

RESEARCH ARTICLE



Seasonal resource selection and movement ecology of free-ranging horses in the western United States

Kathryn A. Schoenecker¹ | Saeideh Esmaeili² | Sarah R. B. King²

¹U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526, USA

²Colorado State University, Natural Resources Ecology Laboratory, 1213 Libbie Coy Way, Fort Collins, CO 80523, USA

Correspondence

Kathryn A. Schoenecker, U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526, USA.

Email: schoeneckerk@usgs.gov

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Abstract

Understanding factors driving resource selection and habitat use of different species is an important component of management and conservation. Feral horses (*Equus caballus*) are free ranging across various vegetation types in the western United States, yet few studies have quantified their resource selection and seasonal use. We conducted a study to determine effects of vegetation community, distance to water, and topographic variables on seasonal resource selection in 2 feral horse populations in Great Basin sagebrush (*Artemisia* spp.) ecosystems of west-central Utah, USA: Conger Herd Management Area (HMA) and Frisco HMA. We deployed global positioning system (GPS) radio-collars on 38 female horses and GPS-transmitters braided and glued into the tail hair of 14 males, collecting locations every 2 hours for 1–4 years between 2016 and 2020. We calculated home range size and core use area of social groups (harems) and bachelor males using autocorrelated kernel density estimators for each biologically defined season (breeding, fall, and winter) per study year. We examined seasonal home range size and overlap of harem groups and bachelor males and compared movement speed of bachelors and harems among seasons. We determined seasonal resource selection in a use-availability framework using resource selection functions. We hypothesized that horses would select for areas of high herbaceous vegetation, that water would be a key variable in

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resource selection models like other equids, and home range size in winter would be largest because horses can eat snow for hydration and could therefore roam farther from surface water. Mean annual home range size was $103.12 \pm 37.38 \text{ km}^2$ (SD) for Conger harems and $117.47 \pm 32.75 \text{ km}^2$ for Frisco harems. At Conger there was no difference in home range size between harem groups and bachelor males, but home range size was smaller in winter than other seasons, whereas winter home range size at Frisco was larger than other seasons. Bachelor males moved at higher speeds than harems during all seasons, and harem groups from both populations had lower movement speeds in winter. Harem groups had distinct winter ranges with little overlap on breeding season ranges. In both populations, all horses selected for herbaceous vegetation types and avoided forest relative to shrubland throughout the year. Harems at Frisco were consistently located closer to water sources, whereas selection for water sources by Conger harems varied seasonally, with winter having the lowest selection. Harem groups at Conger had an average of 10.6% of their home ranges outside the HMA boundary and Frisco harems had up to 66.8% outside, likely because of the horseshoe shape of Frisco HMA in which shrub meadows (foraging areas) comprise the horseshoe center, which is outside the HMA. Our results highlight the importance of water sources, which were a key predictor of horse movement patterns in our study. We emphasize the utility of telemetry devices to understand resource selection of feral horses at a fine scale, enabling management to be more targeted and facilitate planning.

KEYWORDS

Artemisia spp., *Equus caballus*, feral horses, Great Basin, habitat selection, home range, resource selection function, sagebrush ecosystem, Utah

Understanding resource selection by animals is an essential component of wildlife management and conservation (Boyce and McDonald 1999). Resource selection identifies choices made by animals to determine which resources are used and reveals their cost-benefit decisions (Millsbaugh et al. 2020). The foundational idea of resource selection is that use is deemed to be selective when resources are used disproportionately to their availability (Johnson 1980, Boyce and McDonald 1999, Manly et al. 2002). By comparing used and available vegetation types, resource selection function (RSF) modeling quantifies the extent to which animal populations are selective in their choice of food and habitat. It has been applied in studies of social herbivores such as elk (*Cervus canadensis*; Johnson et al. 2000, Mao et al. 2005, Brook and McLachlan 2009, Coe et al. 2011, Proffitt et al. 2011), bison (*Bison bison*; Schoenecker et al. 2015), and bighorn sheep (*Ovis canadensis*; Gedir et al. 2020).

Distance- and speed-related metrics of animals provide quantifiable links between movement behavior and energy use. The pattern of movement and range that animals traverse in a defined period of time informs our understanding of how they navigate their environment (Turchin 1998, Noonan et al. 2019). In addition, seasonal fluctuations in resource availability drive patterns of movement, home range size, and resource selection. Animal movement and home range size are influenced by the need to maintain positive energy balance (Senft et al. 1987, Owen-Smith et al. 2010), such that smaller home range size is associated with greater availability or abundance of resources, and higher seasonal home range overlap from year to year is associated with greater temporal consistency in resource availability. For equids, water availability has been shown to strongly affect movement patterns (King and Gurnell 2005, Kaczensky et al. 2008, Nandintsetseg et al. 2016, Schoenecker et al. 2016). During summer horses (*Equus caballus*) depend on surface water for daily intake, whereas in winter they can consume snow (Mejdell et al. 2005, Kaczensky et al. 2008). Water usage for ungulates is typically higher during lactation. Horses have a gestation of approximately 11.5 months and lactation lasts for 3–6 months, meaning pregnancy and lactation periods for females overlap for several months. This is unlike other North American ungulates that complete lactation prior to the next pregnancy, and likely influences female energetic constraints.

Horses were domesticated in Eurasia over 5,500 years ago (Schubert et al. 2014), long before being introduced to the Americas by Spanish colonists. In the United States, domesticated horses were fundamental to settlement of the West and were used extensively by North American Native peoples (Berger 1986). Their societal utility changed after industrialization, and many domestic horses were released or escaped to the wild becoming feral. Today feral horses inhabit public and tribal lands across the United States (Conant et al. 2011, Schoenecker et al. 2021).

Feral horses are social animals that remain in temporally and spatially distinct harem groups made up of ≥ 1 adult male, with adult females and their juvenile offspring. Males tend their harems in which they move as a social unit and where multiple members can initiate group movements (Krueger et al. 2014). Males attempt to maintain exclusive mating rights with the females in their harem. Bachelors are non-harem-holding males that move across the landscape independently from harems either in small groups of unstable membership or solo (Linklater et al. 1999).

The United States Congress protected horses and burros (*Equus asinus*) under the Wild Free-Roaming Horses and Burros Act of 1971 (PL 92-195) because of their iconic status as a cultural legacy in the United States. Today, horses inhabit many areas of the western United States, but compared to native North American ungulates relatively little is understood about their ecology. There is extensive published literature on all aspects of the biology, life cycle, population dynamics, ecology, ecosystem function, and role of native North American ungulates, yet only a handful of recent studies have characterized habitat use of horses (Girard et al. 2013a, b; Van Beest et al. 2014; LaForge et al. 2016; Hennig et al. 2018; Leverkus et al. 2018). To our knowledge, only 3 published studies have used global positioning system (GPS) technology (Girard et al. 2013a, b; Leverkus et al. 2018; Hennig et al. 2018) to examine horse home range and resource selection in North America.

Our objective was to understand movement patterns and resource selection of horses in a sagebrush (*Artemisia* spp.) ecosystem of the Great Basin on 2 horse populations in western Utah, USA (Figure 1). We sought to quantify habitat selection and mechanisms influencing spatiotemporal variation in resource use of horses relative to social status (harem group, or bachelor male) and season. Further, we sought to determine home range size and seasonal overlap in individual ranges. The 2 study areas were similar in vegetation types, habitat characteristics, population size, and climate. Thus, our first hypothesis was that the 2 horse populations would not differ in home range size and movement patterns. Further, because home range size is inversely correlated with availability of resources (Tufto et al. 1996, McLoughlin and Ferguson 2000), we expected horses in both populations to increase movement distance and have larger home ranges during winter and smaller home range overlap in winter because they are not bound to surface water and groups can distribute farther from one another. Our second hypothesis was that distance to water would be a primary variable predicting horse resource selection, like other members of the family Equidae (Van Soest 1994, Kaczensky et al. 2008). We expected horse selection for water sources to be stronger during the breeding season and warmer months of year and weaker during winter when horses can eat snow for

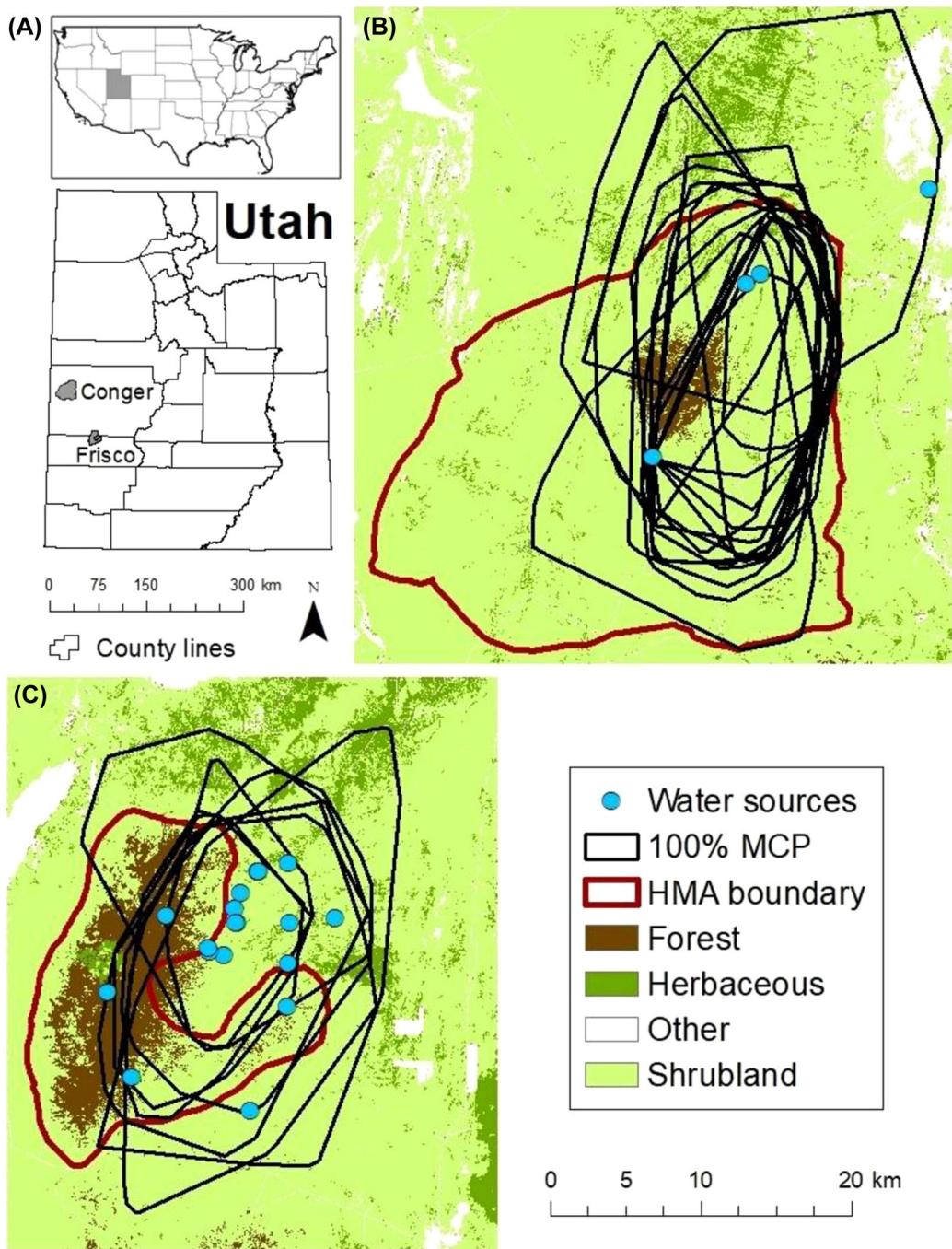


FIGURE 1 A) Location of Conger and Frisco Herd Management Areas (HMAs) in Utah, USA, for study of horse spatial use and resource selection, 2016 to 2020. Total range is represented by a 100% minimum convex polygon (MCP) around all locations collected during the study period (Sep 2016 to Aug 2020) for horses with at least 3 different seasons of data available for B) Conger hares ($n = 17$) and C) Frisco hares ($n = 8$). Land cover classes for resource selection analyses are delineated by color.

hydration. Our third hypothesis was that horses, being grazers, would primarily select vegetation types with high availability of graminoids throughout the year, like other large grazing ungulates (Schoenecker et al. 2015).

STUDY AREA

We conducted our study in Conger and Frisco Herd Management Areas (HMAs) in west-central Utah (Figure 1), which are managed by the Department of Interior, Bureau of Land Management (BLM). Both study areas are in the eastern region of the Great Basin in sagebrush ecosystems. Neither of the HMA boundaries are fully fenced, but a paved highway along the south end of Conger functions as a non-permeable boundary. In addition to horses, both HMAs are managed for human recreation (camping, hiking, hunting), some livestock grazing, wildlife conservation, and other permitted uses.

Conger Herd Management Area

Conger HMA is 69,198 ha, ranging in elevation from 1,433 m to 2,478 m (Figure 1). There are 3 permanent water sources within the HMA and a fourth outside the boundary. Between 2016 and 2020, mean annual precipitation was 192.15 ± 60.27 (SD) mm and temperatures ranged from an average daily mean temperature of $1^\circ\text{C} \pm 2^\circ\text{C}$ in winter to $27^\circ\text{C} \pm 2^\circ\text{C}$ in summer (Remote Automatic Weather Station [RAWS] Tule Valley - Delta 49W Utah). Other wild and domestic ungulates in the area include pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and occasionally elk, with cattle at the south end and domestic sheep at the north end of the HMA during winter.

Conger HMA encompasses the Conger Mountain Wilderness Study Area and is characterized by a series of north-south rocky ridges lined with cliffs to the east of Conger Mountain. Higher elevations are covered by pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.) forest, interspersed with mountain mahogany (*Cercocarpus ledifolius*) and an understory of sagebrush, yucca (*Yucca brevifolia*), and bunchgrasses (needle-and-thread [*Hesperostipa comata*], Idaho fescue [*Festuca idahoensis*], bluebunch wheatgrass [*Pseudoroegneria spicata*], basin wildrye [*Leymus cinereus*], and muttongrass [*Poa fendleriana*]). Lower slopes are dominated by sagebrush, with ephedra (*Ephedra* spp.) and saltbush (*Atriplex* spp.) and a herbaceous layer of perennial bunchgrasses, such as needlegrass (*Achnatherum* spp.), squirreltail (*Elymus elymoides*), and bluegrass (*Poa secunda*), and cheatgrass (*Bromus tectorum*). Valley bottoms are covered with salt desert scrub and semi-desert shrub, with saltbush, sagebrush, various forb and perennial graminoids such as Indian ricegrass (*Achnatherum hymenoides*), blue gramma (*Bouteloua gracilis*), thickspike wheatgrass (*E. lanceolatus*), western wheatgrass (*Pascopyrum smithii*), bluegrass, and cheatgrass. The HMA is surrounded on 3 sides by greasewood (*Sarcobatus vermiculatus*) flats descending to sparsely vegetated salt-flat playas.

Frisco Herd Management Area

Frisco HMA is 24,429 ha, ranging from 1,700 m to 2,895 m at the top of Frisco peak (Figure 1). Frisco has multiple water sources in the form of perennial and ephemeral water seeps, and cattle troughs. Average annual precipitation between 2017 and 2020 was 177.86 ± 104.62 mm and temperatures ranged from a daily average mean of $0 \pm 2^\circ\text{C}$ in winter to $24 \pm 2^\circ\text{C}$ in summer (RAWS Brimstone Res. - Milford 20WSWS Utah). Pronghorn are found on meadow plains, with mule deer and elk in forested areas, and cattle were present in winter.

Frisco HMA is horseshoe shaped (Figure 1) encompassing the high ridge that includes Frisco Peak in the San Francisco Mountains and the lower ridge of Beaver Mountains, whereas the valley between these ridges is outside the HMA. The highest elevations near Frisco Peak have spruce (*Picea* spp.)-fir (*Pseudotsuga menziesii*) forest, with

remaining upper elevations covered in Great Basin pinyon–juniper woodland. There are areas of cliffs, scree slopes, and rocky outcrops. In addition to pinyon pine and juniper, these areas have some ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), and shrubs such as sagebrush and mountain mahogany (*Cercocarpus* spp.). The herbaceous layer consists of bunchgrasses and cheatgrass like Conger. Lower elevation areas in the valley bottom consist of sagebrush shrubland dominated by sagebrush with patches of juniper and sparse grasses such as needlegrass, blue gramma, thickspike wheatgrass, fescue, needle-and-thread, basin wildrye, western wheatgrass, bluegrass, and cheatgrass. At the lowest elevations sagebrush transitions to semi-desert shrub steppe, characterized by grasses such as Indian ricegrass, blue gramma, saltgrass (*Distichlis spicata*), bluegrass, alkali sacaton (*Sporobolus airoides*), needle-and-thread, James' galleta (*Pleuraphis jamesii*), Salina wildrye (*L. salinus*), and cheatgrass, with shrubs including saltbush, sagebrush, rabbitbrush (*Chrysothamnus* spp.), and winterfat (*Krascheninnikovia lanata*).

METHODS

We defined seasons based on reproductive biology of horses and seasonality in the study area: breeding season (Mar–Aug), fall (Sep–Nov), and winter (Dec–Feb). Breeding season for horses is longer than for other North American ungulates; foals can be born as early as February or as late as August (Roelle et al. 2010). We categorized GPS-marked horses by sex and social status (adult female; adult harem-holding male; adult bachelor male). Because animals in the same social group are not independent, we used harem groups as the parameter of interest. We treated bachelor males as individuals because they were independent of social groups and from each other.

Horse locations

We deployed GPS radio-collars (Lotek Wireless, Newmarket, Ontario, Canada) on adult female horses ($n = 28$, Conger; $n = 10$, Frisco) and GPS transmitters (Biotrack Ltd, Dorset, United Kingdom) braided and glued into the tail hair of males at Conger only ($n = 14$) following methods in Schoenecker et al. (2020). All radio-tracking devices collected a location (fix) every 2 hours, and GPS location error was 5–10 m (M. Crawford, Lotek Wireless, personal communication). We censored data from individuals in the same harem group to assure only 1 radio-marked individual represented a group. This ended up being a radio-collared female from each harem because harem-holding males had fewer data points (Schoenecker et al. 2022). We were aware of associations between individuals from direct observations collected by field crews on each radio-marked individual at least once a month year-round for all years of the study, such that membership in each harem was identified and monitored. Horses were also individually identifiable by pelage color differences and a numeric freeze mark on the left hip. For analyses we used GPS locations of 19 harems between 1 September 2016 and 31 August 2020 and 9 bachelor males between 2 June 2017 and 20 May 2018 in Conger HMA, and 9 harems in Frisco HMA collected between 1 March 2017 and 31 August 2020 (we had no data from males at Frisco). We censored horse location data with a dilution of precision >10 (Frair et al. 2010).

Some of the bachelors in our study were castrated as part of another study (King et al. 2022) that reported no differences in behavior or body condition between gelded and intact males. To make sure movement and space use of gelded and intact bachelor males did not differ, we used 2,245 GPS locations of 6 gelded ($n = 1,788$) and 2 non-gelded ($n = 457$) bachelor males, collected between 27 December 2017 (2 weeks after the gelding event) and February 2018, to compare space use and movement metrics of gelded and non-gelded bachelor males. Dates represent months in which we had data on all gelded and non-gelded bachelors. We calculated movement speed (km/hr), 100% minimum convex polygon (MCP) around collected GPS locations (km²), home range size (95% of auto-correlated kernel density estimator, km²), and distance to nearest water sources (km) over the study period (Table S1). We used student *t*-test to compare space use and movement metrics between gelded and non-gelded

bachelor males and logarithmic transformation to meet assumptions of parametric tests wherever it was appropriate. Because we found no difference in movement speed, distance to water sources, MCP range, or home range size between gelded and non-gelded bachelors (Table S1), we pooled bachelors for analyses.

For our analyses, we used 218,168 locations for harems in Conger, 5,066 locations for bachelor males in Conger, and 98,779 locations for harems in Frisco. For seasonal analyses, we assessed if each harem or bachelor male had data spanning the majority of a season (i.e., fixes in ≥ 3 months for breeding season and 1 month for fall or winter); if not we removed that harem or bachelor from analyses for that season. Our final data set included 233 horse-season-years across 2 areas (Conger and Frisco), 4 years (2016–2020), 3 seasons (breeding, fall, and winter), and 37 individuals (Conger harems = 19, Conger bachelor males = 9, Frisco harems = 9).

Horse home range and movement

We defined harem or bachelor seasonal home range (km^2) using the auto-correlated kernel density estimator (AKDE) in a continuous time movement modeling framework using package *amt* (Signer et al. 2019) in program R (R Development Core Team 2016). We calculated the 95% AKDE contour to delineate each harem and individual bachelor's seasonal home range and 50% AKDE contour to delineate core areas for each season per study year. We additionally determined seasonal home ranges by calculating 100% MCP (Mohr and Stumpf 1966) to compare with previous studies. We used location of harems for which we had data for an entire year to calculate annual home range size (95% AKDE).

We did not obtain GPS fix locations of any bachelor male for an entire year because of the short-term duration of tail transmitters on males (Schoenecker et al. 2020, King and Schoenecker 2022). Thus we only report annual home range size for harems. Additionally, for harems that had data for all 3 defined seasons, we calculated 100% MCP using all GPS locations collected over the entire study period to represent total range of harems in each area (Figure 1). To compare movement patterns of horses by sex and social status, and season, we calculated a movement metric of speed (km/hr) of harems and bachelors by dividing total distance traveled every 2 hours by the GPS fix rate (2 hours). To determine how far horses traveled from surface water, we calculated average and maximum distance to water using linear distance from harem and bachelor male locations to nearest water source by season. We calculated spatial extent of horse home ranges (i.e., portion of 95% AKDE) located outside HMA boundaries in each season. To quantify how far harems and bachelors traveled outside HMAs, we calculated linear distance between locations outside the HMA and the HMA boundary in each season.

To evaluate the amount of home range overlap between different harems or different bachelors within each season, we measured pairwise seasonal home range overlap of harems and bachelors over all years within each season by calculating percent overlap in 95% AKDE home ranges using the following equation: $O/(A1 + A2 - O)$, where O is the area of overlap between home range $A1$ and $A2$, and $A1$ and $A2$ are the areas of the 2 home ranges (Millsbaugh et al. 2004, Vander Wal et al. 2014). To test if horses shifted their range between seasons, we measured home range overlap between successive seasonal ranges of each harem or bachelor in the 2 study areas (Van Beest et al. 2010).

Habitat variables for resource selection modeling

We included topographic measures including elevation (m) and slope (%) derived from the digital elevation model of Utah (spatial resolution of 10 m; Archuleta et al. 2017; <https://gis.utah.gov/data/elevation-and-terrain/>, accessed 8 Feb 2021). We classified land cover of the 2 HMAs with the 2016 National Land Cover Dataset (Yang et al. 2018) by combining categories with similar functionality to 4 vegetation types: forest, shrubland, herbaceous, and other (Figure 1; Appendix A). The herbaceous category comprised rangelands that were dominated by grasses and forbs without significant shrub or tree components. To measure availability of surface water in study areas, ground crews

identified all water sources (i.e., troughs or springs) known to be available to horses by visual observation. We analyzed all spatial data at 30-m resolution. We measured distance to water by calculating linear distance from each harem or bachelor location in respective study areas to the nearest water point. We standardized continuous variables by subtracting each value from the mean and dividing by standard deviation to improve model fit and for easier interpretation of results.

Statistical analysis

At Conger where we had data from both sexes, we compared movement and space use parameters (speed, seasonal home range, core areas, percent home range overlap) between harem groups and bachelor males during different seasons using 2-way analysis of variance (ANOVA) including interaction of sex and season (Zar 1999) followed by *post hoc* Tukey's honest significance tests using log transformation to meet parametric test assumptions, or we used a Kruskal-Wallis test followed by a pairwise Wilcoxon test with Bonferroni adjustment for *P*-value as appropriate for distribution of data. Because our sample size for bachelor males in fall was 1, we removed bachelors from our analyses in fall. In Frisco HMA where we only had data from females, we compared movement and space use parameters of harems in different seasons using a 1-way ANOVA, followed by a Tukey's honest significance *post hoc* test, or a Kruskal-Wallis test followed by a pairwise Wilcoxon test with Bonferroni adjustment for *P*-value as appropriate for distribution of data. Finally, we compared annual home range size of harems between Conger and Frisco using a *t*-test.

To characterize seasonal resource selection by horses, we calculated RSFs within a use-availability design (Boyce et al. 2002, Fortin et al. 2008). For each horse location (used point), we generated 10 random points (available points) within the 100% MCP of each bachelor male or female (representing a harem) location for each season and year (third-order habitat selection; Johnson 1980, Meyer and Thuiller 2006) and extracted habitat variables for both used and available points. We developed RSFs using binomial logistic regressions to estimate coefficients for habitat variables (Manly et al. 2002, Johnson et al. 2006) with a weight of 1,000 assigned to available points (Muff et al. 2020). We generated separate models for each season and included individual identity-year as a random intercept in all models to account for individual and year variability in resource selection (Conger harems: $n = 54$ identity-years for breeding, $n = 47$ for fall, $n = 53$ for winter; Conger bachelor males: $n = 4$ for breeding, $n = 8$ for winter; Frisco harems: $n = 20$ for breeding, $n = 27$ for fall, $n = 19$ for winter). Before presenting habitat variables to models, we screened collinearity among them using pairwise correlations with a threshold of ($|r| > 0.6$). We combined uncorrelated variables into a global model for each study area and season. For Conger, we developed models for harems and bachelor males separately. Variables used for models in both Conger and Frisco included elevation (m), slope (%), distance to nearest water source (km), and land cover categories extracted from the National Land Cover Dataset (Yang et al. 2018) with shrubland, the most common category in both areas, as the reference category. We were not able to use distance to livestock as a parameter in our winter model (the season when livestock were present) because we had no data on livestock movements. We conducted analyses in program R using package raster (Hijmans et al. 2015) and sf (Pebesma 2018) for spatial analysis and package amt (Signer et al. 2019) for home range estimates and RSF models.

RESULTS

Home range and movement

Mean annual home range (95% AKDE) of harems at Conger was $103.12 \pm 37.38 \text{ km}^2$ (range = $42.52\text{--}199.92 \text{ km}^2$, $n = 33$ harems per year) and at Frisco was $117.47 \pm 32.75 \text{ km}^2$ (range = $85.03\text{--}170.85 \text{ km}^2$, $n = 11$ harems per year). We found no difference in mean annual home range size of harems by HMA ($t_{19,45} = -1.21$, $P = 0.24$).

Mean seasonal home range of harems (95% AKDE) at Conger varied from $49.9 \pm 38.0 \text{ km}^2$ in winter to $85.7 \pm 33.7 \text{ km}^2$ in breeding season, and at Frisco varied from $69.2 \pm 22.8 \text{ km}^2$ in breeding season to $83.4 \pm 33.60 \text{ km}^2$ in winter (Table 1; Figure 2). Seasonal range of harems and bachelor males at Conger did not differ for either home range size ($F_{1,162} = 1.39$, $P = 0.24$) or core area ($F_{1,162} = 0.40$, $P = 0.53$) but differed in size among seasons (home range: $F_{2,162} = 29.41$, $P < 0.001$; core area: $F_{2,162} = 28.78$, $P < 0.001$; Figure 2A–C). Home range and core area sizes for Conger bachelors and harems were smaller in winter compared to fall and breeding seasons ($P < 0.001$; Table 1). Movement speed of harems at Conger was slower in winter than fall and breeding season (Kruskal-Wallis $H_2 = 78.98$, $P < 0.001$; Wilcoxon rank sum exact test for winter season: $P < 0.001$; Figure 2D). Bachelor males moved at similar speeds among seasons but faster than harems in all seasons (Wilcoxon rank sum test $W = 1,304$, $P < 0.01$). At Frisco there was no effect of season on size of home range or core area of harems (home range: Kruskal-Wallis $H_2 = 2.70$, $P = 0.26$; core area: $H_2 = 4.74$, $P = 0.13$; Table 1). Harems in Frisco had different movement speeds among seasons ($H_2 = 28.58$, $P < 0.001$; Figure 2D), with the fastest movement speed in fall and slowest in winter (Wilcoxon rank sum test for all seasons: $P < 0.001$).

Percent seasonal home range overlap (95% AKDE) was highest in breeding season and lowest in winter for harems at Conger ($H_2 = 88.10$, $P < 0.001$; Table 2), with overlap being different among seasons (Wilcoxon rank sum test for all seasons: $P < 0.001$). Data indicated moderate evidence that percent seasonal home range overlap in bachelor males differed between breeding and winter seasons ($W = 70$, $P = 0.06$). At Frisco, harems had higher home range overlap during breeding season compared to fall and winter ($H_2 = 12.60$, $P = 0.002$; Wilcoxon rank sum test for breeding and fall, and breeding and winter: $P \leq 0.01$; Table 2), and percent home range overlap between fall and winter seasons did not differ for Frisco harems (Wilcoxon rank sum test for fall and winter: $P = 1.0$).

Home range overlap (95% AKDE) among seasons for each Conger harem was highest between breeding and fall home ranges ($45.0 \pm 12.9\%$; $F_{2,129} = 12.42$, $P < 0.001$), compared to $33.3 \pm 13.8\%$ between fall and winter, and $25.8 \pm 13.6\%$ between winter and breeding season. We did not have enough data to measure home range overlap in bachelor males at Conger. In Frisco harems, home range overlap was higher between fall and winter ($48.2 \pm 13.4\%$) compared to winter and breeding ($33.8 \pm 14.6\%$) and breeding and fall comparisons ($35.9 \pm 13.2\%$; $F_{2,54} = 6.06$, $P = 0.004$).

TABLE 1 Mean seasonal home ranges of horses at Conger ($n = 19$ harems and $n = 9$ bachelor males) and Frisco ($n = 9$ harems) Herd Management Areas in Utah, USA, between September 2016 and August 2020. Breeding season was March to end of August, fall was September to end of November, and winter was December to end of February. Home range represents 95% auto-correlated kernel density estimator (AKDE) home range ($\text{km}^2 \pm \text{SD}$), with 50% AKDE representing core range ($\text{km}^2 \pm \text{SD}$). Total range ($\text{km}^2 \pm \text{SD}$) represents 100% minimum convex polygon (MCP) around all locations collected during study area for harems with ≥ 3 different seasons of data available ($n = 17$ at Conger and $n = 8$ at Frisco). Different capital letters indicate significant differences within a column ($P < 0.05$). No bachelor male had data from all 3 seasons.

Social group	Season	Conger			Frisco		
		Home range	Core range	Total range	Home range	Core range	Total range
Harems	Breeding	^A 85.7 ± 33.7	^C 22.1 ± 9.4	124.3 ± 46.3	69.2 ± 22.8	16.6 ± 5.6	105.7 ± 31.7
	Fall	^A 82.4 ± 43.7	^C 19.9 ± 10.7	118.1 ± 55.2	75.7 ± 35.2	18.7 ± 9.1	102.6 ± 47.9
	Winter	^B 49.9 ± 38.0	^D 12.4 ± 9.6	68.6 ± 48.9	83.4 ± 33.6	21.5 ± 9.8	108.4 ± 39.6
	Total range			228.1 ± 89.3			239.3 ± 85.9
Bachelor males	Breeding	^A 84.1 ± 38.2	^C 20.7 ± 8.62	98.3 ± 27.4			
	Fall ^a						
	Winter	^B 56.2 ± 21.2	^D 12.6 ± 5.6	80.6 ± 29.4			

^aSample size of 1 bachelor male in fall precluded determining mean and standard deviation.

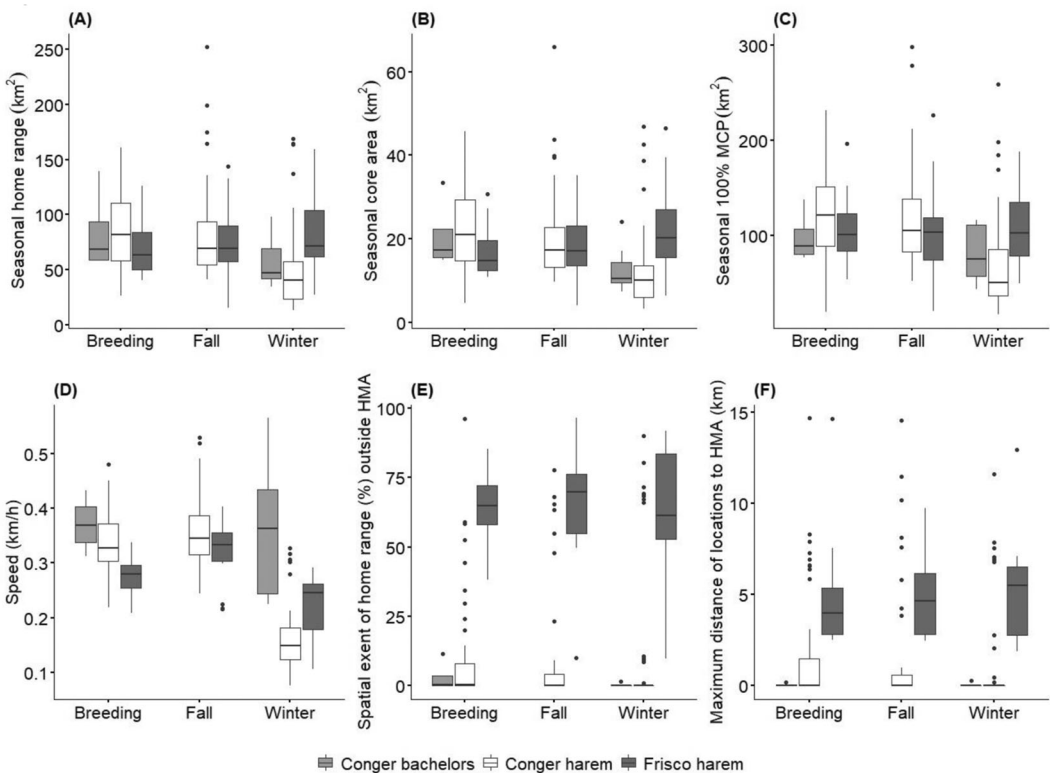


FIGURE 2 A) seasonal home range size (95% auto-correlated kernel density estimator [AKDE]), B) seasonal core areas (50% AKDE), C) seasonal 100% of minimum convex polygon (MCP) around horse locations, D) movement speed, E) spatial extent of horse home ranges (95% AKDE) outside the Herd Management Area (HMA), and F) maximum distance of horse location to the boundary of HMA of 19 harems ($n = 152$ harem-season-years) in Conger HMA, Utah, USA, and 9 harems ($n = 66$ harem-season-years) in Frisco HMA in Utah, for winter, breeding, and fall seasons between September 2016 and August 2020. Boxes indicate median, 25%, and 75% quartiles, whiskers represent 10th and 90th percentiles, and dots show outliers. Sample size of $n = 1$ bachelor male in fall precluded comparing movement and home range parameters with harems in fall (i.e., no data).

TABLE 2 Mean seasonal pairwise percent home range overlap (SD) by social status (harems and bachelor males) and Herd Management Area (HMA; Conger or Frisco) of horses in 2 populations of the Great Basin, Utah, USA, 2016–2020. Different letters indicate significant difference within a row. P -values represent Kruskal-Wallis test results for Conger harems (n : breeding = 347, fall = 268, winter = 337 overlap in pairs of home range), Wilcoxon rank sum test results for Conger bachelors (n : breeding = 3, winter = 28 overlap in pairs of home range), and Kruskal-Wallis test results for Frisco harem (n : breeding = 84, fall = 59, winter = 53 overlap in pairs of home ranges) seasonal home range overlap.

HMA (social status)	Season			P
	Breeding	Fall	Winter	
Conger (harems)	^A 27.8 (19.6)	^B 18.1 (19.2)	^C 16.0 (19.5)	<0.001
Conger (bachelor males)	43.5 (29.9)		18.0 (28.2)	0.06
Frisco (harems)	^A 37.2 (17.0)	^B 28.8 (16.8)	^B 27.5 (18.3)	0.002

Mean spatial extent of horse home ranges outside HMA boundaries at Conger was 9.4 ± 19.4 for harems and $3.1 \pm 5.6\%$ for bachelor males in breeding season, $9.5 \pm 21.3\%$ for harems in fall, and $10.4 \pm 25.1\%$ for harems and $0.2 \pm 0.6\%$ for bachelor males in winter (Figure 2E). In contrast, harems at Frisco on average had $64.0 \pm 11.7\%$, $66.8 \pm 19.7\%$, and $62.0 \pm 23.3\%$ of their seasonal home ranges outside the HMA boundary in breeding, fall, and winter, respectively (Figure 2E). The maximum linear distance harems moved from the HMA boundary was 14.7 km at Conger (max. = 14.7 km in breeding, 14.6 km in fall, and 11.6 km in winter), and 14.7 km at Frisco (max. = 14.7 km in breeding, 9.7 km in fall, and 12.9 km in winter). Maximum linear distance that bachelor males moved outside the HMA was 277 m at Conger (Figure 2F). All horses had greater average distance to water in winter compared to breeding season or fall, and the maximum distance any harem traveled from a known surface water source was 16.8 km (Table 3).

Resource selection

Resource selection function models showed slightly different patterns for harems and bachelor males in different seasons (Table 4). In Conger, harems selected for higher elevations particularly in winter (odds ratios changed from 1.09 to 1.48 for an increase in 1 standard deviation of elevation in winter and breeding seasons, respectively) and avoided steeper slopes (selection decreased by 0.92 in winter and 0.89 in breeding season for each increase in 1 standard deviation of slope). Selection for water was variable by season for harems at Conger. In breeding season, they selected for closer distance to water (odds ratio = 1.04) and avoided it in winter (odds ratio = 0.72), with no clear selection or avoidance in fall. Harems also selected for herbaceous vegetation types (with the strongest and weakest selections in fall and winter, respectively) and avoided forest (with strongest avoidance in fall and weakest avoidance in winter) relative to shrublands (reference category) in all seasons. Frisco harems consistently selected for herbaceous vegetation types and avoided forest relative to shrubland in all seasons (Table 4), with selection for herbaceous cover being stronger in winter compared to other seasons. Unlike Conger, Frisco harems selected for closer distances to water (with a stronger selection in fall, odds ratio = 1.06) and steeper slopes (with a stronger selection in winter, odds ratio = 1.22) during all seasons (Table 4).

Bachelor males avoided closer distances to water in breeding season and winter (Table 4). Bachelors selected for herbaceous vegetation types relative to shrublands (the reference category) in breeding and winter season. They showed no clear selection or avoidance for the other category in either season and avoided steep slopes and forest in all seasons (Table 4). Selection for herbaceous cover and avoidance of forest were strongest in breeding and winter seasons, respectively.

TABLE 3 Mean and maximum distance to nearest water source ($\pm$ standard deviation) of GPS radio-marked harems and bachelor males by season and Herd Management Area (HMA) from 2016 to 2020 in a Great Basin sagebrush ecosystem of Utah, USA. Sample size of $n = 1$ bachelor male in fall precluded calculations for that season (no data).

HMA (social status)	Distance to surface water (km)								
	Breeding			Fall			Winter		
	$\bar{x}$	SD	Max.	$\bar{x}$	SD	Max.	$\bar{x}$	SD	Max.
Conger (harems)	4.8	2.5	15.4	5.3	2.3	16.3	7.1	2.0	16.8
Conger (bachelor males)	5.6	2.8	14.9				6.3	3.1	15.4
Frisco (harems)	2.2	1.5	12.7	2.3	1.7	11.2	2.4	1.4	11.1

TABLE 4 Resource selection function parameter estimates and 95% confidence intervals (lower [L] and upper [U] confidence interval [CI]) for models describing seasonal resource selection for harem and bachelor males at Conger Herd Management Area (HMA) and for harems at Frisco HMA, Utah, USA, 2016–2020. Breeding season was March to end of August and winter was December to end of February. In all models shrubland, which was the most common category in both areas, is the reference category. All parameters have been standardized. Sample sizes (identity-year) differed for each season (Conger harems: $n = 54$ for breeding, $n = 47$ for fall, $n = 53$ for winter; Conger bachelor males: $n = 4$ for breeding, $n = 8$ for winter; Frisco harems: $n = 20$ for breeding, $n = 27$ for fall, $n = 19$ for winter). Because of small sample size, we were not able to model habitat selection for bachelor males in fall.

HMA	Social status	Parameter	Breeding			Fall			Winter		
			Estimate	L 95% CI	U 95% CI	Estimate	L 95% CI	U 95% CI	Estimate	L 95% CI	U 95% CI
Conger	Harems	Elevation	0.09	0.08	0.10	0.18	0.16	0.19	0.39	0.37	0.40
		Slope	-0.11	-0.12	-0.10	-0.13	-0.14	-0.12	-0.08	-0.09	-0.07
		Distance to water	-0.04	-0.05	-0.04	0.01	-0.01	0.01	0.33	0.32	0.34
		Forest	-2.79	-2.88	-2.69	-3.24	-3.40	-3.08	-1.73	-1.85	-1.61
		Herbaceous	0.55	0.53	0.58	0.68	0.65	0.72	0.43	0.39	0.46
		Other	-0.08	-0.15	-0.01	0.09	-0.01	0.19	0.36	0.27	0.45
Frisco	Harems	Elevation	0.06	0.05	0.07	-0.07	-0.09	-0.05	0.09	0.07	0.11
		Slope	0.08	0.07	0.09	0.03	0.01	0.05	0.20	0.18	0.21
		Distance to water	-0.01	-0.02	0.00	-0.06	-0.07	-0.05	-0.04	-0.06	-0.03
		Forest	-1.23	-1.26	-1.19	-1.31	-1.39	-1.24	-1.09	-1.16	-1.02
		Herbaceous	0.64	0.60	0.67	0.34	0.28	0.40	0.81	0.76	0.87
		Other	0.16	-0.67	0.99	1.11	0.52	1.69	-0.92	-2.00	0.15
Conger	Bachelor males	Elevation	0.51	0.44	0.57				0.74	0.69	0.79
		Slope	-0.09	-0.15	-0.03				-0.11	-0.15	-0.07
		Distance to water	0.14	0.07	0.20				0.51	0.45	0.56
		Forest	-1.50	-1.84	-1.16				-1.93	-2.11	-1.76
		Herbaceous	0.77	0.55	0.99				0.51	0.29	0.74
		Other	-0.58	-1.97	0.80				0.40	-0.22	1.02

DISCUSSION

Our results provide fine-scale understanding of horse space use, movement patterns, habitat needs, and range use in 2 Great Basin populations. Because home range size is an indication of resource availability, the similarity of harem home range size between the 2 populations (103.12 km² and 117.47 km²) suggests comparable resource availability in the sagebrush ecosystems we studied.

Few studies have examined home range size of horses based on GPS collar data. Earlier studies in North America that relied on visual observations reported wide variation in horse home range sizes, between 2.6 km² and 48 km² (Pellegrini 1971; Feist and McCullough 1976; Berger 1977, 1986; Salter and Hudson 1982; Miller 1983). Results from earlier studies reported consistently smaller home range sizes than what we found using GPS telemetry data (mean annual 95% AKDE of 103.12 km² and 117.47 km² for Conger and Frisco harems, respectively), which were also larger than 95% kernel home ranges reported for feral horses in forests in Canada (48.4 km²; Girard et al. 2013a), and open shrublands of Wyoming, USA (40.4 km²; Hennig et al. 2018) where GPS-marked horses were studied. Both the Wyoming and Canada horse populations were in habitats with abundant water sources, unlike harems in both Great Basin populations of our study, which had greater home range sizes likely to accommodate longer distances to water and potentially less forage availability, although we did not measure forage cover or biomass in our study. Both Conger and Frisco HMAs were not fully fenced; thus, HMA boundaries did not limit home range size of horse groups.

Harems in both HMAs we studied had distinct breeding season and winter ranges with little overlap, and seasonal home range overlap (spatial range overlap of multiple harems within a season) also indicated harems had highest overlap in breeding relative to other seasons. This site fidelity is likely related to pregnant and lactating females needing to remain near established water sources because of increased hydration needs (Fischhoff et al. 2007) and has been demonstrated in other equids as well (King 2002, King and Gurnell 2005, Kaczensky et al. 2008).

Seasonal movements of ungulates are strongly influenced by seasonal vegetation biomass and availability (Salter and Hudson 1982, Kaczensky et al. 2008), which subsequently influences home range (McLoughlin and Ferguson 2000). We expected home range size in winter to be larger than in breeding season; however, both home range and core area of harems and bachelors were smaller in winter. Harems also had less overlap and were spread-out in a more dispersed distribution in winter, especially once snow became available at higher elevations. The presence of snow allows harems to move farther from surface water, particularly in Conger HMA where there were only 4 water sources that often froze in winter. Frisco had many natural water sources in the form of creeks and seeps making it less limiting to Frisco harems, although harems still moved to higher elevation in winter, suggesting they also relied on snow for hydration. Conger and Frisco harems did not select for different vegetation types in winter compared to breeding season and fall (highest selection was for herbaceous vegetation types in all seasons), so movement to winter range is more likely related to reduction or depletion of forage resources on breeding range and potentially avoidance of social stress and competition for forage by moving farther from other harems. Further, in winter horses can maintain hydration from eating snow (Mejdell et al. 2005) and are thus freed from traveling between water sources and foraging areas. We predicted eating snow would allow horses to roam farther, but instead it allowed them to reduce movements in a critical time of year for energy balance. Similar to other North American ungulates that experience resource limitation in winter (McCabe et al. 2010, Murie 2017), Conger harems relocated to areas in the south of the range where they could access forage resources that were too far from surface water during breeding season. Harems in both populations also moved at significantly slower speeds in winter than breeding and fall seasons and had a smaller spatial extent of movement. In winter, Przewalski horses (*Equus przewalskii*) are reported to spend more time feeding than moving or other activities to address seasonal energetic balance constraints (King 2002), which is likely what harems at Conger and Frisco are doing as well.

Our hypothesis for winter home range size was not accurate for Conger harems, but at Frisco winter home range was larger than other seasons, although season had no influence on home range size. Frisco had more water sources naturally dispersed especially at higher elevations and harems were on average only approximately 2.3 km

from the nearest known water source, likely reducing the influence of water as a driver of movement. These different results by HMA emphasize the important role of water in movement and space use of horses.

Horse home ranges included areas outside HMA boundaries, particularly at Frisco where the horseshoe shape of the HMA and location of herbaceous vegetation in the horseshoe center meant horses crossed the boundary to access foraging areas. At Conger, movement outside the HMA was largely by 3 harems, 1 that was mostly found on open terrain north of the HMA and 2 others that moved to the opposite side of a ridge that was outside the HMA. Both populations were near the target population size or appropriate management level (AML) and drought indices in Millard and Beaver counties did not go into the most severe levels during this study. We do not know why horses moved outside HMAs but suggest it was not because of a lack of resources or solely density related. Horses are large bodied grazers that can travel long distance and roam widely.

To our knowledge, information on bachelor males is sparse in the literature. Harem groups are typically easier to find by ground observation compared to bachelors because harems are generally larger than bachelor groups (Linklater 2000). Finding a single male and tracking or following him is difficult without radio telemetry. The GPS tail transmitters we used did not function for a full year, which limited our ability to compare space use and movement patterns of bachelors with harem groups in all seasons, and may have influenced our biological interpretation. But we were able to compare breeding and winter season space use, and those results indicated similar home range size and resource selection, except that bachelors tended to roam faster than harems. Bachelor males had significantly higher movement speeds than harems during all seasons, similar to observations of males spending more time moving than females in other populations (King et al. 2016). This is possibly because, in comparison to bachelor males, harem group movement speed is constrained by the needs of pregnant and lactating females that spend more time feeding, and by the needs of foals that spend more time in recumbent rest than adults (King et al. 2016).

Horses used almost all areas of each HMA except densely forested areas and steeper slopes in both study areas, and there was strong similarity in resource selection and spatial use of harems. Horses are large grazers (Van Soest 1994), and their foraging strategy includes consuming sizable amounts of variable and low-quality forage (Schoenecker et al. 2016) while compensating for their high digestive pass-through rate by exhibiting higher daily food intake than ruminants (Duncan et al. 1990). Horses in both study areas selected for vegetation types with higher graminoid and herbaceous productivity, that is, areas with greater biomass to enhance foraging efficiency (Fleurance et al. 2009). Horses have been shown to select for taller swards (Edouard et al. 2009) in which their intake is assumed to be higher (Naujeck et al. 2005) but also for short grass regrowth (Fleurance et al. 2009) and much shorter grasses than ruminants (Menard et al. 2002); they have been reported to select graminoids over forb or browse (Salter and Hudson 1979, Schoenecker et al. 2016) when available, especially during summer (King 2002, King and Gurnell 2005, Girard et al. 2013b, King and Schoenecker 2019). Both populations we studied selected for habitats with greater herbaceous vegetation cover, consistent with other studies in which horses select for grassland herbaceous vegetation types (Smith 1986, Crane et al. 1997, King 2002, King and Gurnell 2005).

Leverkus et al. (2018) reported horses avoided woodlands in a population in Canada. We also found horse avoidance of forest in all seasons. Forest canopy cover limits herbaceous vegetation abundance in the understory, and dead and downed trees may inhibit horse movement and access to forage, which may lead to horse avoidance (Leverkus et al. 2018). Forest cover can also provide hiding places for predators. Girard et al (2013b) determined that horse use was positively related to distance to forest edge. In heavily forested environments that lack grasslands, horses have been found to select disturbed areas such as roadside edges (Girard et al. 2013b) where herbaceous production is high (Irving 2001).

Terrain influences habitat selection, with horses in general more likely to occupy flat pastures or gently sloping ridgetops (Ganskopp and Vavra 1986) than steep slopes. Our results validated these results, except in Frisco where harems were slightly selecting for sloped terrain in all seasons because the HMA includes 2 mountain ranges, so Frisco harems could not avoid slopes. Conger harems and bachelors selected for higher elevations of the HMA more strongly in winter than other seasons. In summer, selecting for higher elevation is thought to be related to horses escaping from insects or hot ambient temperatures (King and Gurnell 2010), thermoregulation, avoiding

human disturbance at lower elevations, or travel between foraging and watering sites. But in winter, snow is more available at higher elevations, which harems and bachelors both selected for strongly in winter. These areas of higher elevation presumably had ample snow for hydration, with wind swept slopes for forage access.

Our research highlights the importance of water sources, which explained horse movement patterns in our study. Horses have a cecal digestive system that is less efficient than ruminants in terms of water use; they excrete a lot of water during digestion making water a critical resource need. Ruminant ungulates can extract water from the vegetation they eat (Leslie and Douglas 1979, Krausman et al. 1999, Sanchez-Rojas and Gallina 2000, deVos and Miller 2005, Cain et al. 2010), whereas horses rely almost entirely on surface water or snow. Access to surface water has been shown to influence spatial distribution and movement pattern of horses (Rubenstein 1981, Berger 1986, Franke Stevens 1988, Rozen Rechels et al. 2015) and predict foal survival (LaForge et al. 2016). Horse response to surface water is reported to vary from positive associations in summer (Girard et al. 2013a) to no particular influence throughout the year (Salter and Hudson 1979). It has been reported as a significant variable for feral horse habitat selection (Arandhara et al. 2020) and used to predict probability of khulan (*Equus hemionus hemionus*) occurrence (Nandintsetseg et al. 2016). In our study, selection for closer distances to water differed by population and social status. Harems selected for closer distances to water during breeding season at Conger where only 4 permanent water sources existed and avoided it in winter when they could eat snow. Frisco harems had access to dispersed natural water sources across the HMA where it was seemingly non limiting, explaining why Frisco harems selected for areas close to water in all seasons. Bachelor males avoided closer distances to water in all seasons, being free to travel longer distances to access prime forage, to avoid or join conspecifics, or to move farther from water in summer because they are not limited by associations with lactating females, and in winter they had access to snow.

We did not measure forage quality or quantity directly, but these variables are likely important factors influencing horse seasonal movement and resource selection that should be investigated. Another limitation of our study was retention of radio marks on males. We were able to collect over 281,000 GPS locations from harems in both populations but only 5,000 from bachelor males (in only 1 population). Males have been found to be difficult to mark (Schoenecker et al. 2020) and this makes obtaining GPS location data from males challenging. A longer lasting method is needed to mark male horses; our GPS tail transmitters did not remain in place for more than 1 year.

The BLM is required by law to manage for multiple use of renewable and nonrenewable resources including recreation, wildlife, rangelands, minerals, and wild horses and burros, amongst others. Fine-scale information about seasonal horse use and habitat selection on the landscape could be useful to managers as they make the most judicious use of public lands to support these multiple uses. Horse populations are increasing across the West (Schoenecker et al. 2021), so knowing which areas horses select for and use seasonally relative to wildlife and permitted livestock can assist in planning spatially targeted management.

MANAGEMENT IMPLICATIONS

The BLM manages HMAs as the bounded areas where wild horses are intended to live. When wild horses leave designated HMAs, they may be considered excess animals, subject to removal. Lands surrounding both HMAs in this study were mostly under BLM management; however, when wild horses stray onto private lands, it can cause conflict and landowners can request that those stray animals be removed. Our results showed that water sources outside of an arid HMA such as Conger can attract wild horses. Thus, horse range use and movements outside of HMAs could be mitigated by strategic placement of water sources, where possible. Our research highlighted how this species is especially vulnerable to drought as harem movements were closely connected to water sources, especially in breeding season. Herd management sometimes includes manipulating sex ratio to have relatively more males; this reduces the per capita population growth rate and could benefit habitat conditions by reducing concentrations of horses because bachelor males had higher movement rates than harems.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Methods were approved by the United States Geological Survey Animal Care and Use Committee (FORT-2015-10; plus extensions).

DATA AVAILABILITY STATEMENT

Data generated during this study are available as a United States Geological Survey data release (Schoenecker et al. 2022).

ORCID

Kathryn A. Schoenecker  <http://orcid.org/0000-0001-9906-911X>

Sarah R. B. King  <https://orcid.org/0000-0002-9316-7488>

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SUPPORTING INFORMATION

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APPENDIX A: LAND COVER CLASSES

Table A1 and Table A2

TABLE A1 Land cover classes at Conger Herd Management Area (HMA) based on National Land Cover Dataset (NLCD) 2016, Utah, USA. showing land cover classes used for analyses, and the similar land cover classes that are combined. Area and percent cover are given within the HMA boundary, and within all horses'100% minimum convex polygon (MCP).

Land cover class	Land cover classes in NLCD	Area (ha) within HMA boundary	Percent cover within HMA boundary	Area (ha) within horses' 100% MCP	Percent cover within horses' 100% MCP
Forest	Evergreen forest	2,911	4	2,887	4
Shrubland	Shrub and scrub	63,763	92	68,660	85
Herbaceous	Herbaceous	1,949	3	6,200	8
Other	Developed open space, developed low intensity, developed medium intensity, developed high intensity, barren land, hay or pasture, woody wetlands, emergent herbaceous wetlands	536	1	80,755	4

TABLE A2 Land cover classes at Frisco Herd Management Area (HMA) based on National Land Cover Dataset (NLCD) 2016, Utah, USA, showing land cover classes used for analyses, and the similar land cover classes that are combined. Area and percent cover are given within the HMA boundary, and within all horses' 100% minimum convex polygon (MCP).

Land cover class	Land cover classes in NLCD	Area (ha) within HMA boundary	Percent cover within HMA boundary	Area (ha) within horses' 100% MCP	Percent cover within horses' 100% MCP
Forest	Deciduous forest, evergreen forest, mixed forest	9,970	41	8,697	15
Shrubland	Shrub and scrub	13,942	57	42,886	74
Herbaceous	Herbaceous	484	2	6,109	11
Other	Developed open space, developed low intensity, developed medium intensity, developed high intensity, barren land	30	0.1	218	0.4