent	2
2.	Macrohair present	3
2.	Macrohair absent	25
3.	Stomata present	4
3.	Stomata absent	17
4.	Prickles present	5
4.	Prickles absent	9
5.	All stomata subsidiary cells with straight sides (9a)	*Koeleria cristata*
5.	Stomata subsidiary cells not as above	6
6.	Prickle height approximates .016 mm (2a)	*Festuca idahoensis*
6.	Prickle height exceeds .016 mm	7
7.	Prickle height approximates .02mm (3a)	*Agropyron spicatum*
7.	Prickle height exceeds .02 mm	8
8.	Prickle height approximates .024 mm (4a)	*Stipa thurberiana*
8.	Prickle height approximates .032 mm (1b)	*Muhlenbergia richardsonis*
9.	Macrohair less than .08 mm in length (6c)	*Hordeum jubatum*
9.	Macrohair exceeds .08 mm in length	10
10.	Macrohair less than .12 mm in length (5a)	11
10.	Macrohair exceeds .12 mm in length	13
11.	Stomata length exceeds .04 mm (7c)	*Elymus cinereus*
11.	Stomata length less than .04 mm	12
12.	Stomata length exceeds .032 mm (5b)	*Sitanion hystrix*
12.	Stomata length less than .032 mm (2b)	*Festuca idahoensis*
13.	Macrohair length less than .16 mm (3b)	*Agropyron spicatum*
13.	Macrohair length exceeds .16 mm	14
14.	Stomata length greater than width (4b)	*Stipa thurberiana*
14.	Stomata length less than or equal to width	15
15.	Stomata subsidiary cells straight (9a)	*Koeleria cristata*
15.	Stomata subsidiary cells convex	16
16.	Stomata subsidiary cells low-dome shaped (8b)	*Bromus tectorum*
16.	Stomata subsidiary cells triangular shaped (1c)	*Muhlenbergia richardsonis*

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17. Macrohair less than .08 mm in length (6c) *Hordeum jubatum*
17. Macrohair exceeds .08 mm in length 18

18. Macrohair less than .12 mm in length 19
18. Macrohair exceeds .12 mm in length 21

19. Cell walls smooth in vicinity of hairs 20
19. Cell walls sinuous in vicinity of hairs (5c) *Sitanion hystrix*

20. Cells relatively short and wide (7d) *Elymus cinereus*
20. Cells relatively long and narrow (2c) *Festuca idahoensis*

21. Macrohairs less than .16 mm in length (3b) *Agropyron spicatum*
21. Macrohairs exceed .16 mm in length 22

22. Macrohairs moderately long and flexuose (4c) *Stipa thurberiana*
22. Macrohairs straight or slightly bent 23

23. Macrohairs with swollen bases (desk pen) (9b) *Koeleria cristata*
23. Macrohairs not as above 24

24. Macrohairs appear rigid with slightly swollen base (1d) *Muhlenbergia richardsonis*
24. Macrohairs appear flexible with sunken base (8c) *Bromus tectorum*

25. Stomata present 26
25. Stomata absent 43

26. Prickles present 27
26. Prickles absent 33

27. All stomata subsidiary cells with straight sides (9a) *Koeleria cristata*
27. Stomata subsidiary cells not as above 28

28. Prickle height approximates .016 mm (2a) *Festuca idahoensis*
28. Prickle height exceeds .016 mm 29

29. Prickle height approximates .02 mm (3a) *Agropyron spicatum*
29. Prickle height exceeds .02 mm 30

30. Prickle height approximates .024 mm 31
30. Prickle height exceeds .024 mm 32

31. Distal outline of prickle straight (6a) *Hordeum brachyantherum*
31. Distal outline of prickle curved (4a) *Stipa thurberiana*

32. Prickle height approximates .028 mm (9d) *Poa sandbergii*
32. Prickle height approximates .032 mm (1b) *Muhlenbergia richardsonis*

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33. All stomata subsidiary cells with straight sides (9a) *Koeleria cristata*
33. Stomata subsidiary cells not as above 34

34. Stomata length exceeds .06 mm (7c) *Elymus cinereus*
34. Stomata length less than .06 mm 35

35. Stomata length exceeds .04 mm (7a) *Hordeum jubatum*
35. Stomata length less than .04 mm 36

36. Stomata length equal to or less than width 37
36. Stomata length exceeds width 38

37. Stomata subsidiary cells low-dome shaped (8b) *Bromus tectorum*
37. Stomata subsidiary cells triangular shaped (1c) *Muhlenbergia richardsonis*

38. Stomata length less than .032 mm 39
38. Stomata length exceeds .032 mm 40

39. Stomata subsidiary cells low-dome shaped or straight sided (4b) *Stipa thurberiana*
39. Stomata subsidiary cells high-domed or triangular shaped (2b) *Festuca idahoensis*

40. Cell wall sinuations shallow (6b) *Hordeum brachyantherum*
40. Cell wall sinuations deeper 41

41. Stomata outline square in appearance (10a) *Poa sandbergii*
41. Stomata outline ovate in appearance 42

Note: Silica cells or bodies must be present for the remainder of this key.

42. Suberose pairs rare (5d) *Sitanion hystrix*
42. Suberose pairs common (3c) *Agropyron spicatum*

43. Suberose pairs consist of large cork and small silica cells 44
43. Suberose pairs not as above 46

44. Suberose pairs relatively small (4b) *Stipa thurberiana*
44. Suberose pairs relatively large (8a) *Elymus cinereus*

45. Silica bodies longer than wide with sinuous outline 46
45. Silica bodies not as above 48

46. Bodies small with deep indentation (4d) *Stipa thurberiana*
46. Bodies large with shallow indentation 47

47. Bodies only slightly longer than wide (9c) *Koeleria cristata*
47. Bodies much longer than wide (10b) *Poa sandbergii*

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48. Silica cells square and alternate with cork cells in long rows (1c) *Muhlenbergia richardsonis*
48. Silica cells not as above 49

49. Silica cells rectangular and alternate with cork cells in long rows (6c) *Hordeum brachyantherum*
49. Silica cells not as above 50

50. Silica cells much longer than wide with straight sides (8d) *Bromus tectorum*
50. Silica cells not as above 51

51. Silica cells are mid-length between long and cork cells (2d) *Festuca idahoensis*
51. Silica cells appear as silicified long cells 52

52. Silica cell sides deeply indented (5b) *Sitanion hystrix*
52. Silica cell sides less deeply indented 53

53. Silica cells appear between the veins (3d) *Agropyron spicatum*
53. Silica cells appear over the veins (7b) *Hordeum jubatum*

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KEY NUMBER 2

1.	Cells usually longer than 4 times width	2
1.	Cells usually shorter than 4 times width	33
2.	Prickles present (10c)	*Carex spp.*
2.	Prickles absent	3
3.	Macrohairs present	4
3.	Macrohairs absent	12
4.	Branched hair present (19a)	*Descurainia pinnata*
4.	Hair not as above	5
5.	Two-armed hair present (19d)	*Artemisia arbuscula*
5.	Hair not as above	6
6.	Uniserrate, multicellular hair (pod-like) present (21a)	*Lepidium perfoliatum*
6.	Hair not as above	7
7.	Uniserrate multicellular hair with knees present (13a)	*Leptodactylon pungens*
7.	Hair not as above	8
8.	Arachnoid multicellular hair present (14a)	*Phlox hoodii*
8.	Hair not as above	9
9.	Large unicellular hair present (exceeds .2 mm) (12a)	*Iris missouriensis*
9.	Hair not as above	10
10.	Short, stout unicellular hair with rounded tip present (21d)	*Arenaria spp.*
10.	Hair not as above	11
11.	Short unicellular hair with rounded tip (13b)	*Leptodactylon pungens*
11.	Short unicellular hair with pointed tip (23b)	*Penstemon spp.*
12.	Crystals present	13
12.	Crystals absent	15
13.	Rod-like crystals present (12b)	*Iris missouriensis*
13.	Clustered crystals present	14
14.	All cells linear in arrangement (22a)	*Arenaria spp.*
14.	Linear cells in bands, bordered by irregular cells (20a)	*Artemisia arbuscula*
15.	Stomata present	16
15.	Stomata absent	24

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16. Stomata arranged in rows 17
16. Stomata arranged randomly 20

17. Interstomatal distance exceeds 3 times cell width (22b) *Arenaria spp.*
17. Interstomatal distance less than 3 times cell width 18

18. Interstomatal distance approximates or exceeds twice stomata length (21b) *Lepidium perfoliatum*
18. Interstomatal distance approximates stomata length 19

19. Cell walls straight (11c) *Allium spp.*
19. Cell walls sinuous (10d) *Carex spp.*

20. Cell walls strongly lobed (13c) *Leptodactylon pungens*
20. Cell walls essentially straight 21

21. All cells linear in arrangement (19b) *Descurainia pinnata*
21. Linear cells in bands bordered by irregular shaped cells 22

22. Cells essentially square at joint (23c) *Penstemon spp.*
22. Cell juncture not as above 23

23. Cell wall appears dashed at certain focus (20a) *Artemisia arbuscula*
23. Cell wall appears entire at any focus (14b) *Phlox hoodii*

24. Cell walls strongly lobed (13d) *Leptodactylon pungens*
24. Cell walls not as above 25

25. Cell walls sinuous (grass-like) (11a) *Carex spp.*
25. Cell walls not as above 26

26. Cells elongate-hexagon (11d) *Allium spp.*
26. Cells not as above 27

27. Cell length exceeds 10 times cell width 28
27. Cell length less than 8 times cell width 30

28. Cells extremely elongate-hexagon (12c) *Iris missouriensis*
28. Cells not as above 29

29. Cells so long, juncture difficult to locate (21b) *Lepidium perfoliatum*
29. Cell length barely exceeds 10 times width (19b) *Descurainia pinnata*

30. Cell walls appear "dashed" at certain focus 31
30. Cell walls appear entire at any focus (14b) *Phlox hoodii*

31. All cells linear in arrangement (22a) *Arenaria spp.*
31. Linear cells in bands bordered by irregular shaped cells 32

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32. Cells usually irregular at juncture (20a) *Artemisia arbuscula*
32. Cells usually square at juncture over 2 cell widths from irregular shaped cells (23c) *Penstemon spp.*

33. Stalked capitate glands present *Zigadenus spp.*
33. Stalked capitate glands absent 34

34. Hairs present 35
34. Hairs absent 42

35. Branched hairs present 36
35. Hair not as above 37

36. Branches less than .03 mm in length (35d) *Arabis spp.*
36. Branches greater than .04 mm in length (34c) *Astragalus spp.*

37. Heavy pointed unicellular hair present (exceeds .2 mm) (12a) *Iris missouriensis*
37. Hair not as above 38

38. Heavy rounded unicellular hair present (24a) *Zigadenus spp.*
38. Multicellular uniserrate hairs present 39

39. Hair cells approximately equal in length 40
39. Terminal cell of hair elongated 41

40. Hairs erect, perpendicular to plant surface (36a) *Castilleja spp.*
40. Hairs lie at angle to plant surface (15a) *Chrysothamnus viscidiflorus*

41. Hair base cell moderately dumbbell shaped (24d) *Balsamorhiza hookeri*
41. Hair base cell moderately ovate (25c) *Balsamorhiza sagittata*

42. Crystals present 43
42. Crystals absent 44

43. Rod-like crystals present (12b) *Iris missouriensis*
43. Crystals in bundles (24b) *Zigadenus spp.*

44. Stomata present 45
44. Stomata absent 49

45. Stomata length exceeds .04 mm 46
45. Stomata length less than .03 mm 47

46. Cells hexagon in outline (24c) *Zigadenus spp.*
46. Cell walls parallel (straight and curved) (15b) *Chrysothamnus viscidiflorus*

47. Cell walls sinuous (11b) *Juncus spp.*
47. Cell walls straight 48

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48. Cell junctures perpendicular to cell wall (12d) *Iris missouriensis*
48. Cell junctures variable (pointed to square) (35c) *Arabis spp.*

49. Cells hexagon in appearance 50
49. Cell walls essentially parallel 51

50. Cell length essentially equal, hexagon shape strong (24c) *Zigadenus spp.*
50. Cell length variable, hexagon shape weak (12d) *Iris missouriensis*

51. Cell outline appears "dashed" under certain focus (35c) *Arabis spp.*
51. Cell outline appears entire at any focus 52

52. Hair base cell holes numerous (34b) *Astragalus spp.*
52. Hair base cell holes sparse 53

53. Hair base cell holes ovate (15b) *Chrysothamnus viscidiflorus*
53. Hair base cell holes round 54

54. Cells modified around hair base cell holes (25a) *Balsamorhiza hookeri*
54. Cells surrounding hair base cell holes not modified (36d) *Castilleja spp.*

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KEY NUMBER 3

1. Papilla present 2
1. Papilla absent 3

2. Cell outline distinct, elongate papilla cells appear as separate from epidermal cells (13d) *Leptodactylon pungens*
2. Cell outline indistinct, papilla appears to be part of epidermal cells (14c) *Phlox hoodii*

3. Macrohair present 4
3. Macrohair absent 10

4. Hair uniserrate, multicellular, terminal cell whip-like (26a, 26b) *Achillea millefolium*
4. Hair not as above 5

5. Hair uniserrate, multicellular with enlarged base, cells of equal length (26d) *Erigeron austinae*
5. Hair not as above 6

6. Hair long, pod-like in appearance (21a) *Lepidium perfoliatum*
6. Hair not as above 7

7. Hair unicellular with swollen tips (36c) *Frasera spp.*
7. Hair not as above 8

8. Hair long, arachnoid, multicellular (14a) *Phlox hoodii*
8. Hair not as above 9

9. Hair long, uniserrate, multicellular, cells short and wide (28b) *Taraxacum officinale*
9. Hair uniserrate, multicellular with enlarged junctures or short unicellular hairs with blunt tips (13a, 13b) *Leptodactylon pungens*

10. Cells much longer than wide, linear in arrangement 11
10. Cells may be longer than wide, but not arranged linearly 12

11. Lobes seldom exceed one-half cell width (13c) *Leptodactylon pungens*
11. Lobes often equal to or greater than cell width, may be bordered by straight sided cells (14b, 14d) *Phlox hoodii*

12. Numerous cells elongate but not linear in arrangement (26c) *Achillea millefolium*
12. Few cells elongate 13

13. Modified macrohair base cells present (27a) *Erigeron austinae*
13. Not as above 14

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14. Cells diverse in shape but generally of one size (36d) *Frasera spp.*

14. Cells diverse in shape and size 15

15. Cells appear coarse, broad lobed (21c) *Lepidium perfoliatum*

15. Cells appear less coarse, narrow lobed (28c) *Taraxacum officinale*

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KEY NUMBER 4

1.	Hair present	2
1.	Hair absent	15
2.	Stalked capitate gland present (29a)	3
2.	Not as above	4
3.	Hair short stout, unicellular (29b)	*Potentilla spp.*
3.	Hair long, multicellular (36a)	*Castilleja spp.*
4.	Branched hairs present	5
4.	Hairs not as above	6
5.	Cells random in arrangement, generally round (35d)	*Arabis spp.*
5.	Cells arranged in circular patterns, generally oblong (19c)	*Descurainia pinnata*
6.	Hair unicellular with enlarged tip	7
6.	Hair not as above	8
7.	Hair short (.04 mm), flexuose (29d)	*Chenopodium rubrum*
7.	Hair long (.08 mm), straight (36c)	*Frasera spp.*
8.	Hair cylindrical, unicellular with round tip (22c)	*Penstemon speciosus*
8.	Hair not as above	9
9.	Hair uniserrate, multicellular	10
9.	Hair not as above	11
10.	Hair stands perpendicular to surface (36a)	*Castilleja spp.*
10.	Hair lies parallel to surface (30c)	*Rumex spp.*
11.	Hair unicellular, straight, long or short	12
11.	Hair unicellular, long, arachnoid	14
12.	Hair long, straight or curved with modified base (31b, 31c, 31d)	*Lupinus spp.*
12.	Hair not as above	13
13.	Hair robust, straight or curved with enlarged base (29b)	*Potentilla spp.*
13.	Hair less robust, lacking enlarged base (32a, 32b)	*Symphoricarpos parishii*
14.	Hair of one size, crystals lacking, hair base cells location independent of cell structure (37a, 37b)	*Tetradymia canescens*
14.	Hair of two sizes, crystals may or may not be present, hair base cells always at juncture of four or more cells (16a, 16b, 16c)	*Eriogonum spp.*

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15.	Crystals present	16
15.	Crystals absent	18
16.	Cell walls thick (30d, 31a)	*Rumex spp.*
16.	Cell walls thin	17
17.	Hair subcell holes always at juncture of four or more cells (16c)	*Eriogonum spp.*
17.	Hair subcell holes lacking or not evident (30a)	*Chenopodium rubrum*
18.	Stomata round	19
18.	Stomata ovate	20
19.	Diameter small (16d)	*Eriogonum spp.*
19.	Diameter larger (22d)	*Penstemon speciosus*
20.	Length exceeds .04 mm (36d)	*Frasera spp.*
20.	Length less than above	21
21.	Length exceeds .036 mm (30b) (23a)	*Chenopodium rubrum* or *Penstemon speciosus*
21.	Length less than above	22
22.	Length exceeds .03 mm (32c)	*Symphoricarpos Parishii*
22.	Length less than above	23
23.	Small, less than .024 mm long, low domed (35c)	*Arabis spp.*
23.	Larger than above	24
24.	Stomata numerous (16d)	*Eriogonum spp.*
24.	Stomata sparse (29c)	*Potentilla spp.*

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KEY NUMBER 5

1.	Hairs present	2
1.	Hairs absent	21
2.	Hairs two- or three-armed	3
2.	Hairs not as above	5
3.	Hairs two- and three-armed to complex (32d)	*Agoseris spp.*
3.	Hair always two-armed (20c)	4
4.	Irregular cells accompanied by linear cells (20a)	*Artemisia arbuscula*
4.	All cells irregular in shape (20d)	*Artemisia tridentata*
5.	Hairs multicellular, uniserrate silicified (37c)	*Astor scopulorum*
5.	Hairs not as above	6
6.	Hair branched (34c)	*Astragalus spp.*
6.	Hair not as above	7
7.	Hair unicellular	8
7.	Hair multicellular	14
8.	Hair tip enlarged (36c)	*Frasera spp.*
8.	Hair not as above	9
9.	Hair short	10
9.	Hair long	12
10.	Hair stout, "dagger-like", clumpy (17a, 17b)	*Purshia tridentata*
10.	Hair not as above	11
11.	Hair appears flexible, enlarged base (18a)	*Oenothera tanacetifolia*
11.	Hair appears stiff, shorter than above (23b)	*Penstemon spp.*
12.	Hair arachnoid (17a, 17b)	*Purshia tridentata*
12.	Hair tends to be straight or abruptly bent	13
13.	Hair long, curving, base modified (33c, 33d)	*Astragalus purshii*
13.	Hair with abrupt bends, linear cells may be present (14a, 14b)	*Phlox hoodii*
14.	Hair composed of only 2 cells	15
14.	Hair composed of more than 2 cells	17
15.	Terminal cell flattened, hair base unmodified (27c, 27d)	*Erigeron bloomeri*
15.	Terminal cell round, hair base modified (25c)	16

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16. Base cell "dumbbell" shaped, enlarged cell juncture (24d, 25b) *Balsamorhiza hookeri*
16. Base cell ovate, cell juncture not enlarged (25c) *Balsamorhiza sagittata*

17. Hair long, cells short and wide (28b) *Taraxacum officinale*
17. Hair not as above 18

18. Hair robust, length less than five times base cell length (34d) *Haplopappus acaulis*
18. Hair less robust, length greater than five times base cell length 19

19. Base cells compressed, terminal cells elongate (26d, 27b) *Erigeron austinae*
19. Cells of approximate equal length 20

20. Hair long, oriented parallel to vegetative surface (15a) *Chrysothamnus viscidiflorus puberulus*
20. Hair shorter, oriented perpendicular to vegetative surface (15c) *Chrysothamnus visicidiflorus lanceolatus*

21. Crystals present 22
21. Crystals absent 23

22. Crystals formed as a bundle (18b, 18c) *Oenothera tanacetifolia*
23. Crystals formed as a cluster (17c) *Purshia tridentata*

23. Stomata round 24
23. Stomata ovate 25

24. Stomata diameter exceeds .03 mm (28a) *Erigeron bloomeri*
24. Stomata diameter less than .03 mm (23d) *Penstemon spp.*

25. Stomata length equals or exceeds .04 mm 26
25. Stomata length less than .04 mm 31

26. Stomata width equals or exceeds .04 mm (33a, 33b) *Agoseris spp.*
26. Stomata width less than .04 mm 27

27. Stomata width equals or exceeds .036 mm (15d) *Chrysothamnus visicidiflorus*
27. Stomata width less than 036 mm 28

28. Stomata elongate length exceeds width by .02 mm (36d) *Frasera spp.*
28. Stomata ovate, length exceeds width by less than .02 mm (20b) *Artemisia arbuscula*

29. Stomata length less than .03 mm 30
29. Stomata length exceeds .03 mm 32

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30. Stomata appears elevated from vegetative surface (17d) *Purshia tridentata*
30. Stomata not as above 31

31. Stomata numerous, hair base cells much larger than surrounding cells (26d, 27a) *Erigeron austinae*
31. Stomata sparse, hair base cells modified but much smaller than above (34a) *Astragalus purshii*

32. Cell outline irregular to the point of appearing jagged (18d) *Oenothera tanacetifolia*
32. Cell outline not as above 33

33. Cell walls thick, stomata numerous (37d) *Astor scopulorum*
33. Cell walls thin, stomata numerous or few 34

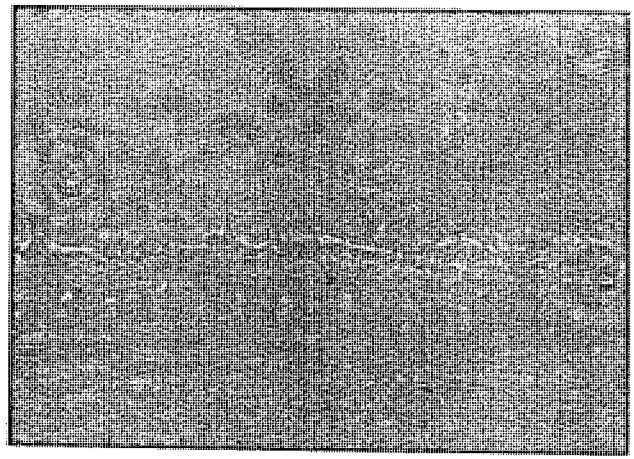
34. Stomata numerous 35
34. Stomata rare 36

35. Cell outline appears dotted (35a, 35b) *Haplopappus acaulis*
35. Cell outline appears entire (25c) *Balsamorhiza sagittata*

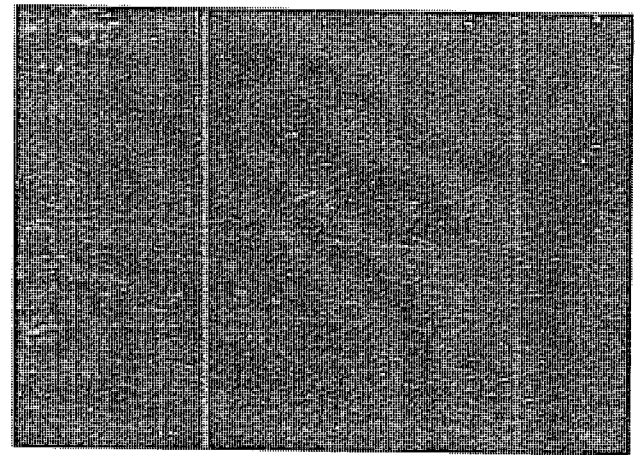
36. Cell smaller, more elongate, with more distinct angles (20d) *Artemisia tridentata*
36. Cell larger, rounder, with few distinct angles (28d) *Taraxacum officinale*

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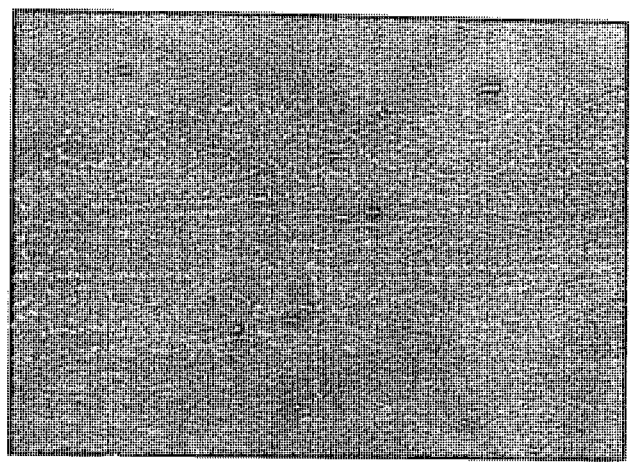
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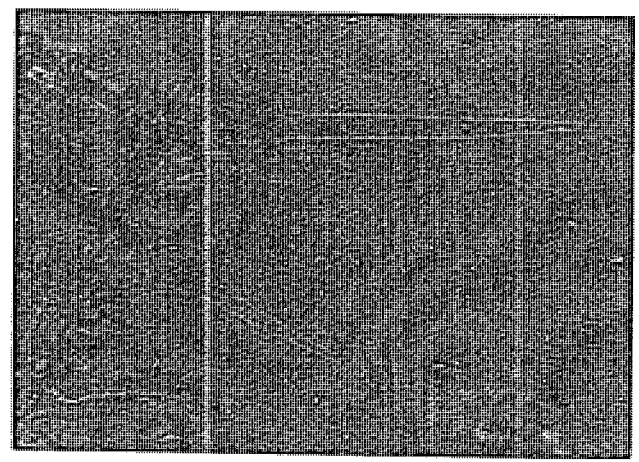
1a. *Muhlenbergia richardsonis*



1b. *Muhlenbergia richardsonis*



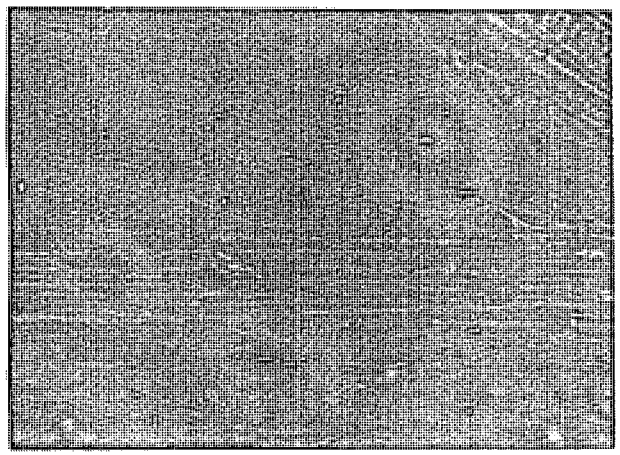
1c. *Muhlenbergia richardsonis*



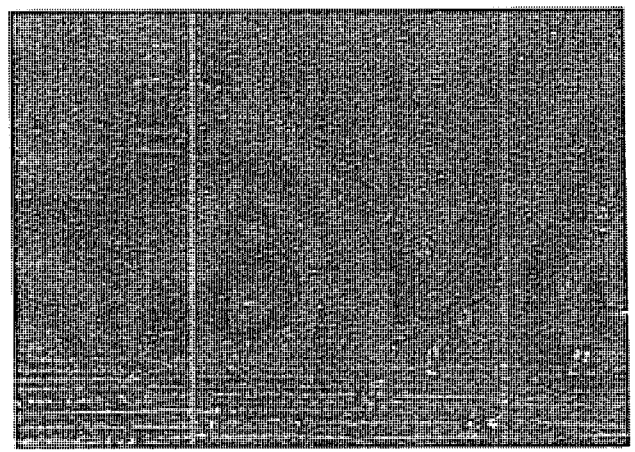
1d. *Muhlenbergia richardsonis*

Plate 1

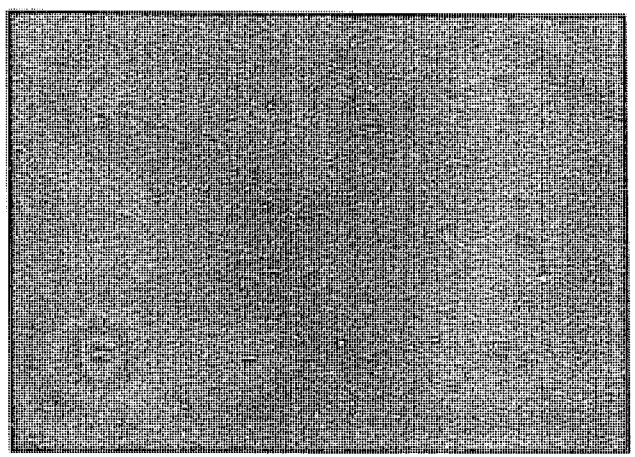
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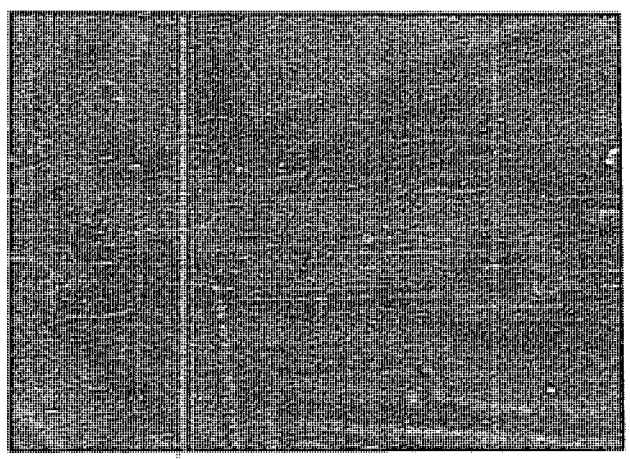
2a. *Festuca idahoensis*



2b. *Festuca idahoensis*



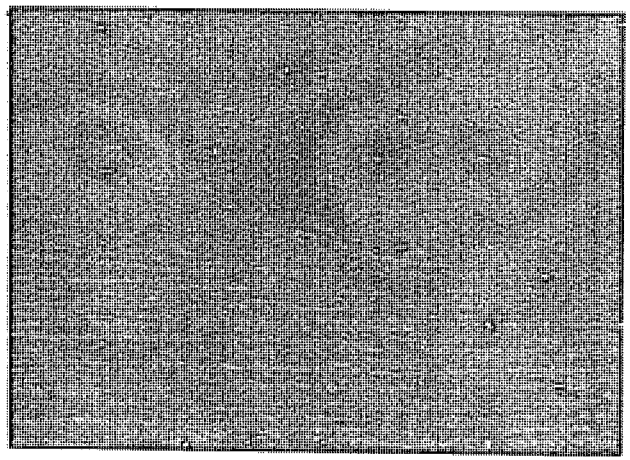
2c. *Festuca idahoensis*



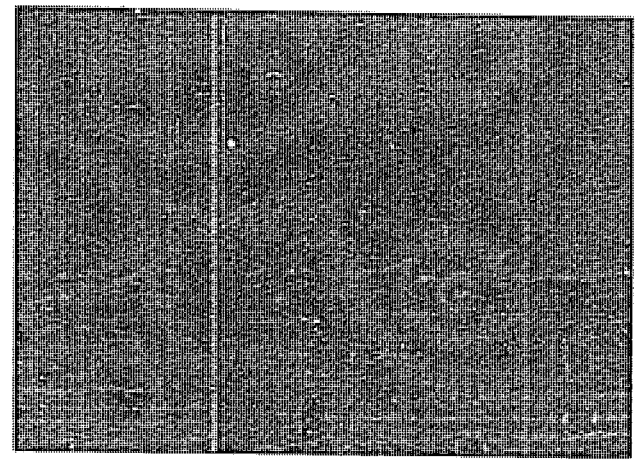
2d. *Festuca idahoensis*

Plate 2

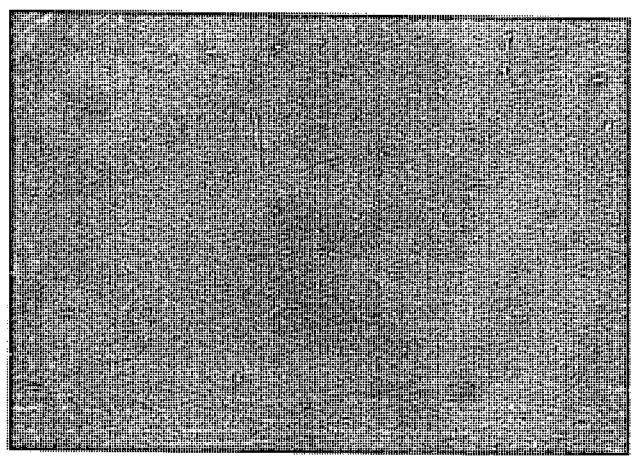
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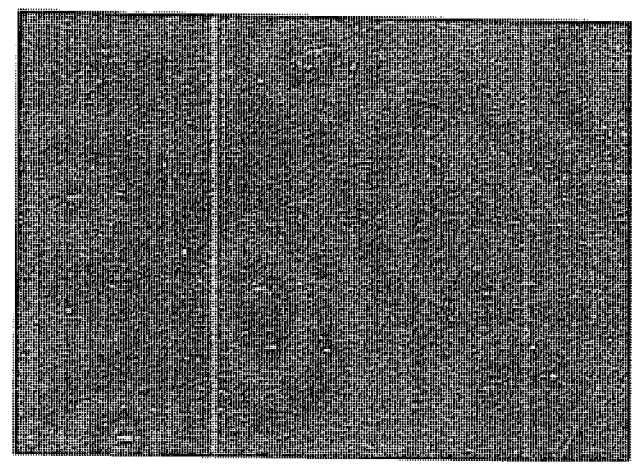
3a. *Agropyron spicatum*



3b. *Agropyron spicatum*



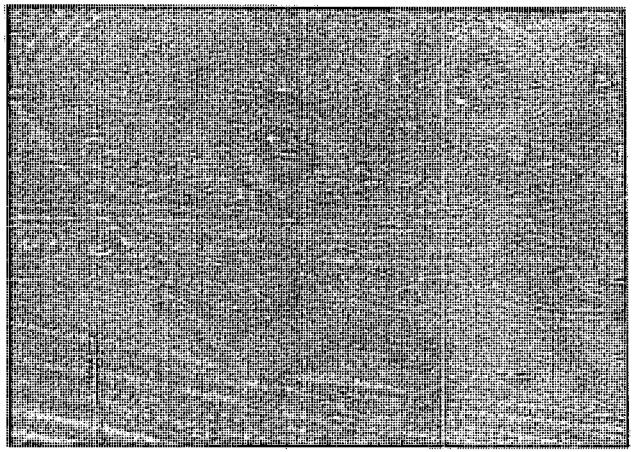
3c. *Agropyron spicatum*



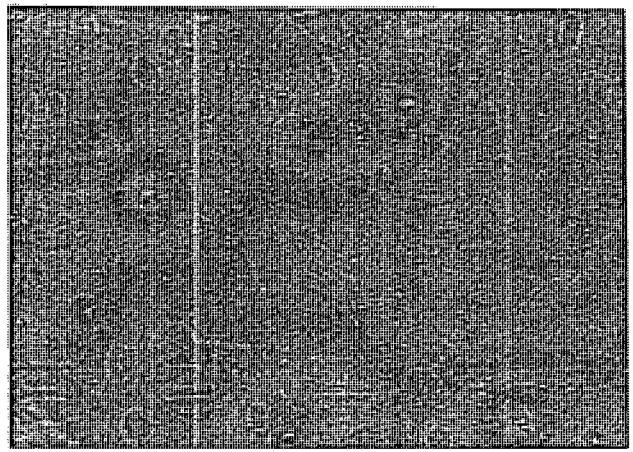
3d. *Agropyron spicatum*

Plate 3

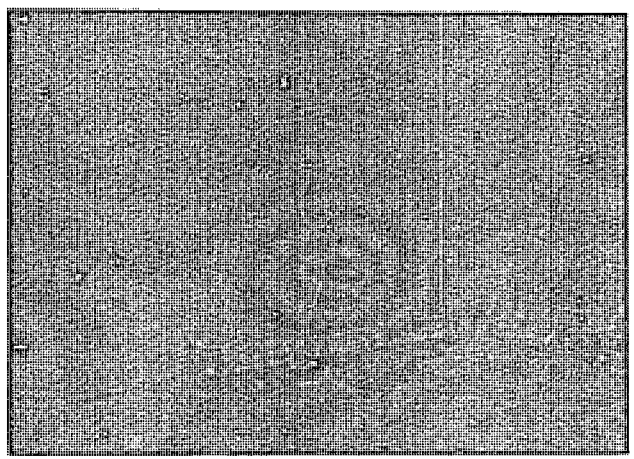
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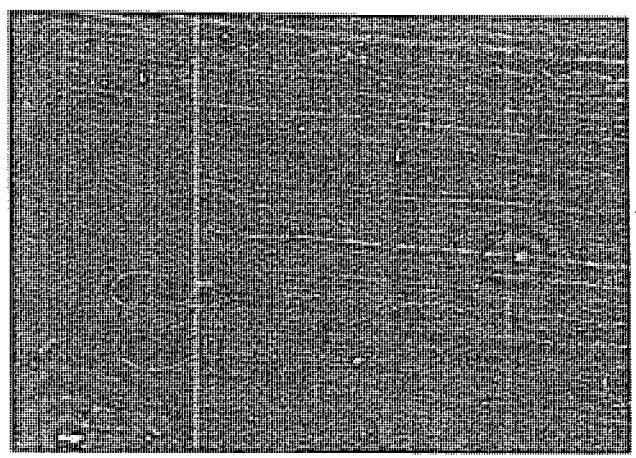
4a. *Stipa thurberiana*



4b. *Stipa thurberiana*



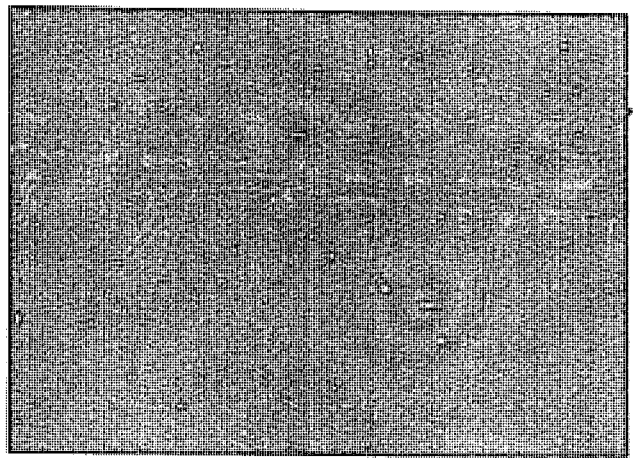
4c. *Stipa thurberiana*



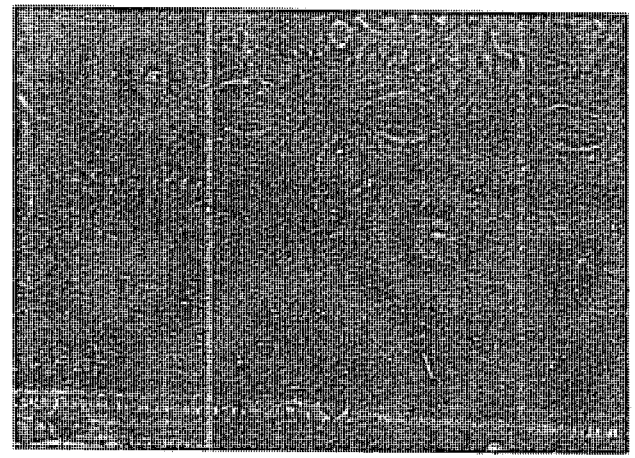
4d. *Stipa thurberiana*

Plate 4

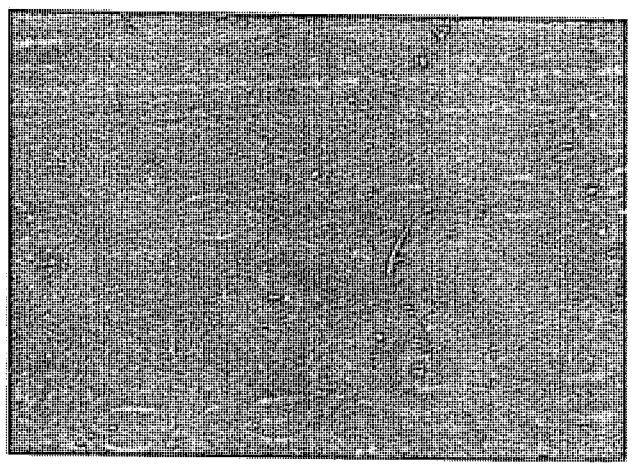
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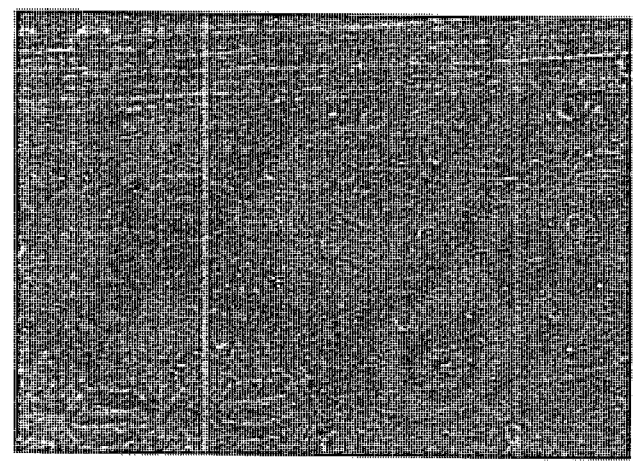
5a. *Sitanion hystrix*



5b. *Sitanion hystrix*



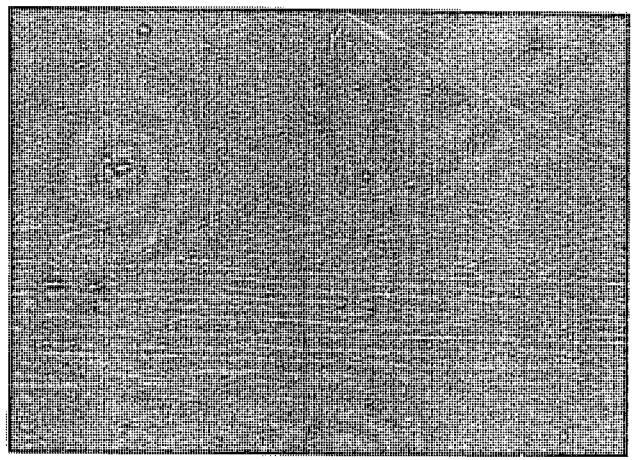
5c. *Sitanion hystrix*



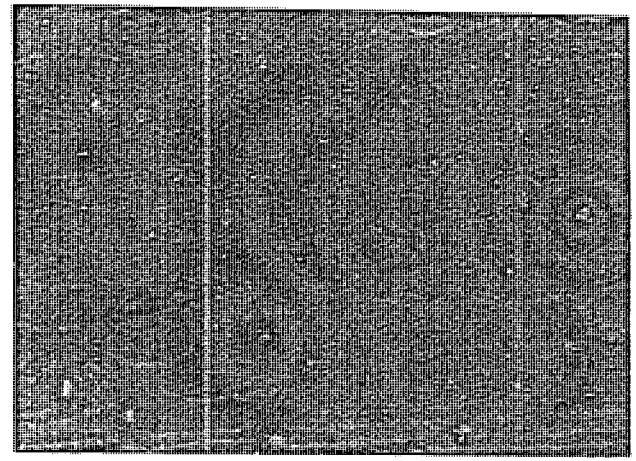
5d. *Sitanion hystrix*

Plate 5

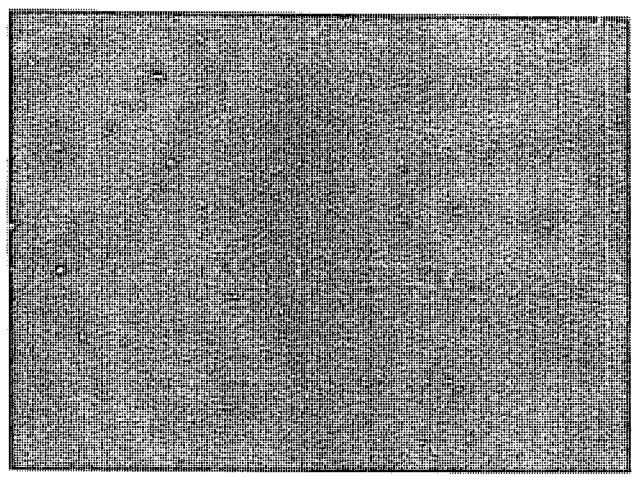
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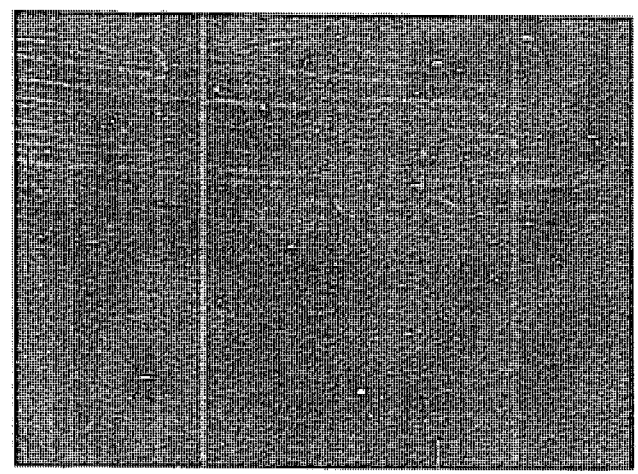
6a. *Hordeum brachyantherum*



6b. *Hordeum brachyantherum*



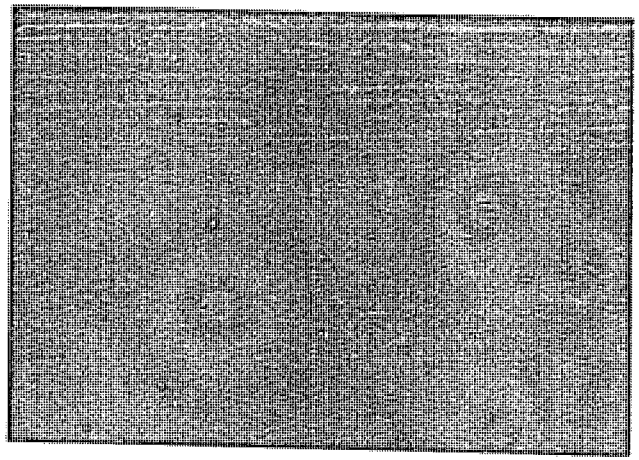
6c. *Hordeum brachyantherum*



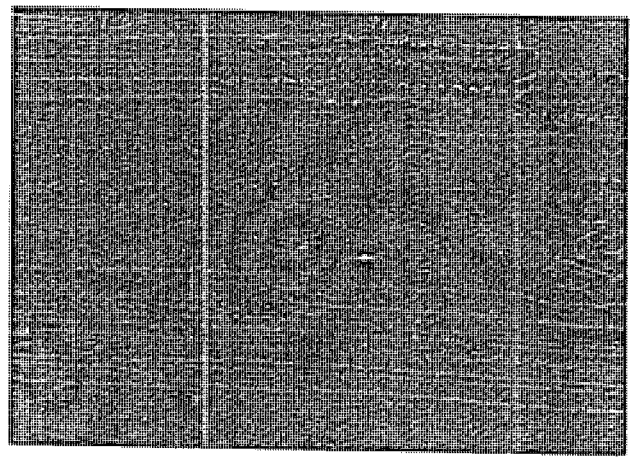
6d. *Hordeum jubatum*

Plate 6

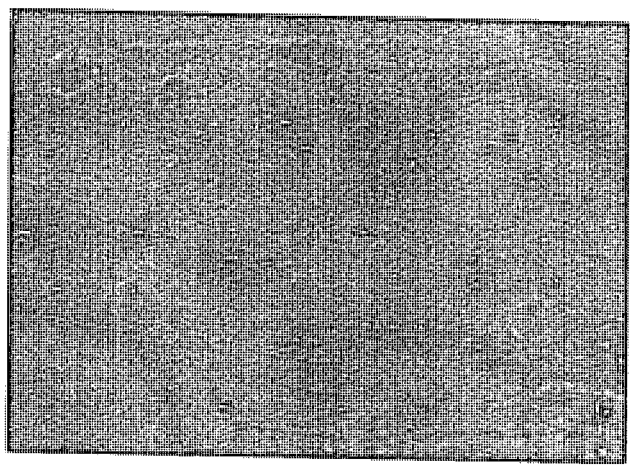
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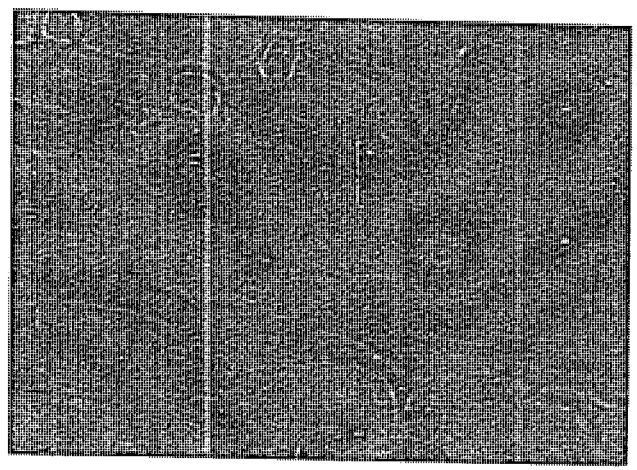
7a. *Hordeum jubatum*



7b. *Hordeum jubatum*



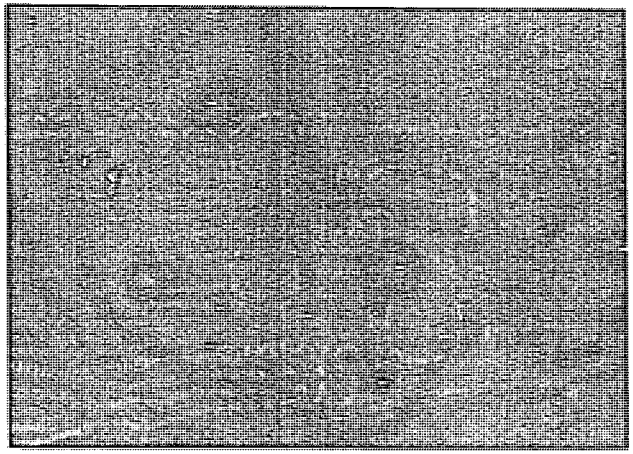
7c. *Elymus cinereus*



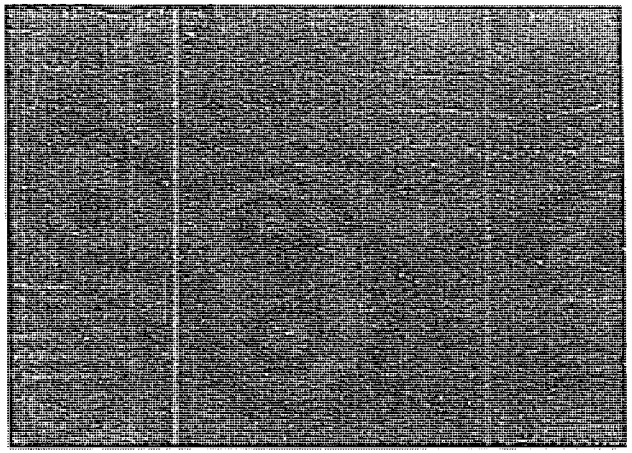
7d. *Elymus cinereus*

Plate 7

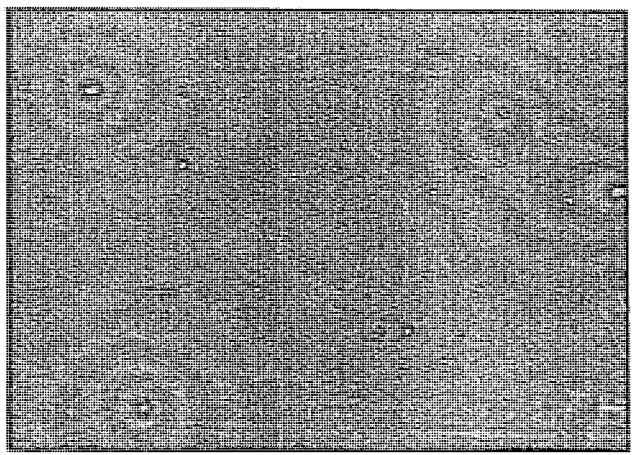
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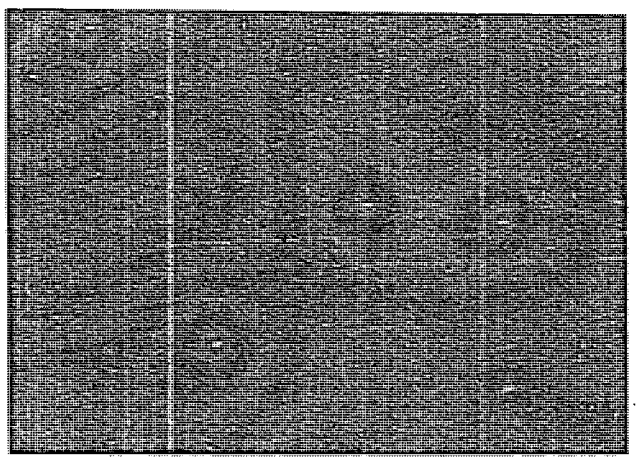
8a. *Elymus cinereus*



8b. *Bromus tectorum*



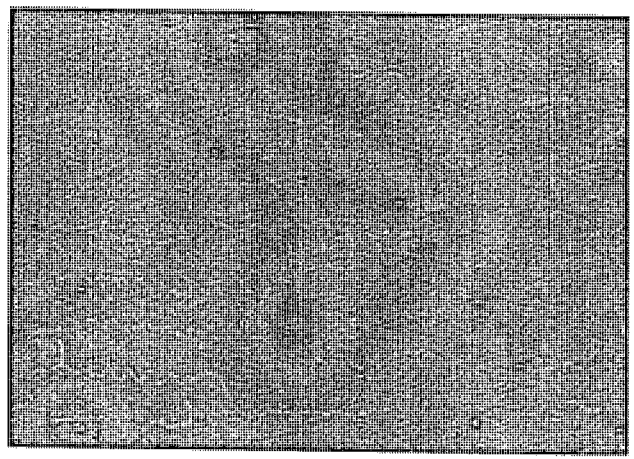
8c. *Bromus tectorum*



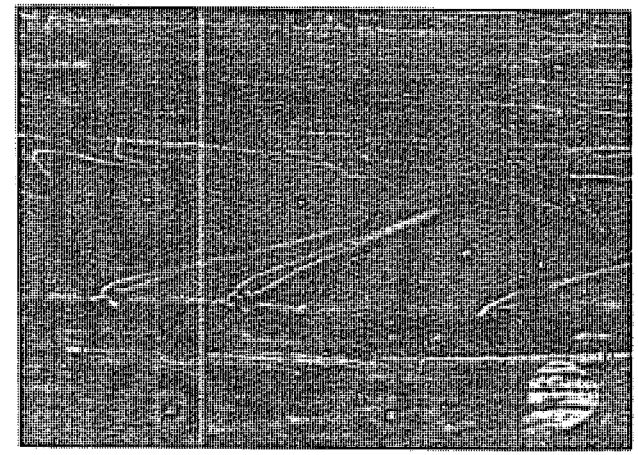
3d. *Bromus tectorum*

Plate 8

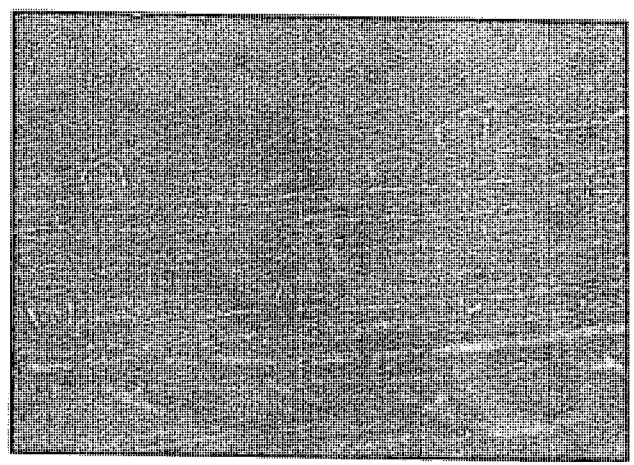
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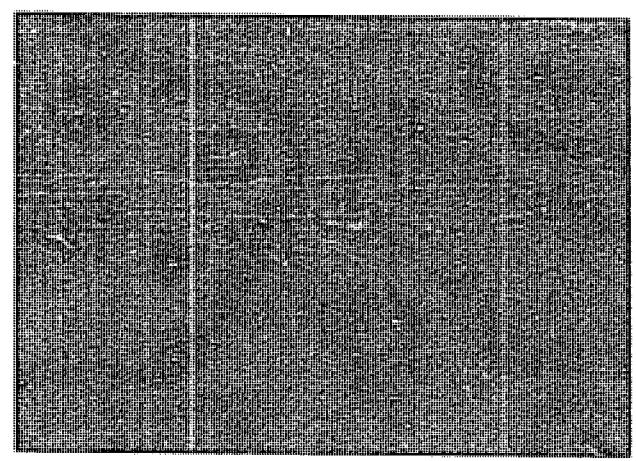
9a. *Koeleria cristata*



9b. *Koeleria cristata*



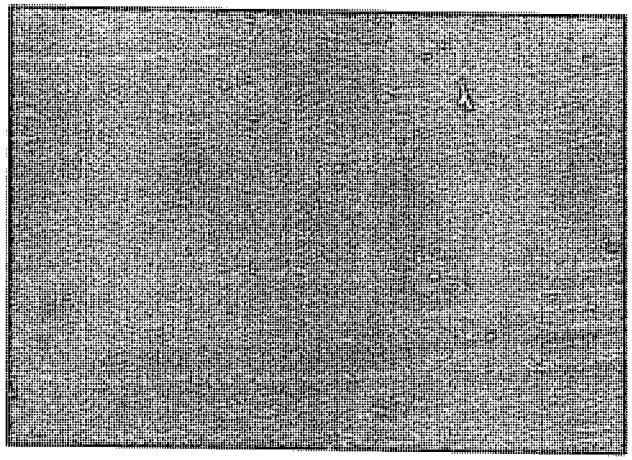
9c. *Koeleria cristata*



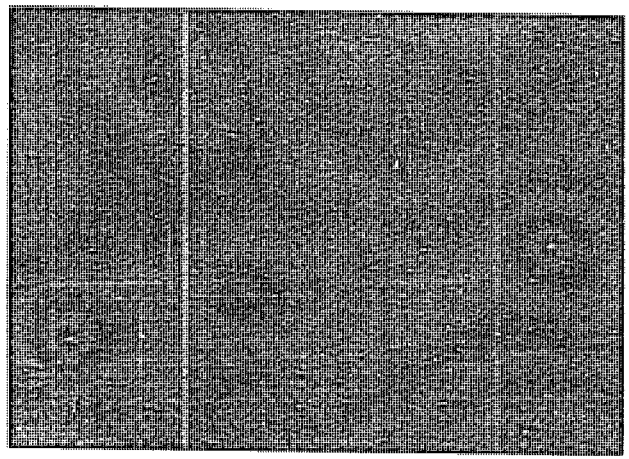
9d. *Poa sandbergii*

Plate 9

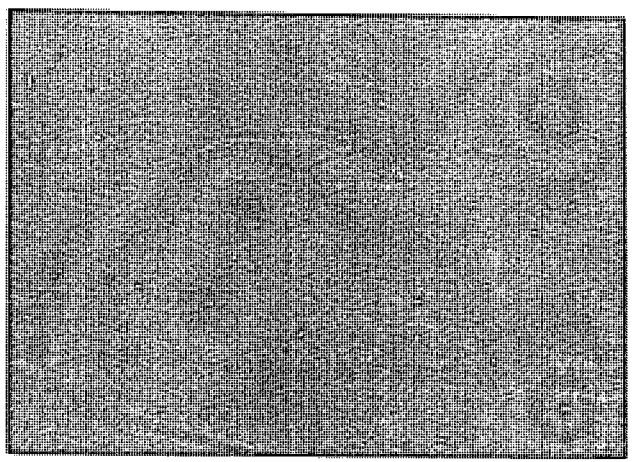
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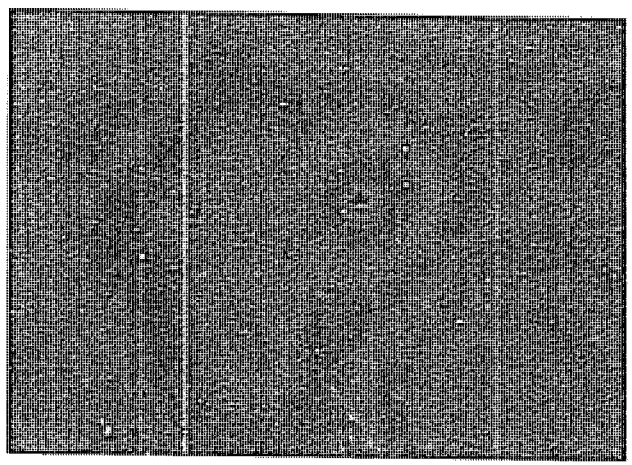
10a. *Poa sandbergii*



10b. *Poa sandbergii*



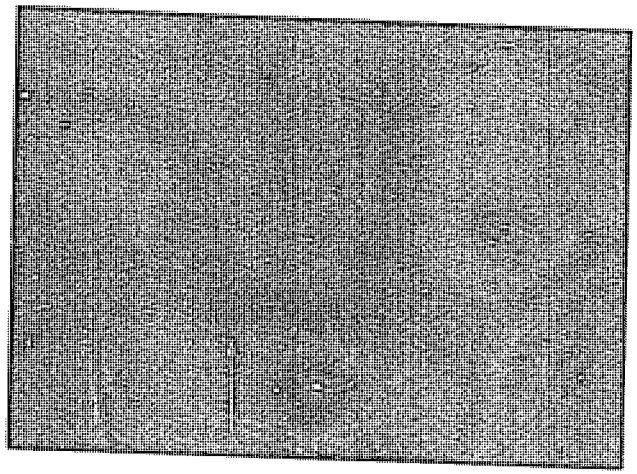
10c. *Carex spp.*



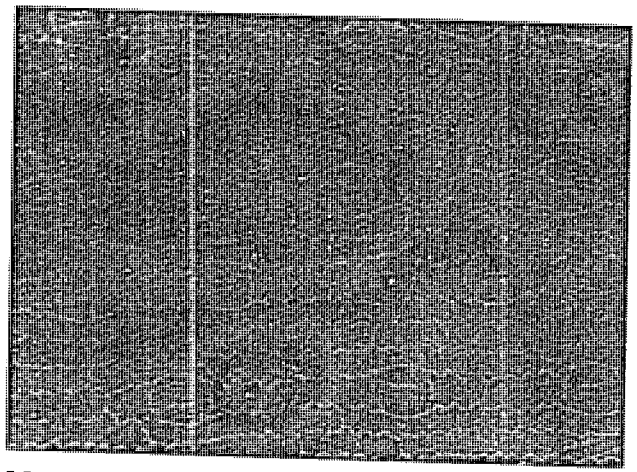
10d. *Carex spp.*

Plate 10

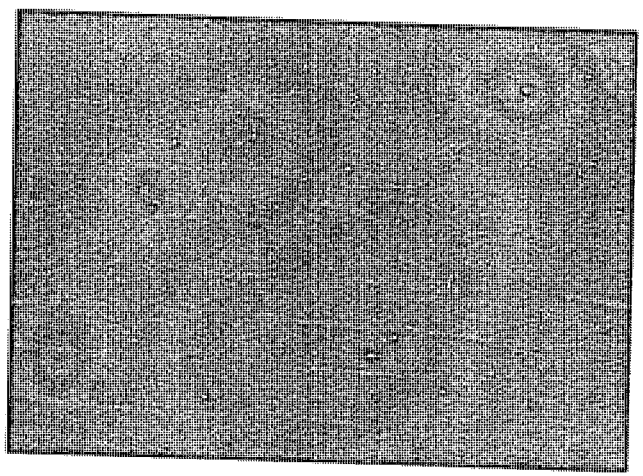
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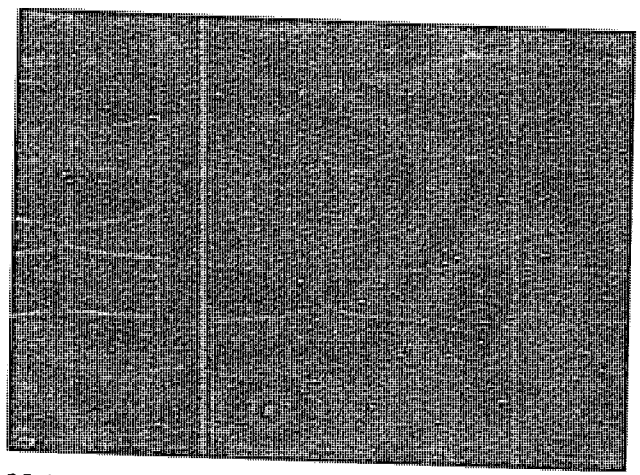
11a. *Carex spp.*



11b. *Juncus spp.*



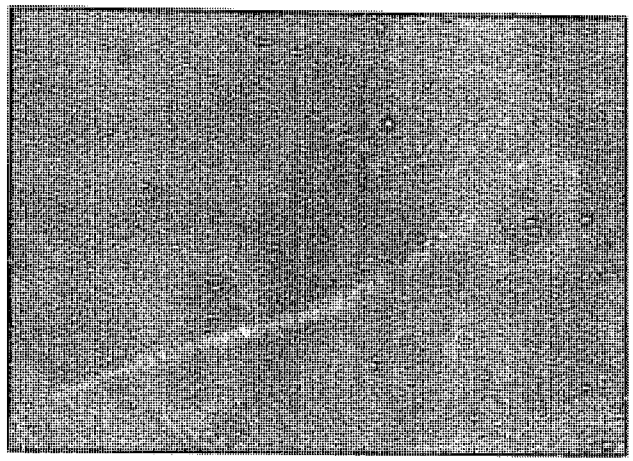
11c. *Allium spp.*



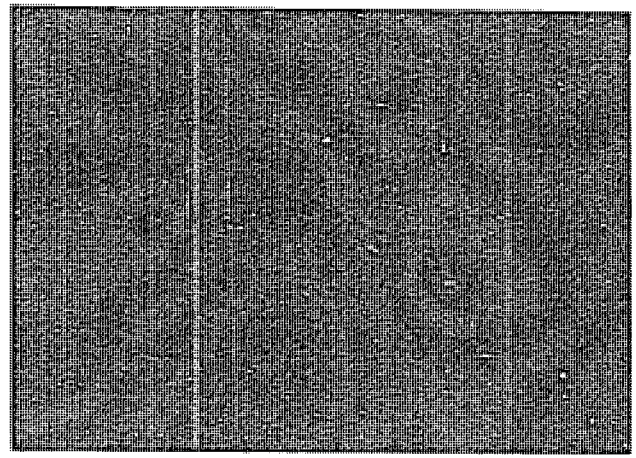
11d. *Allium spp.*

Plate 11

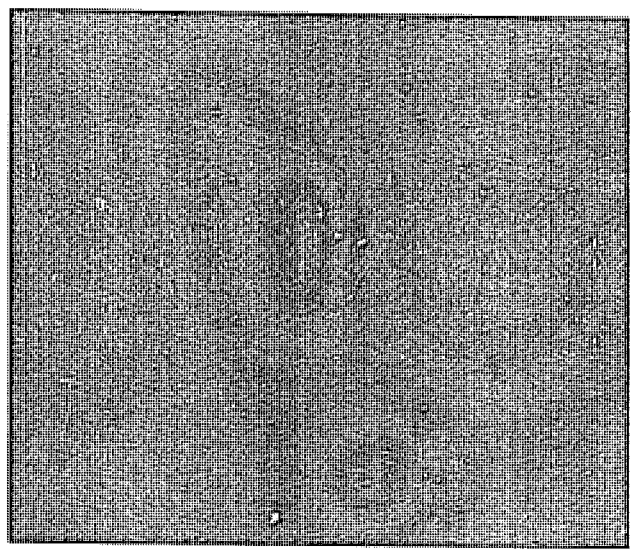
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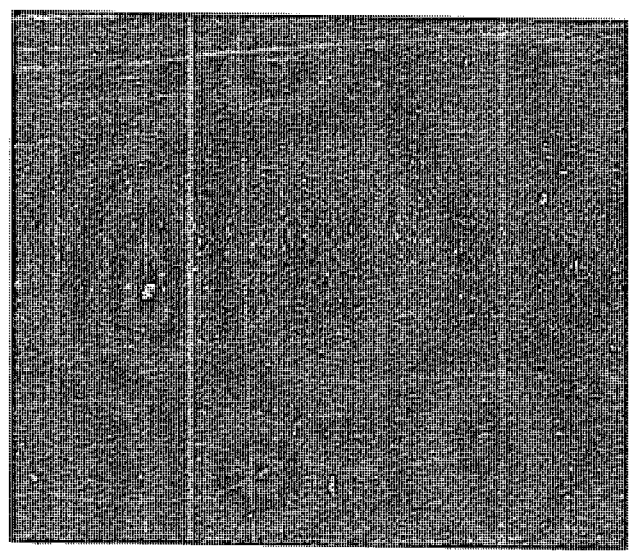
12a. *Iris missouriensis*



12b. *Iris missouriensis*



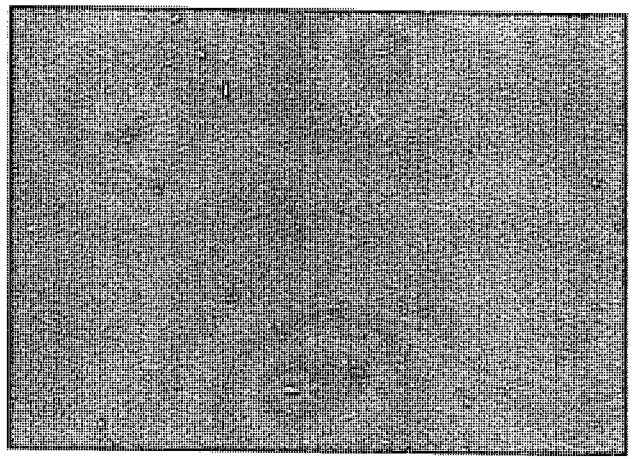
12c. *Iris missouriensis*



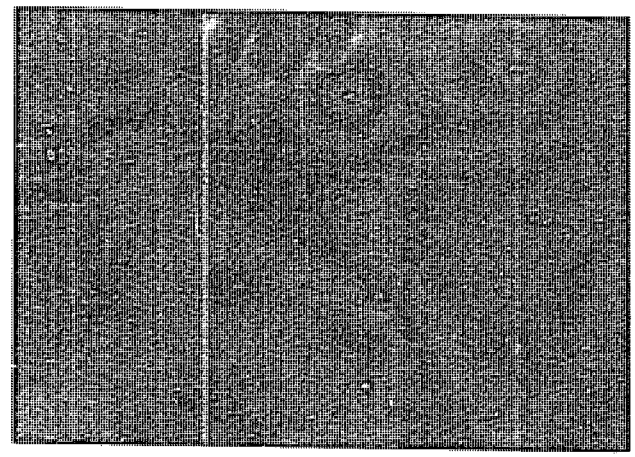
12d. *Iris missouriensis*

Plate 12

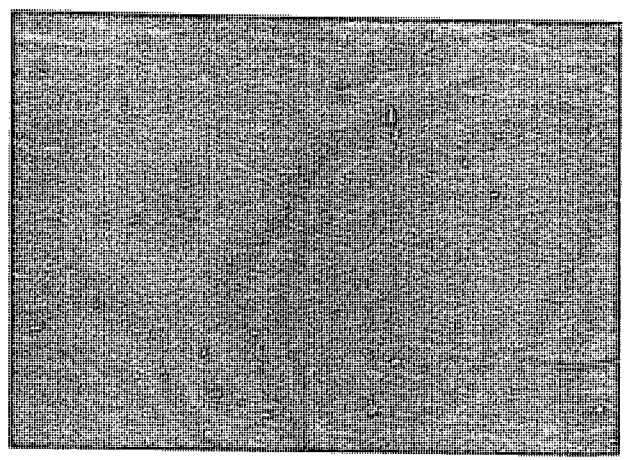
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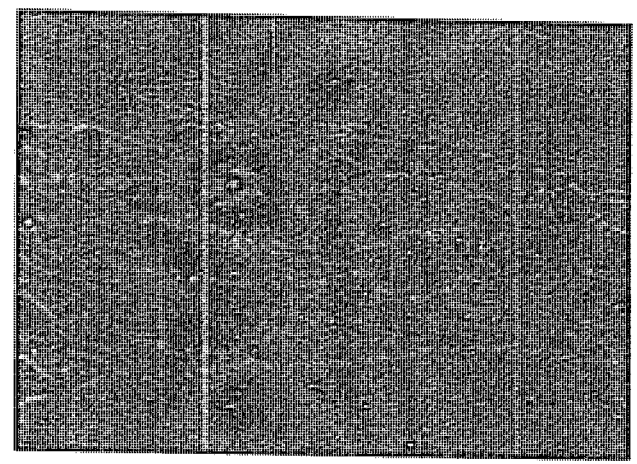
13a. *Leptodactylon pungens*



13b. *Leptodactylon pungens*



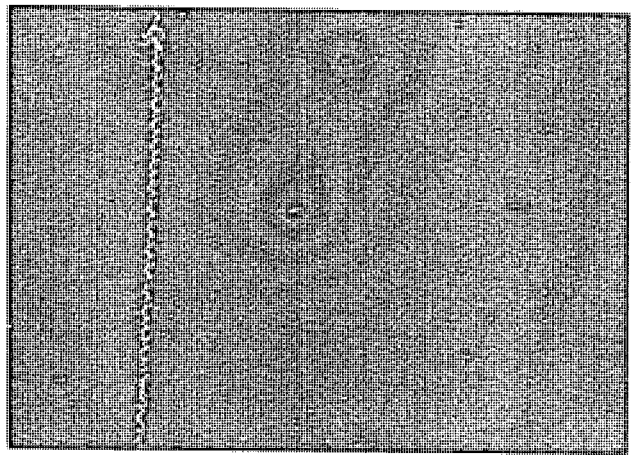
13c. *Leptodactylon pungens*



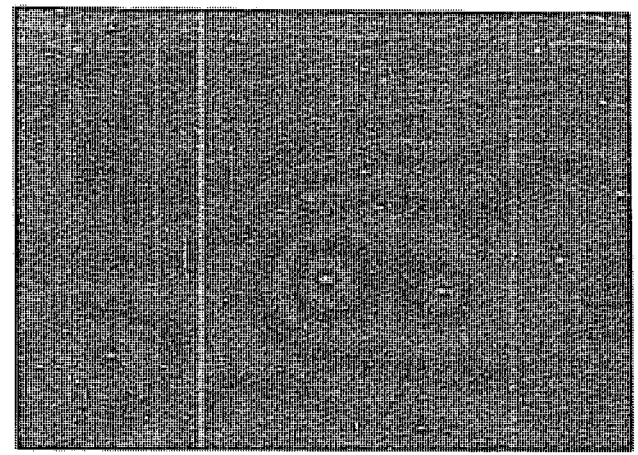
13d. *Leptodactylon pungens*

Plate 13

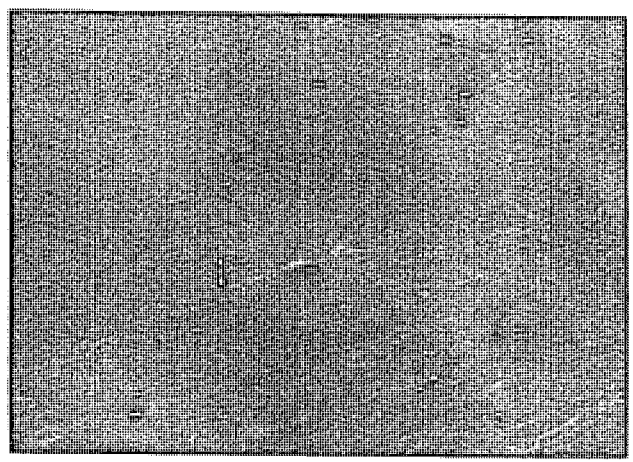
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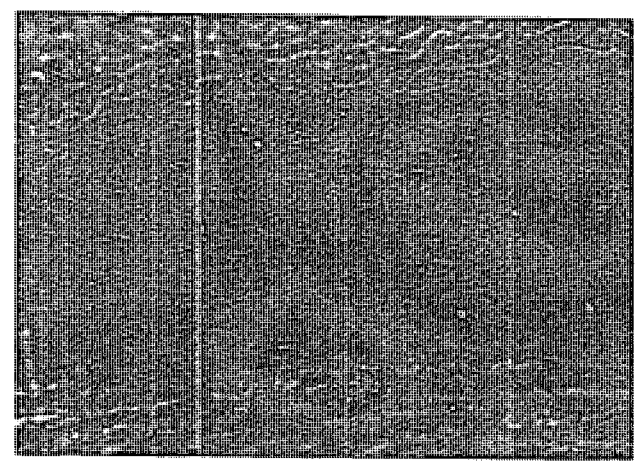
14a. *Phlox hoodii*



14b. *Phlox hoodii*



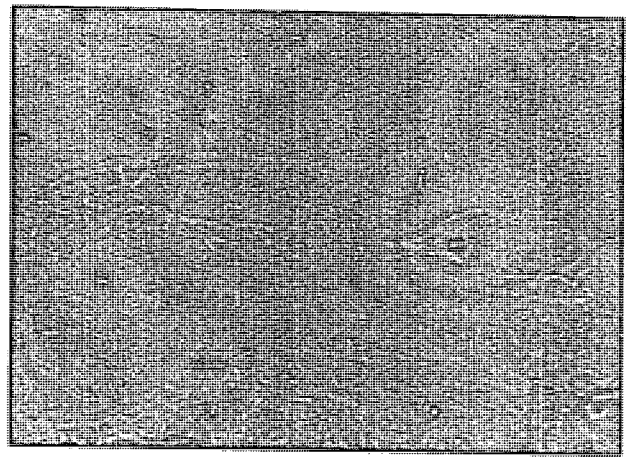
14c. *Phlox hoodii*



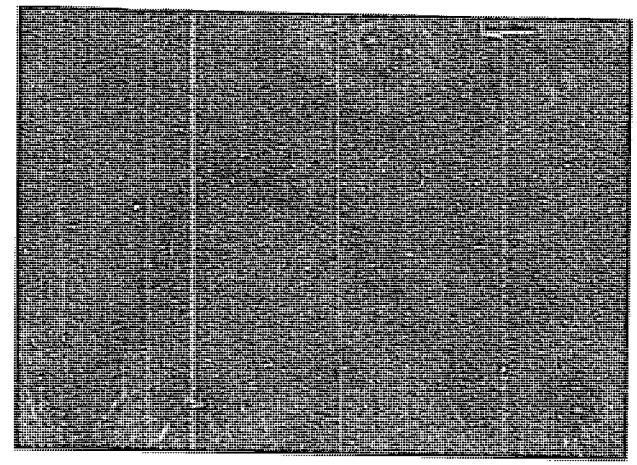
14d. *Phlox hoodii*

Plate 14

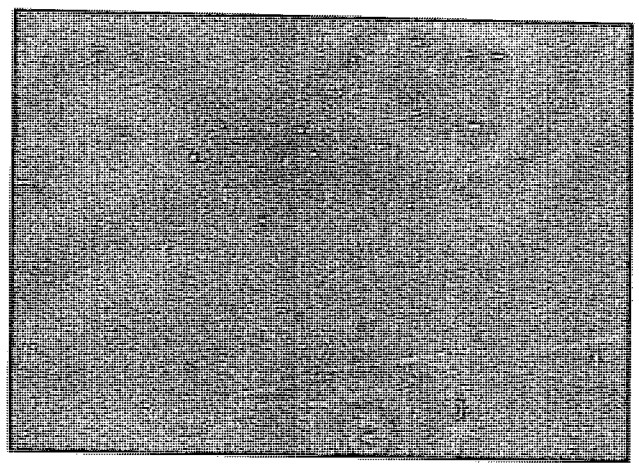
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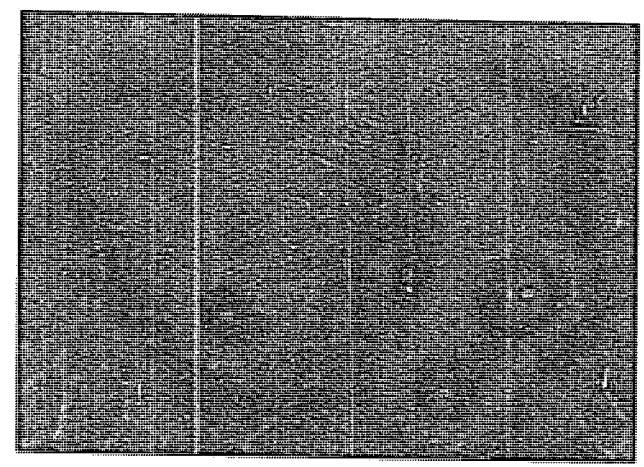
15a. *Chrysothamnus viscidiflorus*



15b. *Chrysothamnus viscidiflorus*



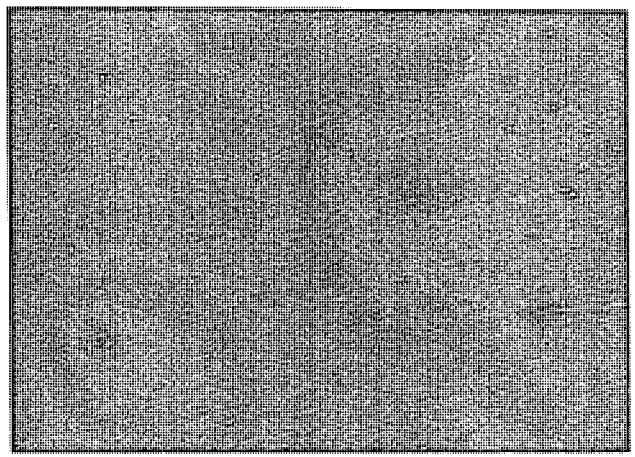
15c. *Chrysothamnus viscidiflorus*



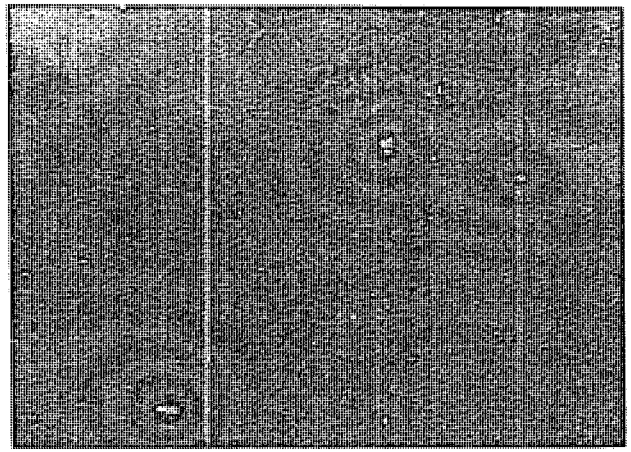
15d. *Chrysothamnus viscidiflorus*

Plate 15

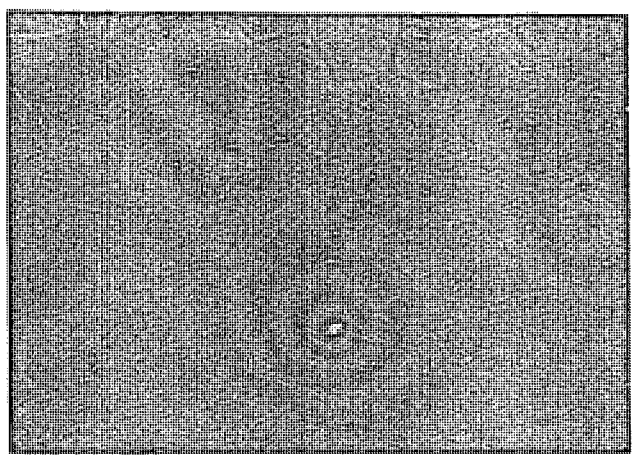
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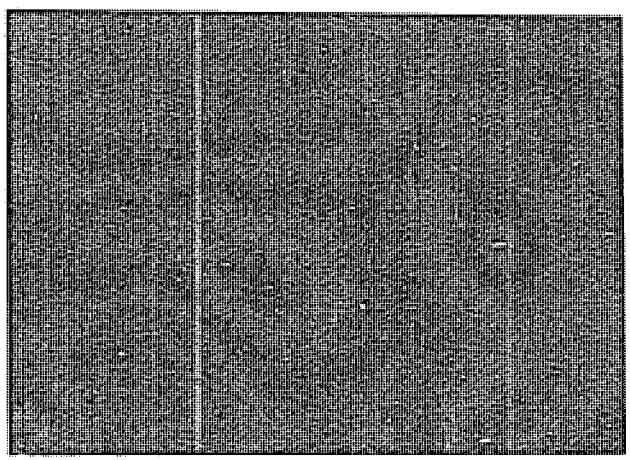
16a. *Eriogonum spp.*



16b. *Eriogonum spp.*



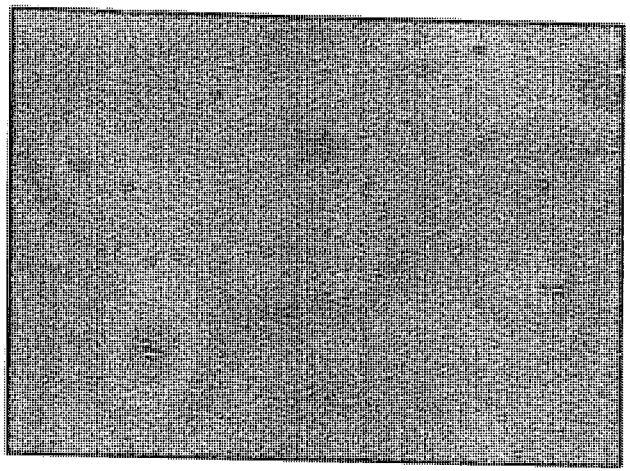
16c. *Eriogonum spp.*



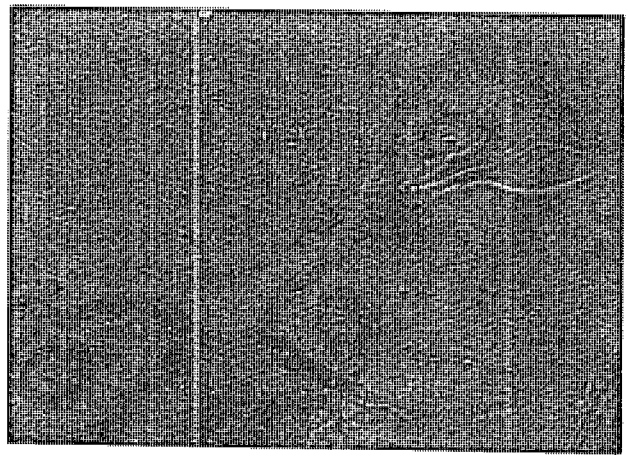
16d. *Eriogonum spp.*

Plate 16

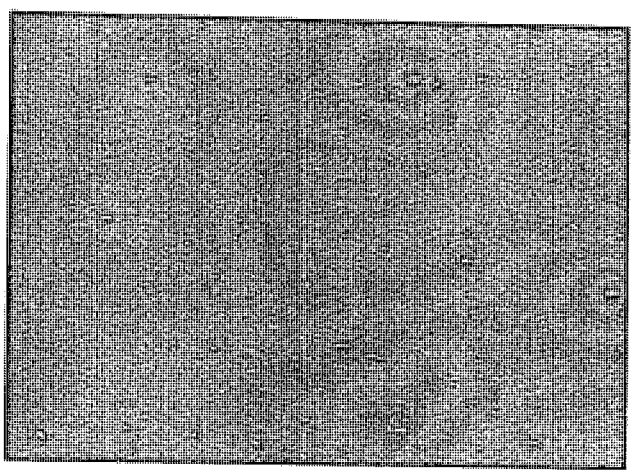
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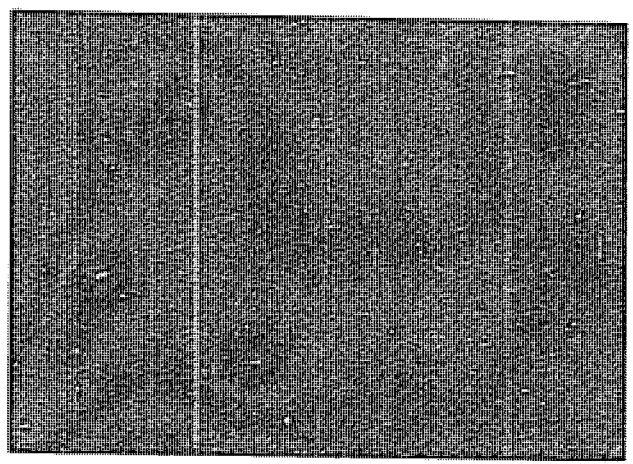
17a. *Purshia tridentata*



17b. *Purshia tridentata* (100X)



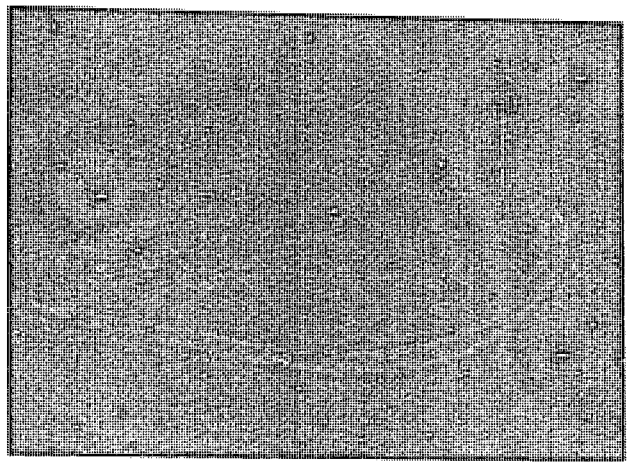
17c. *Purshia tridentata*



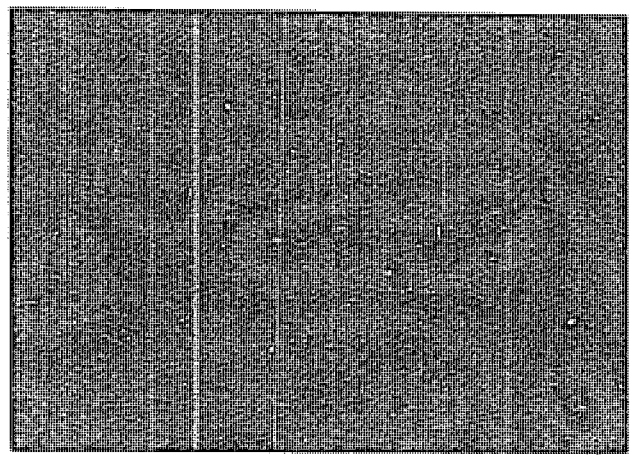
17d. *Purshia tridentata*

Plate 17

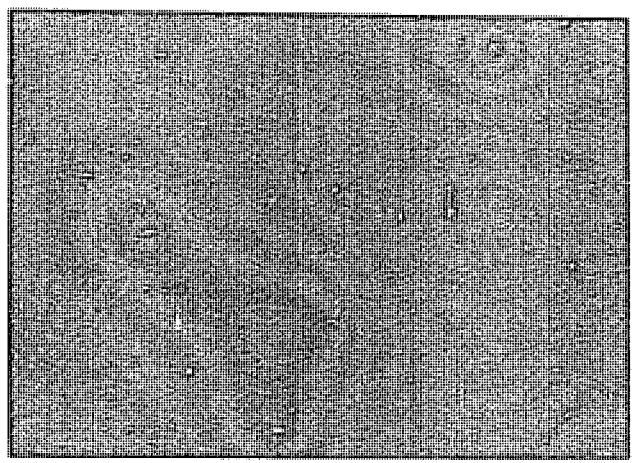
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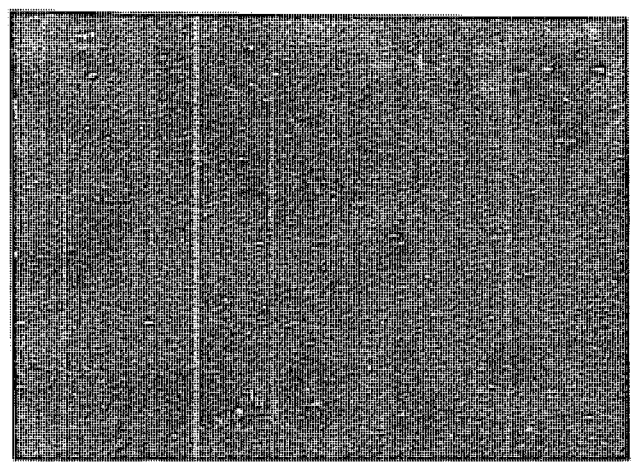
18a. *Oenothera tanacetifolia*



18b. *Oenothera tanacetifolia*



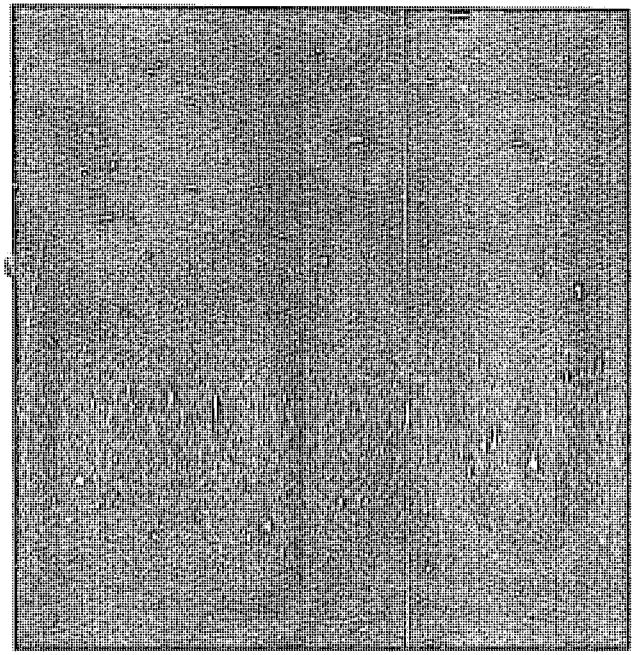
18c. *Oenothera tanacetifolia* (100X)



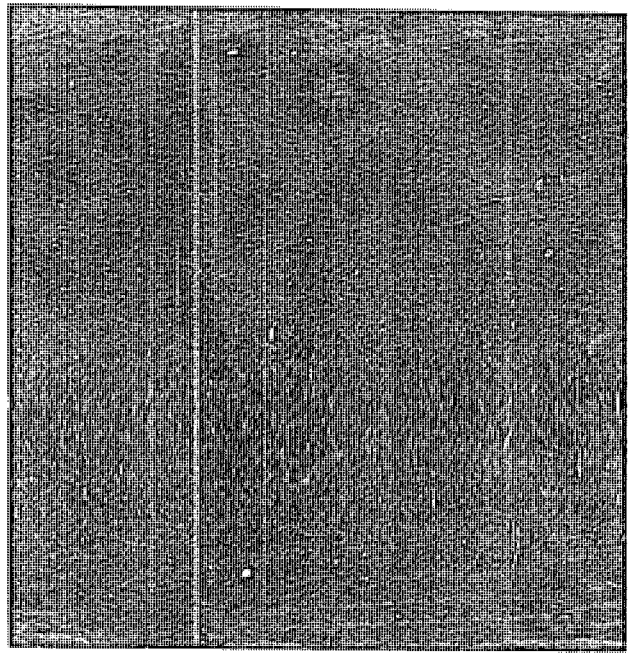
18d. *Oenothera tanacetifolia*

Plate 18

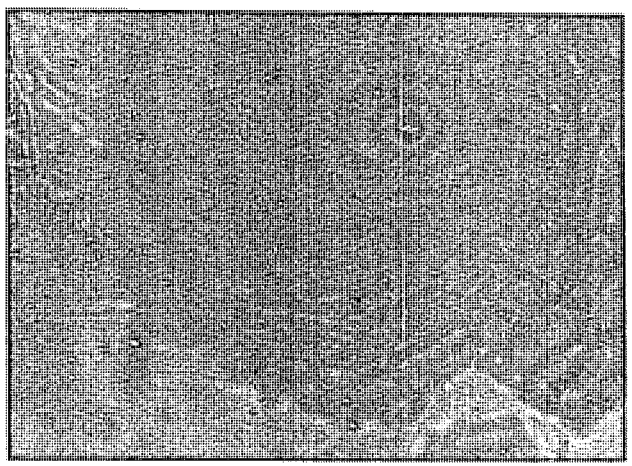
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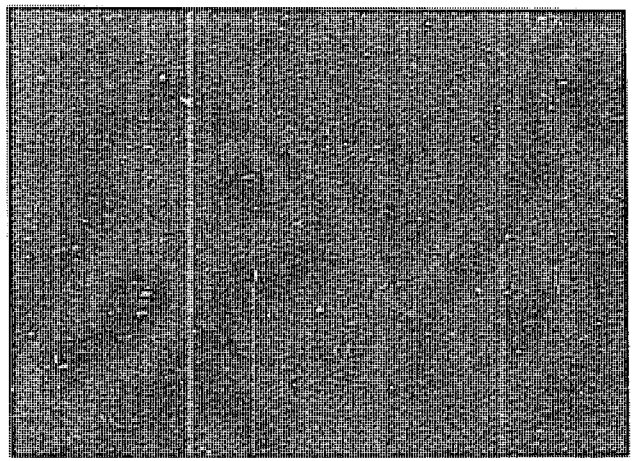
19a. *Descurainia pinnata*



19b. *Descurainia pinnata*



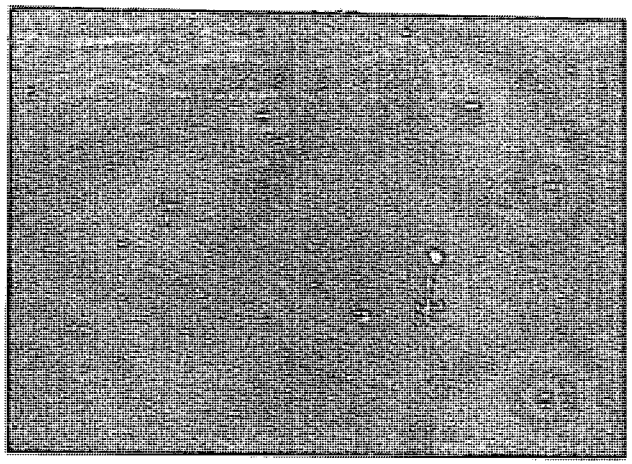
19c. *Descurainia pinnata*



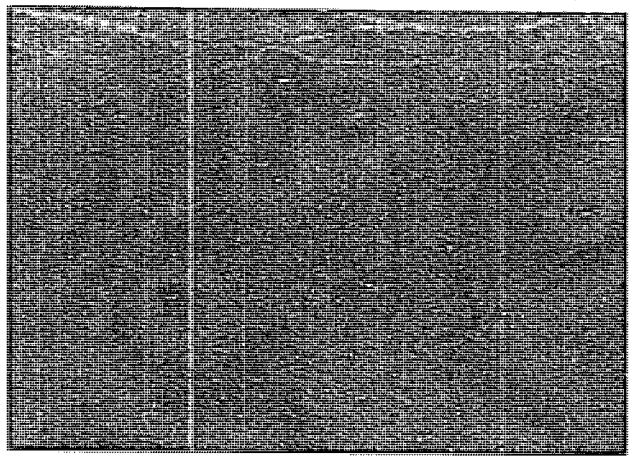
19d. *Artemisia arbuscula*

Plate 19

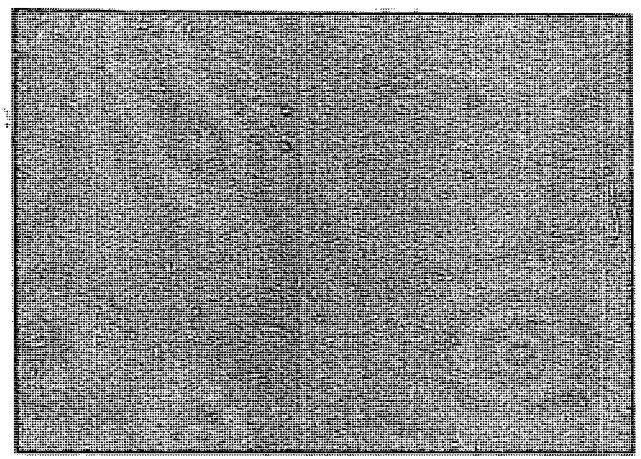
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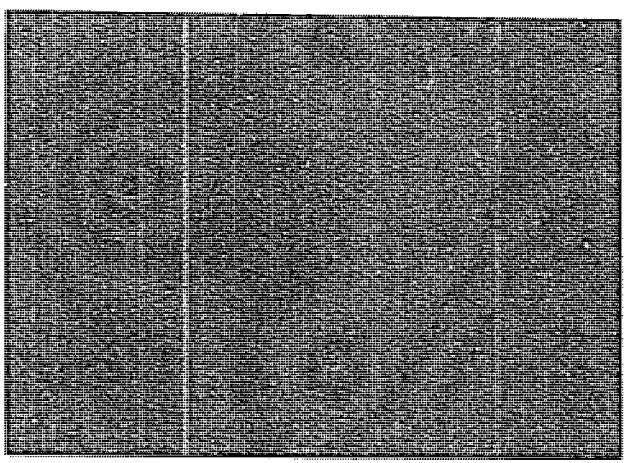
20a. *Artemisia arbuscula*



20b. *Artemisia arbuscula*



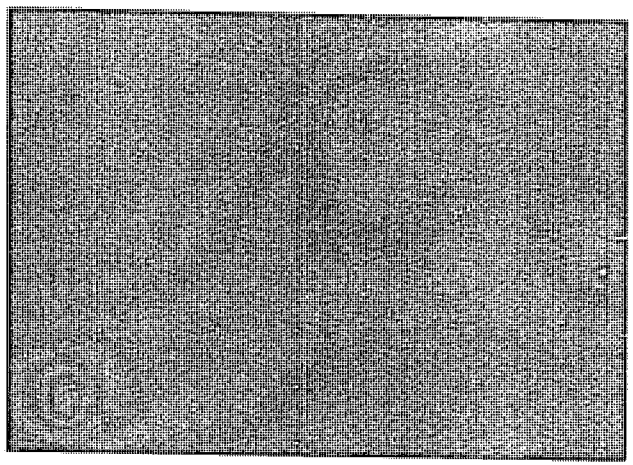
20c. *Artemisia tridentata*



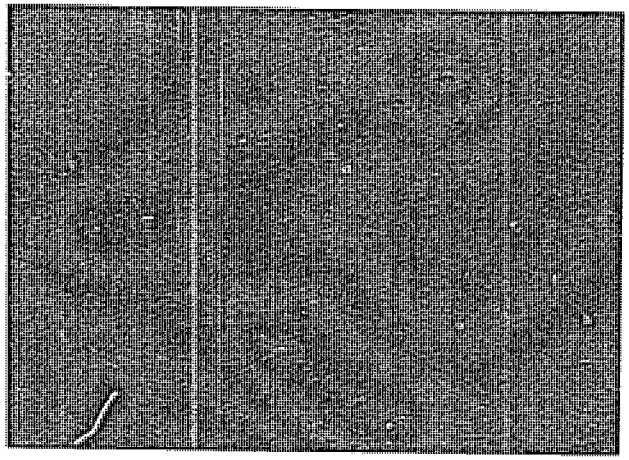
20d. *Artemisia tridentata*

Plate 20

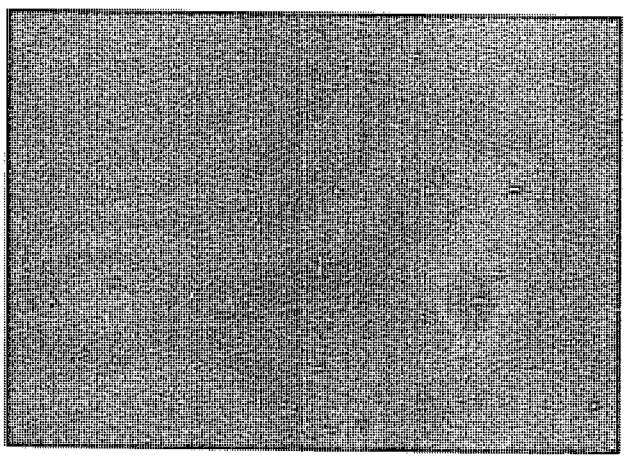
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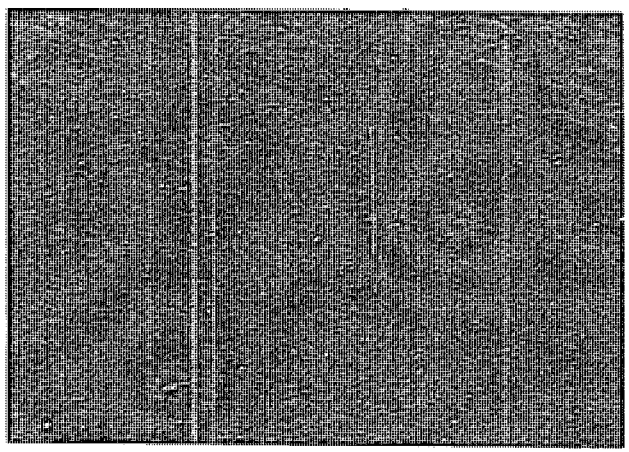
21a. *Lepidium perfoliatum* (100X)



21b. *Lepidium perfoliatum*



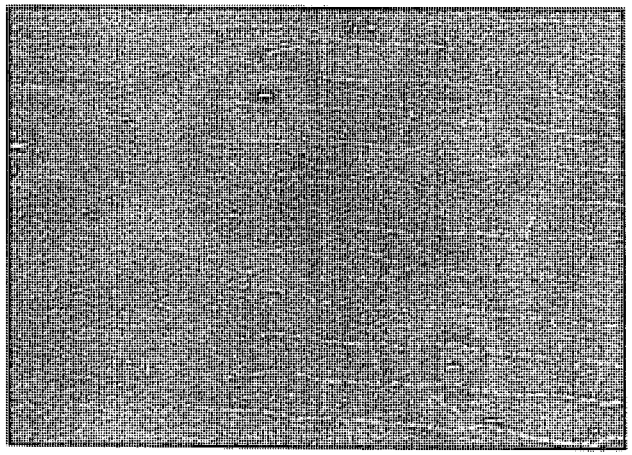
21c. *Lepidium perfoliatum*



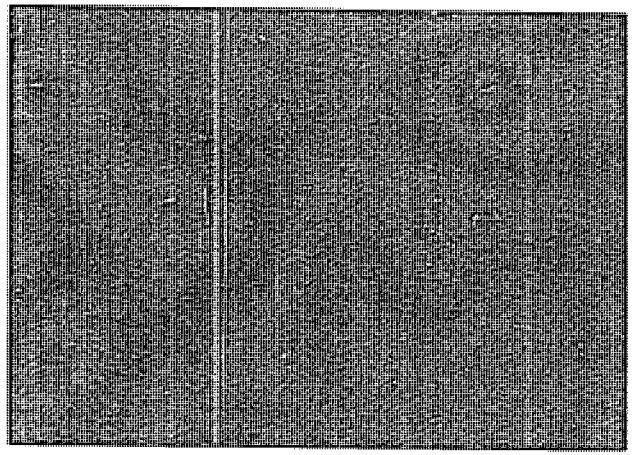
21d. *Arenaria spp.*

Plate 21

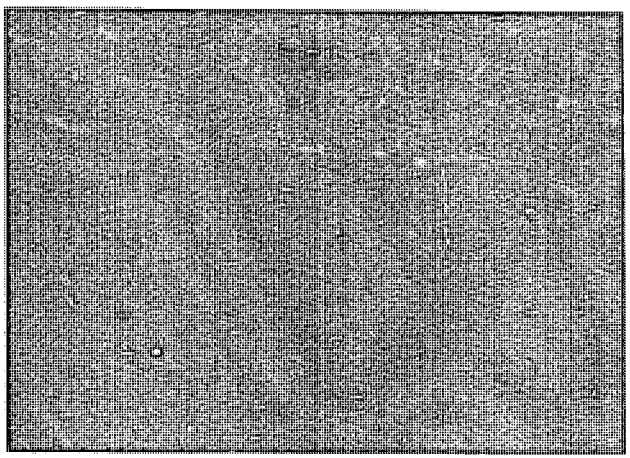
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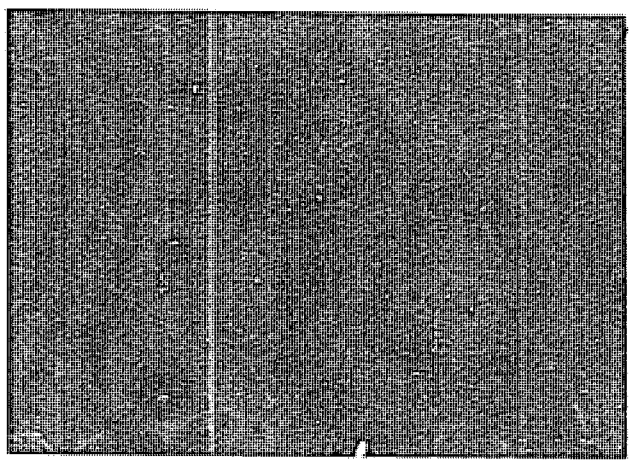
22a. *Arenaria spp.*



22b. *Arenaria spp.*



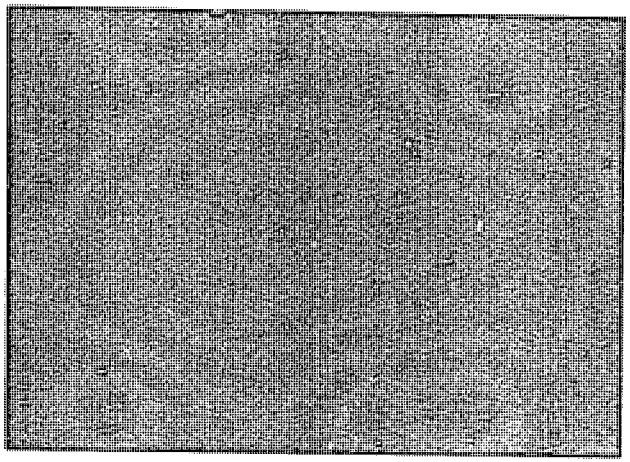
22c. *Penstemon speciosus*



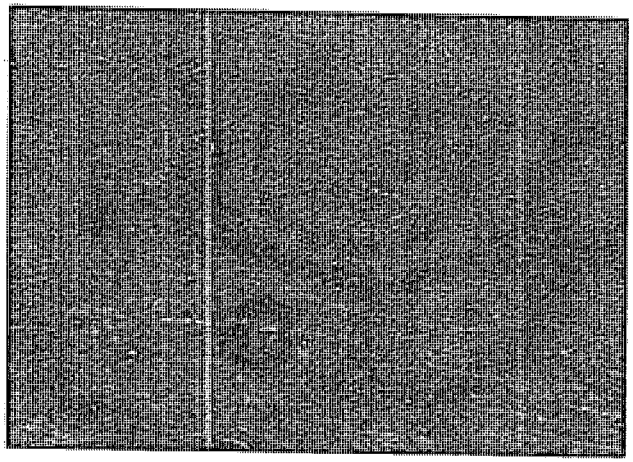
22d. *Penstemon speciosus*

Plate 22

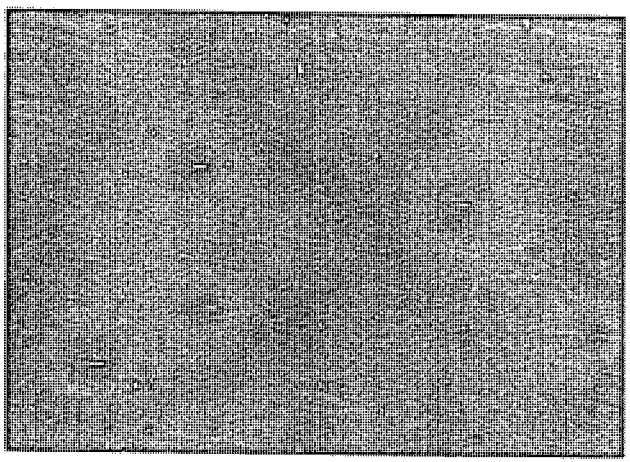
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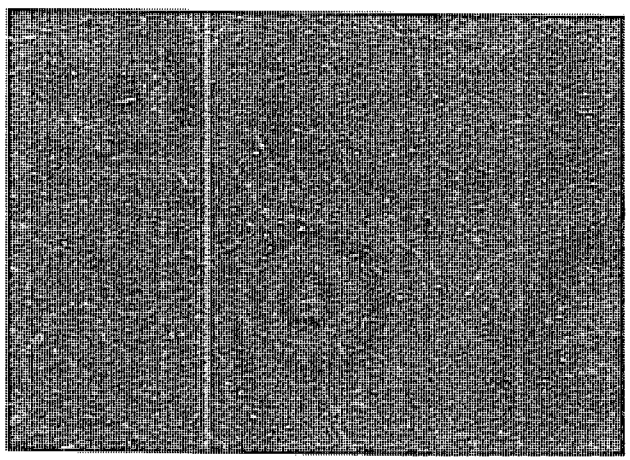
23a. *Penstemon speciosus*



23b. *Penstemon spp.*



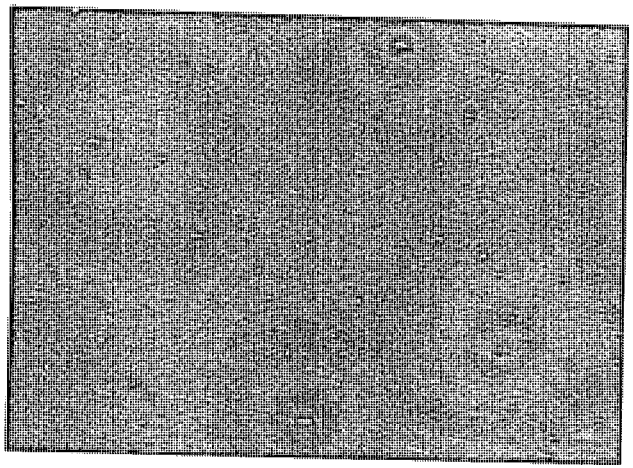
23c. *Penstemon spp.*



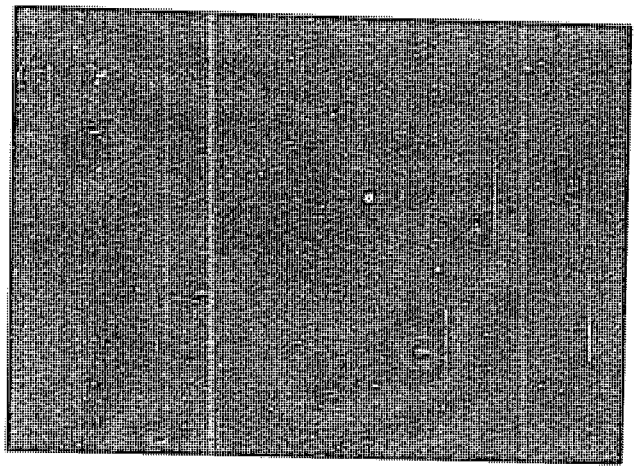
23d. *Penstemon spp.*

Plate 23

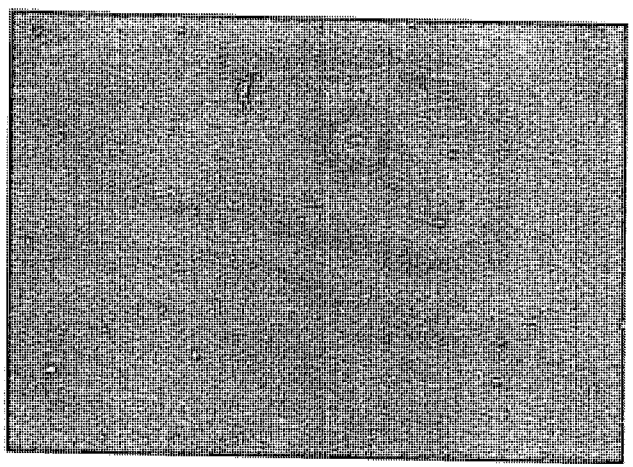
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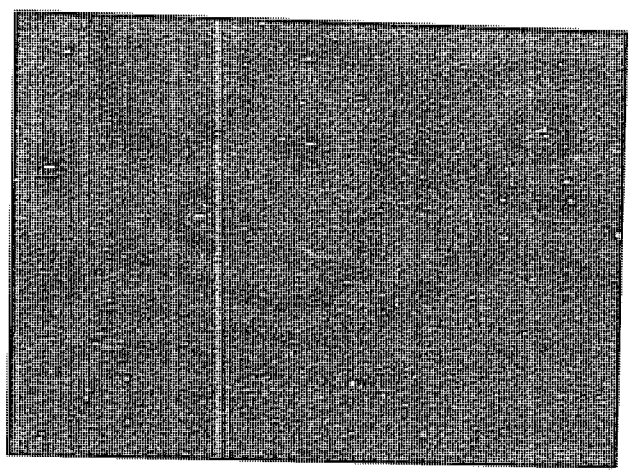
24a. *Zigadenus spp.*



24b. *Zigadenus spp.*



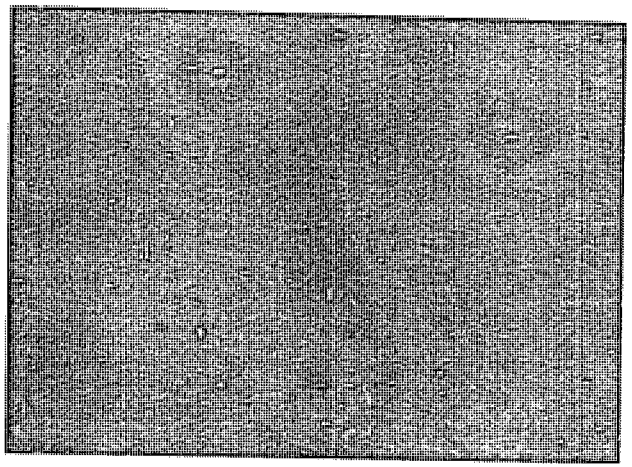
24c. *Zigadenus spp.*



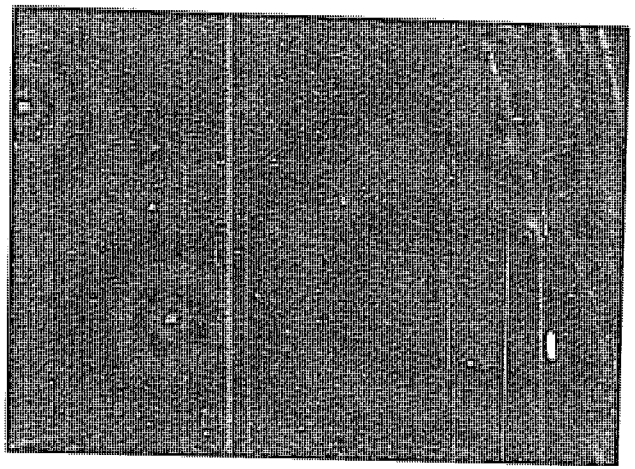
24d. *Balsamorhiza hookeri*

Plate 24

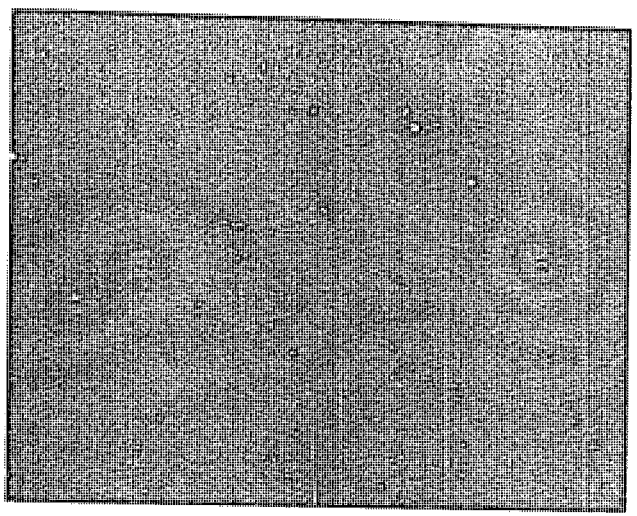
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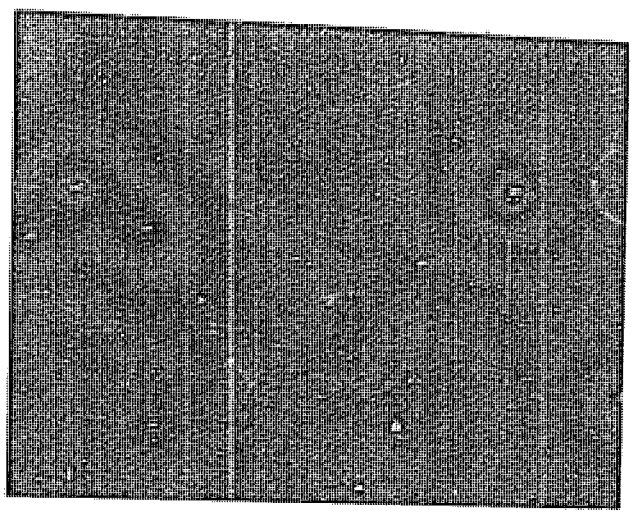
25a. *Balsamorhiza hookeri*



25b. *Balsamorhiza hookeri*



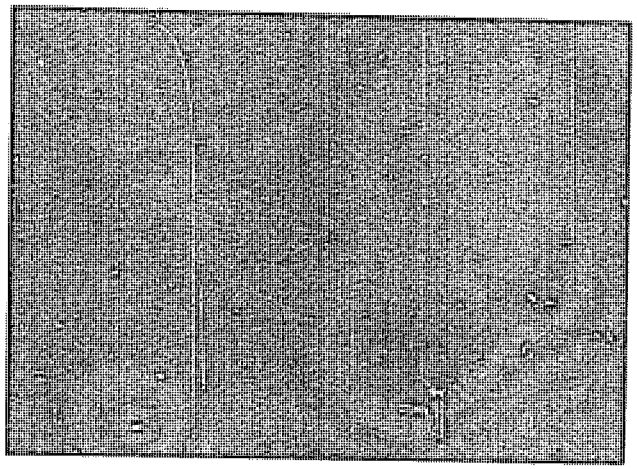
25c. *Balsamorhiza sagittata*



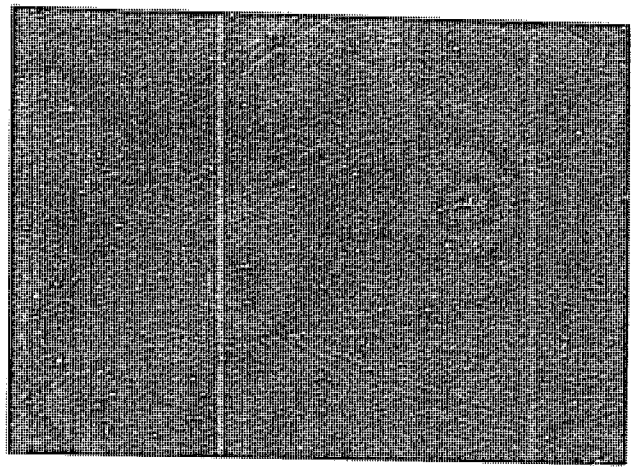
25d. *Balsamorhiza sagittata*

Plate 25

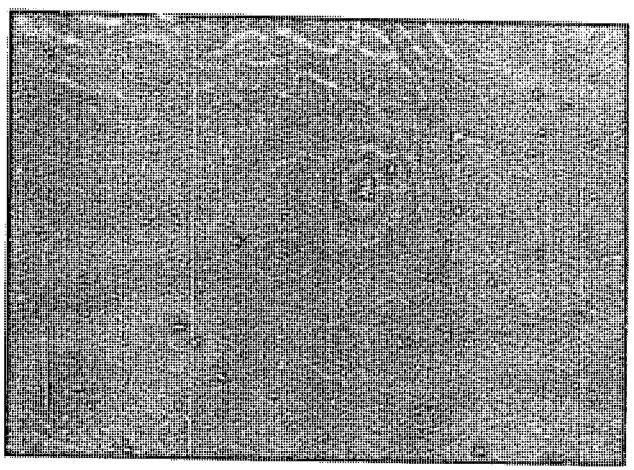
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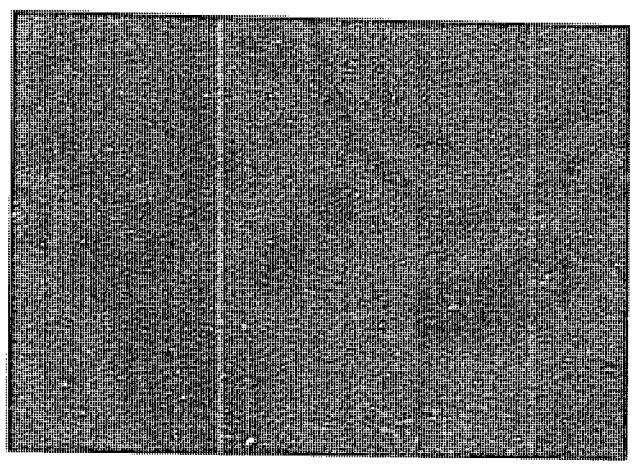
26a. *Achillea millefolium* (400X)



26b. *Achillea millefolium* (100X)



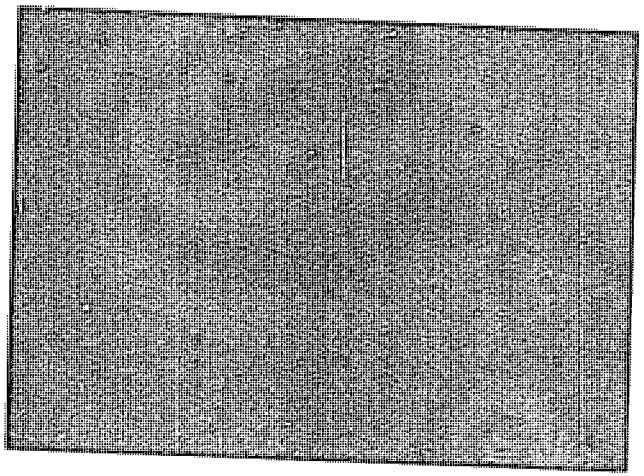
26c. *Achillea millefolium*



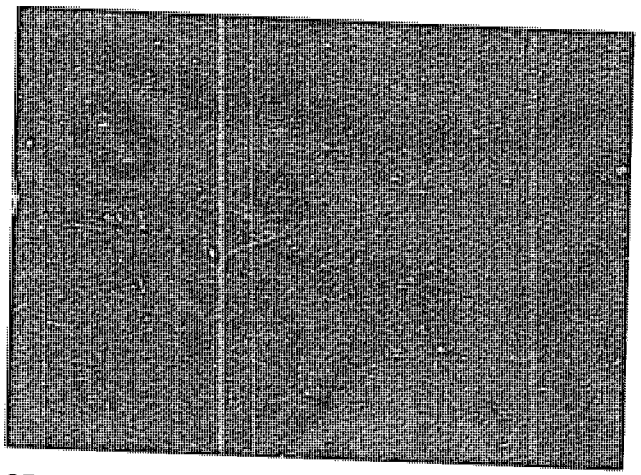
26d. *Erigeron austinae* (100X)

Plate 26

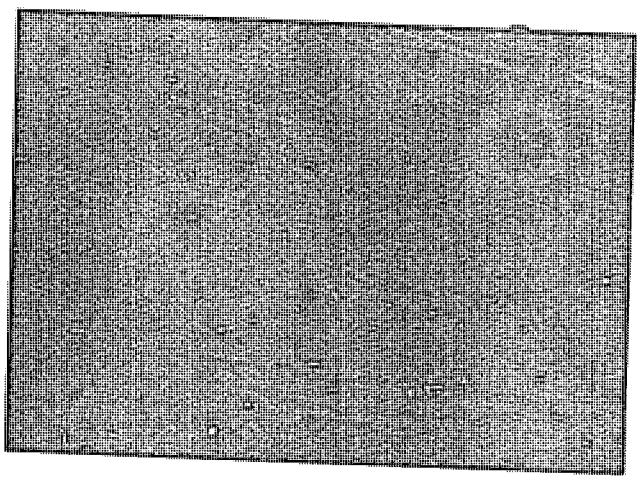
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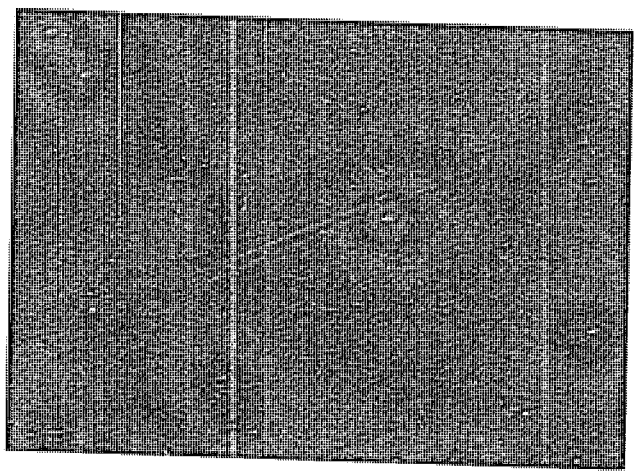
27a. *Erigeron austinae*



27b. *Erigeron austinae* (100X)



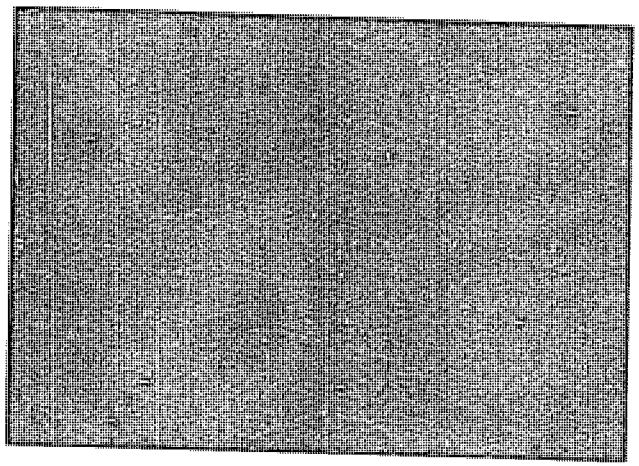
27c. *Erigeron bloomeri*



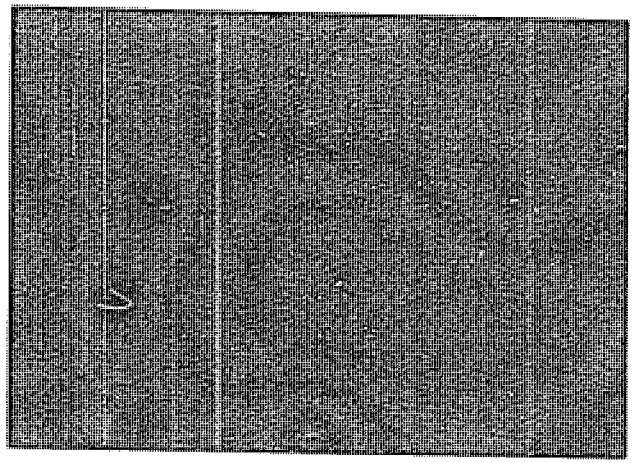
27d. *Erigeron bloomeri*

Plate 27

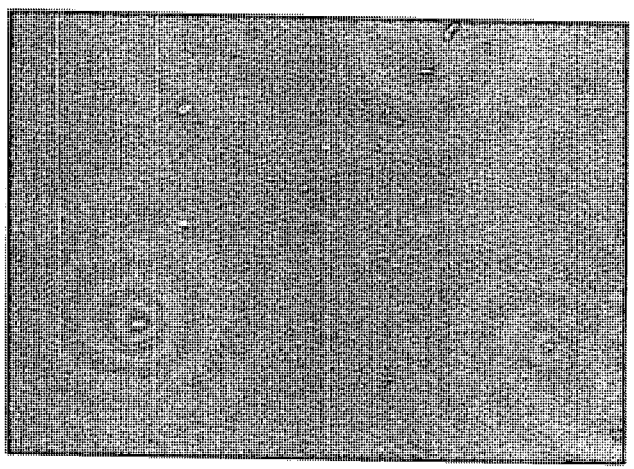
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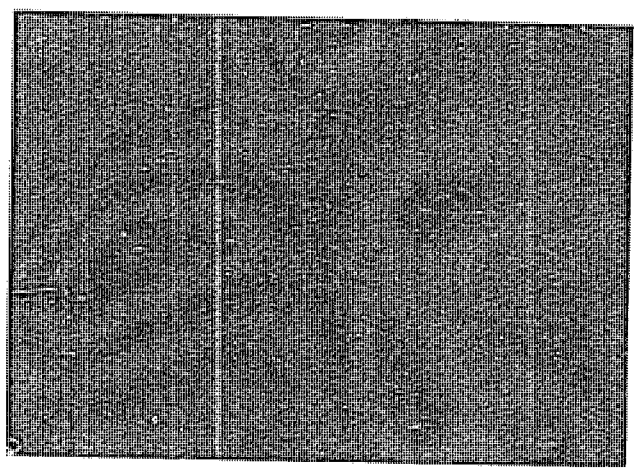
28a. *Erigeron bloomeri*



28b. *Taraxacum officinale*



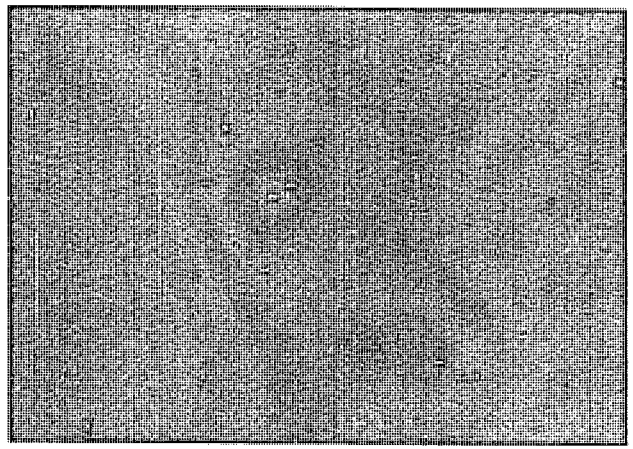
28c. *Taraxacum officinale*



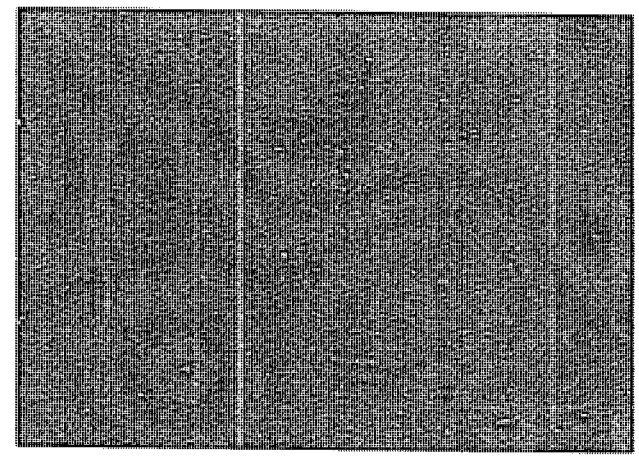
28d. *Taraxacum officinale*

Plate 28

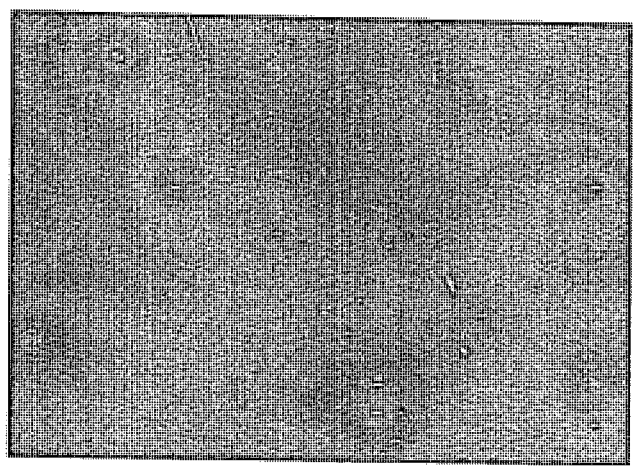
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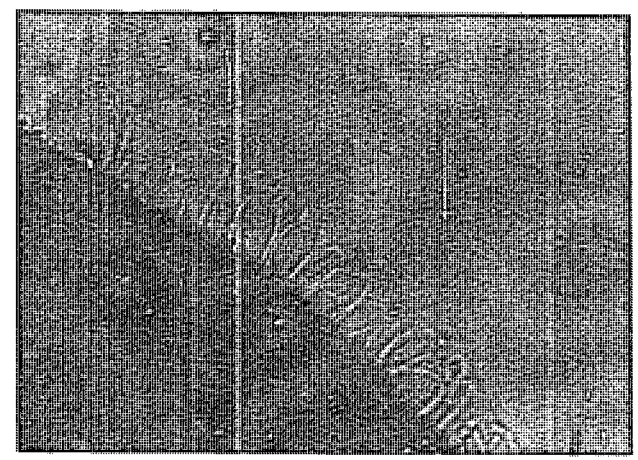
29a. *Potentilla spp.*



29b. *Potentilla spp.*



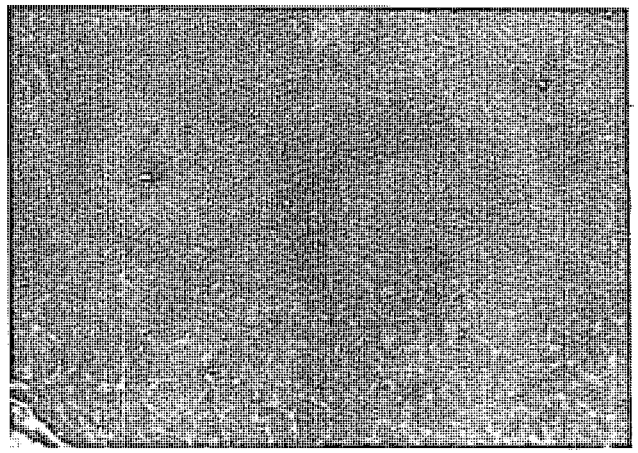
29c. *Potentilla spp.*



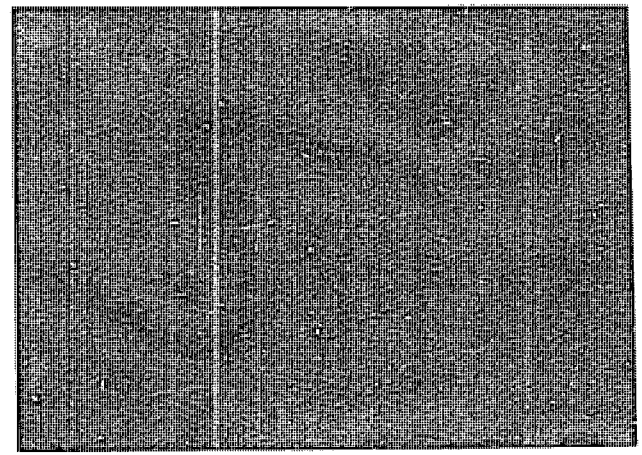
29d. *Chenopodium rubrum*

Plate 29

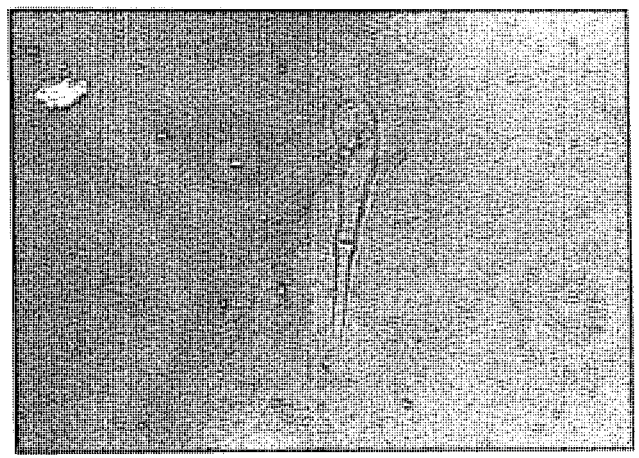
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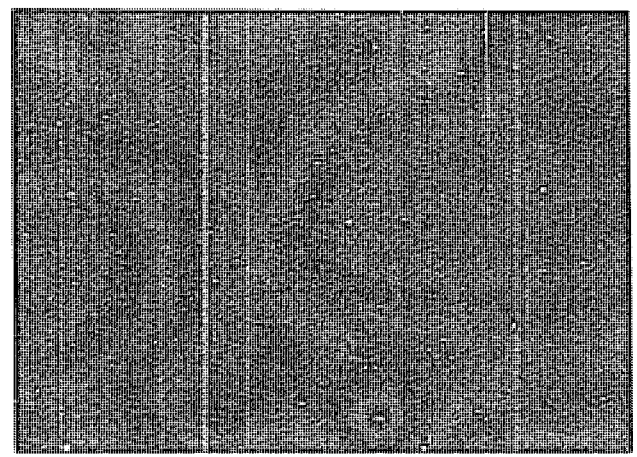
30a. *Chenopodium rubrum*



30b. *Chenopodium rubrum*



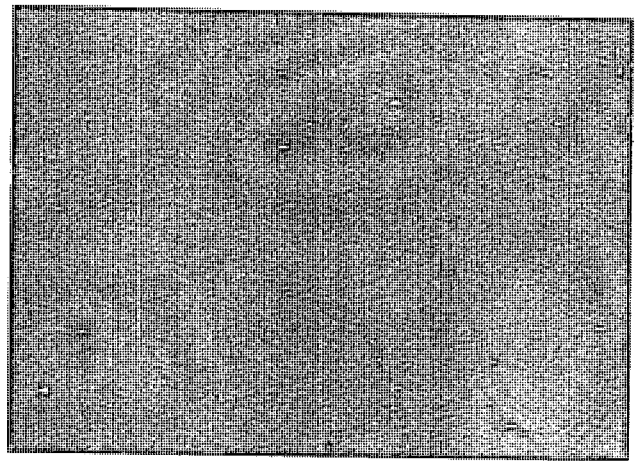
30c. *Rumex spp.*



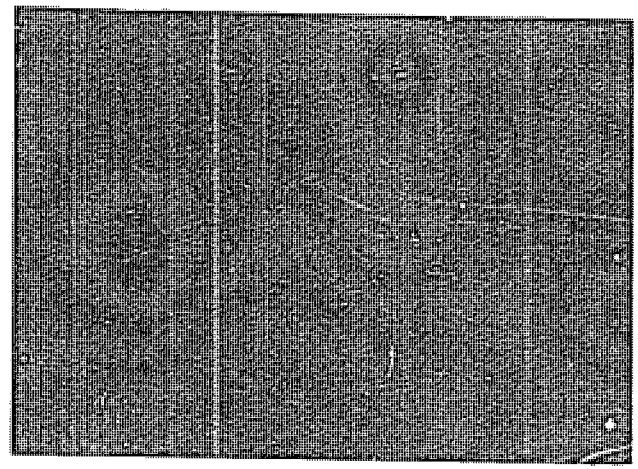
30d. *Rumex spp.*

Plate 30

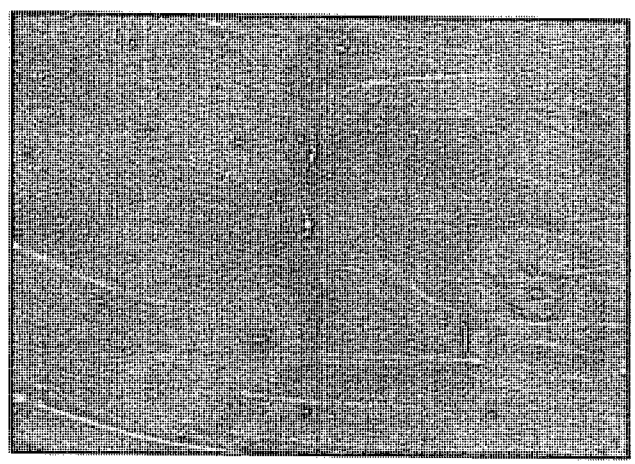
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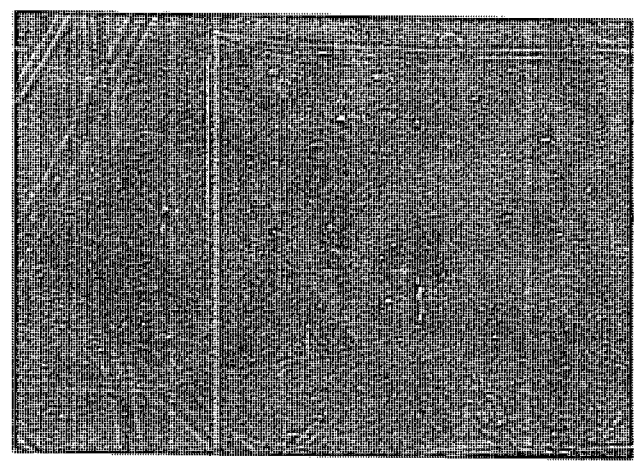
31a. *Rumex spp.*



31b. *Lupinus spp.*



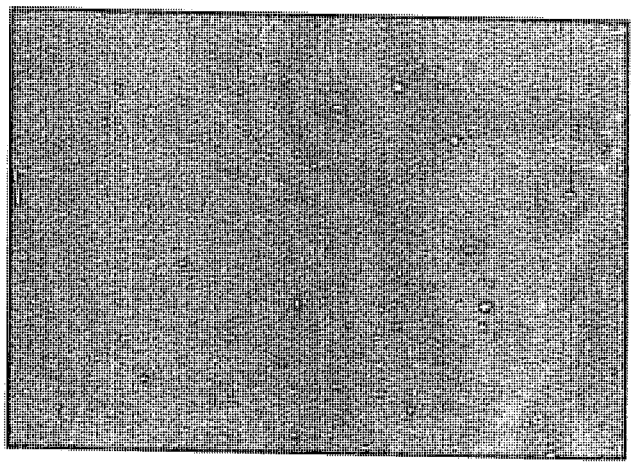
31c. *Lupinus spp.*



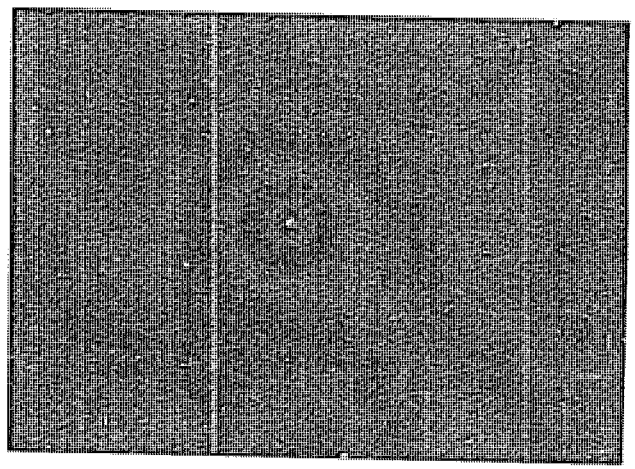
31d. *Lupinus spp.* (100X)

Plate 31

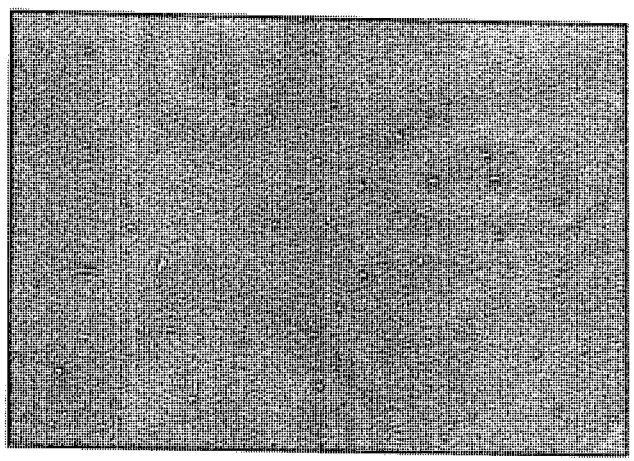
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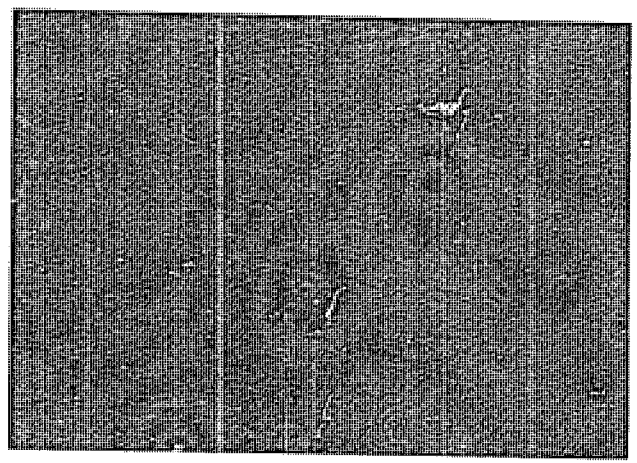
32a. *Symphoricarpos parishii*



32b. *Symphoricarpos parishii*



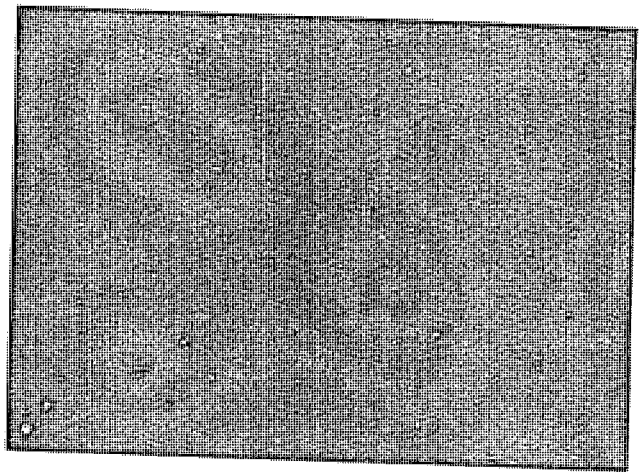
32c. *Symphoricarpos parishii*



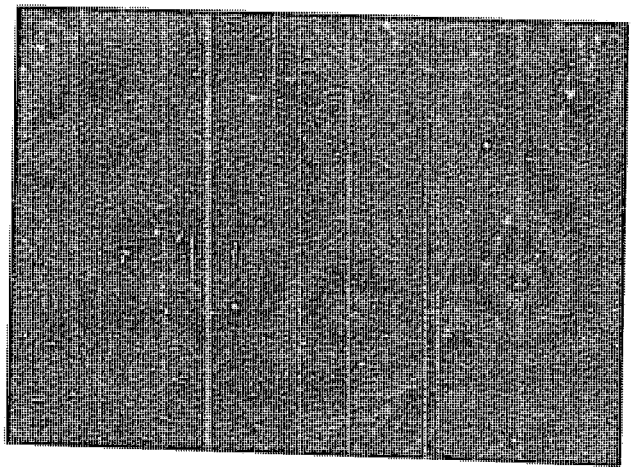
32d. *Agoseris spp.* (100X)

Plate 32

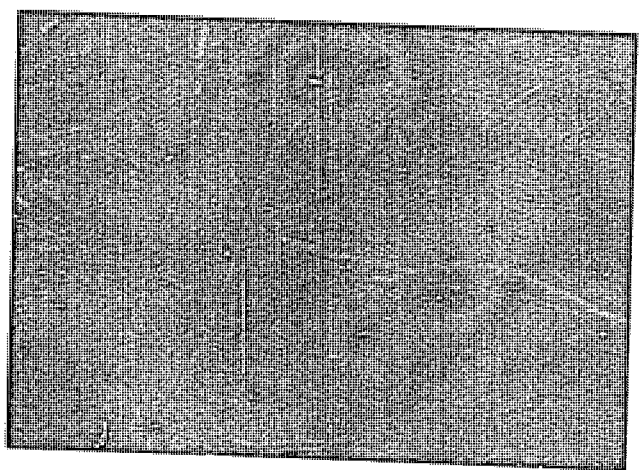
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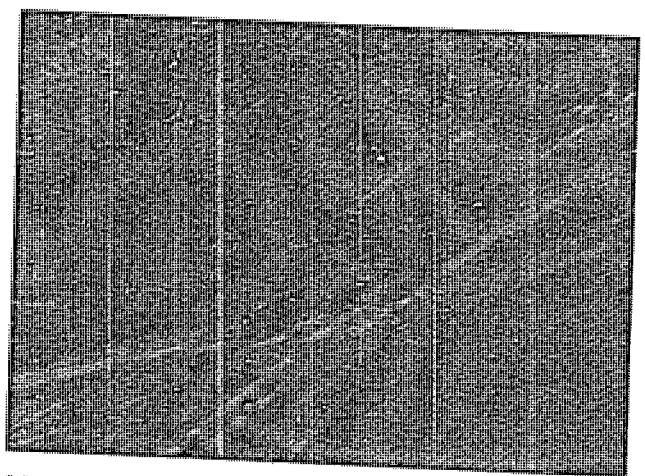
33a. *Agoseris spp.*



33b. *Agoseris spp.*



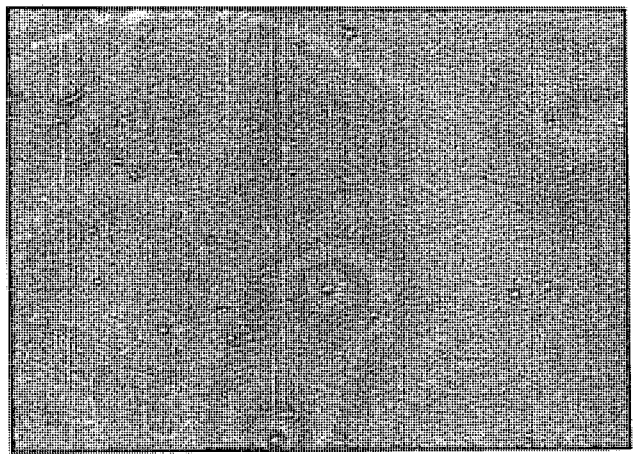
33c. *Astragalus purshii* (100X)



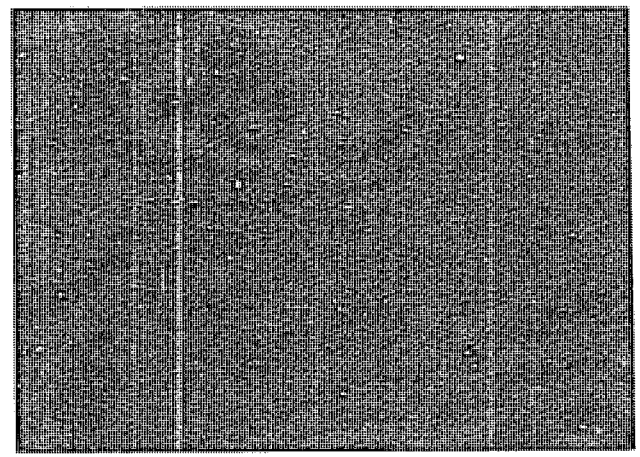
33d. *Astragalus purshii*

Plate 33

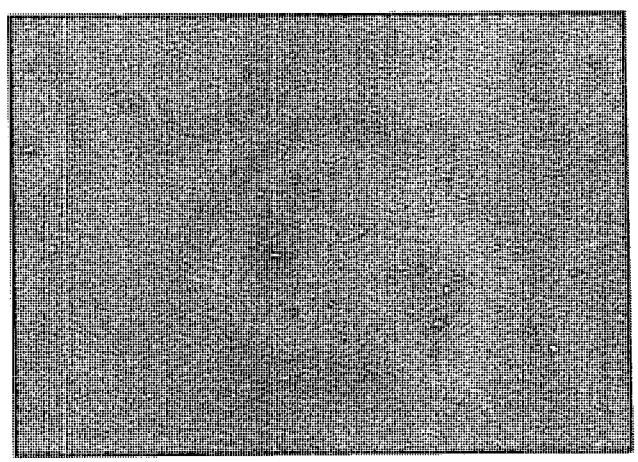
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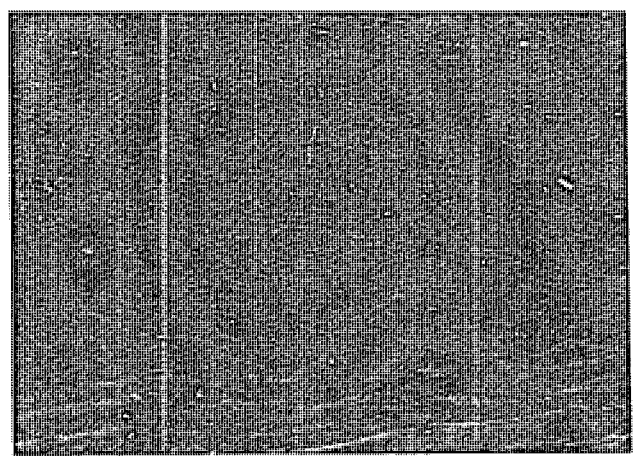
34a. *Astragalus purshii*



34b. *Astragalus spp.*



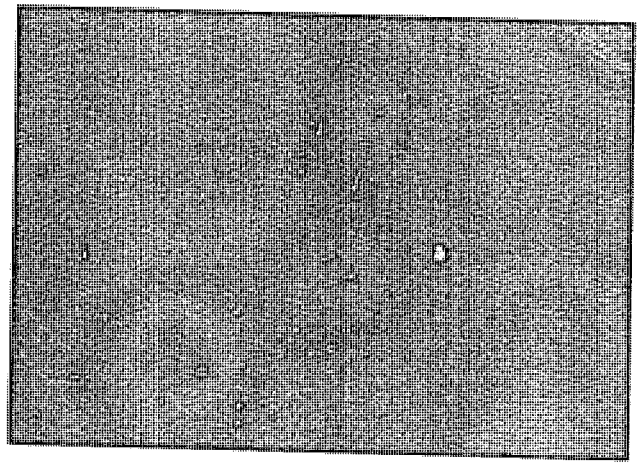
34c. *Astragalus spp.*



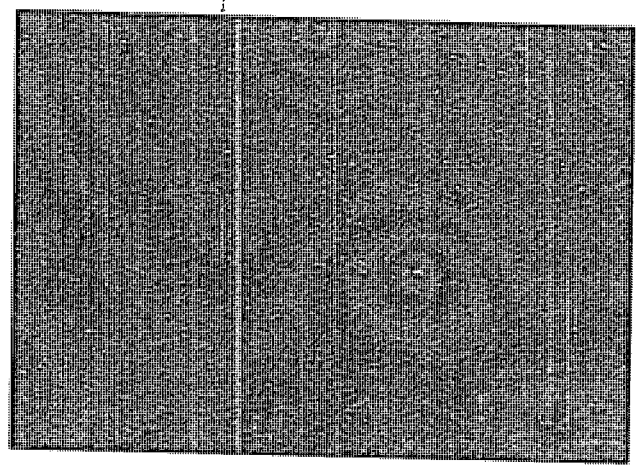
34d. *Haplopappus acaulis*

Plate 34

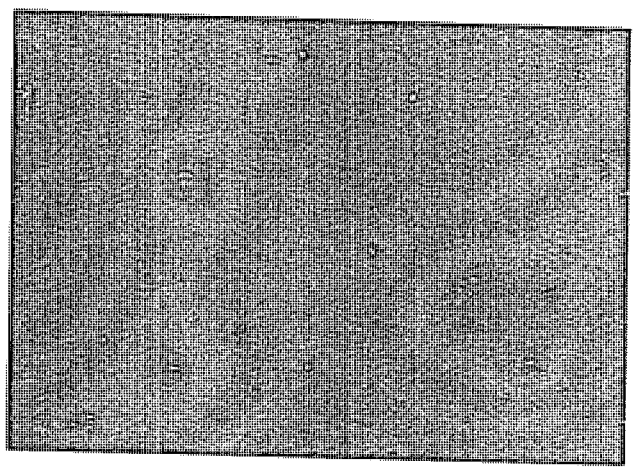
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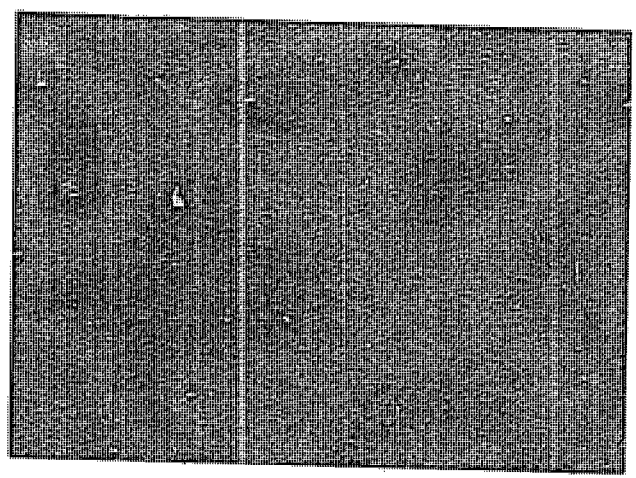
35a. *Haplopappus acaulis*



35b. *Haplopappus acaulis*



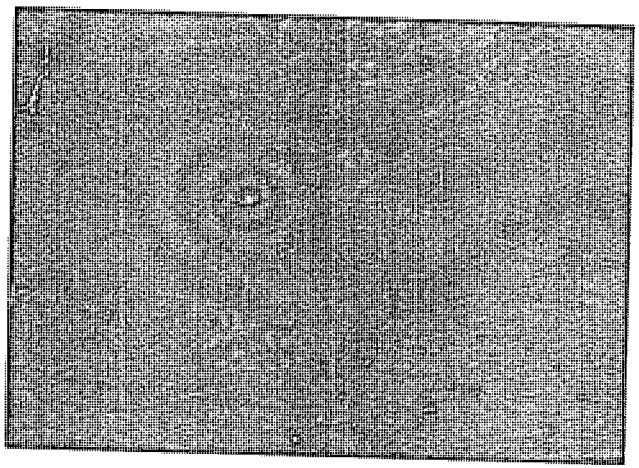
35c. *Arabis spp.*



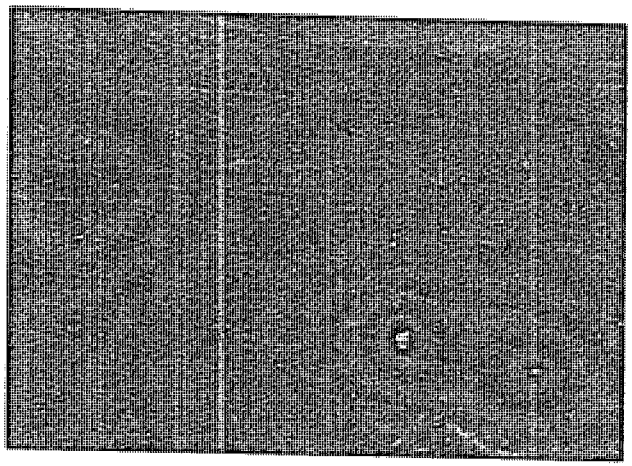
35d. *Arabis spp.*

Plate 35

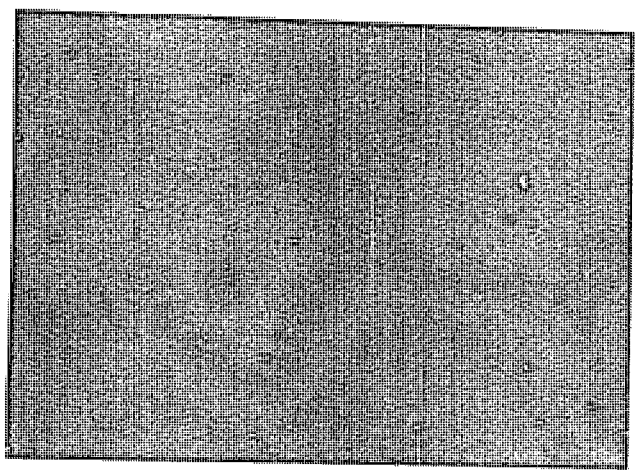
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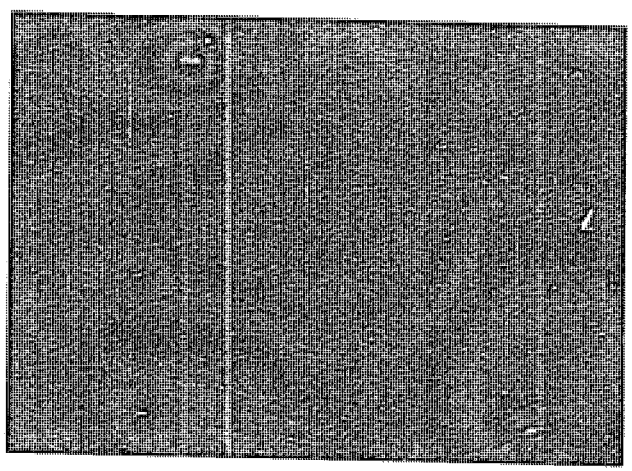
36a. *Castilleja spp.*



36b. *Castilleja spp.*



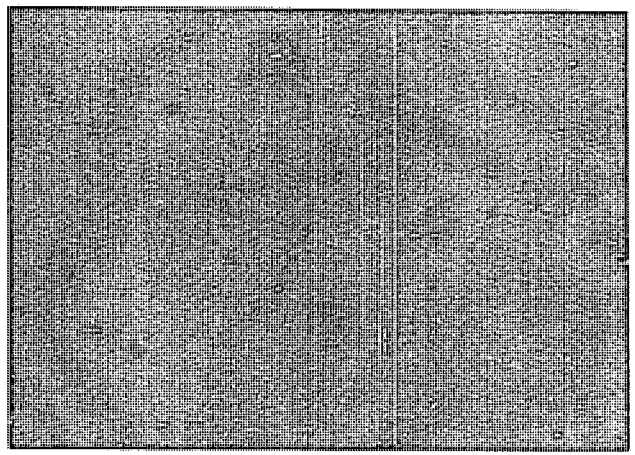
36c. *Frasera spp.*



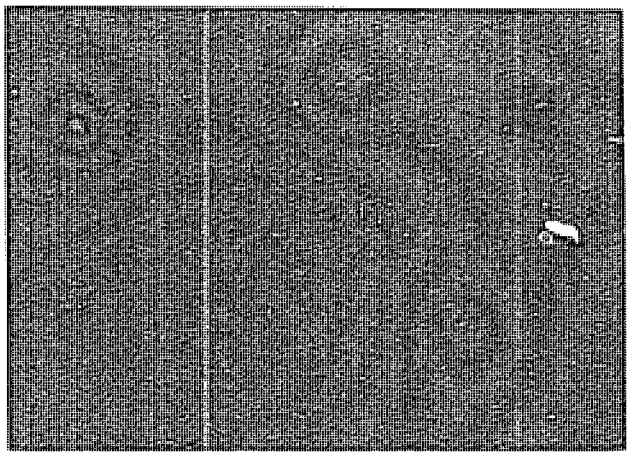
36d. *Frasera spp.*

Plate 36

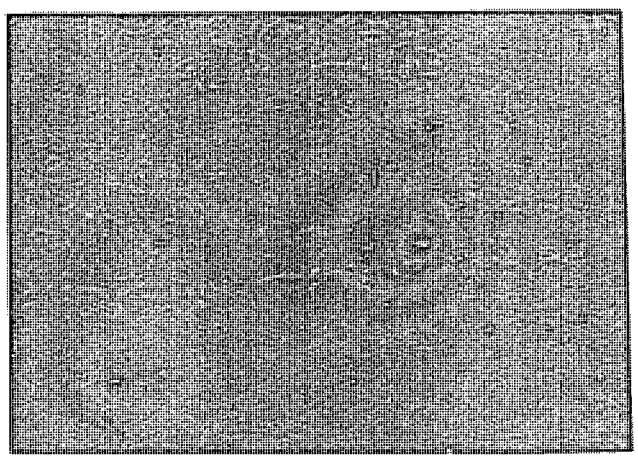
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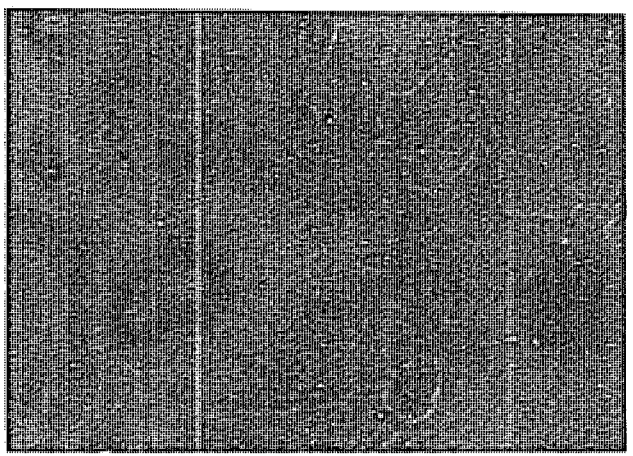
37a. *Tetradymia canescens*



37b. *Tetradymia canescens*



37c. *Aster scopulorum*



37d. *Aster scopulorum*

Plate 37

Journal of Arid Environments 184 (2021) 104304

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Free-roaming horses disrupt greater sage-grouse lekking activity in the Great Basin

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ARTICLE INFO

Keywords:
Cattle
Free-roaming horse
Galliformes
Leks
Mule deer
Pronghorn
Ungulates

ABSTRACT

Greater Sage-Grouse (*Centrocercus urophasianus;* hereafter, sage-grouse) and free-roaming horses (*Equus caballus*) co-occur within large portions of sagebrush ecosystems within the Great Basin of western North America. In recent decades, sage-grouse populations have declined substantially while concomitant free-roaming horse populations have increased drastically. Although multiple studies have reported free-roaming horses adversely impacting native ungulate species, direct interactions between free-roaming horses and sage-grouse have not been documented previously. We compiled sage-grouse lek count data and associated ungulate observations during spring of 2010 and 2013–2018. We used Bayesian multinomial logistic models to examine the response of breeding male sage-grouse to the presence of native (i.e. mule deer, pronghorn) and non-native (i.e. cattle, free-roaming horses) ungulates on active sage-grouse leks (traditional breeding grounds). We found sage-grouse were approximately five times more likely to be present on active leks concurrent with native ungulates compared to non-native ungulates. Of the four different ungulate species, sage-grouse were least likely to be at active leks when free-roaming horses were present. Our results indicate that free-roaming horse presence at lek sites negatively influences sage-grouse lekking activity. Because sage-grouse population growth is sensitive to breeding success, disruption of leks by free-roaming horses could reduce breeding opportunities and limit breeding areas within sage-grouse habitat.

1. Introduction

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) are a sagebrush-obligate species that require specific habitat types within sagebrush communities during various life-history stages, such as nesting, brood-rearing, and wintering (Patterson, 1952). Accordingly, population viability largely hinges on a diversity of habitats across large spatial extents and resulting population trends can serve as a proxy for the ecological integrity of sagebrush ecosystems (Rowland et al., 2006). In recent decades, greater sage-grouse populations have declined substantially throughout their range in western North America (Garton et al., 2015). Declining populations have been attributed to multiple perturbations affecting sagebrush ecosystems in different portions of their range, including anthropogenic alterations associated with energy development (Green et al., 2017), wildfire and invasive grasses (Coates et al., 2016), and pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) expansion (Baruch-Mordo et al., 2013).

Expanding populations of free-roaming horses (*Equus caballus*) represent another significant stressor to sagebrush ecosystem processes (Beever et al., 2018; Boyd et al., 2017). Although native North American horses became extinct following the Pleistocene, non-native horses imported during European settlement are now well-established across western North America (Beever et al., 2018). Free-roaming horse establishment was largely facilitated by The Wild Free-Roaming Horses and Burros Act of 1971 (Public Law 92–195, 1971) which, as amended, afforded protections to free-roaming equids on public lands and tasked the Bureau of Land Management (BLM) with managing the population on those lands. The BLM primarily manages free-roaming horses in designated Horse Management Areas (HMAs) and sets lower and upper population bounds that define an Appropriate Management Level (AML) to facilitate long-term management of these large herbivores within a designated area (BLM, 2010). The AML upper bound represents the threshold for range deterioration (BLM, 2010). Free-roaming horses are particularly ubiquitous in Nevada within the Great Basin, and the current population estimate of 46,974 horses in that state's HMAs exceeds the AML upper bound of 11,987 by 367% (BLM, 2020). The BLM also oversees Herd Areas (HAs) which are not managed with AMLs but comprise public lands that were occupied by horses when the Wild

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https://doi.org/10.1016/j.jaridenv.2020.104304
Received 2 May 2019; Received in revised form 29 July 2020; Accepted 4 September 2020
Available online 5 October 2020
0140-1963/© 2020 Published by Elsevier Ltd.

Horse and Burro Act passed (BLM, 2010). Currently, HMAs contain a majority of the free-roaming horses on public lands relative to HAs (BLM, 2020). However, population estimates within HMAs are not representative of the entire free-roaming horse population. Horses also use areas outside the jurisdiction of the BLM such as on state, private, and tribal lands (Beever et al., 2018; Hennig et al., 2018). Furthermore, population estimates for free-ranging large mammals are often difficult to calculate because detectability is compromised over large areas with heterogeneous terrain (Lubow and Ransom, 2016).

Given the rapid population increase, growing evidence suggests that free-roaming horses can directly and indirectly disrupt native wildlife populations inhabiting sagebrush ecosystems, yet most research has focused on intra-guild competition among large herbivores. For example, free-roaming horses monopolize and actively exclude native ungulates from limited water sources through interference competition (Hall et al., 2018). In contrast, relatively few studies have evaluated interspecific interactions between free-roaming horses and avian wildlife in sagebrush ecosystems, including sage-grouse. Potential for direct interactions exists given the high degree of range overlap between sage-grouse and free-roaming horses (Beever and Aldridge, 2011). Authors have suggested indirect impacts on sage-grouse by reductions in perennial vegetation cover and arthropod abundance, increases in annual grass cover and soil-surface hardness, and multiplicative effects with cattle grazing and drought (Beever and Aldridge, 2011; Davies et al., 2014). Aggressive or dominant behavior exhibited by free-roaming horses (Berger, 1985) that is directed towards sage-grouse, or avoidance by sage-grouse of space occupied by horses, could manifest as a type of competitive interaction that negatively affects sage-grouse reproduction but remains largely unquantified.

During spring, male sage-grouse congregate on traditional breeding grounds, known as leks, to court and mate with visiting females (Schroeder et al., 1999). Counts of males attending leks are a widely used index of sage-grouse population abundance (Connelly et al., 2003), so factors that influence behavior at leks have important ramifications on breeding success and accurate population estimation. Although sage-grouse demonstrate high site fidelity to individual leks (Fremgen et al., 2017), they are also sensitive to natural and anthropogenic disturbances that can reduce attendance rates and ultimately drive lek abandonment (Hess and Beck, 2012). Persistent disruptions at leks may present additional obstacles for population maintenance (Green et al., 2017) for a species that is already sensitive to relatively low reproductive rates (Taylor et al., 2012).

Our study objective was to identify outcomes of interactions between large herbivores on breeding sage-grouse by quantifying male sage-grouse lekking activity in relation to the presence of non-native (horses, cattle) and native (mule deer, pronghorn) ungulates across multiple leks at 14 sites in the Great Basin during 2010 and 2013–2018. Based on literature documenting intra-guild competition between horses and ungulates (Berger, 1985; Hall et al., 2018), we hypothesized that free-roaming horses would be most disruptive to sage-grouse lekking activity.

2. Methods

We compiled ungulate observations from two sources. Because of limited data during 2010, we compiled ungulate sightings recorded during lek counts within field notes. Ungulate sightings were not recorded during 2011 and 2012. By 2013, we established a protocol that recorded native and non-native ungulates on leks during lek counts. We conducted 3–4 surveys per known lek site during spring (March–May) across 14 study areas within California, Idaho, and Nevada during 2013–2018 (Fig. 1). Lek surveys typically lasted 10–15 min, were equally spaced through the breeding season and conducted between 30 min before sunrise and 90 min after sunrise in accordance with standardized lek survey protocols (Connelly et al., 2003). We used binoculars or a spotting scope to survey sage-grouse from a suitable location with view of the entire lek. At lek survey locations, we recorded presence and behavior of all native and non-native ungulates when they were present within or on the lek perimeter boundary. While subjective to an extent, the boundary was determined by the perimeter of the outermost males with an approximate 10–20 m buffer. We categorized each lek as active or inactive. A lek was considered active if two or more breeding males were observed during at least two of the previous 5 years and inactive if two or more males had been observed only once during the previous 5 years. We compiled a subset of data consisting of counts for all active leks in which free-roaming horses or cattle (non-native ungulates), or mule deer or pronghorn (native ungulates) were observed at least once. Although burros were present at some sites, we did not observe them occupying sage-grouse leks. Lek surveys without any ungulates present were classified as "none". We categorized male sage-grouse activity into three classes: present, absent, and flushed. Sage-grouse were considered present if they remained on the lek for the entire duration of the count without flushing; absent if they were not present at the established lek coordinates during a lek count, even if fresh sign was present or if a satellite lek was found in the vicinity; and flushed if they were present but then displaced from the lek by ungulate activity. We did not include five lek surveys in which multiple ungulate species were observed to simplify the analysis and facilitate interpretation.

We used a Bayesian multinomial logistic model (Darrah et al., 2018) to estimate the likelihood of sage-grouse activity in the presence of ungulates. The model took the form:

$$y_i \sim multinomial\left(\left[P_{pi},\ P_{ai}, P_{fi}\right], 1\right)$$

where sage-grouse activity y_i at each lek i follows a multinomial distribution. Possible sage-grouse activities were present (p), absent (a), and flushed (f). We then regressed predictors of ungulate presence (i.e. horse, cattle, pronghorn, mule, none) on the likelihood of each sage-grouse activity. For example, the equation for sage-grouse absence took the form:

$$\eta_{ai} = \beta_0 + \beta_h x_i + \beta_c x_i + \beta_p x_i + \beta_m x_i + \beta_n x_i$$

where η_{ai} is the probability that sage-grouse were absent at lek i. The variable β_0 represents the average rate of sage-grouse absence while β_h, β_c, β_p, β_m, and β_n represent the effects of presence of horse (h), cattle (c), pronghorn (p), mule deer (m), and no ungulates (n), respectively, on rates of sage-grouse absence, given conditions (x) at lek i.

We conducted the Bayesian multinomial model analysis in R 3.4.3 (R Core Team, 2018) and JAGS 4.2.0 using the package rjags (Plummer, 2016). We ran 10,000 iterations of three chains with a thinning rate of two and a burn-in of 1000. We evaluated chain convergence visually using trace plots and numerically using the Gelman-Rubin diagnostic (R-hat; Gelman and Hill, 2007). We determined that chains had converged when R-hat < 1.1 for all parameters in the model. We used uninformative priors with normal distributions of mean zero and precision 0.01 for all parameters.

3. Results and discussion

We observed free-roaming horses on leks at five study areas: Desatoya, Huntington Valley, Midway, Monitor Range, and Northern SWIP. Excluding Huntington Valley, these overlapped with the Desatoya HMA, Pancake HMA, Butler Basin HA, and Triple B HMA, respectively. We compiled data from 255 lek surveys for 2010 and 2013–2018 and recorded 89 instances of single native (n = 74) and non-native (n = 15) ungulate species at active sage-grouse leks at all study areas. Pronghorn were the most commonly observed ungulate during surveys (n = 60, 67.0% of ungulate observations), followed by mule deer (n = 14, 16.0%), free-roaming horses (n = 9, 10.0%), and cattle (n = 6, 7.0%). Of the six lek surveys where cattle were present, male sage-grouse were present at two (33.3%), absent at three (50.0%), and flushed at one

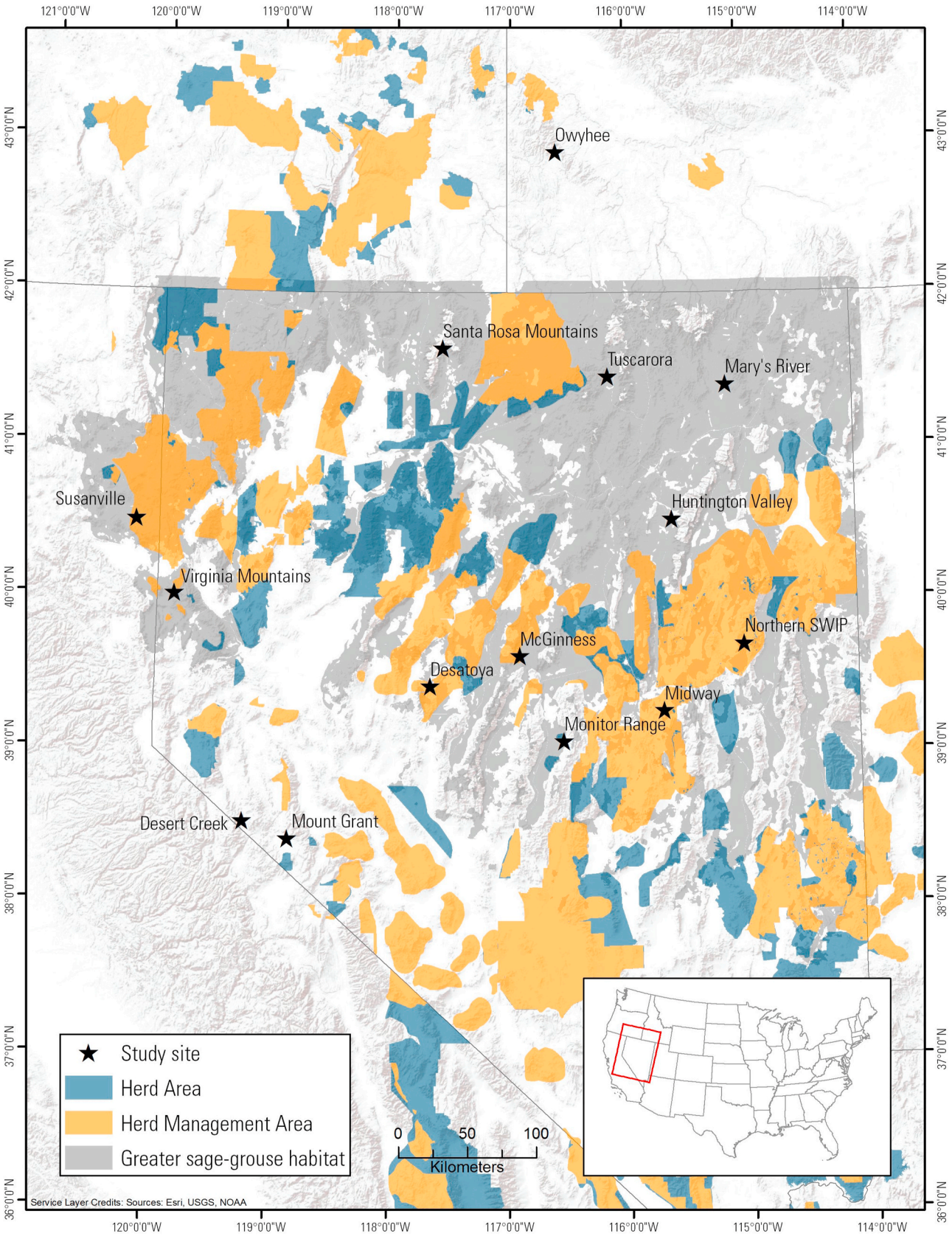


Fig. 1. Study sites of sage-grouse lek surveys and ungulate surveys in relation to Herd Areas, Herd Management Areas, and sage-grouse habitat (Coates et al., 2020) during 2010 and 2013–2018.

(16.7%). Of the nine lek surveys where free-roaming horses were present, male sage-grouse were present at one (11.1%), absent at seven (77.8%), and flushed during one (11.1%). Of the 74 lek surveys where single native ungulate species were present, male sage-grouse were present at 54 surveys (73.0%), absent at 17 (23.0%), and flushed during three (4.0%). Pronghorn appear to have been responsible for the three flushes. Otherwise, observers generally noted that sage-grouse appeared unperturbed by pronghorn and mule deer and continued displaying.

Sage-grouse activity varied significantly according to ungulate status and species (Fig. 2). Sage-grouse were approximately 5 times more likely to be present concurrent with native ungulates (median: 62.92%, 85% CI: 25.17–85.71%) than when non-native ungulates were present (12.85%, 85% CI: 2.07–44.14%; Fig. 2a) on the lek. Additionally, sage-grouse were 2.6 times more likely to flush in the presence of non-native ungulates (13.75%, 85% CI: 0.88–65.33%) than in the presence of native ungulates (5.28%, 85% CI: 0.75–25.02%). Mule deer and pronghorn were comparatively innocuous, with predicted probabilities of sage-grouse absence at 24.6 (85% CI: 2.04–46.39%) and 19.4% (85% CI: 7.11–32.66%; Fig. 2b), respectively. Predicted probabilities for sage-grouse being present concurrently with mule deer or pronghorn or in the absence of all ungulates were 74.4 (85% CI: 52.76–96.75%), 75.6 (85% CI: 62.84–88.29%), and 83.6% (85% CI: 52.01–96.36%), respectively (Fig. 2b). Meanwhile, predicted probabilities for sage-grouse being present concurrently with cattle or horses were 43.0 (85% CI: 17.15–76.04%) and 17.1% (85% CI: 4.81–38.83%), respectively. Furthermore, the predicted probabilities for sage-grouse absence in the presence of cattle or horses were 44.1 (85% CI: 13.0–73.82%) and 75.4% (85% CI: 50.94–91.40%), respectively. Overall, sage-grouse were least likely to be present and more likely to be absent when horses were on the established leks.

Our findings suggest that male sage-grouse respond differently to native and non-native ungulates on leks (Fig. 3). When pronghorn or mule deer were present, sage-grouse generally appeared unperturbed and continued displaying. In contrast, sage-grouse were usually not detected when free-roaming horses or cattle were on the lek. To our knowledge, our observations are the first recorded interactions between free-roaming horses and male sage-grouse on leks. We only directly observed one event in which horses flushed sage-grouse but, knowing that horses were near other leks, we surmise that similar events occurred outside of the lek count observation period for vacant leks or that the presence of horses discouraged sage-grouse from occupying the lek. This inference is supported by our discovery of a horse-occupied lek containing fresh sage-grouse fecal droppings. Other instances occurred where sage-grouse were absent from a lek only when free-roaming horses were present. For example, one lek averaged 12 male sage-grouse and another averaged nine males when horses were absent. In contrast, both leks were devoid of sage-grouse when horses were present. Lastly, sage-grouse did not return to some leks at subsequent lek counts following visitation by horses but may have formed or moved to nearby satellite leks. Since we did not individually mark sage-grouse

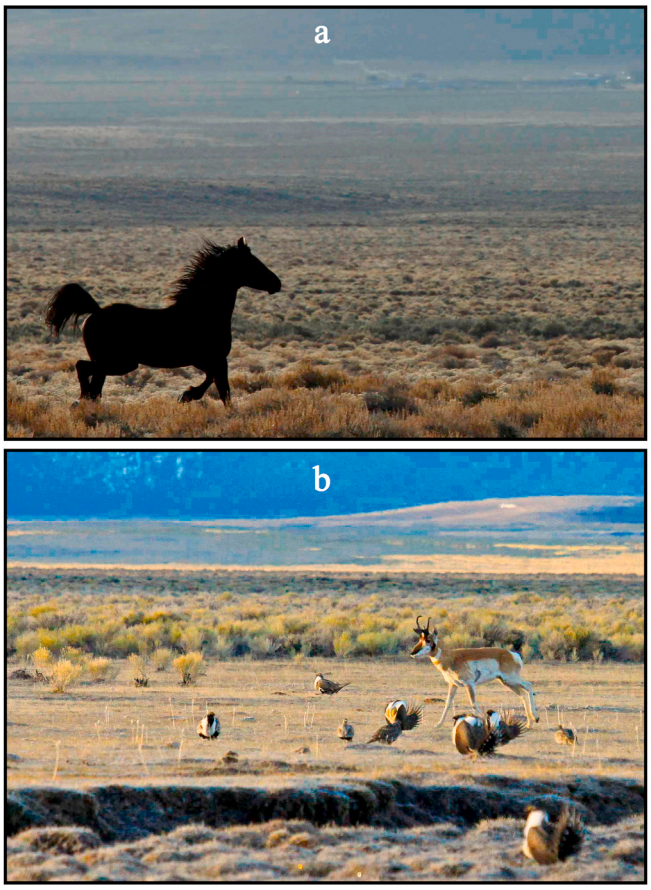


Fig. 3. Ungulates on leks: (a) Free-roaming horse exhibiting aggressive posturing towards observer (b) Pronghorn crossing lek in presence of sage-grouse. Photos by Tatiana Gettelman.

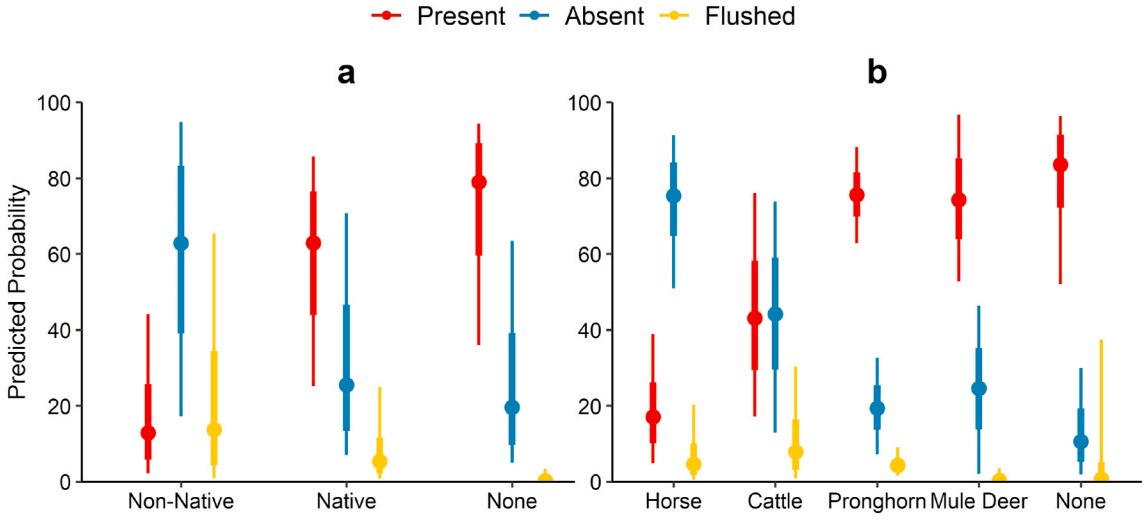


Fig. 2. Estimated median probabilities of sage-grouse activity according to ungulate (a) native status and (b) species in 2010 and 2013–2018. Points represent posterior median estimates, thick lines represent 50% credible intervals, and thin lines represent 85% credible intervals.

with identifiable markers, it is difficult to ascertain whether the satellite leks were composed of the same individuals as the original leks. Nevertheless, we no longer detected male sage-grouse at the original location following intrusion by free-roaming horses. Although we seldom observed concurrent occupation of a lek by both sage-grouse and horses during our lek surveys, we have previously observed at least two occasions of horses exhibiting aggressive (e.g. kicking) or playful behavior towards sage-grouse.

We speculate that differences in sage-grouse lekking activity may be influenced potentially by differences in size, novelty, or behavior of Great Basin ungulates. First, sage-grouse were most likely to be absent in the presence of cattle and horses, which were the largest ungulates observed in our study. Sage-grouse may assess ungulates as a threat beyond a certain body size threshold that pronghorn and mule deer fall under. Second, sage-grouse may be less accustomed to free-roaming horses and cattle introduced to the Great Basin during European settlement in comparison to native ungulates. Finally, behavioral differences between ungulate species may account for the variation in sage-grouse response. Despite similarities in time since introduction and size, sage-grouse were more likely to be present when cattle were present relative to horses. Although our data do not allow identification of the behavioral mechanisms driving decreased lekking activity in association with free-roaming horses, competitive amensalism, where one organism causes a negative effect on another without being affected in return (Odum, 1983), is possible given well-documented aggressive behavior displayed by horses towards conspecifics and native ungulates (Berger, 1985; Hall et al., 2018). Although we do not know whether this behavior manifests through current (e.g. horses kicking and chasing sage-grouse) or past (e.g. sage-grouse vacating leks when horses come near because of past negative experience) interactions, future studies that utilize remote videography on leks likely to encounter horses would help answer this important question.

Free-roaming horses present a unique management problem in the United States (Beever et al., 2018; Scasta et al., 2018). Although cattle distribution and grazing impacts on native wildlife can be limited through fencing, appropriate grazing practices, and permitting; free-roaming horse management heavily relies on managing population levels (Beever and Aldridge, 2011). The BLM currently attempts to limit horse population growth through immunocontraception and by periodic gathers where animals are removed from the range and brought into captivity for adoption (Beever et al., 2018). Protections under the Wild Free-Roaming Horse and Burro Act of 1971 severely limit the development of additional management options that could mitigate the potential impact of free-roaming horses on sage-grouse. This is especially important owing to extensive overlap of the two species and mutual need for limited resources (e.g. water, herbaceous forage) across large portions of the Great Basin (Fig. 1).

Mating success for male sage-grouse is conditional on the amount of time that they spend displaying on the lek (Gibson and Bradbury, 1985). Despite our limited sample sizes for non-native ungulates, our results strongly indicate that free-roaming horses reduce lekking activity when they do visit leks and constitute a non-trivial stressor to sage-grouse population growth through reduced breeding opportunities to a species already sensitive to disturbance. Negative effects on sage-grouse population growth can compound further as the reproductive cycle progresses, particularly when mesic resources required during the brood-rearing phase become degraded by horse utilization (Beever and Aldridge, 2011; Davies et al., 2014). Improved understanding of free-roaming horse resource use and movements within sagebrush ecosystems, and sage-grouse response to free-roaming horse presence and behavior at crucial life stages may help develop practices that mitigate ecological impacts of free-roaming horses. We propose that managers and researchers account for free-roaming horse presence as a potential source of bias when conducting annual sage-grouse lek surveys, as our results suggest that they can influence observed counts. Population assessments may be underestimated if free-roaming horses disrupt lek activity prior to counting male sage-grouse during the survey.

Finally, the ecological impacts of free-roaming horses are not limited to the United States. Free-roaming horses occupy a wide range of ecosystems across multiple countries and are associated with reductions in environmental quality, ecosystem function, and plant community composition (Eldridge et al., 2020). Community composition, which includes measures of species diversity and richness, appears particularly susceptible to free-roaming horse activity in arid environments (Eldridge et al., 2020). Globally, most studies on free-roaming horse impacts have primarily focused on plants and soil while few have investigated responses by other animals (Eldridge et al., 2020). However, studies on responses by birds, reptiles, and small mammals to free-roaming horses are increasing (Hall et al., 2016; Cherubin et al., 2019). Our study has filled a much-needed gap in our understanding of how native non-ungulate animals respond to free-roaming horses outside of a direct competition perspective. Additional research on interactions between free-roaming horses and wildlife both in the United States and abroad is imperative to allow a more comprehensive understanding of free-roaming horse impacts on biodiversity and ecosystems. Ultimately, filling such knowledge gaps will help inform management decisions, especially those involving species of conservation concern.

CRediT authorship contribution statement

Diana A. Muñoz: Data curation, Formal analysis, Writing - original draft, Visualization, Methodology, Writing - review & editing. **Peter S. Coates:** Conceptualization, Investigation, Supervision, Project administration, Funding acquisition, Visualization, Methodology, Writing - review & editing. **Mark A. Ricca:** Project administration, Funding acquisition, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was not funded by any public, commercial, or not-for-profit agency. We followed all relevant state and federal laws while conducting this work. We are grateful to the numerous field technicians, interns, and volunteers who diligently collected data at our study areas throughout the Great Basin. We thank Tatiana Gettelman for bringing this topic to our attention and inspiring the ensuing investigation. We also thank Brianne Brussee and Brian Prochazka for assistance in designing and implementing the statistical model. Lastly, we thank Michael Chenaille for map-making assistance. The use of firm, trade, or brand names in this report is for identification purposes only and does not constitute endorsement by the U.S. Government.

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nature COMMUNICATIONS

ARTICLE

https://doi.org/10.1038/s41467-021-27439-6 OPEN

Collapse of the mammoth-steppe in central Yukon as revealed by ancient environmental DNA

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The temporal and spatial coarseness of megafaunal fossil records complicates attempts to to disentangle the relative impacts of climate change, ecosystem restructuring, and human activities associated with the Late Quaternary extinctions. Advances in the extraction and identification of ancient DNA that was shed into the environment and preserved for millennia in sediment now provides a way to augment discontinuous palaeontological assemblages. Here, we present a 30,000-year sedimentary ancient DNA (sedaDNA) record derived from loessal permafrost silts in the Klondike region of Yukon, Canada. We observe a substantial turnover in ecosystem composition between 13,500 and 10,000 calendar years ago with the rise of woody shrubs and the disappearance of the mammoth-steppe (steppe-tundra) ecosystem. We also identify a lingering signal of *Equus* sp. (North American horse) and *Mammuthus primigenius* (woolly mammoth) at multiple sites persisting thousands of years after their supposed extinction from the fossil record.

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Humans evolved and dispersed throughout the continents in an epoch dominated by giant terrestrial mammals. Megafauna (body mass ≥ 44 kg) only exist in comparable densities today within small refugia (mainly Africa) where most of their populations are in states of decline, and many of these species are threatened or endangered[1,2]. The ecological reverberations associated with the Late Pleistocene (130,000–11,700 years before present [BP]) loss of approximately 101 of 150 genera[3] of Earth's largest terrestrial animals is thought to have restructured the terrestrial biosphere, impacting vegetation composition and diversity, biogeochemistry, and climate feedback systems[4–13]. This rearrangement of terrestrial ecosystems, including massive biogeographic range shifts, local extirpations, and widespread extinctions, is argued by some to be the direct result of rapid climate change and attendant environmental feedbacks during the late Pleistocene[14–17]. Others contend[18–23] that factors unique to the last glacial period are to blame, such as the coincident dispersal of a new predator—*Homo sapiens*. It is likely that no single factor can account for the staggered magnitude of such losses globally, but rather that each ecosystem experienced a variable set of locally compounding pressures[17,24,25]. Taphonomic processes challenge attempts to tease apart the palaeoecological nuances of the late Quaternary extinctions (LQE), necessitating relatively precise estimates for megafaunal population declines and last appearance dates[26,27], for timings of ecological shifts (e.g. changes in plant community structure), as well as for robust archaeological evidence of anthropogenic impacts.

In the case of eastern Beringia (unglaciated regions of Yukon, Canada and Alaska, U.S.A.), Guthrie[16], Mann et al.[28,29], and Rabanus-Wallace et al.[30] argue that the expansion of woody shrubs and peatlands following an increased moisture regime during the late Pleistocene was the leading contributor to the loss of megafaunal grazers, including mammoth, horse, and bison. By contrast, Zimov et al.[23,31] contend that megafaunal extirpations preceded a rise in woody shrubs, with the loss of keystone megaherbivores having led to the disappearance of the graminoid and forb dominated, mammoth-steppe biome[5,31–33]. Disentangling the relative timings of ecological restructuring versus megafaunal population declines often exceeds the resolution[34] of Quaternary records.

Here, we present hybridization capture enriched sedimentary ancient DNA (sedaDNA) data derived from loessal silts preserved in permafrost (Fig. 1, Table 1) and recovered from four sites in the Klondike goldfields—an unglaciated region of west-central Yukon Territory, Canada[35]—dating to ca. 30,000–4000 calibrated (calendar) years before present (cal BP). This work builds on the methodological results reported in Murchie et al.[36] in which North American horse (*Equus caballus*) and woolly mammoth (*Mammuthus primigenius)* DNA was unexpectedly identified in a permafrost sample dating to ~9700 cal BP. This post-dates the last macrofossil evidence (such as bones, teeth, and soft-tissues) of these animals in Alaska by some 3300 years. Such a late date is indicative of a substantial ghost range (cryptic population)—an extended spatio-temporal range derived from palaeoecological proxies that post-date the last macrofossil remains[37].

Our aims here are two-fold. The first is to assess how our permafrost sedaDNA dataset can be used to assess the plausibility of two competing explanatory models of Beringian extinctions. These are the bottom-up "shrub/peatland expansion" model of Guthrie[16] and Mann et al.[28–30], and the top-down "keystone megaherbivore decline" model of Zimov et al.[5,23]. The shrub/peatland expansion model argues that climate change drove ecosystems into new equilibrium states that were unfavourable for megafaunal herbivores in eastern Beringia[25]. In contrast, the keystone-decline model posits that megaherbivores were active ecological engineers. When their populations began to decline (from anthropogenic or environmental pressures), it triggered numerous knock-on effects including the disappearance of mammoth-steppe vegetation and its replacement by shrublands and wet tundra. Our second objective is to replicate and test the extent of the sedaDNA ghost ranges for *Equus* sp. and *Mammuthus* as identified in Murchie et al.[36].

Background

Late Quaternary losses on the eastern mammoth-steppe. Megafaunal extinctions and extirpations after 40,000 cal BP in the Holarctic (i.e., northern Eurasia, Beringia, and North America) arguably followed a two-stage pattern suggested by dated macrofossils[27] (Supplementary Table 1). The first wave seems to have occurred prior to or during the Last Glacial Maximum (LGM, 26,500–19,000 cal BP)[38] which in eastern Beringia included the loss of *Homotherium latidens* (scimitar-toothed cat) and *Arctodus simus* (short-faced bear). The second wave occurred between 15,000–10,000 cal BP, which in mainland Beringia included Equidae (caballine and stilt-legged horses), *Mammuthus primigenius* (woolly mammoth), *Panthera spelaea* (cave lion), and *Saiga tatarica* (saiga antelope), while at least 20 genera went extinct or were extirpated in North America south of the continental ice sheets. Other species such as *Bison priscus* (steppe bison) survived until at least ~6000 years ago in southern Yukon[39], with genetic data supporting a *B. priscus* persistence until as recently as a few hundred years ago[40]. *M. primigenius* survived on Wrangel (Russia) and St. Paul (Alaska) islands until about 4000 and 5500 cal BP, respectively[41,42]. Holarctic faunal assemblages of Pleistocene predators, species with small populations, and taxa living in understudied regions are expectedly sparse. This has led some to argue that these two late Pleistocene extinction/extirpation pulses are an artifact of an inadequate record and the Signor-Lipps effect[43,44], and that the true wave of losses occurred during or after the Younger Dryas, ca. 12,900 cal BP[25,37,45].

Beringia's environment during the late Pleistocene has been characterized as a graminoid and forb-dominated steppe-tundra mosaic generally referred to as the mammoth-steppe[31,33,35,46–50]. It is thought to have been the most extensive terrestrial biome on Earth during the late Pleistocene, stretching from the Iberian Peninsula eastward across Eurasia and into Canada[31,50–52], although the extent and character of this ecosystem remains controversial for some[53]. This paradoxically productive[54,55] high-latitude mosaic biome supported a diverse abundance of large bodied fauna[31,50,52], facilitating higher biotic productivity (energy and nutrient turnover) than many habitats existing at high latitudes today[23,56].

Owen-Smith[32] proposed the keystone herbivore hypothesis based on the ecology of extant African megafauna to explain the role of megaherbivores in transforming vegetation structure and composition[57–63]. Nutrients locked in leaves and stems are liberated when used by fauna, accelerating biogeochemical cycling[11]. In this top-down model, megafauna are critical for maintaining and promoting biodiversity in open-mosaic environments, and for controlling the abundance of woody vegetation that can limit biodiversity[5]. A severe reduction of these megafaunal engineers[64–66] is proposed to have resulted in the conversion of mosaic, steppe grasslands and wood pastures to more uniform forests and prairies, shrinking mosaic ecotones—high productivity transition areas between biological communities[67]—thereby reducing the carrying capacity of terminal Pleistocene environments. This in turn could have led to a positive-feedback response wherein diminishing populations of megafauna were increasingly unable to control woody shrub

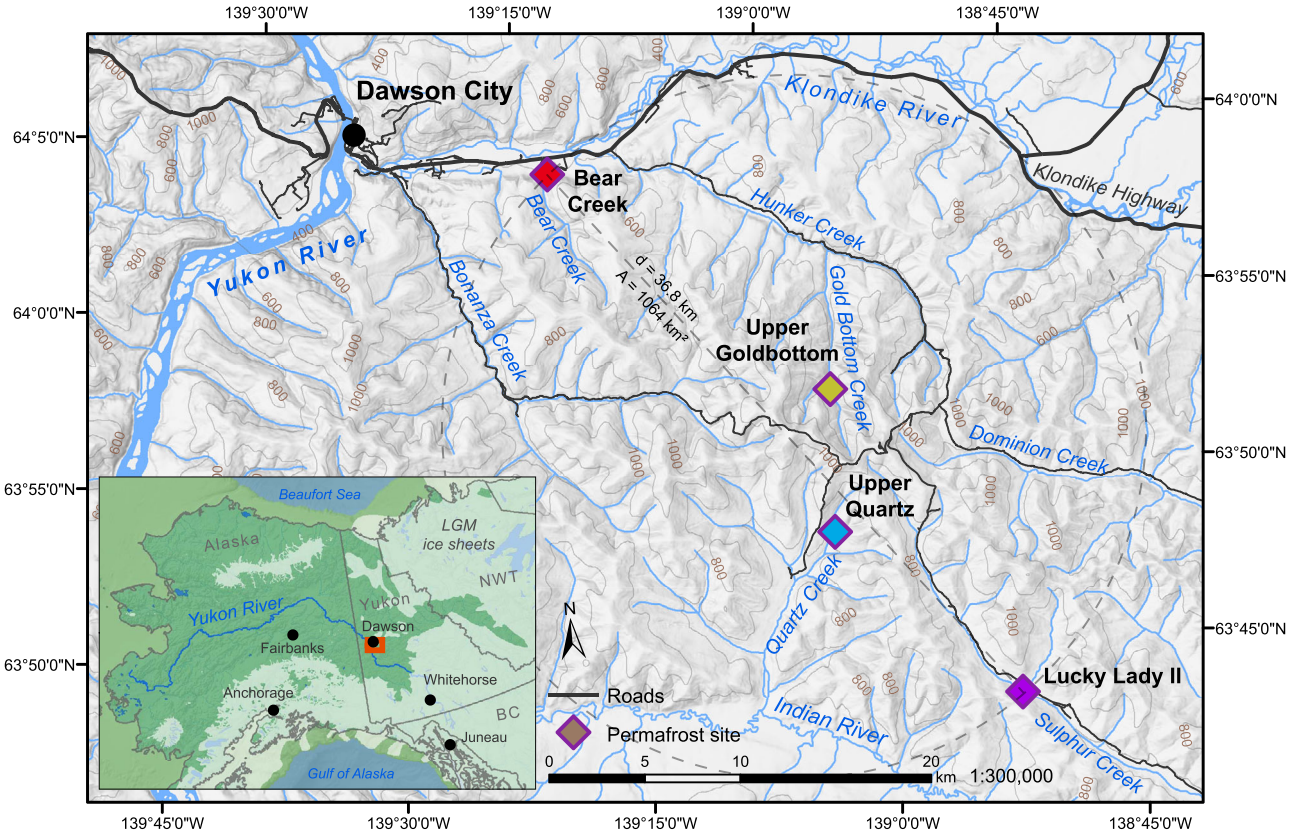


Fig. 1 Permafrost sites from the Klondike region of Yukon, Canada. Base map data retrieved from GeoYukon (hosted by the Government of Yukon); contours elevation unit: meters above sea level. See Supplementary Fig. 2 for a description of inset map data sources.

expansion, further reducing the biotic productivity of the mammoth-steppe.

Alternatively, an increasing moisture regime during the Bølling–Allerød interstadial (ca. 14,690–12,890 cal BP)[68] is argued to have caused the rise of mesic-adapted woody shrubs that were highly defended against herbivory, replacing the diet of Pleistocene grazers (woolly mammoth, steppe bison, and horse)[16,28–30], along with the paludification of Beringia (the spread of peatlands). In this line of bottom-up arguments, climate change and attendant environmental feedbacks led to the disappearance of the mammoth-steppe in eastern Beringia, along with the megafauna it supported.

Power and limits of sedimentary ancient DNA. Much of the LQE debate has been limited by the inability of dated macrofossils (primarily from detrital contexts) to convey the spatio-temporal resolution necessary to untangle the causative versus correlative ecological transformations associated with the Pleistocene-Holocene transition. Molecular (micro) methods[69] are increasingly able to augment discontinuous macrofossil records. This can aid in identifying cryptic populations (or ghost ranges)[37,70,71], independently assess population declines, and estimate the timings of functional extinctions/extripations[15,72]—the point at which undercrowding and inbreeding depression lead to a loss of fitness through Allee effects[73–75] to the degree that a species no longer significantly contributes to ecosystem functioning, becoming a trace presence in records before completely disappearing.

Ancient environmental DNA (eDNA)[76] is a powerful method for directly assessing the local[77] presence of animals, plants, fungi, and microbiota through time[33,36,37,41,78–82]. Most eDNA is quickly metabolized by bacteria or otherwise degraded through a variety of chemical and physical processes. SedaDNA (referring to a subset of ancient eDNA sample types[83]) can survive these degradative processes, even in the absence of visible fossils, because cellular material can bind to sedimentary minerals[84–91], protecting these molecular fragments for millennia, especially when perennially frozen[92,93]. Sediment samples as small as 100 mg can contain tens of billions of DNA fragments from all forms of life in a local ecosystem. However, there are several sedaDNA challenges to be aware of: (1) determining whether the recovered sedaDNA is stratigraphically accurate[91]; (2) whether the wet-lab recovery and targeting strategy, genetic reference databases, and taxon assignment approach (bioinformatic parameters) can accurately assess the breadth of eDNA or is prone to false-positive/negative assignments[36,94]; (3) assessing whether eDNA abundance retains a correlation with a population's living biomass[95,96]; and (4) determining the degree to which sedimentary inhibitors or differential degradation may bias the sedaDNA signal[36]. Of particular importance for the kinds of permafrost sedaDNA analyzed in this report are the factors of reworked sedaDNA and leaching.

Perennially frozen sedaDNA has the potential to undergo erosion and redeposition while remaining chemically intact. Arnold et al.[91] found evidence of reworked periglacial sediments in high-energy fluvial contexts within large catchments and local thermokarst deposits. They caution against sampling from settings where DNA can be readily reworked and redeposited within younger materials. In this study, we targeted loessal silts to mitigate the potential for fluvial reworking, although aeolian processes are certainly capable of reworking nanoscale sedaDNA complexes. Further, there is evidence throughout the Klondike of an early Holocene thaw unconformity[97–99] that Mahony[100] identified at Upper Goldbottom and Upper Quartz (among other

Table 1 SedaDNA permafrost samples.

Site	Core[a]	ID[b]	Calibrated age-model[c] (2σ)			Input[d]	Total raw reads	PalaeoChip mapped & *MEGAN* assigned[e]
			Median	From	To			
Bear Creek	BC 4-2B	PHP-1	≳30,000			1.05	5,650,809	241,143 (4.27%)
Lucky Lady II	LL2S-189-E	PHP-2	8707	8919	8637	0.9	8,667,496	9,908 (0.11%)
	LL2S-253-D1	PHP-3	9177	9485	8950	0.6	9,303,528	491,487 (5.28%)
	LL2C-118-C	PHP-4	13,176	13,250	13,119	0.6	7,749,177	178,973 (2.31%)
	LLII 12-84-3	PHP-6	13,335	13,393	13,277	0.6	10,235,721	806, 601 (7.88%)
	LL2C-205-B	PHP-5	13,510	13,596	13,401	1.35	4,997,824	48,226 (0.96%)
	LL2C-243-A2	PHP-7	14,113	14,245	13,975	0.6	5,820,472	54,700 (0.94%)
	LLII 12-170-6	PHP-8	14,750	14,897	14,595	0.3	1,331,181	17,628 (1.32%)
	LLII 12-217-8	PHP-9	15,500	15,651	15,339	1.05	3,115,296	38, 566 (1.24%)
Upper Goldbottom	MM12-118B	PHP-11	9,246	9869	8604	1.35	7,983,085	541,521 (6.78%)
	MM12-119B	PHP-12	10,051	10,181	9909	1.5	18,409,441	1,823,618 (9.91%)
	MM12-115b	PHP-14	19,704	20,320	19,070	0.3	2,320,965	35,539 (1.53%)
	MM12-116b	PHP-13	20,787	20,955	20,554	0.3	1,624,580	174,890 (10.77%)
	MM12-117b	PHP-15	21,232	22,424	20,568	0.3	1,910,387	164,997 (8.64%)
Upper Quartz	MM12-QC-10	PHP-19	3849	3899	3727	0.6	9,244,928	190,555 (2.06%)
	MM12-QC-9	PHP-20	5776	5929	4590	0.6	5,913,447	312,597 (5.29%)
	MM12-QC-8	PHP-21	5909	5992	5744	0.6	5,142,454	265889 (5.17%)
	MM12-QC-6	PHP-22	12,860	12,989	12,758	0.6	6,080,182	114,978 (1.89%)
	MM12-QC-4	PHP-23	14,939	15,958	13,988	0.9	14,729,646	68,186 (0.46%)
	MM12-QC-3	PHP-24	15,759	16,862	14,720	0.3	1,129,623	17,162 (1.52%)
	MM12-QC-2	PHP-25	16,563	17,810	15,469	0.3	1,568,411	29,419 (1.88%)
Blanks	Extraction (9) & library (4) negative controls						102,440	81 (0.08%)
						TOTAL	132,928,653	5,626,583 (4.23%)

Core identifications as per D'Costa et al.[106] for Bear Creek, Mahony[100] for Lucky Lady II, Upper Goldbottom, and Upper Quartz, and Sadoway[109] for Lucky Lady II.
[a]Lucky Lady II subsamples from vertical cores. Bear Creek, Upper Goldbottom, and Upper Quartz are horizontal samples taken from permafrost exposures.
[b]PHP = Pleistocene-Holocene Permafrost sedaDNA ID. See Supplementary Table 14 for a breakdown of sedaDNA replicates by core.
[c]See Supplementary Figs. 5–7 for Bayesian age-models. Dates reported as calendar/calibrated years before present (cal BP).
[d]Sediment input across extraction replicates.
[e]Sequenced reads that pass quality filters for de-duplication, adaptemer removal, minimum size (24 bp), and map to the PalaeoChip references[36] that could then also be *BLASTn* aligned and taxonomically binned in *MEGAN*. Percent on-target reads (those that map to the PalaeoChip references) of total raw sequenced reads.

sites) that presents the possibility for the localized reworking of sedaDNA during our early Holocene core samples. The Lucky Lady II section by contrast is continuous from >16,500– 8500 cal BP, sits toward the middle of a broad valley, and shows no evidence of erosion or redeposition by slope wash or thermokarst-induced slumping—suggesting that reworked early Holocene sedaDNA is of less concern at the Lucky Lady II site.

The vertical movement of free DNA has been found to be negligible in perennial frozen settings[91]. Studies have found synchronous palaeoecological shifts when comparing palynological and macrofossil evidence with sedaDNA reconstructions[101,102], in addition to age-dependent DNA damage patterns[103–105]. Leaching is not considered to be a problem in perennially frozen sediment because there is minimal movement of liquid water[33,37,102,106–108].

Results

Age-modelling and palynology. Age-depth models were first reported for cores used in this study by Sadoway[109] and Mahony[100]. To refine the chronologies of these records we developed Bayesian age-depth models for each site using Oxcal v.4.4.2[110] and the IntCal20 calibration curve[111] (Supplementary Figs. 5–7 and Supplementary Table 3). Some outlier dates from the model were observed (Supplementary Figs. 6–7). As such, remodelled ages are reported here as 2σ maximum/minimum ranges to account for this uncertainty for comparing samples within and between sites (Table 1). A selection of subsamples were also analysed with palynology as a secondary proxy to the eDNA data. Most samples were nearly barren of palynomorphs, with only the Holocene-aged samples having preserved large numbers of pollen grains—in this case predominantly spruce (*Picea*) (Supplementary Table 4).

SedaDNA palaeoecology. Through the targeted capture[36] of organelle eDNA preserved in loessal permafrost silts (Supplementary Fig. 4), *Bison priscus* (steppe bison), *Mammuthus primigenius* (woolly mammoth), *Equus* sp. (specifically limited to caballine horse), and *Lagopus lagopus* (willow ptarmigan) constitute most of the identifiable DNA reads of direct interest within Animalia (Fig. 2). This is in addition to less abundant organisms such as *Rangifer tarandus* (caribou/reindeer), and *Ovis sp.* (likely Dall sheep). Many reads expectedly lack taxonomic specificity at species and genus ranks (as many regions of the mitochondrial genome are variably conserved), and as such a large portion of reads could only be confidently assigned to higher ranks such as Caprinae, Pecora, Perissodactyla, and Elephantidae. In some cases, such as with hits to order Perissodactyla and superorder Afrotheria, we can be confident that they represent *Equus* (or its familial relative, *Haringtonhippus* [stilt-legged horse]), and *Mammuthus*, respectively, as unique members of their clades in the late Quaternary record of this region. There is also a low biomolecular signal from predators in this dataset including *Canis lupus* (grey wolf) and *Martes* sp. (marten). A variety of rodents were identified, including *Urocitellus* sp. (likely arctic ground squirrel), *Microtus xanthognathus* (taiga vole), and *Dicrostonyx groenlandicus* (northern collared lemming). Human DNA was identified despite not being targeted with the PalaeoChip baits. However, human DNA was also observed in the

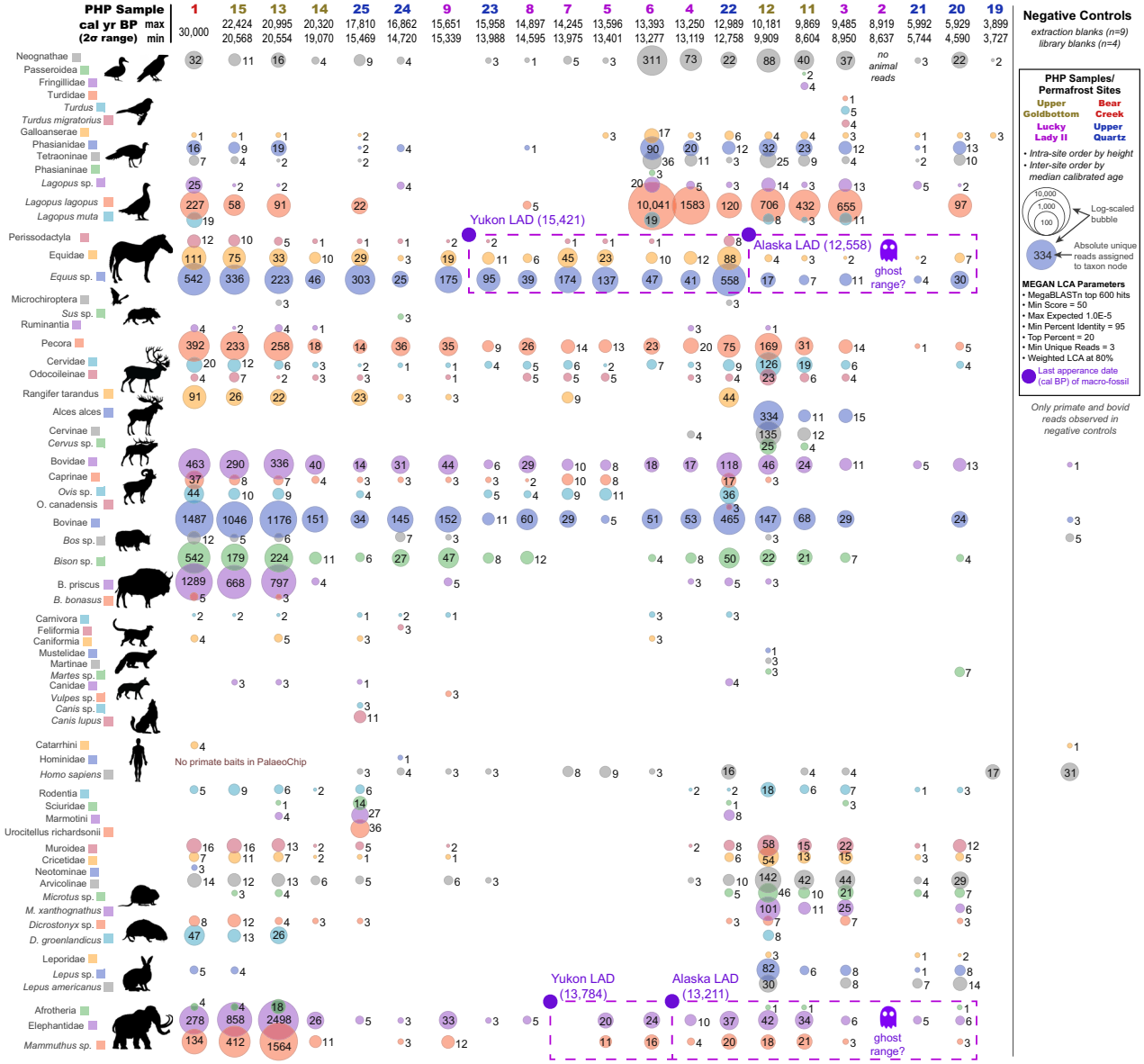


Fig. 2 Metagenomic comparison of animal reads assigned using BLASTn to MEGAN. Values indicate unique reads assigned to that taxon node. Source data are provided as a Source Data file.

negative controls. We do not consider this human signal to be reliable without further investigation.

Overall, this taxonomically rich sedaDNA dataset reflects a gradual decline in the megafauna signal through time (Fig. 3). Elephantidae is one of the first to decrease in sedaDNA abundance after ~20,000 cal BP. This is followed by declining signals for Bovidae and Equidae (Fig. 2), until a punctuated decrease occurs near the Pleistocene-Holocene transition as their sedaDNA signals almost disappear while those for *Alces alces* (moose) and *Cervus sp.* (likely *Cervus canadensis* [elk/wapiti]) enter the dataset. Our admittedly temporally coarse set of permafrost samples suggests a delay in the disappearance of megafaunal grazing species in the Klondike to between ca. 13,000–10,000 cal BP, but we also observe a lag in the final appearance of *Equus* and *Mammuthus* sedaDNA as late as ca. 6000 cal BP. Cores from Lucky Lady II, Upper Goldbottom, and Upper Quartz retain 100+ DNA sequences assignable to those taxa well beyond their last dated macrofossils (Fig. 2).

Plant sedaDNA clearly reflects a major environmental turnover between 13,500–10,000 cal BP (Figs. 3–4). Pleistocene graminoids (grass-like, herbaceous [non-woody] plants) such as Poaceae (grasses), Cyperaceae (sedges), along with a variety of forbs (herbaceous flowering plants) such as *Artemesia* (sagebrush), *Lupinus* (lupine), *Saxifraga* (rockfoil), *Papaver* (poppy), and *Ranunculus* (buttercup) were identified in relative sedaDNA abundance from 30,000–13,500 cal BP. Woody taxa such as *Salix* (willow), *Populus* (poplar), *Betula* (birch), *Rhododendron*, *Arctous* (bearberry), and *Picea* (spruce) were identified with increasing relative sedaDNA abundances after ~13,500 cal BP, along with *Equisetum* (horsetail), *Gymnocarpium* (oak ferns), and *Sphagnum* (peat moss). Our data suggests that forbs and graminoids (in this case Poaceae and Asteraceae) were dominant from ~30,000–13,500 cal BP while woody shrubs were comparatively rare (Fig. 3), indicating that the conventional idea of the mammoth-steppe holds until at least this late.

Assessing aDNA authenticity. All 13 negative controls had negligible library adapted molecules prior to indexing (Supplementary Fig. 8) and had minuscule molarities after targeted

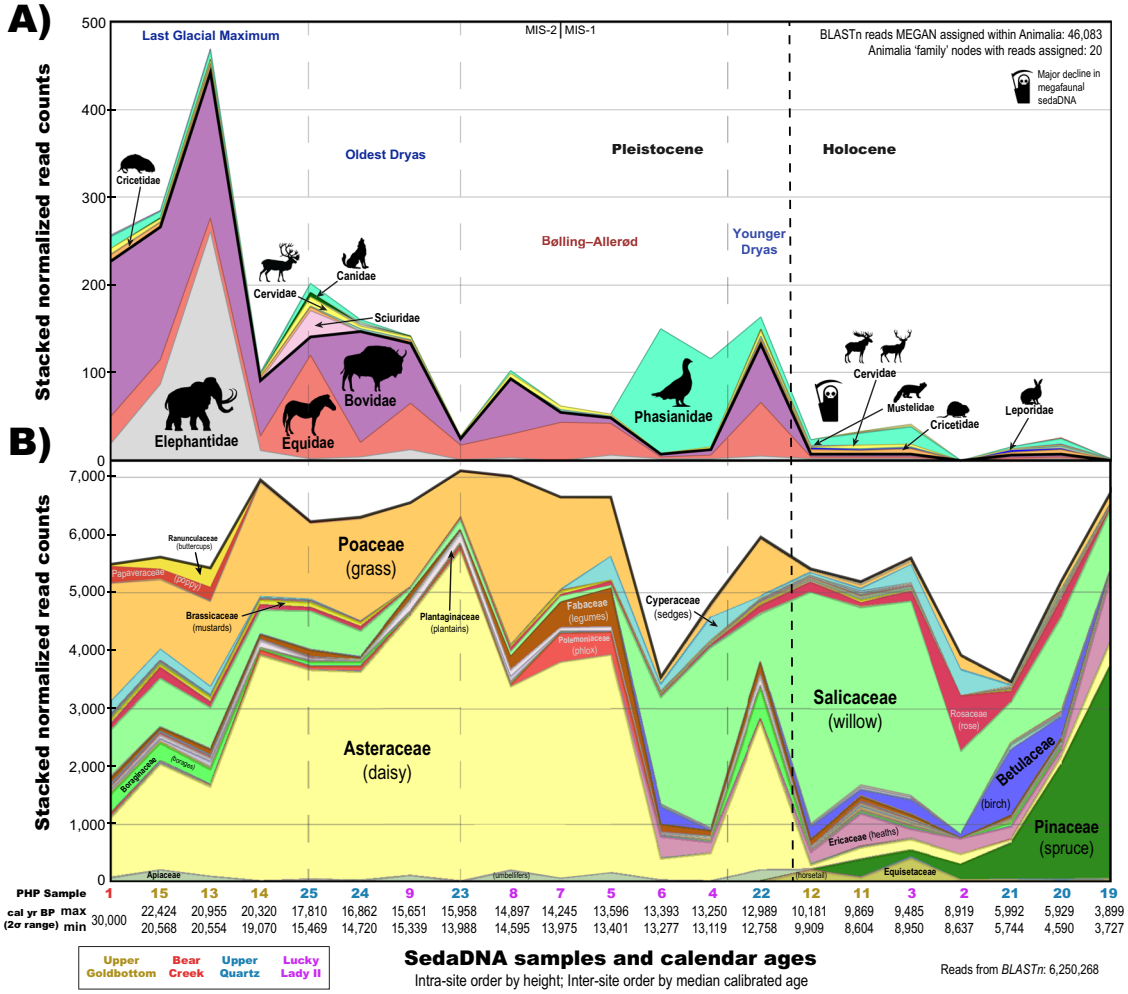


Fig. 3 Major taxonomic shifts in relative sedaDNA read assignment through time. Stacked normalized reads assigned to the rank 'family' in (**A**) Animalia (insects excluded) and (**B**) Viridiplantae. See Supplemental Figs. 10–12 for a metagenomic breakdown of samples by site. Source data are provided as a Source Data file. Note: sedaDNA abundance is likely affected by variable taphonomic intensity through time (such as temperature, moisture, and acidity) among other known and unknown micro-environmental conditions and recovery biases. While eDNA abundance and biomass arguably retain some correlation upon initial release, many other factors influence this relationship. As such, relative abundances with sedaDNA must be interpreted cautiously pending further research.

enrichment (Supplementary Fig. 9). Despite using the entire post-enrichment eluate for each of the controls during equimolar pooling, these blanks received minimal sequenced reads (102,440) and even fewer reads that could be taxonomically binned (81, 0.08%). Shotgun sequencing blanks processed with a subset of these libraries in Murchie et al.[36] were almost entirely (>95%) adaptemers (adapter chimeric DNA), and likewise contained no signal of the ecologically relevant organisms under investigation here or in that previous work. As all 13 negative controls were processed identically in parallel with the permafrost subsample replicates (Supplementary Figs. 34–54), and yet contain none of the same sedaDNA signal (Figs. 2, 4, Supplementary Fig. 55), we can conclude that the trends observed here originate from the sediments themselves and are not the result of contamination.

We observe ancient DNA characteristic damage profiles where sufficient reads could be mapped to MEGAN and PIA identified references (Fig. 5, Supplementary Figs. 13–28), confirming that these molecules are ancient and not modern contaminants. The taxonomic constituents of these samples are also correlated more with age than site (Fig. 6), with 90% of the variance being explained by principal components 1/2 as driven by the proportions of Pinaceae, Asteraceae, and Salicaceae. These libraries also exhibit age- and climate-related damage patterns (Supplementary Figs. 29–33), suggesting that reworking and leaching have contributed minimally (if at all) to the ecological reconstructions.

Discussion

We observe four main trends within this dataset. (1) There is a surprising taxonomic richness and spatio-temporal consistency in the metagenomic signal across all sampling locations, suggesting that these reconstructions are representative of palaeoecological trends in the Klondike region. (2) Megafaunal sedaDNA declines gradually after the LGM with the *Mammuthus primigenius* signal being the first to drop out, followed by *Bison priscus* and *Equus*. (3) Signal dominance for forbs and graminoids is coeval with grazing megafauna, whereas the local transition towards woody shrubs is associated with a diminished faunal signal. Megafaunal sedaDNA reduces substantially after the Younger Dryas, by which time grazing megafauna had become functionally extirpated in the Klondike. (4) Despite this turnover, a low megafaunal sedaDNA signal persists into the Holocene. This signal—identified as a ghost range here—is suggestive of a late persistence of megafauna in a high latitude refugium, apparently outliving the

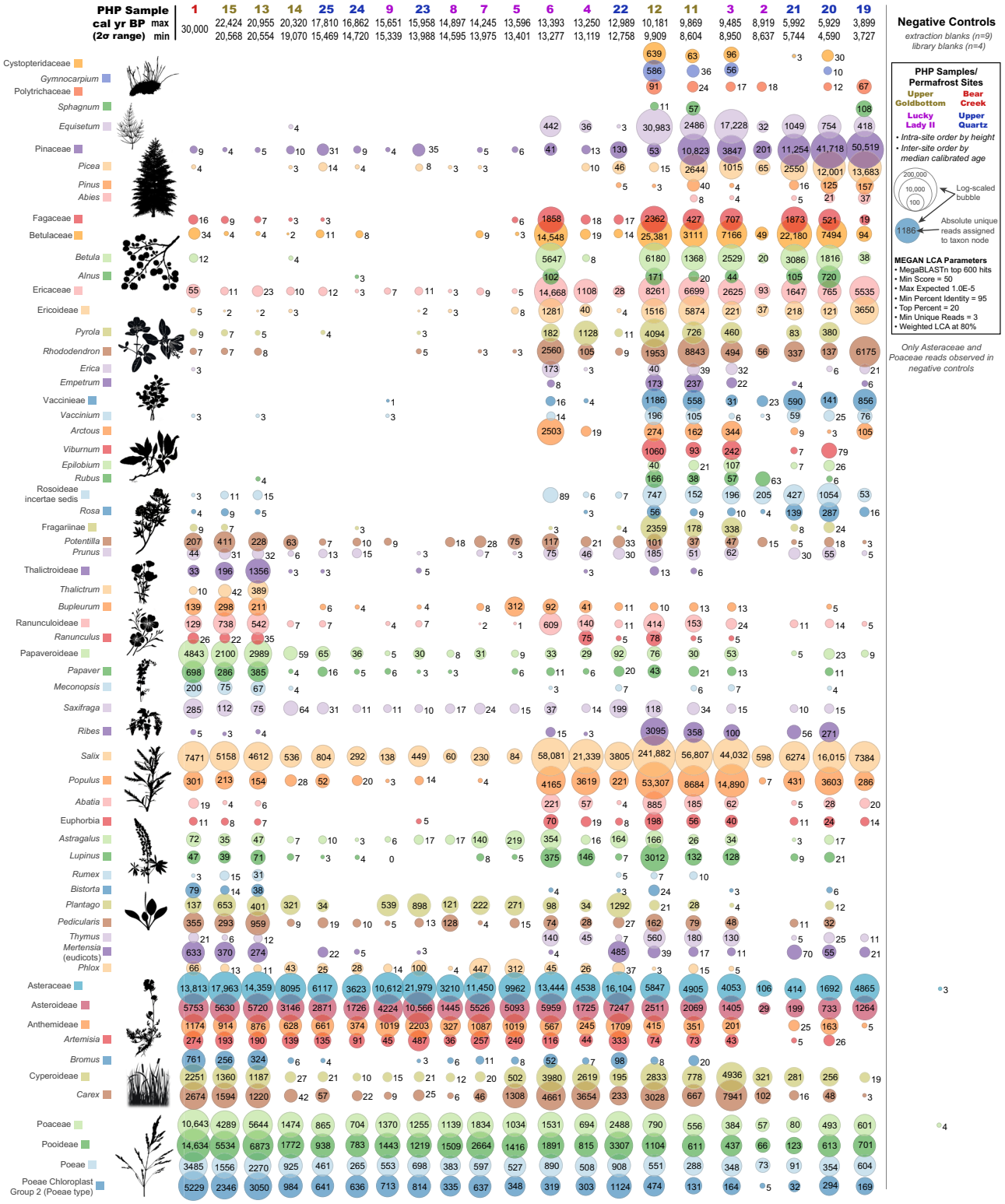


Fig. 4 Viridiplantae metagenomic comparison of permafrost core subsamples analyzed using *BLASTn* to *MEGAN* assigned reads. Values indicate unique reads assigned to that taxon node. Select taxon nodes depicted. Source data are provided as a Source Data file.

functional extinction and complete loss of other continental populations.

Ecological turnover and collapse of the mammoth-steppe. *Mammuthus, Equus*, and *Bison* presence are closely associated in our dataset with forbs and graminoids characteristic of the mammoth-steppe biome. During the relative sedaDNA rise in Salicaceae (likely willow shrubs) ca. 13,500 and 10,000 cal BP, Asteraceae and Poaceae correspondingly decline in relative sedaDNA abundance while grazing megafaunal DNA largely disappears from our dataset. This suggests that, at least in the Klondike, *Mammuthus primigenius* may have been the first

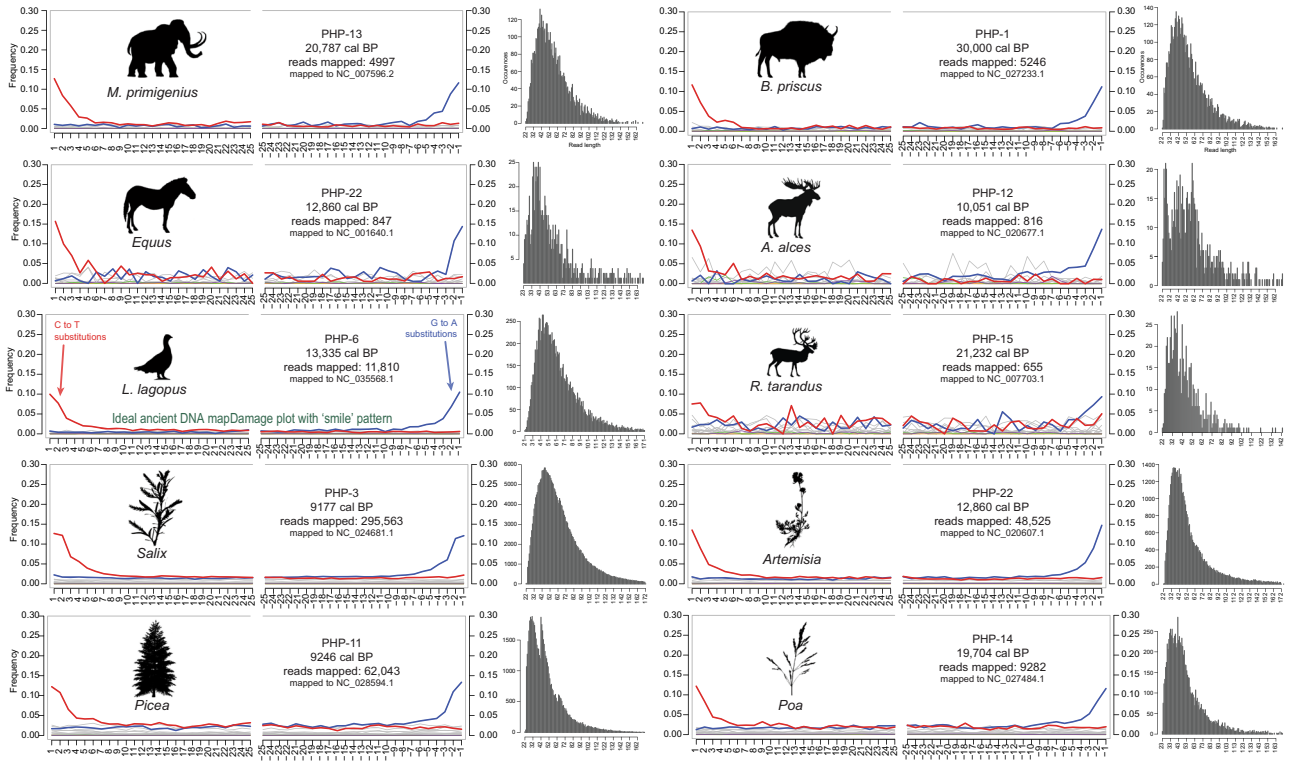


Fig. 5 Example mapDamage plots. Minimum size 24 bp, minimum map quality 30. See Supplementary Figs. 13–28 for a full breakdown of fragment misincorporation plots and a discussion of on/off target mapping. Source data are provided as a Source Data file.

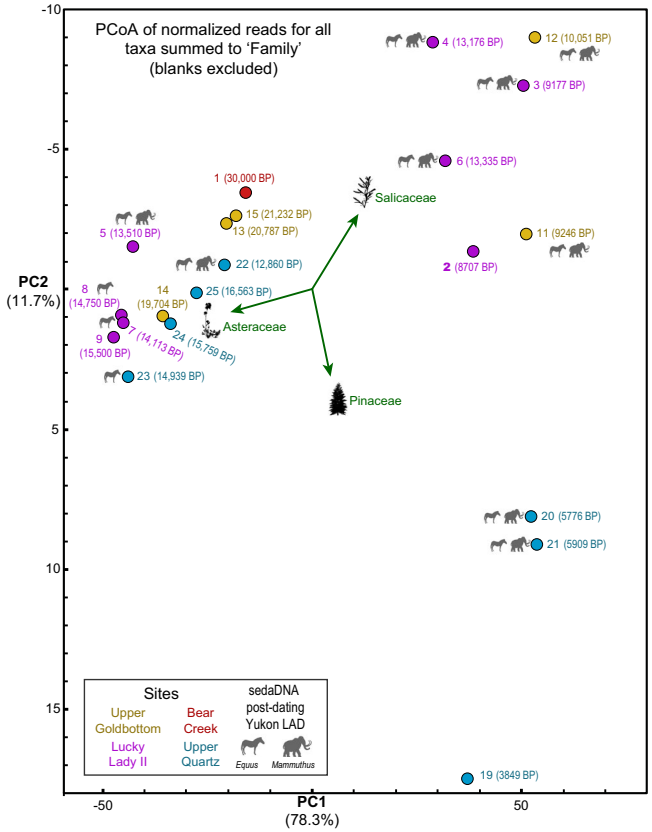


Fig. 6 Metagenomic Principal Coordinates Analysis (PCoA) produced in MEGAN using a chi-square ecological index[187]. LAD last appearance date based on dated macrofossils (Fig. 2). Source data are provided as a Source Data file.

megafaunal species to undergo a local population reduction after ~20,000 cal BP.

It is difficult to say whether sedaDNA signal decay reflects an actual reduction in the regional abundance of animals or is reflective of other stochastic and unknown[34] factors unique to this proxy such as variable eDNA release and turnover[95], biochemical changes to eDNA stabilization processes such as organo-mineral binding[90], or shifting microbial and other taphonomic pressures. As *Equus* sedaDNA remains relatively consistent until the rise of mesic-hydric woody shrubs during the Allerød warming (~13,500 cal BP) (Fig. 3B), this is suggestive of longer-term local declines of *Mammuthus* (and perhaps *Bison*) eDNA input rather than a shifting of biomolecular taphonomy because we would generally expect animal eDNA to breakdown or become mineral-bound[88] at similar local rates. Further, *Lagopus* DNA spikes during major declines in megafaunal DNA. Again, implying local ecological rather than just taphonomic or methodological factors driving shifts in relative animal sedaDNA recovery. As this study used a capture enrichment approach targeting organelle genomes[36] (with replicates [Supplementary Table 14]) rather than PCR metabarcoding amplicons[76,112], relative changes in metagenomic signal abundance are arguably somewhat correlated with shifting eDNA inputs[95,96,113–116] during periods of otherwise stable climate. As such, we suggest that major shifts in relative DNA abundance, such as *Mammuthus* sedaDNA nearly dropping out of the dataset after 20,000 cal BP, are ecologically informative.

The decline in local mammoth abundance that we infer from this sedaDNA record is consistent with a low frequency of ^{14}C-dated mammoth macrofossils from the Klondike. *M. primigenius* macrofossils are comparatively rare in central Yukon relative to more northerly sites around Old Crow (Supplementary Fig. 1), but still relatively few of those northern macrofossils have been successfully radiocarbon dated because most are beyond

radiocarbon range[117,118]. Much of the <30,000-year fossil record in Beringia is represented by a small number of well-preserved, and logistically accessible sites (Supplementary Fig. 1). Our faunal sedaDNA dataset somewhat conflicts with these macrofossil abundances in that the highest frequencies of DNA reads identified as *Mammuthus*, *Equus*, or *Bison* are distributed between 30,000–15,000 cal BP. Conversely, dated faunal remains of *Mammuthus* and *Bison* in eastern Beringia have a median concentration around 15,000 cal BP, with only *Equus* bones being predominant nearer to 25,000 cal BP (Supplementary Fig. 1).

Relative *Bison* and *Equus* sedaDNA signals decrease in read counts after ~15,000 cal BP. However, there is a subsequent increase around the onset of the Younger Dryas (ca. 12,900 cal BP) that may be associated with previously described *Bison* dispersals[40,119] or other local factors (e.g. shifting mosaic vegetation patches[25], herbivore land use, or taphonomy). It is worth noting that this inference is limited by there only being a single Younger Dryas core sample in this dataset. After the Younger Dryas (during the early Holocene) grazer sedaDNA nearly disappears (Fig. 3), which is correlated with the ecological turnover from forbs and graminoids to woody shrubs—predominantly *Salix* sp.—and a rise in avian fauna, rodents, and cervid browsers. There is a pronounced transition in the ecological signal after ~13,500 cal BP from forbs and graminoids to woody shrubs in the Lucky Lady II cores, with rises in *Salix* reads tightly associated with a sharp increase of *Lagopus lagopus* (willow ptarmigan) sedaDNA—a grouse whose habitat and subsistence patterns are based on woody shrubs[120] (Fig. 3). Keesing and Young[121] observed on the African savanna that when large grazing mammals were removed from an area, the rodent populations doubled, which increased the populations of predators that target small-bodied animals. Our data mirrors this observation with an increase in rodent sedaDNA after ~10,000 cal BP (Fig. 2), along with the appearance of the small forest dwelling carnivore *Martes* sp. (martens) who may also now be present because of trees on the landscape.

After *Mammuthus primigenius* and *Equus* sp. were functionally extirpated from the Klondike, the local ecosystem began transitioning towards boreal taxa with an associated rise in *Picea* (spruce) and mosses (Fig. 4). Despite significant declines in grazing megafaunal DNA, reads extend beyond their last dated macro-remains—perhaps even as late as the mid-Holocene—which has already been observed for *Bison priscus*[39,40].

Our plant dataset is consistent with Willerslev et al.[33] in which forbs were found to proportionally dominate their metabarcoded sedaDNA signal during and after the LGM. Nichols et al.[112] argue that the forb dominance observed in Willerslev et al.[33] was partly caused by polymerase and GC biases of their PCR metabarcoding approach favoring forbs over graminoids with the Platinum HiFi Taq polymerase targeting the short *trnL* (P6 loop) locus[122]. We have used a capture enrichment approach (indexed and reamplified with the KAPA SYBR FAST qPCR Master Mix) targeting much larger regions of the chloroplast genome (*trnL* [~500 bp], *rbcL* [~600 bp], and *matK* [~800 bp])[36] where overall GC content is generally equivalent between the three major target families identified in Fig. 3 (see Supplementary Fig. 56). We suspect that beyond the PCR biases argued to have influenced Willerslev et al.[33] (i.e. the greater relative abundance of forb sedaDNA compared to graminoids and woody plants) that this is likely the result of eDNA release and preservation characteristics of forbs with higher rates of biomass turnover. This more rapid turnover thus potentially leads to an eDNA over-representation of forbs compared with typical palynological findings. It has been argued that interpreting relative floral abundances with eDNA requires calibration. Yoccoz et al.[95], for example, observed that their above-ground vegetation surveys were accurately mirrored in modern environmental soil DNA, but that functional groups (woody plants, graminoids, and forbs) varied in their proportional eDNA representation. Woody plants were most affected by this trend, being proportionally under-represented in eDNA compared to above ground biomass by 1:5[95], while graminoids were under-represented by 1:1.5. Conversely, forbs were over-represented by 2.5:1. GC and polymerase bias coupled with eDNA release variation, beyond simple growth form categories, complicates this further[112]. Nevertheless, the substantial abundance of forb DNA, even if cut by half, likely reflects an abundance of flowering herbs on the Pleistocene mammoth-steppe. This may also be under-represented palynologically due to varied pollen production between entomophilous (insect-pollinated) forbs and anemophilous (wind-pollinated) gramminoids[123].

The rise in Pinaceae (notably spruce, see Fig. 4) around ~10,000 cal BP, and its growing dominance through our mid-Holocene samples, is consistent with other records from Yukon in regard to the initial development of the taiga/boreal forest[124–129], and is consistent with pollen grains identified in samples younger than ca. 9200 cal BP (Supplementary Table 4). We observe similar relative sedaDNA increases in boreal flora (Fig. 4), albeit with a comparatively less abundant signal for *Betula*. Palynological studies frequently report an abundance of *Betula* with a comparatively small initial influx of *Salix* in the Alaskan-Yukon interior during the terminal Pleistocene shrub expansion[125]. While we observe a distinct rise in relative *Betula* sedaDNA during the Bølling–Allerød and post-Younger Dryas chronozones that persists into the Holocene, the number of *Betula* sedaDNA molecules are comparatively dwarfed by the immense abundances of Salicaceae (*Salix* [willow]) (Figs. 3–4) DNA. *Betula* is known to be over-represented by pollen, whereas *Salix* is often under-represented[130–133]. Our sedaDNA data suggests that *Salix* was more important in Beringian shrub expansion than palynological records have yet indicated.

The relative over-abundance of *Salix* sedaDNA compared to *Betula* is relevant to testing the shrub-expansion extinction model of Guthrie[16], who contended that an increasing moisture regime and rise of mesic-hydric vegetation, with chemical defenses against herbivory (notably *Betula nana exilis* [resinous dwarf birch], but also including *Salix*)[134–136], drove regional extirpations of grazing megafauna in eastern Beringia. If *Salix* was substantially more abundant in the Beringian shrub expansion than *Betula* as our sedaDNA dataset suggests, this questions whether the rise of defensive vegetation was a major driver in the extirpations as *Salix* is the most preferred and palatable shrub among extant subarctic browsers[135,137]. While *Bison* and *Equus* are considered closer towards the obligate grazer end of dietary guilds[50,138], both have been observed to exhibit variable grazing and even mixed feeding[139,140]. *Mammuthus, Equus*, and *Bison* coprolites suggest that these taxa had a diet variably rich in forbs and graminoids, with a smaller but notable proportion of woody shrubs/trees (including alder [*Alnus*], birch [*Betula*], larch [*Larix*], spruce [*Picea*], and willow [*Salix*])[33,141,142].

If mammalian sedaDNA abundances are rough indicators of palaeo-biomass (a correlation in need of further research), it is unclear why *Mammuthus primigenius* and *Bison priscus* (Fig. 2) relative sedaDNA signals decline prior to an expansion of woody shrubs during the Bølling-Allerød warming (Fig. 3). The abrupt increases in Cyperaceae (*Carex* [sedges]), Ericaceae (*Arctous* [bearberry], *Rhododendron*), Betulaceae, and Salicaceae during the Allerød are suggestive of a transition toward a moist dwarf-shrub ecosystem by ca. 13,500 cal BP. The presence of these plants suggests more continuous ground cover, better insulation, shallower permafrost, and likely boggy, wet conditions. The early Allerød rise of Fabaceae sedaDNA (particularly *Astragalus* and

Oxytropis, Fig. 4) may also be indicative of a rise in flora with anti-herbivory defenses as these locoweeds are toxic to grazing fauna. Notably, despite otherwise rapid faunal and floral turnover, our single Younger Dryas core sample may suggest that the mammoth-steppe locally persisted through the Bølling-Allerød chronozone in the Klondike.

Mann et al.[28,29] and Rabanus-Wallace et al.[30] contend that a shifting moisture gradient from xeric to mesic-hydric, with the paludification of eastern Beringia, best accounts for the loss of dryland-specialists (*Equus, Mammuthus*), whereas mesic and mixed feeding seasonal fauna (*Rangifer, Cervus, Ovibos*) retained suitable habitats and hydric specialists (*Alces, Homo sapiens*) were able to invade new Beringian niches. While warming, an increasing moisture regime, the arrival of cervid browsers, and the rise of woody shrubs may explain much of the terminal signal decay observed for grazing specialists, this does not explain the relative declines of *Mammuthus* and *Bison* sedaDNA prior to the Bølling–Allerød chronozone (assuming that sedaDNA abundance retains a correlation with palaeo-biomass). Guthrie[143] found that horses had undergone body-size declines after the LGM until their extirpation in Beringia, which likewise suggests longer-term pressures predating shrub expansion. The rise of woody plants in this dataset thus may be partially explained by both the gradual reduction in local megaherbivore ecosystem engineering over millennia and by a warming climate and shifting moisture regimes.

Unknowns in sedaDNA release, preservation, and recovery restrict what we can confidently infer from differences in relative signal abundance, but there are indications of both top-down and bottom-up contributions to the collapse of the mammoth-steppe in central Yukon. While the decline of faunal sedaDNA is likely influenced to some degree by shifting taphonomic processes (such as warming and increasing moisture causing more DNA degradation), substantial declines in megafaunal sedaDNA predates the Bølling–Allerød interstadial (14,690–12,900 cal BP)[68]. This could be seen as partially supporting Zimov and colleagues'[5,23] keystone megaherbivore decline model that these animals were increasingly unable to maintain suitable steppe habitats due to declining populations. However, there is a substantial time lag in our dataset between a declining megafaunal sedaDNA signal after 20,000 cal BP and the relative rise of woody shrub sedaDNA ca. 13,500 cal BP. By contrast, the rise of mesic-hydric woody shrub DNA during the Allerød oscillation (13,900–12,900 cal BP) and early Holocene are clearly associated with an abrupt decline in megafaunal sedaDNA, strongly supporting the climate-induced shrub and peatland expansion model of Guthrie[16] and Mann et al.[28–30]. There is potential support in this dataset for both bottom-up and top-down pressures influencing megafaunal extirpations in the Klondike. Further research is needed to determine whether indications of longer-term top-down pressures are real or an artifact of sedaDNA methodology, and to what degree each Beringian megafaunal species was differentially impacted and/or responsive to shifting ecological pressures.

The degree to which humans may have been involved in any of these transformations is hard to gauge from available evidence (see Supplementary Notes 1.2). Early (>14,000 cal BP) human presence in eastern Beringia is controversial but has been suggested based on possible anthropogenic cutmarks at Bluefish Caves[144–147] and the identification of allegedly human fecal biomarkers and a coinciding rise of fire activity on the Alaskan North Slope[148–151]. However, these records lack unambiguous artifacts, features, or other clear indications of middle Upper Palaeolithic lifeways as seen in eastern Siberia[152–156]. At this time, there is no clear evidence for an ecologically significant human presence in eastern Beringia prior to ca. 14,000 cal BP (Supplementary Figs. 2–3). Thereafter, low fecundity megafauna[72,157], who had already undergone millennia of oscillating climatological and ecological pressures, may have been vulnerable to novel anthropogenic forces[25,158–162] that lack archaeological visibility due to the emergence of post-LGM, high mobility lifeways[156,163]. Currently, evidence of anthropogenic contributions to the ecological turnover in eastern Beringia remain functionally absent, being at most but one enigmatic component in a synergistic set of compounding pressures[25]. SedaDNA analyses of Pleistocene permafrost targeting human DNA may prove key to addressing lingering unknowns in the peopling of Beringia.

Evidence of a cryptic refugium. The persistence of *Equus* and *Mammuthus* until ~9200 cal BP and perhaps as late as ~5700 cal BP (Fig. 2), as suggested by our sedaDNA records, lies well beyond the last dated macrofossils for these taxa (Fig. 7). However, interpreting cryptic populations with sedaDNA necessitates caution. As noted previously, Arnold et al.[91] found that although permafrost contains a wealth of well-preserved eDNA, the favourable characteristics of perennially frozen ground increases the likelihood for allochthonous organics to survive transport and be redeposited within younger strata. They argue that while reworking is of lesser concern when assessing first appearance dates and "abundant" sedaDNA signals, reworking of older sediments can be an inherent problem when assessing last appearance dates in high-energy fluvial contexts or in areas of thermokarst where older sediments thaw and mobilize followed by potential re-aggradation of permafrost. Arnold and colleagues highlight the careful analysis of loess sediments from the Stevens Village site in central Alaska where Haile et al.[37] utilized ^{14}C, OSL, extensive eDNA sampling on and off site, and careful sedimentological analyses to plausibly infer the late survival of *Mammuthus* and *Equus* to as late as ~10,000 cal BP. While the sediments targeted here are also loessal silts[100], these materials were not recovered in the field with ancient DNA in mind, but were instead later reselected to follow-up on results presented by Murchie et al.[36]. Although we acknowledge that the signals for late megafaunal persistence should be interpreted with careful skepticism, and require additional supporting evidence for verification (particularly given early Holocene thaw unconformities[97–99] in the Klondike as identified at Upper Goldbottom and Upper Quartz[100]), these signals are reasonable and worthy of further study for the following reasons.

First, the ghost range signals observed for *Mammuthus* and *Equus* is observed at three different sites in 9 (*Mammuthus*) to 12 (*Equus*) separate permafrost cores and are correlated with substantial and consistent changes in vegetation. In samples younger than ~13,500 cal BP there is a complete restructuring of vegetation. To our knowledge, no plant taxa completely disappeared during the transition, which limits our ability to use the plant data to chronologically test for allochthonous sedaDNA. However, the megafaunal signal observed in the alleged ghost range cores are comparable to those observed during periods of known presence. It is reasonable to ask how many reads are sufficient to say an organism was truly present, but there cannot be any simple answer to that question. At the same time, >50 unique sedaDNA molecules identified as Elephantidae at ~9500 cal BP is significant relative to older cores considering the otherwise substantial ecological turnover.

Certainly in the case of cores with sediments younger than 13,000 cal BP, the presence of *Mammuthus* and *Equus* extending to ~9500 cal BP is highly consistent with other investigations in both northern Asia and northwestern North America[37,41,42,164]. Furthermore, reads for these megafaunal taxa are observed at two

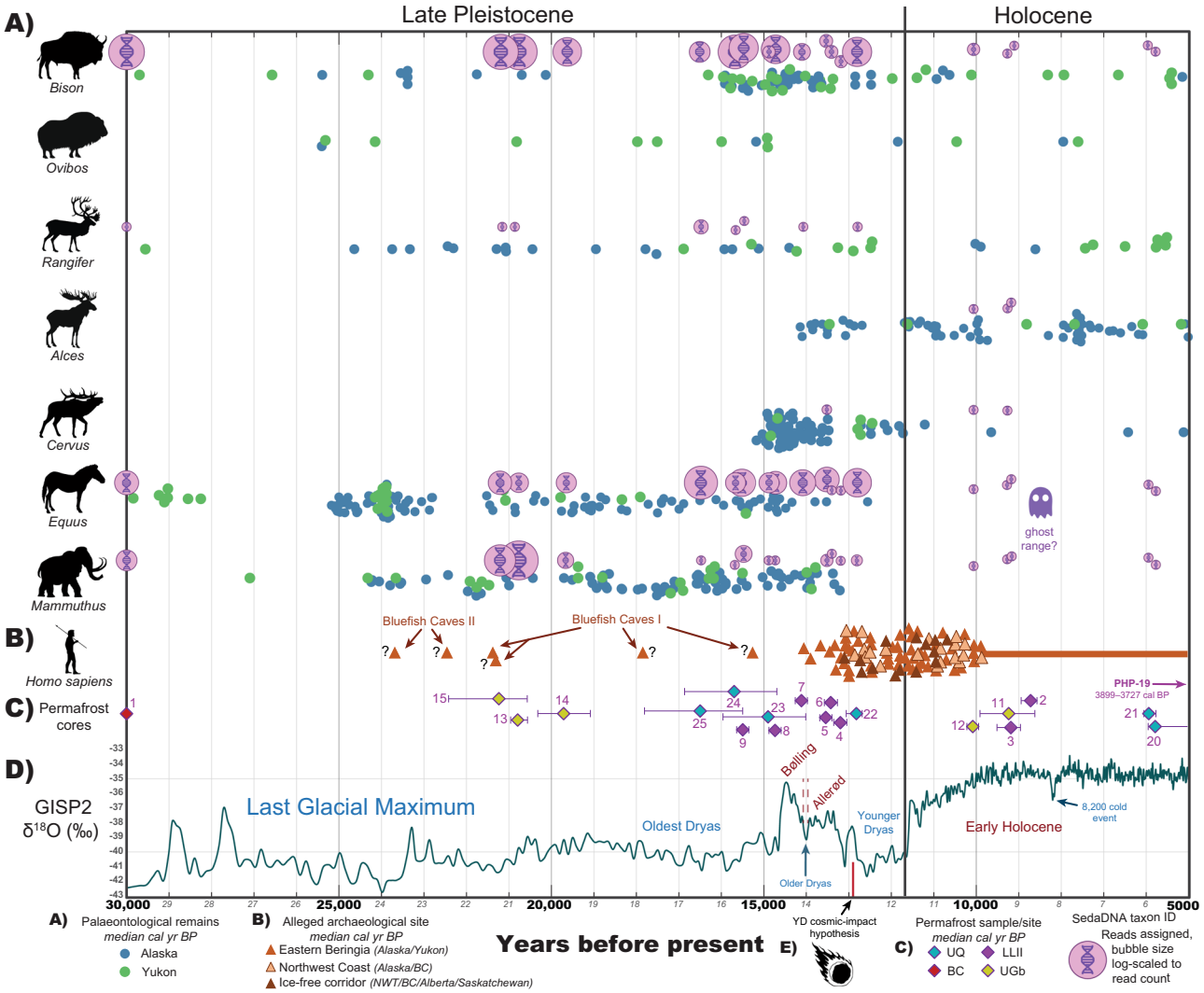


Fig. 7 Synthesis of palaeontological, archaeological, climatological, and megafaunal sedaDNA data. Source data are provided as a Source Data file, see the following references for original data sources. **A** Dated fossils of select megafaunal taxa in eastern Beringia[165], see Supplemental Fig. 1. **B** Earliest archaeological sites in northwestern North America[188], see Supplemental Figs. 2–3 and Supplemental Table 2. **C** Central Yukon permafrost samples analyzed in this study with 2σ modelled age ranges, see Supplementary Figs. 5–7. **D** Greenland Ice Sheet Project 2 (GISP2) oxygen isotope profiles at 2 m intervals[189]. **E** Onset of the Younger Dryas, and alleged cosmic impact hypothesis[190].

sites across all subsampled replicates and are associated with a completely different plant ecological signature. Here the point is that we would expect both floral and faunal sedaDNA would be reworked at roughly similar rates, which is not what is observed. Graminoids and forbs do persist, as would be expected, but there is no obviously mixed ecological signal as woody species dominate the plant metagenomics data (Fig. 4); this is despite otherwise having been observed in modern experiments to be proportionally under-represented genetically compared to their biomass by a factor of ~1:5[95].

The youngest signatures for *Equus* and *Mammuthus* (ca. 5700 cal BP) are of great interest because they imply local survival of these taxa long after the Pleistocene-Holocene transition. Aside from very late insular occurrences of mammoths from the Bering and Chukchi Seas[41], there are no accepted radiocarbon dates on mammoth or horse fossils in mainland Beringia that fall anywhere close to the mid-Holocene (Figs. 2, 7, Supplementary Fig. 1). Although the authenticity of the identifications is not in question (Supplementary Fig. 57), the wide temporal gap between these sedaDNA molecules and dated bones is concerning. This difference needs to be evaluated in context. Palaeontological and archaeological records across much of the Arctic and Subarctic are notably sparse. Small refugial populations might have survived in remote pockets at sizes too small to be readily detected by macrofossil collections derived largely from a small set of resource extraction and development sites. The case of *Mammuthus* survival on St. Paul and Wrangel islands, until 5500 and 4000 cal years BP, respectively[41,42], is interesting because until recent decades neither population was known to have persisted into the mid-Holocene. *Bison priscus* was likewise discovered to have survived throughout the Holocene in southern Yukon[39,40]. Conroy et al.[165] observed the presence of coprophilous fungi in the Alaskan interior at Windmill and Jan Lakes until ~9000 cal BP and 4500 cal BP. This abundance of spores postdates the megafaunal turnover and is perhaps most likely related to a replacement with browsing cervids. Alternatively, it is also possible that cryptic, refugial populations of Pleistocene grazers were contributing sources. The way forward is through further testing and confirmation, which can be achieved through multiproxy sampling from a broader suite of high latitude sites where reworking is negligible, and conditions favour the widest possible metagenomic spectra.

Summary. This taxonomically rich sedaDNA dataset tracks the ecological turnover of fauna and flora in central Yukon across the Pleistocene-Holocene transition. We identify the coeval eDNA turnover of megafaunal grazers with forbs and graminoids relative to the rise of woody shrubs and boreal flora at ca. 13,500–13,000 cal BP and after 10,000 cal BP, along with the gradual decline of faunal sedaDNA after 30,000 cal BP. There is also a consistent, multi-site signal of late persistence for *Equus* and *Mammuthus*, perhaps surviving some 7000 years longer than their last dated macrofossils in eastern Beringia would indicate.

Top-down versus bottom-up perspectives on the collapse of the mammoth-steppe cannot be entirely resolved with this dataset, perhaps because both are relevant. The ancient eDNA data presented here have indications of both long term, top-down ecological pressures impacting megafaunal populations in the Klondike, arguably supporting the keystone megaherbivore model of the mammoth-steppe[23,31] (albeit with unknowns regarding sedaDNA abundance and palaeo-biomass, along with a lag in vegetation turnover). There are also clear, short term, bottom-up indicators signifying climate-induced ecological transformations triggering the megafaunal extirpations between 13,500–10,000 cal BP[16,28–30]. The degree to which a decline of megafaunal DNA prior to the Bølling–Allerød interstadial can be interpreted as indicative of declines in the local populations of grazing megafauna is open for debate. But, as *Equus* sedaDNA remains relatively consistent until the rise of mesic-hydric woody flora during the Allerød warming, this is suggestive of longer-term local declines of woolly mammoths and steppe-bison pre-dating the ecological turnover. The abruptness of the transition thereafter is arguably indicative of both a potential lack of megafaunal engineering controlling woody expansion[4,23,31,121,166] and the compounding impacts of significant climate change[25]. The local persistence of mammoth-steppe taxa at our single Younger Dryas point sample suggests that the mammoth-steppe locally persisted through the Bølling–Allerød warming, but that subsequent early Holocene transformations significantly shifted the ecological character of the Klondike by 10,000 cal BP.

The late Pleistocene palaeontological record of Beringian megafauna is extensive compared to many other areas of Eurasia and the Americas[27]. However, even with this richness, it is too sparse in well-dated and geographically diverse macrofossils to effectively tease apart the complexity of factors involved in the Pleistocene-Holocene transition and the collapse of the mammoth-steppe. The data presented in this study highlights the power of environmental DNA for the recovery of highly complex signals of ecological change from exceptionally small sediment inputs (0.3–1.35 grams), even in the absence of macro biological tissues. Using targeted enrichment for sedaDNA is also far more cost effective for high-throughput sequencing applications compared to a shotgun approach. Murchie et al.[36] shotgun sequenced replicates of the same core samples studied here, and in the best sample, a shotgun approach had only 0.007% on-target sequence data (average 0.002%) of ~21 million DNA reads. This contrasts with as much as 10.8% on-target (average 4.2%) here with PalaeoChip enrichments—a 1,538x increase in on-target aDNA. If such a capture enrichment approach were paired with a robust sampling effort focused on sites with clear evidence of stratigraphic integrity across multiple regions and with tight temporal control, these genetic records could prove to be key to unravelling the ambiguities of this extinction event that has confounded Quaternary science since the eighteenth century.

Methods

Ethical approval was not required for this research as no archaeological or palaeontological materials were processed or analyzed and no human DNA was targeted or analyzed. Cores were acquired with Yukon Science and Explorer License research permits issued to DF by the Yukon Government, Department of Tourism & Culture. A description of the sampling sites, palynology, wet lab master mix recipes, qPCR results, additional bioinformatic analyses and results, and a palaeontological and archaeological background summary are included in the Supplementary Information.

Summary. Twenty-one core samples of loessal permafrost silts recovered from the Klondike region of Yukon, Canada (Fig. 1, Table 1)—dating between 30,000–4,000 calibrated years before present (cal BP)—were processed for sedimentary ancient DNA (sedaDNA) to evaluate changing biomolecular signals of plants and animals during the late Pleistocene-Holocene transition in eastern Beringia. We used Bayseian age modelling in conjunction with stratigraphic and cryostratigraphic observations to estimate core dates, and a subset of the core samples were processed in parallel for palynology. Despite the exceptional preservation and richness of the sedaDNA, very few pollen grains could be found in the samples (Supplementary Table 4).

For ancient DNA processing, we utilized a sedaDNA modified Dabney et al.[167] extraction procedure with the long cold spin inhibitor removal technique as described in Murchie et al.[36], and prepared double stranded, dual-indexed libraries[168,169] for targeted enrichment. We used the PalaeoChip Arctic-1.0 plant and animal baits[36] to capture enrich these libraries for chloroplast barcoding loci (*trnL*, *matK*, *rbcL*) of Arctic/Subarctic plants and for whole mitochondrial genomes (or singular loci where mitogenomes were unavailable at the time of bait-design in 2017) of extinct and extant northern animals (focused on megafauna). Libraries were sequenced on an Illumina HiSeq 1500 with 2 × 90 paired-end read chemistry.

After trimming, merging, and filtering the sequenced reads, BLASTn[170] was used to taxonomically identify the reads to the top 600 hits against a July 2019 local copy of the GenBank database[171,172], which was used as the input for MEGAN Community Edition[173,174] (v6.19.7, https://github.com/husonlab/megan-ce) and PIA (Phylogenetic Intersection Analysis, v 5.3, https://github.com/Allaby-lab/PIA)[94]. The outputs from MEGAN are plotted in the main text, while plots of individual extraction replicates from both MEGAN and PIA are included in the supplement (Supplementary Figs. 34–55). MapDamage[175] (v2.0.3, https://ginolhac.github.io/mapDamage/) was used to assess the aDNA damage signals of taxonomically identified taxa (Supplementary Figs. 13–28).

Field sampling. The cores used in this analysis were previously studied by D'Costa et al.[106], Mahony[100], and Sadoway[109] and have since been kept in cold storage at the McMaster Ancient DNA Centre and the Permafrost Archives Laboratory at the University of Alberta. Permafrost cores were collected between June and August of 2010, 2012, and 2013 with research permits issued to DF from the Yukon Heritage Branch. These cores were sampled at placer gold mining exposures chosen for the quality of the exposure and expected age of the sediments. Prior to sample collection by all three original research teams, the sampling area was cleared of eroded materials back to frozen sediments to create a fresh coring surface for a ~10 cm diameter coring tube ~30 cm in length. Horizontal core samples were drilled with a small portable gas-powered drill (Echo), recovered frozen, stored individually in plastic bags, immediately placed in a −20 °C chest freezer, and transported in the freezer to the University of Alberta or McMaster University for subsampling. Core locations were recorded with a GPS in the field and these locations along with stratigraphic information were recorded in a field notebook at the time of sampling. Horizontal permafrost cores were collected from Bear Creek, Upper Quartz, and Upper Goldbottom. Vertical cores were taken from Lucky Lady II (Fig. 1, Supplementary Methods 2.1).

Radiocarbon dating and Bayesian age-depth modelling. Plant macrofossils were picked from thawed samples using a dissecting microscope, dried and pre-treated for AMS dating at the University of Alberta along with known-age wood standards (c.f. Mahony[100]). Pre-treatment of all samples followed standard acid-base-acid procedures. Solutions heated to 70 °C and placed in 1 M HCl for 30 min, followed by 60-min washes in 1 M NaOH until the solution became clear. Finally, samples were placed in 1 M HCl for 30 min and rinsed with ultrapure water until they became neutral. Measurements of CO_2 production, graphitization and radiocarbon abundance in all samples were completed at the Keck-Carbon Cycle AMS facility (UCIAMS).

Age-depth models for Lucky Lady II, Upper Goldbottom and Upper Quartz were first presented by Sadoway[109] and Mahony[100]. To refine the chronologies of these records we developed new Bayesian age-depth models for each study site using Oxcal v.4.4.2[110] and the IntCal20 calibration curve[111]. In each case a P_Sequence depositional model was developed along sampling transects or vertical cores using a variable K parameter (increments per unit length)[176] and a general Outlier_Model, with a 5% prior probability of any ^{14}C date being a statistical outlier[177]. Boundaries were placed at the contacts between sediment units where changes in accumulation rates are likely to have taken place.

The Upper Quartz age-depth model (Supplementary Fig. 5) is developed from two P_Sequence depositional models run either side sedimentological boundary at 3.8 m which represents an unconformity of several thousand years. The lower P_Sequence includes two ^{14}C dates (UCIAMS-114733 and UCIAMS-114710) and provides chronology for SedaDNA samples; PHP-22, PHP-23, PHP-24, and PHP-

25. The upper P_Sequence includes three ^{14}C dates (UCIAMS-114899, UCIAMS-114733, and UCIAMS-114710) and provides chronology for SedaDNA samples; PHP-19, PHP-20, and PHP-21.

Lucky Lady II includes three vertical cores which were sampled for SedaDNA (LLII-12, LL2C, and LL2S) (Supplementary Fig. 6). A prominent palaeo-soil that can be traced laterally for hundreds of metres around the exposure is present in the LLII-12 and LL2C cores, and ^{14}C dates associated with this horizon were used to combine these cores with a single P_Sequence model (UCIAMS-56390, UCIAMS-114725, UCIAMS-143307, and UCIAMS-143308). Core LLII-12 includes three ^{14}C dates (UCIAMS-240139, UCIAMS-122284, and UCIAMS-122273), as well as a palaeo-soil isochron, and provides chronology for SedaDNA samples PHP-9, PHP-8, and PHP-6. Core LL2C includes three ^{14}C dates (UCIAMS-142198, UCIAMS-142197, and UCIAMS-143306) as well the palaeo-soil isochron, and provides chronology for SedaDNA samples PHP-4, PHP-5, and PHP-7. A boundary was placed at 3.5 m (at the contact between units 1 and 2) where grey silts including graminoid vegetation are replaced by organic-rich grey and black silts with in situ shrub vegetation. Core LL2-S includes three ^{14}C dates (UCIAMS-143296, UCIAMS-142212, and UCIAMS-142211) and provides chronology for SedaDNA samples PHP-3 and PHP-2.

The Upper Goldbottom age-depth model (Supplementary Fig. 7) is developed from two P_Sequence depositional models run either side of a sedimentological boundary at 22.5 m which represents an unconformity of several thousand years. The lower P_Sequence provides chronology for sedaDNA samples PHP-14, PHP-13, and PHP-15, and includes six ^{14}C dates (UCIAMS-122282, UCIAMS-114712, UCIAMS-114714, UCIAMS-142208, UCIAMS-114716, and UCIAMS-122274) as well as the Dawson tephra which has been dated to 29,055–29,470 cal BP[178]. The depths of three ^{14}C dates obtained from Arctic ground squirrel middens (UCIAMS-122282, UCIAMS-114712 and UCIAMS-114714) were adjusted by 0.8 m to account for burrowing depth. This is likely to be a conservative estimate of active-layer depths during cold stages in the Yukon which were deeper than present. One ^{14}C date caused a significant age-reversal and so was excluded from the age-depth model (UCIAMS-240141). Boundaries were placed at 12.6 m and 18 m (at the contacts between units 1, 2, and 3). The upper P_Sequence provides chronology for sedaDNA samples PHP-11 and PHP-12 and includes two ^{14}C dates (UCIAMS-114898 and UCIAMS-240143). A further two ^{14}C dates were excluded from the model as they caused significant age-reversals (UCIAMS-114910 and UCIAMS-114906).

The single Bear Creek sample (PHP-1) used in this analysis was not re-dated. This core was recovered from immediately beneath the Dawson tephra[179–182], which is dated to 29,055–29,470 cal BP[178]. As such, this sample can be estimated as being $\gtrsim$ 30,000 cal BP[106]. See Supplementary Methods 2.1 for a site description.

Ancient DNA wet lab. Laboratory work was conducted in clean rooms at the McMaster Ancient DNA Centre, which are subdivided into dedicated facilities for sample preparation (separate facilities for subsampling eDNA and discrete materials), stock solution setup, and DNA extraction through library preparation (collectively "pre-amplification rooms"). The post-indexing amplification clean room (enrichment) is in a physically isolated facility from the Centre's standard aDNA labs, while the subsequent high-copy PCR workspace is in a separate building; the centre has a unidirectional workflow progressing from low-copy to high-copy facilities to reduce the chance of cross-contamination. Each dedicated workspace is physically separated with air pressure gradients between rooms to reduce exogenous airborne contamination. Prior to all phases of laboratory work, dead air hoods and workspaces were cleaned using a 6% solution of sodium hypochlorite (commercial bleach) followed by a wash with Nanopure purified water (Barnstead) and 30 min of UV irradiation at >100 mJ/cm^2.

Subsampling. Permafrost sedaDNA subsamples were only taken from core interiors and care was taken to ensure that none of the sampling tools or interior surfaces were exposed any materials that had come in physical contact with the core exteriors (Supplementary Fig. 4). Permafrost samples from Lucky Lady II had been previously subsampled by Sadoway[109] at the University of Alberta. These subsamples were homogenized by core and transported to McMaster University by Sadoway where they have remained in cold storage. All other subsamples from Upper Quartz and Upper Goldbottom were processed as follows.

Metal sampling tools were cleaned with commercial bleach, rinsed with Nanopure water immediately thereafter, UV irritated on both sides for >30 min, then heated overnight in an oven at ~130 °C. Once the tools had cooled the next day, work surfaces were cleaned with bleach and Nanopure water and covered with sterile lab-grade tin foil. Sediment cores previously split into disks[106,109] and stored at −20 °C had the upper ~1 mm of external sediment chiselled off to create a fresh sampling area free of exogenous contaminants. For those cores that had not yet been split, a bleach and UV decontaminated handsaw was used to create a groove ~1–2 cm deep around the circumference of the core. A ~1 inch chisel was placed into the groove and a hammer was used to gradually split the core through percussion around the circumference. Once split, this opened a fresh interior surface previously unexposed to sampling equipment. For both the previously split and newly split cores, a small (~1/4 inch) decontaminated chisel was then used to carefully remove interior sediment from the core, which was collected in a weigh boat. After enough material was acquired for multiple extractions (~2–5 g), the core was covered in sterile tin foil and re-frozen. The subsampled material in the weigh boat was homogenized by manually stirring using a small metal chisel as the sediment thawed. This sediment was transferred to a 50 mL falcon tube and refrozen. Thereafter, the work area was thoroughly cleaned with bleach and Nanopure water, all plastic-ware was discarded, and metal tools were placed across the room for decontamination. The now decontaminated workspace was prepared again with sterile tin foil and another core sample. Gloves were changed frequently throughout subsampling (multiple times per core) to minimize cross and exogenous contamination. New metal tools that had been bleach, UV, and heat decontaminated from the previous day were used for each new core and all sterile tools remained isolated in the oven during subsampling. The homogenized sediments for each core were later subsampled for subsequent DNA extractions.

Lysis and purification. We followed the lysing and sedaDNA extraction procedure described in Murchie et al.[36]. The first round of sediments (PHP) were lysed with an input of 0.3 g. Subsequent experiments determined that this resulted in a higher inhibitor load for certain samples leading to ~10–20% failed or suboptimal adapter ligation efficiencies during library preparations (Supplementary Figs. 8–9). For the second round of extractions (PHP$_{ii}$), we reduced the input to 0.15 g, but used two PowerBead lysing tubes per sample that were pooled on the same Roche column following the long cold spin.

Subsamples were lysed with a digest solution (Supplementary Table 5) preloaded into Dneasy PowerBead tubes, then vortexed for 20 min using a TissueLyser II. Thereafter, the tubes were briefly centrifuged to remove liquid from the lids, and proteinase K was pipetted into each tube individually. The tubes were then briefly finger vortexed to disturb the sediment-bead pellets that had formed at the base and the tubes and were loaded in an incubator to oscillate overnight at 35 °C. The next day, the PowerBead tubes were centrifuged at 10,000 × g for 5 min and the supernatant was transferred to a 2 mL MAXYMum Recovery tube and stored at −20 °C for later purifications.

For sedaDNA purification, the digestion supernatant (≈1.25 mL) was thawed, briefly centrifuged, and added to ≳16.25 mL (13 volumes) of high-volume guanidinium binding buffer (Supplementary Table 6) in a 50 mL falcon tube and mixed by repeated inversion. The 50 mL tubes were loaded into a refrigerated centrifuge for the Murchie et al.[36] long cold spin, where they were centrifuged at 2500 × g at 4 °C for ~20 h overnight. Thereafter, the falcon tubes were carefully removed from the centrifuge buckets, and the supernatant was decanted, taking care to not disturb the darkly coloured pellet that had formed during the cold spin. The binding buffer was passed through a high-volume silica-column (High Pure Extender Assembly, Roche Diagnostics) over multiple rounds of centrifugation and extraction proceeded as per Dabney et al.[167] with binding and wash centrifugation at 3300 × g, two rounds of PE wash, followed by two 30 s dry spins at 16,000 × g with the tubes rotated 180° between spins to minimize the chance of ethanol retention. Purified DNA was eluted off the silica columns with two volumes of 25 µL EBT (each while waiting 5 min after EBT loading to maximize elution, then centrifuging at 16,000 × g for 1 min). Prior to all subsequent experiments the extracts were centrifuged at 16,000 × g for ≳5 min to pellet any remaining co-eluted inhibitors. Care was taken when subsampling these extracts to avoid disturbing any pellet precipitates.

Library preparation, quantitative PCR, and indexing. Doubled stranded libraries were prepared for each extract as described in Meyer and Kircher[168] with modifications from Kircher et al.[169] and a modified end-repair reaction to account for the lack of uracil excision (Supplementary Table 7). Samples were purified after blunt-end repair with a QIAquick Nucleotide Removal Kit (QIAGEN) (to maximally retain small fragments) and after adapter ligation (Supplementary Tables 8–9) and indexing (Supplementary Table 10) with a MinElute PCR Purification Kit (QIAGEN). Pre-indexing total library adapted DNA concentrations were estimated as a filtering step to determine whether a sample was successfully convereted into libraries with the short amplification qPCR assay (Supplementary Table 11).

Targeted capture with PalaeoChip. In-solution enrichments were carried out using the previously designed PalaeoChip Arctic v1.0 bait set[36]. This bait set targets whole mitochondrial genomes from approximately 180 extinct and extant Holarctic fauna, and the chloroplast barcoding loci (trnL, rbcL, and matK) from approximately 2100 species of plants. See Murchie et al.[36] for further details on the design of PalaeoChip Arctic-1.0.

Enrichments were performed using a modified version of the myBaits v4.1 protocol (Daicel Arbor Biosciences). In summary, hybridization and bait mixes were prepared to the concentrations in Supplementary Table 12. For each library, 7 µL of template was combined with 5 µL of the library block master mix (using xGens, Human Cot-1 DNA, and Salmon Sperm). Hybridization and bait mixes were combined and pre-warmed to 60 °C before being combined with the library-block mixture. The final reaction for batch 1 (PHP) was incubated for 48 h at 55 °C for bait-library hybridization. The second round of libraries (PHP$_{ii}$) were enriched with a hybridization temperature of 60 °C over ~72 h to improve off-target exclusion.

After the hybridization, beads were dispensed (20 µL per reaction [rxn]), washed with 200 µL/rxn of binding buffer, then resuspended in 20 µL/rxn binding buffer and aliquoted into PCR strips. Baits were captured using 20 µL/rxn of the bead binding buffer, incubated at 55 °C for 2.5 min (60 °C for the second round), finger vortexed and spun down, then incubated for another 2.5 min. Beads were pelleted and the supernatant (the non-captured library fraction) was removed and stored at −20 °C as per Klunk et al.[183]. The beads were resuspended in 180 µL of 60 °C Wash Buffer X per tube and washed four times following the Mybaits v4.1 protocol. Beads were resuspended in 18.8 µL EBT, PCR reamplified for 12 cycles (Supplementary Table 10), then purified with MinElute columns following manufacturer's protocols and eluted in 15 µL EBT.

Total quantification, pooling, size selection, and sequencing. Libraries were quantified using the long-amplification total library qPCR assay (Supplementary Table 13) and pooled to equimolar concentrations. Pools were size-selected with gel excision following electrophoresis for molecules ranging between 150–500 bp. Gel plugs were purified using the QIAquick Gel Extraction Kit (QIAGEN), according to manufacturer's protocol, then sequenced on an Illumina HiSeq 1500 with a 2 × 90 bp paired-end protocol at the Farncombe Metagenomics Facility (McMaster University, ON).

Bioinformatics. Reads were demultiplexed with bcl2fastq (v1.8.4), converted to bam files with fastq2bam (https://github.com/grenaud/BCL2BAM2FASTQ), then trimmed and merged with leeHom[184] using ancient DNA specific parameters (–ancientdna). Reads were mapped to a concatenation of the PalaeoChip Arctic-1.0 plant and animal probe references with network-aware-BWA[185] (https://github.com/mpieva/network-aware-bwa) with a maximum edit distance of 0.01 (-n 0.01), allowing for a maximum two gap openings (-o 2), and with seeding effectively disabled (-l 16500). Mapped reads that were merged or unmerged but properly paired were extracted with libbam (https://github.com/grenaud/libbam), collapsed based on unique 5′ and 3′ positions with biohazard (https://bitbucket.org/ustenzel/biohazard) (for PCR deduplication), and converted to fasta files and restricted to a minimum length of 24 bp. Fasta files were additionally filtered to remove any reads with lingering sequence similarity to the Illumina adapter sequences (…/fasta2oneline.pl input.fasta | agrep -v -1 AGATCGGAA | agrep -v -1 TTCCGATCT | tr "\t" "\n" | tail -n + 2 > output.fasta) and were string deduplicated using the NGSXRemoveDuplicates module of NGSeXplore (https://github.com/ktmeaton/NGSeXplore).

These filtered fastas were used as the input for BLASTn[170], which were aligned against a July 2019 local copy of the GenBank NCBI (National Center for Biotechnology Information;[171,172]) nucleotide database set to return the top 600 alignments (unique accession hits) per read with *e*-values less than 1.0E−5 (flags: -num_alignments 600 -max_hsps 1 -evalue 0.00001). The BLASTn outputs were then passed to MEGAN (Community Edition, v.6.19.7)[173,174] where the BLASTn results were filtered through a lowest common ancestor (LCA) algorithm using the following parameters:

- Min-score = 50 (default)
- Max expected (*e*-value) = 1.0E−5
- Minimum percent identity = 95%

  Allows 1 base mismatch at 24 bp, 2 at 50 bp, and 3 at 60 bp to account for cytosine deamination and other aDNA characteristic damage or sequencing errors.
- Top percent consideration of hits based on bit-score = 20%.

  More conservative taxonomic assignments than the 10% default by taking more of the top hits into consideration for LCA assignment.
- Minimum read support = 3

  Number of unique reads aligning to an NCBI accession sequence for that taxon to be considered for LCA binning.
- Minimum complexity = 0.3

  Default minimum complexity filter.
- LCA weighted algorithm at 80%.

  Two rounds of analysis that increases LCA specificity by taking all taxonomic assignments of a library into consideration.

A second set of BLASTn files, identical to those utilized in MEGAN except for being in a different output format (-outfmt "6 std staxids") were passed to PIA (Phylogenetic Intersection Analysis)[94] using default inputs. The PIA output was converted to a MEGAN readable format using scripts available on the PIA-accessories GitHub (https://github.com/Allaby-lab/PIA-accessories). All libraries from both the MEGAN-LCA and PIA taxonomic binning approaches were then compiled using MEGAN's compare feature with absolute read counts. Plant and animal sequences were inspected separately; taxonomic nodes deemed to be ecologically informative (through data exploration prioritizing taxa with high read counts, distinct changes in read abundance through time, or are otherwise known to be ecologically significant organisms) were selected and plotted using MEGAN's built-in bubble chart feature. In these inter-sample comparative charts, absolute assigned read counts are retained, but the bubble sizes are scaled (either square-root or logarithmic) to visually normalize between samples of differing sequence depths. As these logarithmically scaled bubbles make it difficult to see change through time (whereas linearly scaled bubbles obscure all but the most abundant taxon nodes), a normalized set of MEGAN libraries was used to create stacked proportional charts to more clearly observe changing sedaDNA taxon assignments through time by taking sequencing depth into account. A PCoA was also created through MEGAN with these normalized libraries. All MEGAN charts were exported as EPS files and were visually fine-tuned in Adobe Illustrator[186].

Thereafter, the closest available genetic references were obtained for notable taxa identified with the MEGAN-LCA and PIA taxonomic binning approaches. All samples were mapped to these references using the same aforementioned procedures but with an additional map-quality filter set to ≥30 with samtools (https://github.com/samtools/samtools), then assessed for ancient DNA typical damage signals using mapDamage[175] (v 2.0.3).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The sedaDNA sequence data generated in this study that can be mapped to the PalaeoChip bait reference sequences have been deposited as bam files in the NCBI SRA database under BioProject: PRJNA722670, Accessions: SRR14265632– SRR14265692. Metagenomic data derived from these mapped reads are provided in the supplementary information and source data files. PalaeoChip reference and bait sequences are available at https://doi.org/10.5281/zenodo.5643845. Source data are provided with this paper.

Code availability

All software utilized in this analysis are available online and are referenced and linked to here or in the supplementary information.

Received: 4 April 2021; Accepted: 22 November 2021;
Published online: 08 December 2021

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Acknowledgements

Many thanks to the CANA Foundation for their support of a PDF and operating costs to T.J.M. and H.N.P. This work was partially funded by the Belmont Forum and BiodivERsA grants (to D.F. and H.N.P.) for the Future ArcTic Ecosystems (FATE) research consortium, as well as NSERC Discovery grants to D.F. and H.N.P. We wish to also thank the Garfield Weston Foundation for their support of T.J.M., as well as McMaster University, the Arctic Institute of North America, Polar Knowledge Canada, and the Social Sciences and Humanities Research Council of Canada for each funding various components of this research. Thank you to the placer gold mining community of the Klondike and the Tr'ondëk Hwëch'in for their continued support of our research and access to study sites in central Yukon. Additional thanks to Ana T. Duggan for the development and continued maintenance of her ancient DNA pipeline at the McMaster Ancient DNA centre. Further thanks to Brian Golding for providing access to his computational resources. Thanks to Shanti Morell-Hart, Brian Golding, and Peter Heintzman for their guidance and support during T.J.M.'s doctoral research. Thanks to all members and affiliates of the McMaster Ancient DNA Centre for their ongoing support of this work, as well as the admin and faculty of the Anthropology department at McMaster University. Special thanks to Debi Poinar, Melanie Kuch, Jennifer Klunk, Marissa L. Ledger, and Kévin Roche for their wet-lab assistance during the *Quaternary Research* PalaeoChip paper that laid the groundwork for this study.

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Competing interests

T.J.M., H.N.P., and R.D.E.M. are members of the CANA Foundation science advisory board, a non-profit organization with horse re-wilding initiatives. T.J.M. and H.N.P. are currently supported by CANA through a PDF to T.J.M. and consumable costs. The research presented in this paper was completed long prior to funding by CANA. The authors declare no other competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41467-021-27439-6.

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Peer review information *Nature Communications* thanks Eric Capo, Daniel Mann and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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