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Wild and Feral Equid Population Dynamics

Wild equid populations are shaped by births, deaths, emigration, and immigration, each of which is subject to a suite of biological and ecological inputs across space and time. How these inputs influence population dynamics varies between populations as well as among species. In our rapidly changing world, human actions also increasingly affect wildlife populations (Sanderson *et al.* 2002). Fragmented landscapes, hunting of predators, reintroduction of species, invasive species, competition with humans and their livestock for resources, direct killing, and climate change all can influence population dynamics (see chap. 12). Most wild equids occupy arid or semiarid steppe, grassland, and desert environments, but some feral populations also thrive in forests, montane, and coastal environments, and across hot and cold, xeric and mesic, conditions. The array of factors potentially influencing these populations is great, but some fundamental elements influencing birth, survival, and movement are common to all.

Food can be one of the most important natural factors limiting populations of large herbivores (Fowler 1987; Gaillard *et al.* 1998, 2000; Gaidet and Gaillard 2008). As such, some populations may exhibit density dependence and be limited because of their own impact on forage resources, or because population density itself influences age-specific natality, behavior, or survival (Choquenot 1991; Gaillard *et al.* 1998, 2000; Flux 2001; Linklater *et al.* 2004; Bonenfant *et al.* 2009). When such populations lack resources, body condition of individuals can diminish and disease and parasitism can increase, all with the cumulative effect of reducing fecundity and survival, and ultimately limiting population growth (Eberhardt 1977). Some populations may persist without exhibiting density dependence, changing through time without realized self-imposed resource limitation. Those populations may still be limited by predation or climate events (Ellis and Swift 1988; Georgiadis *et al.* 2003). Over time, any given population may move between exhibiting density dependence and apparent density independence as the influencing factors change. Regardless of the specific paradigm, both deterministic and stochastic mechanisms play important roles in shaping populations (Björnstad and Grenfell 2001).

Attempting to draw broad inferences across equid population states, processes, and inputs is a challenging task, but the wild and feral members of family Equidae are perhaps more similar than not in their equation of life on earth. Some species, notably African wild ass (*Equus af-*

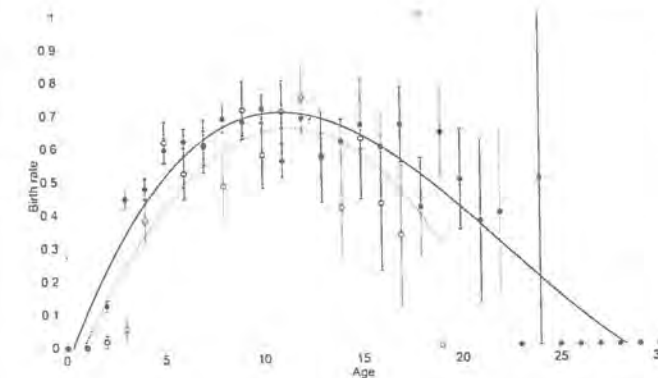


Fig. 6.1 Mean age-specific birth rates of horses $\pm$ standard error, as derived from *E. caballus* (feral) in the western United States (solid dots and solid trend line, $n = 1,013$ births, excluding females that received fertility control treatments) (Ransom *et al.* 2011; J. Ransom, unpublished data), and *E. f. przewalskii* (open dots and dashed trend line, $n = 217$ births, excluding females in the year of their introduction) (Great Gobi B Strictly Protected Area, Mongolia, unpublished data).

ricanus) and kiang (*E. kiang*), are vastly understudied, and considerable gaps persist in our knowledge of even their basic ecology. Other species, such as the feral horse (*E. caballus*), provide rich data sets that can inform us with in depth ecological perspectives. In this chapter, we have synthesized data from studies on equids across the globe toward understanding the common and diverging natural influences acting to shape their populations. The populations in these studies ranged on 6 continents across >91 degrees of latitude, from savannah to mountains and deserts to islands, and thus were influenced by a diversity of biotic and abiotic factors. We focus here on natality, survival, and population growth. We briefly discuss movement into and out of populations, but largely defer that topic to chapter 13. The influence of humans on these populations is a broad topic that can profoundly affect survival, and we must defer that topic to chapter 12.

Natality

All species of wild equid appear to follow the same general distribution of age-specific natality that is observed in horses, with primiparous births most typically occurring from females age 2–5 years, and peak birth rates occurring roughly for females age 6–17 (fig. 6.1). There is some evidence that when forage is abundant, female equids are more likely to give birth at an earlier age (Berger 1986; Saltz and Rubenstein 1995; Tatin *et al.* 2009). When forage and water becomes exhausted, age of primiparous birth can increase and birth rates for all females can decline quickly (Ginsberg 1989). The majority of feral asses (*E. asinus*) in Death Valley, USA, for example, were observed giving primiparous birth at age 24 years while persisting in an extremely harsh environment (Moehlman 1974). (Note that sexual ma-

turity is reached at 1.5 years; Grinder *et al.* 2006.) In the wild, female plains zebra (*E. quagga*) have been documented giving birth as old as age 18 (Klingel 1969), mountain zebra (*E. zebra*) at age >21 (Joubert 1974a), Przewalski's horses (*E. ferus przewalskii*) at age 20 (O. Ganbaatar, unpublished data), and feral horses as old as age 24 (fig. 6.1).

Horses and zebras typically give birth to one offspring annually, though extraordinarily rare cases of twins have been reported (Roelle *et al.* 2010; Vodička 2010). Feral asses have been observed giving birth to either one or two offspring (Grinder *et al.* 2006), as have Asiatic wild asses (*E. hemionus*) (Schook *et al.* 2013). The cases of twins born to Asiatic wild asses all resulted in early mortality of at least one sibling, and it is unknown how frequently twin births occur in the wild. Wild females of all asses are most typically observed with only one offspring of the year. The mean birth rate for equid females ≥ 2 years old across all species and studies we reviewed ranged from 0.20 in mountain zebras to 0.68 in feral asses, with a mean across species of 0.47 (95% confidence interval, or CI = 0.35–0.59) (table 6.1). Note that the lowest value from individual studies in this range arose from Przewalski's horses in the Gobi Desert following a catastrophic winter climate event (birth rate = 0.04) (Kaczensky *et al.* 2011), and the maximum value occurred in a small Asiatic wild ass (onager) population that started to increase rapidly six years after reintroduction (birth rate = 1.00) (Saltz and Rubenstein 1995). Despite these extremes, however, birth rates among wild equid species are remarkably similar when put in context of the pressures selecting for fitness.

Birth rates in wild populations reflect offspring born and observed, rather than pregnancy rate, which is presumably higher in most cases. Pregnancy rates

Table 6.1. Mean birth, survival, and population growth rates of wild and feral equids

Species	Populations	Mean Adult Birth Rate	Mean Foal Survival Rate	Mean Adult Survival Rate	Mean Population Growth Rate (λ)
<i>E. caballus</i> (feral) ¹	Tornquist Park, Argentina; Garden Station, Australia; Alberta, Canada; Sable Island, Canada; La Camargue, France; Namib Desert, Namibia; Kaimanawa Ranges, New Zealand; Peneda-Gerés, Portugal; Vodnyi Island, Russia; Galicia, Spain; Exmoor, UK; New Forest, UK; Snowdonia National Park, UK; Assateague Island, USA; Garfield Flat, USA; Granite Range, USA; Great Basin, USA; Jicarilla Wild Horse Territory, USA; Little Book Cliffs, USA; McCullough Peaks, USA; Montgomery Pass, USA; Pine Nut and Pah Rah, USA; Pryor Mountain, USA; Red Desert, USA; Salmon, USA; multiple locations across western USA	0.56 ± 0.001 (0.23–0.92)	0.84 ± 0.002 (0.09–0.97)	0.90 ± 0.001 (0.79–0.98)	1.18 ± 0.001 (0.84–1.39)
<i>E. f. przewalskii</i> ²	Xinjiang, China; Le Villaret, France; Great Gobi B, Mongolia; Hustai National Park, Mongolia	0.36 ± 0.011 (0.27–0.75)	0.61 ± 0.003 (0.59–0.83)	0.86 ± 0.003 (0.83–0.98)	1.13 ± 0.001 (1.12–1.18)
<i>E. asinus</i> (feral) ³	Dorisvale, Australia; Victoria River, Australia; Bander National Monument, USA; Death Valley, USA; Grand Canyon, USA; Mojave Desert, USA	0.68 ± 0.003 (0.41–0.89)	—	—	1.19 (—)
<i>E. africanus</i> ⁴	Denkelia Desert, Eritrea	0.30 ± 0.066 (0.00–0.71)	—	—	—
<i>E. hemionus</i> ⁵	Qatrouyeh National Park, Iran; Makhtesh Ramon, Israel; Great Gobi B, Mongolia; Badghyz Nature Reserve, Turkmenistan	0.48 ± 0.004 (0.15–0.76)	0.57 ± 0.001 (0.40–0.64)	0.86 (0.85–0.86)	1.04 ± 0.001 (0.95–1.15)
<i>E. kiang</i> ⁶	Tibetan Plateau	0.50 (—)	—	—	—
<i>E. zebra</i> ⁷	Ai-Ais / Fish River Canyon National Park, Namibia; BullsPort Guest Farm, Namibia; Gondwana Cañon Park, Namibia; NamibRand Nature Reserve, Namibia; Camdeboo National Park, South Africa; De Hoop Nature Reserve, South Africa; Karoo National Park, South Africa; Mountain Zebra National Park, South Africa	0.20 ± 0.002 (0.16–0.45)	0.98 ± 0.001 (0.87–0.98)	0.92 ± 0.001 (0.91–0.93)	1.13 ± 0.002 (0.85–1.23)
<i>E. grevyi</i> ⁸	Barsalinga, Kenya; Dvur Kralove Zoological Garden (translocated from Kenya); Laikipia, Kenya; Lewa, Kenya; Ngare Ndare, Kenya; Samburu Buffalo Springs Game Reserve, Kenya	0.64 (—)	0.57 ± 0.084 (0.27–0.90)	0.85 ± 0.002 (0.77–0.88)	1.02 —

Table 6.1. continued

Species	Populations	Mean Adult Birth Rate	Mean Foal Survival Rate	Mean Adult Survival Rate	Mean Population Growth Rate (λ)
<i>E. quagga</i> ⁹	Laikipia, Kenya; Athi-Kapiti Plains, Kenya; Serengeti, Tanzania; Ngorongoro, Tanzania; Hwange National Park, Zimbabwe; iMfolozi-Hluhluwe, South Africa; multiple private reserves, South Africa; Kruger National Park, South Africa; Boland Lanbou, South Africa; Elandsberg Private Reserve, South Africa	0.48 ± 0.056 (0.23–0.75)	0.67 ± 0.120 (0.13–0.96)	0.84 ± 0.025 (0.79–0.88)	0.98 ± 0.028 (0.92–1.01)

Sources:

¹Pellegrini 1971, Tyler 1972, Feist and McCullough 1975, Nelson 1978, Perkins *et al.* 1979, Boyd 1980, Wolfe 1980, Eberhardt *et al.* 1982, Salter and Hudson 1982, Seal and Plotka 1983, Keiper and Haupt 1984, Berger 1986, Simliff *et al.* 1986, Wolfe *et al.* 1989, Garrett and Taylor 1990, Berman 1991, Turner *et al.* 1992, Baker 1993, Monard *et al.* 1997, Greger and Romney 1999, Ashley 2000, Gomes and Oom 2000, Goodloe *et al.* 2000, Ashley and Holcombe 2001, Turner and Morrison 2001, Linklater *et al.* 2004, Greyling 2005, Grange *et al.* 2009, Scoroll and Lopez Cazorla 2010, Contasti *et al.* 2012, Dawson and Hone 2012, Ransom 2012, Spasskaya *et al.* 2012, Stanley and Shultz 2012, Lagos 2013.

²Chen *et al.* 2008, Tatin *et al.* 2009, Kaczensky *et al.* 2011, Usukhjargal and Bandi 2013.

³Moehlman 1974, Norment and Douglas 1977, Mogart 1978, White 1980, Ruffner and Carothers 1982, Johnson *et al.* 1987, Perryman and Muchlinski 1987, Choquenot 1990, 1991.

⁴P. Moehlman, unpublished data.

⁵Solomatin 1973, 1977, Wolfe 1979, Zhironov and Ilyinsky 1986, Saltz and Rubenstein 1995, Feh *et al.* 2001, Ziaee 2008, Nowzari 2011, Hemami and Momeni 2013, Lkhagvasuren *et al.* in review.

⁶Schaller 1998.

⁷Joubert 1971, Penzhorn 1985, Lloyd and Rasa 1989, Novellie *et al.* 1992, 1996, Smith *et al.* 2007, Gosling 2013, Eastern Cape Parks, unpublished data, H. Hrabar, unpublished data, South African National Parks, unpublished data.

⁸Dobroruka *et al.* 1987, Rubenstein 1989, 2010, Rowen 1992, Williams 1998.

⁹Klingel 1965, 1969, Petersen and Casebeer 1972, Spinage 1972, Smuts 1976a,b, Ohsawa 1982, Rubenstein 1989, Hack *et al.* 2002, Georgiadis *et al.* 2003, Grange *et al.* 2004, Barnier *et al.* 2012, Grange *et al.* 2012, 2015, H. Hrabar and G. Kerley, unpublished data.

Note: Table includes some semiwild populations in managed reserves. Mean rates from each source study were weighted by sample size (number of individuals sampled) and length of study (years) to generate the mean values shown for each species ± standard error. The range of individual study means is given in parentheses after the point estimate. Birth rate is total number of foals divided by all females at least 2 years of age, and survival rate for adults represents individuals ≥2 years of age. Foal survival represents individuals surviving from birth to age 1.

have not been rigorously measured across equid species in the wild, but the feral horses of Kaimanawa, New Zealand, exhibited pregnancy rates of 0.79–0.94, with an average birth rate observed at only 0.49 (Linklater *et al.* 2004). Similarly, feral horses in Idaho, USA, exhibited an average pregnancy rate (across all ages) of 0.68, with only 8% of 1- to 3-year-olds becoming pregnant, increasing to 93% of 10- to 12-year-olds becoming pregnant (Seal and Plotka 1983). Plains zebra pregnancy rates in the Serengeti were reported ranging from 0.69 in 3- to 5-year-olds to 0.88 in 13- to 16-year-olds (Grange *et al.* 2004), but birth rates in similar systems of east Africa were reported as only 0.26–0.51 (Klingel 1969; Georgiadis *et al.* 2003). It is possible that in many studies the reported birth rates may be negatively biased because offspring aborted, stillborn, or depredated immediately after birth were undetected by observers. Abortion is extraordinarily unlikely after

three months of gestation in horses, which implies that the environmental conditions early in pregnancy are perhaps most influential in the successful birth of a foal (Roberts 1986).

Interbirth interval (the time between subsequent offspring) among equids can vary depending on individual-level reproductive history and resource availability. Primiparous feral horses, for example, were less likely to foal in the year following their first foal, whereas multiparous females were more likely to foal if they had foaled the previous year (Roelle *et al.* 2010). The interbirth interval among plains zebra, on the other hand, appeared to be longer if the first foal was male (Barnier *et al.* 2012). Feral horses also demonstrated a protracted interbirth interval after producing a male foal under stressed resource conditions (Monard *et al.* 1997).

Both strong physiological and environmental inputs influence the rate and phenology of conception

and subsequent year births in most wild equid populations. Hormones associated with reproduction (such as estradiol, progesterone, and testosterone) fluctuate cyclically through time in both males and females (Kirkpatrick *et al.* 1977; Nuñez *et al.* 2011; Schook *et al.* 2013), reaching an annual apex of reproductive potential when enough sunlight and warm temperatures have stimulated the hormonal cascade (Ransom *et al.* 2013). This mechanism can help regulate birth cycles, and ultimately produces birth pulses that are often synchronized with forage availability. Estrus, birth rates, and birth phenology have been correlated with rainfall in some populations of zebras (Klingel 1969; Joubert 1974b; Williams 1998; Sinclair *et al.* 2000; Rubenstein 2010), feral horses (Siniff *et al.* 1986; Berman 1991; Scorolli and Lopez Cazorla 2010; Ransom *et al.* 2013), and Asiatic wild asses (Saltz *et al.* 2006). This synchrony with forage resources may increase female and neonate survival, especially because nutritional requirements of lactating females are elevated and higher-quality forage can result in increased body condition and nutritional support for neonates (Ginsberg 1989; National Research Council 2007). In a study of three temperate populations of feral horses where birth phenology was perturbed, estimated survival of foals decreased 1.4% for every 10 days after peak forage that parturition occurred (Ransom *et al.* 2013).

Environmental pressures can contribute greatly to birth phenology, and in some cases can truncate the birth season to a short, synchronized pulse. Predation, for example, has been posited to influence the timing of births under the premise that neonates are most vulnerable in their first hours or days of life, and as such predators can only harvest a finite number of young in a short period of time; consequently, if all young are born together, more should survive (Darling 1938; Sinclair *et al.* 2000). Parturition season for Asiatic wild asses in the Mongolian Gobi (where wolves prey on them), for example, typically begins mid-June and concludes around mid-July (P. Kaczensky, personal communication), and similarly the same species in Badkhyz State Reserve, Turkmenistan (13° latitude farther south), was reported to foal primarily between 14 April and 14 May, but some foals were recorded as early as late as 28 July (Wolfe 1979). In contrast, a Sri Lanka feral ass population located almost on the equator and with no predators present exhibited no birth seasonality, and offspring were born uniformly across every month of the year (Santiapillai *et al.* 1999). Predation pressure may not be the primary driver of length of birthing season, however; length of gestation, birth interval, and duration of resource availability can all be impor-

tant factors (Williams 1998). Wildebeest (*Connochaetes taurinus*) sympatric with Grevy's zebra (*E. grevyi*) in Kenya, for example, exhibited a birth season constrained to only two weeks, whereas the Grevy's zebra present in the same environmental conditions gave birth over the course of months (Williams 1998). In that system, rainfall was highly stochastic, and thus seasonal forage availability did not exhibit a pronounced peak.

Gestation period is similar among equid species, though environmental inputs can create plasticity (Howell and Rollins 1951). Average gestation length ranges from 327 to 357 days in horses (Howell and Rollins 1951; Card and Hillman 1993; Monfort *et al.* 1994), 321 to 404 days in asses (Grinder *et al.* 2006; Pagan *et al.* 2009; Schook *et al.* 2013), and 364 to 390 days in zebras (Grubb 1981; Penzhorn 1988; Churcher 1993). Gestation period in kiang is the least quantified, with reports ranging from 210 to 365 days (St-Louis and Côté 2009). Given the nearly yearlong gestation across all equid species, we could expect estrus, reproductive behavior, and conception to peak between the spring equinox and the summer solstice, waning thereafter with subsequent parturition occurring roughly at the same time the following year. Where such empirical data were present in the literature, this pattern was evident across equid species, though it is more variable in populations near the equator (fig. 6.2).

While body condition, resource availability, and biological inputs all contribute to conception and birth success, these factors may also influence sex ratio of young born into the population. Female feral horses in poor body condition at the time of conception have been observed producing more female foals (Cameron *et al.* 1999), for example, aligning with the much-debated Trivers-Willard hypothesis, which posits that when populations are experiencing more stress (and thus individuals have decreased body condition), more female offspring will be produced because they can increase fitness more quickly than inputs of male offspring (Trivers and Willard 1973). Sex ratio of foals across all equid species and populations we reviewed is of course quite variable, precisely because of these environmental inputs, but on average we found that the ratio of males to females born did not differ from parity (1.1 males to 1 female; 95% CI = 0.93–1.29:1). The extreme situations were 2.2 males to 1 female in a population of mountain zebra ($n = 16$ foals; H. Hrabar, unpublished data), and 2.2 males to 1 female in an Asiatic wild ass population that was experiencing a high growth rate ($n = 53$ foals; Saltz and Rubenstein 1995). In the latter case, it is interesting that while more males were being produced in a density-independent environment

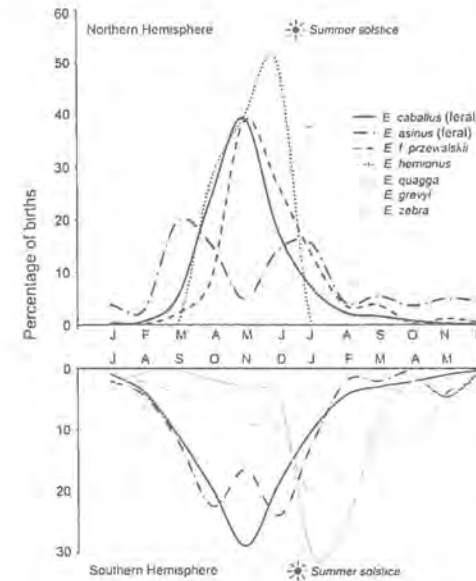


Fig 6.2 Percentage of births by month across equid species. Data are smoothed and shown as the mean across populations. Data for *E. caballus* derived from Tyler 1972, Boyd 1980, Keiper and Houpt 1984, Berger 1986, Berman 1991, Lucas *et al.* 1991, Ashley 2000, Gomes and Oom 2000, Linklater *et al.* 2004, Greyling 2005, Nuñez *et al.* 2010, Scorolli and Lopez Cazorla 2010, Lagos 2013, Ransom *et al.* 2013, and N. Spasskaya, unpublished data; data for *E. asinus* derived from Moehman 1974, McCool *et al.* 1981, Ruffner and Carothers 1982, and Santiapillai *et al.* 1999; data for *E. f. przewalskii* derived from Chen *et al.* 2008, Prague Zoo 2010 (wild and semiwild populations only), and Usukhjargal and Bandi 2013; data for *E. hemionus* derived from Wolfe 1979 and O. Ganbaatar, unpublished data; data for *E. quagga* derived from Klingel 1965, Smuts 1976b, and Sinclair *et al.* 2000, data for *E. grevyi* derived from Dobroruka *et al.* 1987 and Rowen 1992, data for *E. zebra* derived from Joubert 1974b, Penzhorn 1985, Westlin-van Aarde *et al.* 1988, and H. Hrabar, unpublished data.

(in concurrence with Cameron and Linklater 2007), the investigators noted that more female foals were being produced by primiparous mothers of age 2 or 3 years as compared to multiparous mothers of age 4 or 5 years. This may reflect an evolutionary disparity in effective maternal investment, but that hypothesis was not specifically tested. The opposite extreme was observed in a resource-stressed population of plains zebra where the sex ratio was 0.27 males to 1 female ($n = 19$ foals; Hrabar and Kerley 2013) and a feral horse population where the sex ratio of 0.47 males to 1 female was observed ($n = 25$ foals; Stanley and Shultz 2012).

Survival

Most feral horses, feral asses, and some Przewalski's horses and mountain zebra live in environments without significant predation pressure and exhibit relatively high survival rates across all age classes. Most other wild equid populations are subject to predation from a variety of large predators, and thus experience locally reduced survival rates. Despite this dichotomy of population paradigms, age-specific survival is surprisingly comparable among equid species, with some elevated mortality in foals, relative security in the adult cohort, and then a gradual decrease as senescence prevails (fig. 6.3). The resulting age structure of wild populations is also relatively consistent among species and populations, with foals typically comprising 8–15% of a population, juveniles 13–28% of a population, and adults 71–78% of a population (Berman 1991; Tatin *et al.* 2003; Grange *et al.* 2004; Smith *et al.* 2007). Equids are long-lived animals, and where individuals were followed from birth, known ages for individual wild Przewalski's horses exceeded 25 years old (Prague Zoo 2010) and for feral horses exceeded 29 years old (Ransom 2012). Equids generally live longer in captivity owing to more controlled environmental conditions and applied veterinary care; as such, captive Asiatic wild asses >27 years old have been reported (Volf 2010), as have Przewalski's horses >30 years old (Ballou 1994). Mortalities in wild equid populations arise from a variety of causes. Deaths of adult Przewalski's horses ($n = 145$) at Hustai National Park, Mongolia, for example, were attributed to blood parasites (2.1%), endoparasites (1.4%), disease (7.6%), stillbirth (9.7%), injury (12.4%), predation (22.1%), starvation (31.1%), and other/unknown reasons (13.8%) (Usukhjargal and Bandi 2013). Nine percent of foal deaths (25 of 278 foals) in the same study were attributed to infanticide by stallions (box 6.1).

Annual foal survival rates reported across the studies we reviewed averaged 0.71 (95% CI = 0.53–0.88), and adult survival rates averaged 0.88 (95% CI = 0.85–0.90) (table 6.1). Much of the variation in annual survival rates of both foals and adults by population may be attributed to localized predation. A large number of predators have been documented killing both young and adult equids, including African lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), and spotted hyena (*Crocuta crocuta*) for feral horses, zebras, and asses in Africa; wolf (*Canis lupus*) and snow leopard (*Uncia uncia*) for Asiatic asses, Przewalski's horses, and kiang in the Middle East and Asia; wolf and brown bear (*Ursus arctos*) for feral horses in Europe; and puma

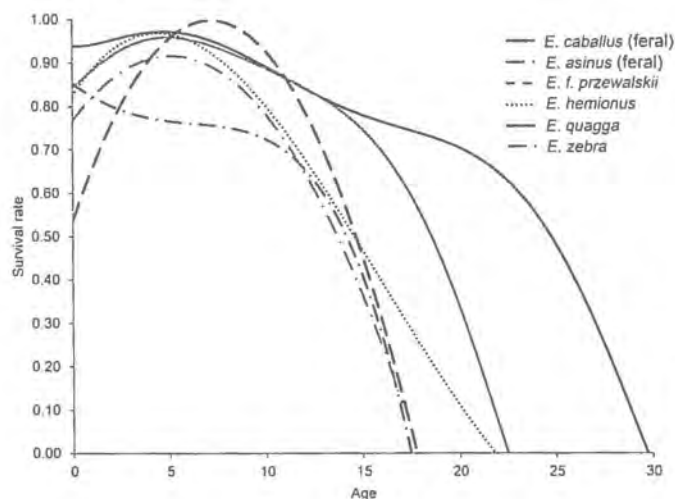


Fig. 6.3 Trend in age-specific survival rates for equid species. Data for *E. caballus* derived from Ransom 2012; data for *E. asinus* derived from McCool *et al.* 1981; data for *E. f. przewalskii* derived from Hustai National Park, unpublished data; data for *E. hemionus* derived from Saltz and Rubenstein 1995 and Lkhagvasuren *et al.* in review; data for *E. quagga* derived from Spinage 1972; data for *E. zebra* derived from Joubert 1974a

(*Puma concolor*) and jaguar (*P. onca*) for feral horses and feral asses in the Americas. In one feral horse population in the western United States, foal survival was reported to be only 27%, and 82% of foal carcasses found showed evidence of being killed by puma (Turner *et al.* 1992); however, most feral horse populations coexist with pumas and experience limited depredation. In the Gobi Desert of Mongolia, 23% of wolf scats analyzed contained remains of Asiatic ass (Feh *et al.* 2001), but it is unknown how many of those samples arose from predation as opposed to scavenging.

Analysis of predator diets has provided some evidence of selection for equids, with a wide range of selection to nonselection across species and seasons. Wolves in northwest Spain clearly selected for feral horses (Ivlev index = 0.99–1.00) (Lagos 2013), but a similarly pack-organized canine, African wild dog (*Lycaon pictus*), specifically avoided hunting zebra even when they were relatively abundant (Hayward *et al.* 2006). In Lewa, Kenya, African lions strongly selected Grevy's zebra over plains zebra, even though plains zebra outnumbered Grevy's zebra four to one (Rubenstein 2010). In the Serengeti, Tanzania, 90% of all spotted hyena kills were adult zebra when the available ungulate assemblage was quite diverse (Kruuk 1972). In systems where feral horses and predators most typically coexist, a high percentage of all mortality is attributed to a sole predator as opposed to disease, accident, or other natural causes. Wolves in Peneda-Gerês National Park, Portugal, for example, have been responsible for 89% of horse mortalities, and in nearby Galicia, Spain, that figure rises to 96% (Gomes and Oom 2000; Lagos 2013).

In systems with multiple predators or sympatric prey species, the percentage of equid mortality attributed to depredation can be somewhat ameliorated, such as plains zebras in the Serengeti, Tanzania, where 59–74% of all mortality was attributed to African lion and spotted hyena (Schaller 1972), or Przewalski's horses in Hustai National Park, where 13–50% of horse mortalities were attributed to wolves (Van Duyn *et al.* 2009).

At a finer scale, predator species may also select for one sex of prey over the other; thus they may affect prey populations differently at long timescales. Spotted hyenas at Ngorongoro, Tanzania, killed 2.25 female plains zebra for every one male, but lions at Serengeti, Tanzania, killed only 0.83 female plains zebra for every one male (Kruuk 1972). Longitudinal studies indicate that shifts in diet can also occur over time, as in the Serengeti, Tanzania, where 19–20% of spotted hyena diet was composed of plains zebra before the 1970s, but after that time it diminished to <9% (Kruuk 1972). The zebra population remained relatively stable over that time period (Hack *et al.* 2002), but changes in other prey populations or competing predator populations could have contributed to the apparent dietary shift.

Some behavioral traits may also influence survival. Group formation in ungulates has been posited to be a function of open environments where foraging can be optimized because groups of animals are more vigilant for predators than isolated individuals can be (Kie 1999). Equids form groups of various sizes and composition, which may influence predation risk (see chap. 2). Schaller (1972) reported that lions were 13% more successful when plains zebras were alone rather than

BOX 6.1 INFANTICIDE AMONG EQUIDS

Infanticide is not common in equids but has been reported in both captive and wild populations. This unique source of mortality arises when a stallion intentionally kills a foal, an action hypothesized to be a fitness-driven evolutionary behavior (Hrdy 1979). The concept posits that if a novel stallion kills an unrelated foal, then the foal's mother may more quickly return to estrus and be fertilized by the assailant male, thus increasing his fitness faster through reduction of interbirth interval. This concept has been discussed most broadly in the classic case of the African lion (Packer and Pusey 1982), but it has drawn the attention of equine ethologists because of their polyandrous mating systems.

Infanticide among the equids appears to be most prevalent in the harem-forming species and has been reported most frequently in captive conditions where artificial social constructs may elevate frequency (Pluháček *et al.* 2006). In the wild, infanticide has been documented at the highest rates in Przewalski's horses, where 9% (25 of 278 foals born 1993–2011) of all foal mortality in Hustai National Park, Mongolia, was attributed to this phenomenon (Usukhjargal and Bandi 2013). It was also reported in the same species at Kalamaili Ungulate Protected Area, China, where 83.3% of all foal mortalities (7 mortalities out of 24 births) was attributed to infanticide in the 5-year period following reintroduction (Chen *et al.* 2008). Nearly half of those deaths occurred in the first year, lending support to the proximate social stresses presented when novel stallions suddenly become available to social groups.

Infanticide was reported in domestic horses (Duncan 1982) and New Forest ponies (Tyler 1972), and attempted infanticide among feral horses has been documented across populations (Tyler 1972; Berger 1986; Gray 2009). When more than one adult male has been present in a band of feral horses, extraordinary maternal protection has also been reported, potentially minimizing the incidents of infanticide (Cameron *et al.* 2003). While the sample size is limited, there is some evidence that intruding stallions may selectively target male foals (all cases reported by Duncan 1982, with additional cases reported by Berger 1986), which could reflect the potential for reducing future competition from unrelated males, but that hypothesis has never been explicitly tested. Induced abortion has also been documented when

novel stallions forcibly copulate with a pregnant female. At the Granite Range, USA, such feticide was reported for 78% of forced copulations by novel feral horse males (Berger 1986).

Harem-forming zebra have also demonstrated infanticide, with three cases being reported in wild mountain zebra (Penzhorn 1975), and multiple cases reported in captive plains zebra (of which several individuals originated from wild populations) (Pluháček *et al.* 2006). In a captive mountain zebra enclosure in Namibia, Joubert (1971) reported an attempted infanticide that failed when the female actively defended her foal, but the stallion then proceeded to kill two sympatric antelope instead. This event illustrates the uncertainties underlying our understanding of mechanisms and motivations related to infanticide (Pluháček *et al.* 2006). It is possible that some cases of infanticide are motivated by a more immediate need: survival. At Hluhluwe Reserve, South Africa, a severely injured plains zebra foal was observed in the center of a band vocalizing continuously and loudly after escaping from a predator attack. All adult members of the band were expressing elevated vigilance behaviors and nervousness, and the band stallion eventually approached and killed the foal with strikes to the head. While the genetic relationship of the stallion and foal was unknown, the silencing of the foal instantly reduced the exposure of the band to local predators (J. Ransom, unpublished data). Infanticide has not been reported for Grevy's zebra, but the territorial organization of this species can result in females not remaining with specific males long enough for the males to benefit from such behavior.



Photo by J. Ransom

in a group. Unlike most equids, where foals closely accompany their dams most or all of the time, Grevy's zebra sometimes leave their foals in aggregated juvenile groups or "kindergartens" (Williams 1998). The source of this behavior may arise from energetic constraints of young, but ultimately it may also place foals at risk of depredation, especially during nocturnal aggregations (Klingel 1974).

Because most equids inhabit arid environments, considerable interannual variance in precipitation and related productivity may also influence survival (Archer *et al.* 1999). One model simulation of zebra populations suggested that survival decreases more rapidly during dry seasons than reproduction increases during wet seasons, which would constrain population growth over time (Georgiadis *et al.* 2003). In contrast, neither wet season nor dry season rainfall at Kruger National Park, South Africa, influenced plains zebra survival in a longitudinal empirical study, though it did affect other ungulates in the system (Owen-Smith *et al.* 2005). Across ungulate species, it appears that interannual variance in precipitation influences juvenile survival more profoundly than it does adult survival (Gaillard *et al.* 1998, 2000). In feral horses, each centimeter of spring rainfall increased foal survival by 1.5%, did not measurably influence survival for animals up to age 19, and then significantly increased survival rates for animals ≥ 20 years old (Ransom 2012).

Population Growth

Quantifying population dynamics is generally not as simple as adding births and subtracting deaths. Understanding population growth and decline is further complicated by movement into and out of populations, and by catastrophic stochastic events that change rates both instantaneously and longitudinally. In addition to that volume of uncertainty, the size of most wild equid populations is not absolutely known or even estimated robustly (Moehlman 2002). We have reviewed studies where some measure of population growth was reported or could be reasonably derived. To discuss this more clearly, we refer to the theta-logistic model because it accommodates the nonlinear density dependence more indicative of equid populations (Gilpin and Ayala 1973):

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right)^\theta$$

In this model, r is the intrinsic rate of increase, N is the population size, K is the carrying capacity, t is time, and θ is the nonlinear modifying parameter for the ratio of

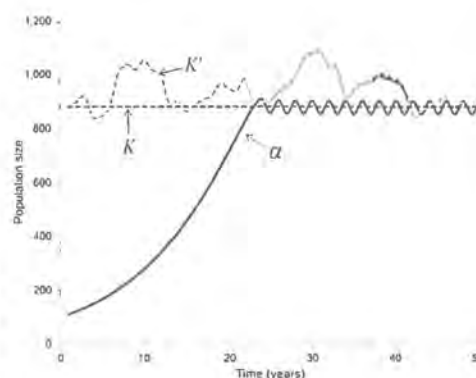


Fig. 6.4 An example of theta-logistic population growth for a simulated equid population over time (black line), where growth rate (r) is fixed and reaches the fixed carrying capacity of K . The same population is simulated with a randomized carrying capacity (K') in gray, illustrating the stochastic effects of resource availability on a single parameter. Point a represents the inflection point where population growth begins to moderate as the population approaches K .

$N:K$. Conceptually, when $\theta < 1$, r decreases rapidly with population size; likewise, the population will quickly approach K when $\theta > 1$. For equids, this is a steeper curve than the classic logistic sigmoid curve, and the inflection point is much closer to K (fig. 6.4). In this example, a simplified deterministic population trajectory is used to illustrate growth of hypothetical equid population. To add a degree of reality, K is randomized (K') to illustrate how carrying capacity can vary annually with the amount and quality of resources available over time, which in turn can influence the maximum number of individuals that could survive at a given time (fig. 6.4, gray lines). Conceptually, when rapid growth is reported for a population, the theta-logistic model suggests that the population is most likely below a (the inflection point) on the sigmoid curve, and when slow growth is observed, the population might be closer to K at that point in time. Many studies report an instantaneous rate of increase (λ) rather than r . This simply reflects the growth rate of a population from one year to the next as if it had instantly occurred, or $\lambda_t = (N_t / N_{t-1})$ where t represents one year. For synthesis and discussion purposes, we have converted r values from individual studies to λ , using $\lambda = e^r$.

Mean annual population growth (λ) in the studies we reviewed averaged 1.12 (95% CI = 1.04–1.19) across all species (table 6.1). While the reported range of growth rates was similar between species, the average

growth rates for Asiatic wild ass, Grevy's zebra, and plains zebra were notably lower than the other species (1.04, 1.02, and 0.98, respectively). It is unknown whether this finding simply reflects the paucity of data for these species, is an artifact of their different life history strategies, or is indicative of a more complex set of factors. Robust population dynamics metrics for African wild ass and kiang are completely missing from the literature, illustrating critical science needs for better understanding equid ecology.

Some variability in population growth rates over time and between studies and species may be explained by the relationship between abundance and resources. Equids are generally well equipped to persist near K because their longevity and high survival rates, low recruitment rates, and low sensitivity to moderate environmental stressors result in relatively durable populations, barring catastrophic mortality events (Saltz 2002). When mass mortality events occur, equids are quite slow to recover because of their inherently low recruitment rates, but at the longitudinal scale, this is when equids should be most productive. For example, a small, reintroduced Asiatic wild ass (onager) population exhibited its maximum growth rate as abundance expanded to the resources available (Saltz and Rubenstein 1995). In feral horses, heavily managed populations that have persisted near K but then experience a large culling event can be suddenly reduced far below a , prompting a compensatory response in increased growth rate (Choquenot 1990; National Research Council 2013).

Focused predation can impart nonrandom influence on population growth, such as at Pryor Mountain, USA, where predation from specific pumas was increasingly limiting the horse population from 1993 to 2004 to a nadir of $\lambda = 0.97$ before the pumas were killed and the predation pressure was dramatically released (Ransom 2012). In a plains zebra population in South Africa, models of population growth including lion predation were far more supported than models of climate factors, though population growth of only one of the two populations was affected by number of lions present (Grange *et al.* 2012). While food, water, and predation have been widely investigated as agents of population constraint, behavior has also been posited to limit equid populations by reduced fecundity arising from social stress (Linklater 2000; Tatin *et al.* 2009).

Perhaps the most unpredictable natural influence on population growth of equids also carries the greatest magnitude of effect: catastrophic climate events such as extreme drought and storms. Such events can have lasting influence on population dynamics and in some

cases can threaten extirpation of populations. The dzud winter (extreme cold with heavy snow) of 2009/2010 in the Mongolian Gobi, for example, suddenly reduced the Przewalski's horse population by 60% in a single season (Kaczensky *et al.* 2011). The population effect from direct mortality was compounded by a severe reduction in per capita births the following year, with only one female foaling. Though not well quantified, the extirpation of Asiatic wild asses from Kazakhstan at the end of the nineteenth century was documented following a similar dzud winter, though hunting by humans and competition with their livestock certainly contributed to the decline (Zhirnov and Ilyinsky 1986). Winter mass mortalities of feral horses in the American West have been documented with a 51% decline in a single winter at Pryor Mountain (Garrott and Taylor 1990) and 12% in a winter at the Granite Range (Berger 1983). The latter study indicated that severe snowstorm mortality might be more common than assumed and also referenced an earlier unpublished event in the Granite Range when 300 horses died (roughly 50% of the population).

Despite the extraordinary capacity of equids to persist in harsh arid environments, drought can still promulgate catastrophe. One severe mass mortality event related to drought was reported for plains zebra at the Tuli Game Reserve in southern Africa in 1983, where 199 carcasses and only 58 live zebra were detected following two years of drought (Walker *et al.* 1987). Hundreds of mountain zebra were reported dead in the Namibian Khomas Hochland during the 1968/1969 drought, with mortalities attributed to starvation, entrapment in mud at waterholes, and behavioral disorientation leading to increased human depredation (Joubert 1971). Large-scale drought-related mortalities are relatively common in the Australian outback, where tens of thousands of feral horses perish during extended drought. Similar events are generally precluded in the United States only by artificial water supplementation.

Severe thunderstorms have also had population-level effects on small equid populations. For example, a thunderstorm overtook Tornquist Provincial Park in Argentina, killing 193 feral horses in 48 hours (28% of the population) (Scorolli *et al.* 2006). Likewise, electrical storms at the high-altitude area of Pryor Mountain have produced fatal lightning strikes to individuals and entire feral horse bands, with an event in 1999 killing 4% of the population with a single lightning strike (US Bureau of Land Management, unpublished data).

Little has been quantified regarding movement of individuals into and out of equid populations in the

context of population growth rate. But one only need consider the migrant case of the plains zebra to understand the ramifications of how migration can quickly influence access to resources and changes in body condition that may influence birth rates, or how such migrations attract predators that might influence survival rates (Naidoo *et al.* 2014). Localized movements of plains zebra in Kruger National Park, South Africa, required travel of 10–15 km every 1–2 days during the dry season for individuals to drink, thus reducing time available for foraging and resting (Cain *et al.* 2012). Feral horses in central Australia also traveled up to 15 km during drought in order to access water, and one population declined 51% in density during a severe drought; it is unknown how many of those animals died as opposed to emigrated from the area (Berman 1991). In a similar xeric environment, feral asses of Death Valley became more prevalent within 1.6 km of a water source in summer (Moehlman 1974). Anthropogenic disturbance at water holes has been implicated in movement of Grevy's zebra, with the energetic costs arising from long-distance movement to and from water being reflected in reduced foal survival (Williams 1998). Whether any of these traveling individuals truly moved from one population to another, affecting population demography, is unknown, but the catalysts for such movement clearly provide an opportunity for immigration and emigration, which ultimately can influence both population dynamics and genetic flow.

Conclusion

The wild and feral equid populations of the world share many common features, and they function similarly for a variety of reasons. Equids can be quite long-lived ungulates and demonstrate relatively low fecundity, meaning that, in the absence of extreme stressors, their populations should be rather stable over time. Unfortunately, this is seldom realized in a changing world where anthropogenic influence permeates nearly all populations (see chap. 12) and climate events can impart severe catastrophes. Recovering from such population decimations requires long timescales for equids. Ultimately, most wild equids persist in a state where extensive conservation measures are needed to prevent extirpation and most feral equids persist at the other end of the curve, where extensive management is necessary to mitigate resource damage.

We aimed in this synthesis to gain a better understanding of equid ecology and what naturally shapes their populations, but such findings are not function-

ally separate from the effects that humans have on these populations. Direct killing, encroachment, and resource competition remain the largest threats to wild equids and profoundly influence the dynamics of most populations. The scale of human impacts thus confounds attempts to understand the natural influences on these species. What we can conclude, however, is that precipitation and phenological rhythms can strongly influence births, whereas survival is more strongly influenced by predation and mass catastrophe. Equids also exhibit complex social behavior that may drive population dynamics in ways we simply have not quantified or fully understand (see chap. 3). Such uncertainties in both the changing environment and our shortfalls in understanding the depth of equid societies demand forward thinking conservation and careful management for a group of species that nearly all persist on the world's threatened and endangered list.

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