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Effects of mountain lion predation on reducing feral horse population growth rates: panacea or pipedream?

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A goal of applied ecology is to evaluate how demographic rates contribute to population growth and how demography might be manipulated to achieve management objectives. In western North America, many feral horse (*Equus caballus*) populations occupying public lands are protected by federal law and managed for site-specific numerical targets. However, feral horses can exhibit population growth rates exceeding 20% per yr, which can lead to overpopulation, and therefore conflict with other permitted land uses. In response, some stakeholder groups have advocated for natural solutions to the problem of rapid growth and overabundance. Mountain lion (*Puma concolor*) predation has been hypothesized to have suppressive effects on horse population growth rates under some conditions. Here, we evaluated the degree to which this phenomenon might reduce feral horse growth rates using elasticity analysis, scenario analysis with simulations, and an empirical state-space model for a horse population in southeastern Nevada subject to chronic predation. Age-specific elasticities revealed that annual population growth rates (λ) were more sensitive to perturbations in foal and yearling survival rates than for older age-classes. This finding, in conjunction with empirical measures indicating that foals comprised approximately 60% of horses killed by mountain lions, suggests that predation may have greater potential to reduce horse population growth rates than previously recognized. Scenario analysis predicted that horse populations could decrease to target levels within 10 years if predation reduced: (1) annual foal survival by 80% each year, or (2) annual survival rates of foals, yearlings, and 2-year olds by >60%. The state-space model indicated that the heavily predated Nevada horse population experienced positive population growth during 2022 and 2023 ($\lambda = 1.07$, both years). Using information on known predation-caused mortalities from 2020–2021, our model predicted that population growth rate in the absence of predation ('predicted λ ') would have been approximately twice as high (predicted $\lambda_{2020} = 1.14$; predicted $\lambda_{2021} = 1.14$ in 2021). Taken together, our results suggest that predation is unlikely to singularly induce stable or negative population growth of feral horses. That said, our findings suggest two aspects of predation that may benefit resource managers. First, chronic predation may reduce λ , thereby increasing the time required for populations to either recover from declines, or exceed management objectives; and second, predation may be most effective in achieving management objectives for horse populations when combined with other interventions, such as removals or fertility control treatments.

KEYWORDS

elasticity analysis, *Equus caballus*, population growth rate, puma, simulation, state-space model, wild horse, wildlife management

Introduction

A major focus of applied ecology is evaluating how demographic rates, such as fertility and survival, contribute to population growth; and consequently, how those rates might be manipulated to achieve management goals. For long-lived, iteroparous mammals, theory from stage-based population models suggests that adult female survival is the key parameter affecting the annual population growth rate (hereafter λ , or simply *growth rates*; Gaillard et al., 1998; Morris and Doak, 2002). In contrast, juvenile survival typically demonstrates high interannual variability, and therefore makes smaller contributions to λ as compared to adult survival (Gaillard et al., 1998; Ruprecht et al., 2024). When adult survival is high and constant, populations can maintain positive growth even while experiencing low juvenile survival (Gaillard et al., 1998). However, variation in juvenile survival can also make meaningful contributions to reductions in population growth (Grange et al., 2004).

Domesticated animals and their descendants living in a free-ranging state in wildland settings independent of human support are considered feral (Gering et al., 2019). Despite multiple generations in the wild, feral species retain traits associated with, and induced by, domestication (Neaux et al., 2020), such that becoming feral does not return these animals to their wild phenotype (Sanchez-Villagra, 2022). Traits that emerge through selective breeding include tameness, early sexual maturation, and high reproductive output; conversely, traits that can be lost through this process include wariness/vigilance, reaction times, and physiological feedbacks to environmental stressors due to protection and care afforded by humans (Driscoll et al., 2009; Sanchez-Villagra, 2022). Feral species often express high fertility acquired through selective breeding (Grange et al., 2009), which can promote growth rates that are exceptional relative to their wild progenitors (Grange et al., 2009; Ransom et al., 2016).

In western North America, feral horse (*Equus caballus*) populations are distributed discontinuously across Federal, Tribal, and State lands (Schoenecker et al., 2021). In the United States, many herds occupying Bureau of Land Management (BLM) Herd Management Areas or U.S. Forest Service (USFS) Wild Horse Territories are designated as “Wild” horses and protected by the Wild and Free-roaming Horses and Burros Act (hereafter, the ‘Act’; Public Law 92-195, 1971). Each herd unit is managed for a given population range, termed the “Appropriate Management Level” (AML), and defined as the number of horses or burros (*Equus asinus*) that can be supported alongside other permitted land uses in a thriving ecological balance (NRC, 2013). Because monitoring population size is key to maintaining AML, in the decades since the passage of the Act, much of the research on feral horses (hereafter, horse) has focused on estimating demographic rates and determining how those rates contribute to population growth (e.g., Wolfe, 1980; Garrott et al., 1991; Roelle et al., 2010; Folt et al., 2023). Similar to many other large mammal species, survival rates in horse populations are high and consistent for adult females (Garrott and Taylor, 1990; Schoenecker et al., 2023), but variable for juveniles (Schoenecker et al., 2023). These life history characteristics can lead to positive growth rates that commonly

reach or exceed 20% per year (Wolfe, 1986; Garrott et al., 1991, NRC, 2013, Ransom et al., 2016).

Horses are gregarious with a female defense polygynous social system, in which a dominant male defends one or more females and their offspring in a social group (King and Schoenecker, 2025). A population (or herd) is comprised of many polygynous groups, plus bachelor males that have either lost, or not yet acquired, females. They display a capital breeding strategy with an 11-month gestation period, producing 1 foal per year (Keiper and Houpt, 1984), starting as early as age two (Wolfe et al., 1989), and can live in excess of 20 years (Wolfe, 1980, Garrott et al., 1991; Ransom et al., 2016; Schoenecker et al., 2023). In western North America, mares give birth from March to August each year (Ransom et al., 2016). The cecal digestive system of horses affords them a wide dietary niche compared to more specialized ruminants (Van Soest, 1994). This physiological trait helps facilitate adult survival rates between 93% and 99% in highly variable environmental conditions (Garrott and Taylor, 1990).

Feral horses retain several traits derived from domestication (Neaux et al., 2020), including high fertility and foaling rates (Grange et al., 2009; Grant et al., 2021). These qualities allow horse populations to rapidly exceed AML, thereby resulting in management interventions that attempt to reduce one or more vital rates driving growth (BLM, 2010). The two prevailing population control techniques are contraception (e.g., Bechert et al., 2022), which attempts to reduce overall fertility and subsequent birth rates; and large-scale round-ups, called “gathers” (BLM, 2010), which remove sexually mature animals from target populations, thereby mimicking a reduction of adult survival rates. However, horses are valued for cultural and aesthetic reasons, and so management interventions used to curtail growth and hold populations at or near AML have been scrutinized and criticized by the public (Hennig et al., 2023). Alone or in conjunction, gathers and certain forms of contraception have proven controversial, and often inadequate to stem long-term growth rates at the levels applied. Because of this, stakeholder groups have looked for alternative mechanisms to reduce population growth that fall within the Act and are deemed more natural — and therefore potentially more acceptable — to broad constituencies.

One possible solution proffered by various stakeholders is predation (e.g., Phillips, 2018). Most equid populations are subject to some degree of predation (Boyce and McLoughlin, 2021). Perhaps the most widely recognized example of predator-equid relationships is lion (*Panthera leo*) predation on plains zebras (*Equus burchelli*) in east Africa. Grange et al. (2004) argued that zebra population growth was limited by foal survival, but that predation was inadequate to explain observed mortality rates and speculated that other factors were interacting with predation to limit zebra populations. In central Asia, Van Duyne et al. (2009) documented wolf (*Canis lupus*) predation on reintroduced Przewalski's horses (*Equus przewalskii*). The authors found that predation on this small population was inversely correlated with the abundance of red deer (*Cervus elaphus*), the preferred prey of wolves in that system. In southeastern Australia, Watts et al. (2020) found evidence that dingos (*Canis familiaris dingo*) consumed feral horses, but based on scat analyses, it was unclear whether this was the result of predation or scavenging.

Although predation on equids is well documented, previous research involved species that were undomesticated (Grange et al., 2004), naïve (Van Duyne et al., 2009), or took place in ecosystems in which horses were an incidental part of the predator's diet (Watts et al., 2020). In the tropical and temperate latitudes of the western hemisphere, mountain lions (*Puma concolor*) are the most widely distributed and abundant predator of ungulates (Pierce and Bleich, 2003). In western North America, they also exhibit the most habitat overlap with horses relative to other large-bodied carnivores such as wolves or black bears (*Ursus americanus*). Mountain lions exhibit a stalk and ambush hunting strategy, often using steep, rugged terrain to capture prey up to 5 times their own body mass (Pierce and Bleich, 2003). Mule deer (*Odocoileus hemionus*) are their most commonly reported prey (Ackerman et al., 1984; Pierce and Bleich, 2003; Stoner et al., 2018), which has led to their characterization as deer specialists (Berger and Wehausen, 1991). However, in mixed-prey communities they have been documented hunting a wide variety of ungulates, including elk (*Cervus canadensis*; Hornocker, 1970), moose (*Alces alces*; Ross and Jalkotzy, 1996; Knopff et al., 2010), pronghorn (*Antilocapra americana*; Ockenfels, 1994), bighorn sheep (*Ovis canadensis*; Sawyer and Lindzey, 2002), feral pigs (*Sus scrofa*; Maehr et al., 1990), and free-ranging cattle (*Bos taurus*; Cunningham et al., 1999). Collectively, these findings suggest a high degree of plasticity in mountain lion prey use based on local availability.

Investigations into the effects of mountain lion predation on ungulate populations have shown mixed results (Ballard et al., 2001; Hurley et al., 2011). Studies conducted in the western United States have documented reductions in adult survival rates on several mountain lion prey species, including elk (Proffitt et al., 2020), bighorn sheep (Logan and Sweanor, 2001; Sawyer and Lindzey, 2002), and mule deer (*Odocoileus hemionus*; Robinson et al., 2002). Mountain lions have also been implicated in declines of small populations of mountain caribou (*Rangifer tarandus caribou*) at the southern end of their distribution (Kinley and Apps, 2001; Wittmer et al., 2005). There is a small but growing literature demonstrating that mountain lions can be a pervasive source of mortality in some horse populations (Turner et al., 1992; Andreasen

et al., 2021; Iacono et al., 2024). Furthermore, some investigators have hypothesized that predation can have suppressive effects on horse population growth rates under certain circumstances (Turner et al., 1992; Greger and Romney, 1999; Roelle et al., 2010). However, among larger-bodied prey species (> ~ 150 kg), including horses, mountain lion predation on adults is rare; instead, juveniles and to a lesser extent, yearlings, are more frequently selected as prey (Ross and Jalkotzy, 1996; Knopff et al., 2010; Andreasen et al., 2021). Because mountain lions are limited to this narrow subset of the ungulate population age structure, it raises questions of whether predation could effectively reduce growth rates of horses, and if so, what frequency would be sufficient to alter population trajectories (NRC, 2013).

Despite the intuitive appeal of predation as a panacea to potentially control horse growth rates, this simple notion neglects a large body of research on mammalian predator-prey relationships suggesting that the ability of predators to limit or regulate prey populations is temporary, context-dependent, and subject to numerous local contingencies (Ballard et al., 2001; Hurley et al., 2011; Clark and Hebblewhite, 2021). Nevertheless, given extensive habitat overlap between horses and mountain lions, growing observations of predation on juvenile horses (< 1 yr; Figure 1), and legal, logistic, and financial constraints on management interventions, we sought to evaluate whether predation could meaningfully reduce horse population growth rates. We used a combination of simulation modeling and empirical analysis with a case study to address three objectives: (1) we used elasticity analysis to understand how sensitive horse population growth is to reductions in age-specific survival rates; (2) we used simulation modeling to estimate predation mediated reductions in survival that would be necessary to stabilize horse population growth; (3) we used empirical information in a state-space model framework to estimate population growth rates in a free-roaming horse population subject to chronic mountain lion predation in southeastern Nevada. Lastly, we used the model to predict what population growth rate might have been in the absence of predation and thus inferred the effects of this source of mortality on annual population growth.



FIGURE 1

An approximately 8-week old feral horse (*Equus caballus*) preyed by a female mountain lion (*Puma concolor*) in the Clover Mountains, Nevada, May 2023 (Photo credit: H. Klugman).

Materials and methods

Elasticity analysis

Natural resource practitioners aim to understand how management interventions can effectively manipulate population parameters to achieve measurable objectives. Different demographic sensitivity analyses can be used to decipher how changes to specific vital rates such as fertility and survival, can influence population growth rates (λ ; Morris and Doak, 2002). Thus, we first sought to evaluate the relative sensitivity of horse population growth rates to variation in demographic rates using elasticity analysis (de Kroon et al., 2000; Morris and Doak, 2002). Garrott (1991) explored demographic sensitivity for horse populations using a stage-based model to estimate sensitivity of λ to changes in fecundity, juvenile survival, and adult survival. He found that λ was most sensitive to changes in survival of the adult stage class. However, that analysis used a stage-based model with only two stages (i.e., foals, adults; Garrott, 1991), which may have been unable to elucidate additional age-specific patterns of demographic sensitivity that could be estimated with a similar analysis using an age-based model (Caswell, 2001). This is an important distinction in modeling approaches because of the early sexual maturity and long-lifespans exhibited by horses.

We built an age-based, female-only, post-breeding population model (Leslie, 1945; Morris and Doak, 2002) in the statistical Program R (R Core Team, 2023). To populate the model, we used demographic parameter estimates from the horse population occupying the Garfield Flat Herd Management Area in western Nevada (Jenkins, 2002; Table 1). Estimates of fertility, survival, and λ from this population are typical of those measured elsewhere (NRC, 2013). We conceptualized horse demography as having 21 age classes: one class for each year of age from 0 (foals) to 19, and a final stage pooling all individuals ≥ 20 years old. During a given time-step, individuals in each age class had a probability of surviving and transitioning to the next age class until they reached age 20; all individuals ≥ 20 years old were modeled as a single stage class with a probability of surviving and staying within that stage. Females ≥ 2 years old had a probability of reproducing (foaling) and recruiting juveniles into the age-0 class. No incidents of predation were reported from the Garfield Flats reference herd (Jenkins, 2002), which largely falls outside of mapped mountain lion range in Nevada (Ashman et al., 1983). Because the model only included females, we removed males by assuming an equal sex ratio at birth (Garrott, 1991) and multiplying the overall foaling rates from Jenkins (2002) by 0.5. Female-only models are commonly used in demographic studies of polygynous mammals because demographic rates of sexually mature females are what limit population growth (Morris and Doak, 2002), and horse populations are more sensitive to perturbation of this demographic (Garrott and Siniff, 1992). Post-breeding models assume that the population is censused immediately following parturition, so new offspring are included in the population size during each time-step. The model generated a deterministic λ value of 1.206.

We compiled the demographic parameter estimates from Jenkins (2002) into a deterministic demographic matrix (Table 1)

to evaluate whether age-specific patterns of survival could offer more nuanced or variable effects on λ using elasticity analysis. Elasticity analysis is used as an alternative form of sensitivity analysis that quantifies how proportional changes in demographic rates drive proportional changes in λ , with values summing to 1 (Benton and Grant, 1999; de Kroon et al., 2000). We performed an elasticity analysis on the demographic matrix to estimate the relative contribution of reproductive rates and survival for each horse age class from 0– ≥ 20 years using the ‘elasticity()’ function from package ‘popbio’ (Stubben and Milligan, 2007).

Scenario analysis

Our second objective was to understand how much mountain lion predation would be necessary to eliminate positive population growth rates (i.e. $\lambda \leq 1.0$) using a stochastic predictive population model and a scenario analysis. We built an age-structured, stochastic predictive modeling framework (Morris and Doak, 2002) in R that projected a horse population 10 years into the future under different levels of predation-caused mortality and corresponding reductions in survival. We assumed a female-only population of 125 individuals and a maximum AML of 100 females (i.e., 25% above AML); this baseline scenario represents a population that is marginally above the target size range, which is a common attribute of BLM-managed horse populations in recent years (e.g., 79% exceeded maximum sizes in 2022; Bureau of Land Management, 2022). We accounted for uncertainty in demographic parameters across simulation replicates within each scenario. For each replicate, we modeled: (1) initial population size as a normally-distributed variable with a mean of 125 and a standard deviation of 6.25; (2) age-specific survival rates as beta-distributed variables with mean values from the deterministic matrix and variance values that resulted in 95% of random values falling within ± 0.02 of the mean; and (3) age-specific reproductive rates as beta-distributed variables with mean values from the deterministic matrix and variance values that resulted in 95% of random values falling within ± 0.1 of the mean. We partitioned individuals from the population estimate into different age classes by multiplying the random estimate of initial population size by the stable-age distribution estimated from the deterministic demographic matrix. Within each replicate, age-specific survival and reproduction were simulated for each time-step with random binomial draws of success at surviving and reproducing.

Among horses, mountain lion predation primarily affects juveniles and yearlings (Iacono et al., 2024). To understand how much predation on young horses (i.e., 0–2 year olds) would be necessary to limit population growth rate, we built 12 additional scenarios in addition to the baseline scenario. Each scenario varied in the declines in survival rates of foals, yearlings, and 2-year olds due to predation. The baseline scenario assumed no predation-induced reductions in survival (i.e., a ‘null model’) and projected a predator-free population, given reasonable estimates of parametric uncertainty and environmental stochasticity (Jenkins, 2002). Similar to the deterministic model, the baseline, stochastic scenario model yielded a median population growth rate of 1.207. Among the additional 12 scenarios, four assumed that predation

TABLE 1 Deterministic demographic matrix used to estimate the sensitivity of population growth rate to changes in individual demographic rates for a female-only, post-breeding, age-based population of feral horses (*Equus caballus*).

	Age0	Age1	Age2	Age3	Age4	Age5	Age6	Age7	Age8	Age9	Age10	Age11	Age12	Age13	Age14	Age15	Age16	Age17	Age18	Age19	Age20+
Age0	0	0	0.258	0.333	0.376	0.44	0.374	0.441	0.429	0.442	0.384	0.384	0.384	0.384	0.384	0.357	0.357	0.357	0.357	0.357	0.222
Age1	0.919	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age2	0	0.996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age3	0	0	0.994	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age4	0	0	0	0.993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age5	0	0	0	0	0.99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age6	0	0	0	0	0	0.988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age7	0	0	0	0	0	0	0.985	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age8	0	0	0	0	0	0	0	0.981	0	0	0	0	0	0	0	0	0	0	0	0	0
Age9	0	0	0	0	0	0	0	0	0.976	0	0	0	0	0	0	0	0	0	0	0	0
Age10	0	0	0	0	0	0	0	0	0	0.971	0	0	0	0	0	0	0	0	0	0	0
Age11	0	0	0	0	0	0	0	0	0	0	0.947	0	0	0	0	0	0	0	0	0	0
Age12	0	0	0	0	0	0	0	0	0	0	0	0.947	0	0	0	0	0	0	0	0	0
Age13	0	0	0	0	0	0	0	0	0	0	0	0	0.947	0	0	0	0	0	0	0	0
Age14	0	0	0	0	0	0	0	0	0	0	0	0	0	0.947	0	0	0	0	0	0	0
Age15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.947	0	0	0	0	0	0
Age16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.87	0	0	0	0	0
Age17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.87	0	0	0	0
Age18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.87	0	0	0
Age19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.87	0	0
Age20+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.87	0.591

Values in the first row are reproductive rates; offset-diagonal values and the final cell value are age-specific survival rates. Demographic rates were derived from the horse population inhabiting the Garfield Flat, Nevada Herd Management Area (Jenkins, 2002). Life table results yielded a deterministic population growth rate of 1.206.

would reduce foal survival by 20%, 40%, 60%, or 80%; four assumed that predation would reduce survival of foals and yearlings by 20%, 40%, 60%, or 80%; and the last four scenarios assumed that predation would reduce survival of foals, yearlings, and 2-year-olds by 20%, 40%, 60%, or 80%. These reductions in survival are assumed to be the sole product of predation, and do not include other, independent sources of mortality acting on these age classes reflected in the baseline survival rates (Table 1).

We simulated each scenario by projecting the population with 1,000 independent simulation replicates for 10 years. We summarized results for each scenario by calculating the median and 95% confidence limits (CL) among replicates for the predicted population size in each year. Our objective was to portray how predation of one or more age classes at different intensities might reduce population growth and therefore total population size through time (Morris and Doak, 2002).

Case study

Our final objective was to estimate the degree to which mountain lions might reduce horse λ when the two species co-occur under field conditions. We used a Bayesian state-space modeling framework to explore a counterfactual scenario: what would population growth have been in the absence of documented mountain lion predation? To achieve this, we used a population modeling approach with empirical estimates of horse abundance (Schoenecker et al., 2026) and observations of mountain lion predation on horses from the Delamar-Clover study area in Lincoln County, Nevada (Figure 2; Iacono et al., 2024). The study

area measures 3,160 km², with elevations spanning 1,370–2,450 m. The region exhibits a continental climate, with mean temperatures ranging from -7 to 8.3 °C in winter, and 15 to 35 °C in summer. Mean annual precipitation was 237 mm, with approximately 40% falling as snow from December to March, and 24% as summer thunderstorms (Caliente, NV, elev: 1,343 m; <https://www.usclimatedata.com>). The study area straddles the ecotone between the Mojave Desert and Great Basin ecoregions (Bailey, 1983, Figure 2), with plant communities reflecting this transition. Mid-elevations are dominated by Great Basin flora, including semi-arid piñon-juniper woodlands (*Pinus monophylla*, *Juniperus osteosperma*) and sagebrush steppe (*Artemisia tridentata*), with basins and foothills reflecting intrusions of Mojave Desert flora, including Joshua trees (*Yucca brevifolia*), blackbrush (*Coleogyne ramosissima*), and creosote bush (*Larrea tridentata*). Small pockets of ponderosa pine (*Pinus ponderosa*) and aspen (*Populus tremuloides*) are found on mesic sites at high elevations. Cheatgrass (*Bromus tectorum*) is common on disturbed sites throughout the study area (Kricher and Morrison, 1993). The Clover Mountains represent the southwestern-most edge of Gambel oak (*Quercus gambelii*) distribution — a notable species because of its importance as a food resource for mule deer (Newmark and Rickart, 2012). Over 98% of the study area falls under the jurisdiction of the BLM, with the remainder in private ownership, largely along waterways and floodplains. Approximately 61% of BLM lands in the study area are designated horse or burro Herd Areas (HAs). These include the entirety of Applewhite, Delamar Mountain, Clover Mountain, and Clover Creek HAs, and portions of Blue Nose Peak, Little Mountain, Highland Peak, and Meadow Valley Mountains.

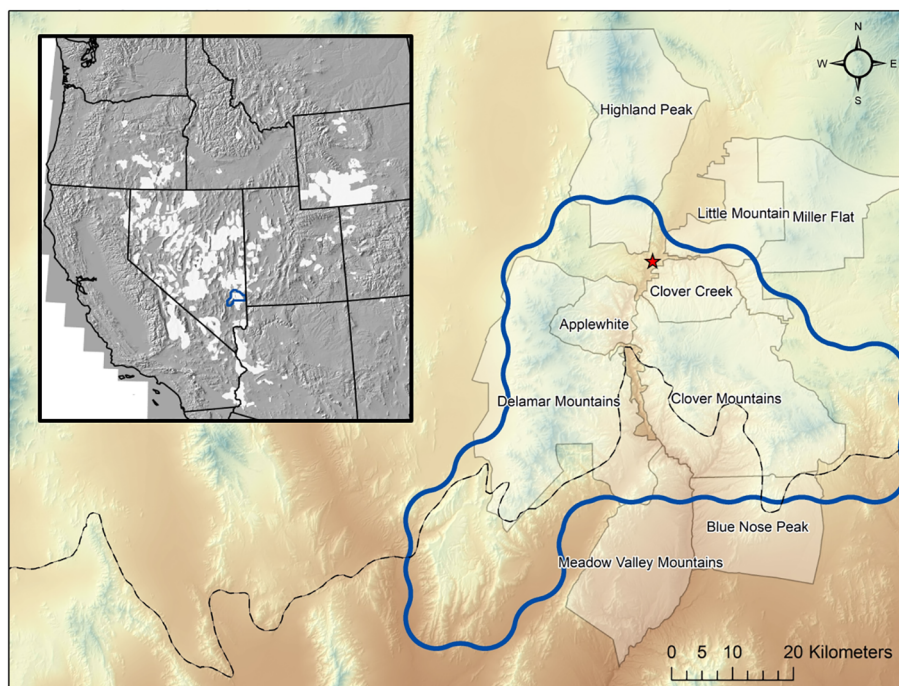


FIGURE 2

Delamar-Clover Mountains study area in southeastern Nevada (blue polygon). Approximately 61% of the study area encompasses all or parts of nine different Wild Horse Herd Areas managed by the Bureau of Land Management (BLM). Black hashed line delineates the boundary between the Great Basin (north) and Mojave Desert (south) ecoregions. Caliente, Nevada is denoted by the red star. Inset, white polygons represent the distribution of all BLM and US Forest Service wild horse management units in the western United States.

Miller Flat, and Meadow Valley Mountains HAs (Figure 2). All of these HAs are contiguous with no limiting geographic boundaries between them, forming one large study area within which horses can roam indiscriminately. Herd Areas receive less management than HMAs in general, because the target population size for HAs is zero. However, model results indicate the horse population during our study period averaged 821 animals. Additional land-uses include livestock grazing, railroad-based cargo transportation, electrical transmission lines and associated maintenance, off-road vehicle recreation, hunting, and other forms of non-motorized recreation. In addition to feral horses, other ungulates commonly or occasionally preyed upon by mountain lions include mule deer, elk, bighorn sheep, pronghorn antelope, feral cattle, and feral pigs (Iacono et al., 2024).

The BLM conducts aerial horse surveys to obtain population estimates that are used in management decision-making (Griffin et al., 2020). Aerial survey and analytical methods have followed guidance from National Research Council (2013), which called for estimates to be made while accounting for imperfect detection of animals, and to properly measure and account for any uncertainties. We used population estimates and associated uncertainties from two recent aerial survey efforts conducted over the affected HAs and our study area during February of 2022 and 2024 (BLM, 2023, BLM, 2025, Schoenecker et al., 2026). Additionally, we incorporated information about management removals of horses conducted during our investigation (239 and 216 horses from the Delamar Mountains and Meadow Valley, respectively, in December 2020).

The aerial surveys occurred well after the end of the birthing season, but also when foals have grown large enough to be difficult to distinguish from adults when observed from the air (Griffin et al., 2020). Given this potential source of error, we pooled all ages into a single, unstructured population for this analysis and conceptualized horse population dynamics using a post-breeding model. Because of the timing and precision of surveys, these efforts provided a consistent estimate of the population size each year.

To infer potential annual impacts of mountain lion predation on horse population growth, we used data on the number, sex-age class, and date of horses predated by GPS-collared mountain lions in the study area between 20 February 2020 and 19 February 2022 from Iacono et al. (2024). At least 132 horses were predated by mountain lions in the study area during this period. Predation rates on horses by individual mountain lions varied by sex and by season, averaging 0.55 and 0.33 horses/week in summer and winter, respectively (averaged across sexes; Iacono et al., 2024). Of documented predation events on horses, 60.5% were foals (<1 year old), 13.2% were yearlings (1–2 years old), 15.8% were adults (2+ year old); for the remaining 10.5% of horses, age class could not be determined from residual field evidence (Iacono et al., 2024). Sex could only be attributed to 35.6% of the horse kills for which age class could be determined. Among those animals, the sex-ratio of the kill was 50:50 for foals and yearlings, but approximately 2:1 (males:females) among adults (Iacono et al., 2024). All procedures related to mountain lion capture, collaring, data collection at kill sites, and parameter estimation are reported in Iacono et al. (2024).

We accounted for horses removed from the population by management practices (gathers and removals) in order to

estimate biological λ . However, to infer a potential effect of predation on reducing horse λ through model prediction, we also wanted to know how many horses were killed by mountain lions. Regardless of cause, the time of year a horse is removed from the population might influence λ (i.e., before or after the spring reproductive pulse), so we counted the number of horses removed by managers or predators during two time periods of each year: spring (March–April) and summer-fall-winter (May–February).

We built a statistical model that estimated λ and population size (N) during February 2022–February 2024 [Equations 1–6]. Because our primary data source was population estimates with non-normal uncertainty from previous agency analyses (90% confidence limits), we sought to propagate estimation uncertainty from original analyses (Schaub and Kéry, 2021). To this end, we used a hierarchical, exponential, state-space model (SSM; Schaub and Kéry, 2021) that modeled uncertainty in population size estimates while estimating λ . The SSM was defined by the following equations:

$$N_1 \sim \text{Lognormal}[\log \hat{N}_1, \sigma^2 \log \hat{N}_1] \quad (1)$$

where N_1 (initial population size) was a random, log-normal variable with a log-mean of the initial population size estimate ($\log \hat{N}_1$) and log-scale variance, $\sigma^2 \log \hat{N}_1$, calculated from the confidence limits around the population. We modeled changes in population size with:

$$N_{t+1} = (N_t * \lambda_t) - \text{Removals}_t \quad (2)$$

in which λ represented the multiplicative population growth rate, N represented population size, and *Removals* was the number of adults removed in the fall, respectively, of each year, t . We constrained N_{t+1} to be non-negative.

We modeled the log of λ ($\text{Log } \lambda_t$) as a random, normally-distributed variable with:

$$\text{Log } \lambda_t \sim \text{Normal}(\mu, \sigma_\lambda^2) \quad (3)$$

where μ was the log-mean and σ_λ was the standard deviation of the residual error. We then exponentiated $\text{Log } \lambda_t$ to calculate λ_t on its natural scale, which is bounded from 0 to ∞ . λ_t represents estimates of annual population growth in the presence of mountain lion predation; we refer to this as ‘Estimated λ ’ in instances below.

We accounted for observation error in population estimates by treating \hat{N} as a log-normally distributed variable with:

$$\hat{N}_t \sim \text{Lognormal}[\log N_t, \sigma_{\log-obs}^2] \quad (4)$$

$$\sigma_{\log-obs} = \sqrt{\ln(1 + cv_{obs}^2)} \quad (5)$$

where \hat{N} was centered on the true population size, N_t , and varied due to observation error with log-variance, σ that scaled as a consequence of a coefficient of variation, cv_{obs} . This allowed variance in observation error to increase with larger population size estimates.

We tallied the number of horses killed by mountain lions on the study area from 20 February 2020 to 19 February 2021 (i.e., 2020)

and 20 February 2021 to 19 February 2022 (i.e., 2021; [Iacono et al., 2024](#)); these dates coincided with the approximate aerial survey dates in 2022 and 2024. To understand the potential effects of predation on population growth, we used the estimation model to ‘hindcast’ and make predictions about population size in February 2020 and February 2021. To do so, we assumed that λ in 2020 and 2021 were similar to estimates from 2022 and 2023; we accomplished this by randomly drawing a value from 2022 or 2023 for the years 2020 and 2021. To understand what effect predation may have had on λ during the years for which we had information on predation events (2020 and 2021), we used the model to make predictions of what λ may have been in the absence of predation (‘Predicted λ ’) using:

$$\text{Predicted } \lambda_t = \frac{[(N_t + DS_t) * \lambda_t] + DF_t}{N_t} \quad (6)$$

where DS and DF were the number of predated horses in the spring (DS) and summer-fall-winter (DF) in each year, t . This added predated horses back into the population to calculate what λ may have been in the absence of predation in 2020 and 2021.

Our estimation exercise had limited information for the model to learn from: only two population estimates (2022, 2024) over a two-year interval, with no information in between. This made it difficult for the model to estimate observation error around population estimates, N , and λ . Thus, we used informed priors to make assumptions about how parameters might be shaped so as to aid in model convergence and to permit this comparison. We used a normal distribution for the μ prior (mean = 0.07, SD = 0.02), which roughly approximates the log- λ observed during 2022–2024, and a truncated normal distribution for σ_λ (mean = 0.075, SD = 0.04). For the coefficient of variation for observation error, cv_{obs} , we also used a truncated normal distribution (mean = 0.11, SD = 0.02), following estimates of observation error observed in other aerial surveys of horses ([BLM, 2023](#), [BLM, 2025](#)). More generally, this exercise also assumes that predation on horses was purely additive, such that inferred potential effects of mountain lions on population growth may represent a maximum effect in those years. This seems reasonable, due to very high reported survival rates of horses (exceeding 95%) but given the limited data and assumptions we made, we view this exercise more as a simulation exploration than a strict estimation process.

We estimated λ , N , and derived predictions using the state-space model in JAGS ([Plummer, 2003](#)), which we implemented using the statistical Program R and the ‘jagsUI’ package ([Kellner, 2016](#); [R Core Team, 2023](#)). We ran three independent chains of 1,500,000 iterations with a burn-in of 500,000 iterations and adaptation period of 10,000 iterations. We thinned chains by 3,000, which gave us 999 samples from the posterior distribution. We assessed model convergence by evaluating the \hat{R} statistic and visually examining traceplots for convergence ([Schaub and Kéry, 2021](#)). We considered convergence on the posterior distribution adequate when all parameters had $\hat{R} < 1.1$ and the traceplots were ‘grassy’. We report median values and 95% highest posterior distribution (HPD) limits for N , λ , and derived predictions.

Results

Elasticity analysis

Elasticity analysis revealed that λ was more sensitive to changes in survival than reproductive rates ([Figure 3](#)). Survival and reproductive rates accounted for 0.859 and 0.141 of elasticities, respectively. Examination of age-specific elasticities revealed variation among age-classes and vital rates, as λ was more sensitive to perturbations in survival for younger age-class horses than older ones. For example, the two demographic rates with the greatest contributions to λ were foal and yearling survival (both 0.141; [Figure 3](#)), and the summed survival elasticities of horses age 0–2 was 0.403 of all elasticities. When considered cumulatively as a single stage class, the survival elasticity of adults aged ≥ 3 years old, accounted for 0.456 of all elasticity.

Scenario analysis

Our null-model scenario suggested that, in the absence of predation and density-dependent regulatory mechanisms, the horse population would exhibit exponential growth over a 10-year period ([Figure 4A](#)). Scenarios simulating mountain lion predation on foals predicted reduced population growth relative to the control scenario, and the ‘Foal predation – 80%’ scenario reduced horse growth rates, such that population size was relatively stable through time ($\lambda \approx 1.0$; [Figure 4B](#)). Scenarios with predation on both foals and yearlings experienced greater reductions in growth compared to foal-only scenarios ([Figure 4C](#)). The scenarios with 60% and 80% reductions in foal and yearling survival caused population size to decrease through time, and the 80% reduced survival scenario resulted in the population decreasing beneath the maximum management targets over the projection interval. Scenarios in which predation affected foals, yearlings, and 2-year olds experienced even greater reductions in population growth compared to all other scenarios. When reductions of survival for these age classes reached 60% to 80%, populations decreased beneath low AML over the 10-yr simulation ([Figure 4D](#)).

Case study

The state-space model estimated that the Delamar-Clover horse population experienced a median λ of 1.07 during 2022 (0.92–1.24, 95% HPD) and 1.07 during 2023 (0.93–1.25, 95% HPD; [Figure 5](#)). These growth rates caused the initial population size in February 2022 (median = 787 horses; 726–860, 95% HPD) to grow to 844 horses in 2023 (726–988, 95% HPD) and 900 horses in 2024 (770–1,060, 95% HPD; [Figure 5](#)). Model predictions for population size in 2020 and 2021 suggested that there were 1,116 horses in February 2020 (900–1,362, 95% HPD) and 735 horses in 2021 (631–848, 95% HPD), after accounting for the removal of 455 horses in December 2020 and subsequent growth ([Figure 5](#)). Model predictions for λ in the absence of mountain lion predation (‘Predicted λ ’) suggested that growth rates could have been 1.14 during 2020 (0.98–1.35, 95% HPD) and 1.14 in 2021 (0.99–1.33, 95% HPD; [Figure 6](#)).

	Age0	Age1	Age2	Age3	Age4	Age5	Age6	Age7	Age8	Age9	Age10	Age11	Age12	Age13	Age14	Age15	Age16	Age17	Age18	Age19	Age20+
Age0	0	0	0.019	0.02	0.019	0.018	0.013	0.012	0.01	0.008	0.006	0.004	0.003	0.003	0.002	0.002	0.001	0.001	0.001	0	0
Age1	0.141	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age2	0	0.141	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age3	0	0	0.122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age4	0	0	0	0.102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age5	0	0	0	0	0.083	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age6	0	0	0	0	0	0.065	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age7	0	0	0	0	0	0	0.052	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Age8	0	0	0	0	0	0	0	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0
Age9	0	0	0	0	0	0	0	0	0.031	0	0	0	0	0	0	0	0	0	0	0	0
Age10	0	0	0	0	0	0	0	0	0	0.023	0	0	0	0	0	0	0	0	0	0	0
Age11	0	0	0	0	0	0	0	0	0	0	0.017	0	0	0	0	0	0	0	0	0	0
Age12	0	0	0	0	0	0	0	0	0	0	0	0.013	0	0	0	0	0	0	0	0	0
Age13	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0
Age14	0	0	0	0	0	0	0	0	0	0	0	0	0	0.007	0	0	0	0	0	0	0
Age15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0	0	0	0	0
Age16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	0	0	0	0	0
Age17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0	0	0	0
Age18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0
Age19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0
Age20+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

FIGURE 3 Results of an elasticity analysis describing the relative contribution of demographic parameters to population growth rate (λ) of a feral horse (*Equus caballus*) population. Each value describes the proportional change in population growth rate that results from a proportional change in a demographic vital rate. Cell color indicates effect magnitude, with darker (i.e., red) cells having greater relative effects on population growth rate than lighter (i.e., tan) cells.

Discussion

Interest in the potential for predation to serve as a natural solution to the challenge of horse population management in North America has prompted new research on the demographic effects that native predators may have on non-native prey species (NRC, 2013; Andreassen et al., 2021; Iacono et al., 2024). Although intuitively appealing, empirical evidence demonstrating the potential for mountain lions to continually suppress population growth rates or total abundance of widely distributed native ungulates is rare (Ballard et al., 2001; Hurley et al., 2011; Pierce et al., 2012). By extension, this gap in our knowledge also applies to feral horses — a large-bodied exotic species with a legacy of domestication and associated high reproductive capacity (Grange et al., 2009). Regardless, quantifying the potential effects of predation on horse growth rates is a step toward evaluating variation in population trajectories among herds occupying different climatic zones and habitat conditions. It can also be used to understand the degree to which faunal communities and associated ecological relationships may affect rates of change in horse populations in western North America, which might inform expectations for managers about the role predators have in shaping horse population growth.

Previous research has found that adult survival — often treated as a single “stage class” — is typically the most important demographic parameter determining population growth rates in horses and other large mammals (Garrott, 1991; Gaillard et al., 1998; Forrester and Wittmer, 2013). Our analysis supported this principle, as summed elasticities from foal and yearling survival rates were less than the summation of all reproductive adult age classes combined (i.e., 18 adult age classes). However, our results also provide a more nuanced

assessment of how individual age classes may contribute differently to overall population growth. We estimated age-specific patterns of demographic elasticity and the survival of individual age classes of younger horses (e.g., foals, yearlings). Our results accounted for the potential 20-yr reproductive lifespan of horses and suggested that the survival rates of foals and yearlings have a relatively greater influence on λ than the survival or reproductive components of older age classes. Given that these age classes are more vulnerable to predation than adults (Andreassen et al., 2021; Iacono et al., 2024; Figure 5), our results suggest that mountain lions may have greater potential to reduce growth rates in large horse populations than previously assumed (NRC, 2013).

Our stochastic simulation model suggested that mountain lions would have to drive relatively large reductions in survival rates of young horses to reduce population growth to stable or declining trajectories. Specifically, predation would have to result in > 40% annual reductions of survival rates of foals, yearlings, and 2-yr olds simply to maintain stable population growth (i.e., $\lambda \approx 1.0$). To reduce λ below 1 (i.e., negative population growth), predation, either alone or in concert with other sources of mortality, would have to decrease survival of the three youngest age classes by 60% per yr. However, if adult horses were relatively immune from predation, then 80% reductions in survival of both foal and yearling age classes would be required to achieve the same result. Lastly, if foals were functionally the only demographic affected by predation, mountain lions would have to reduce survival of this age class by > 80% to prevent the population from increasing.

Field studies have found that foal survival rates vary widely among North American horse populations (27–96%; Roelle et al.,

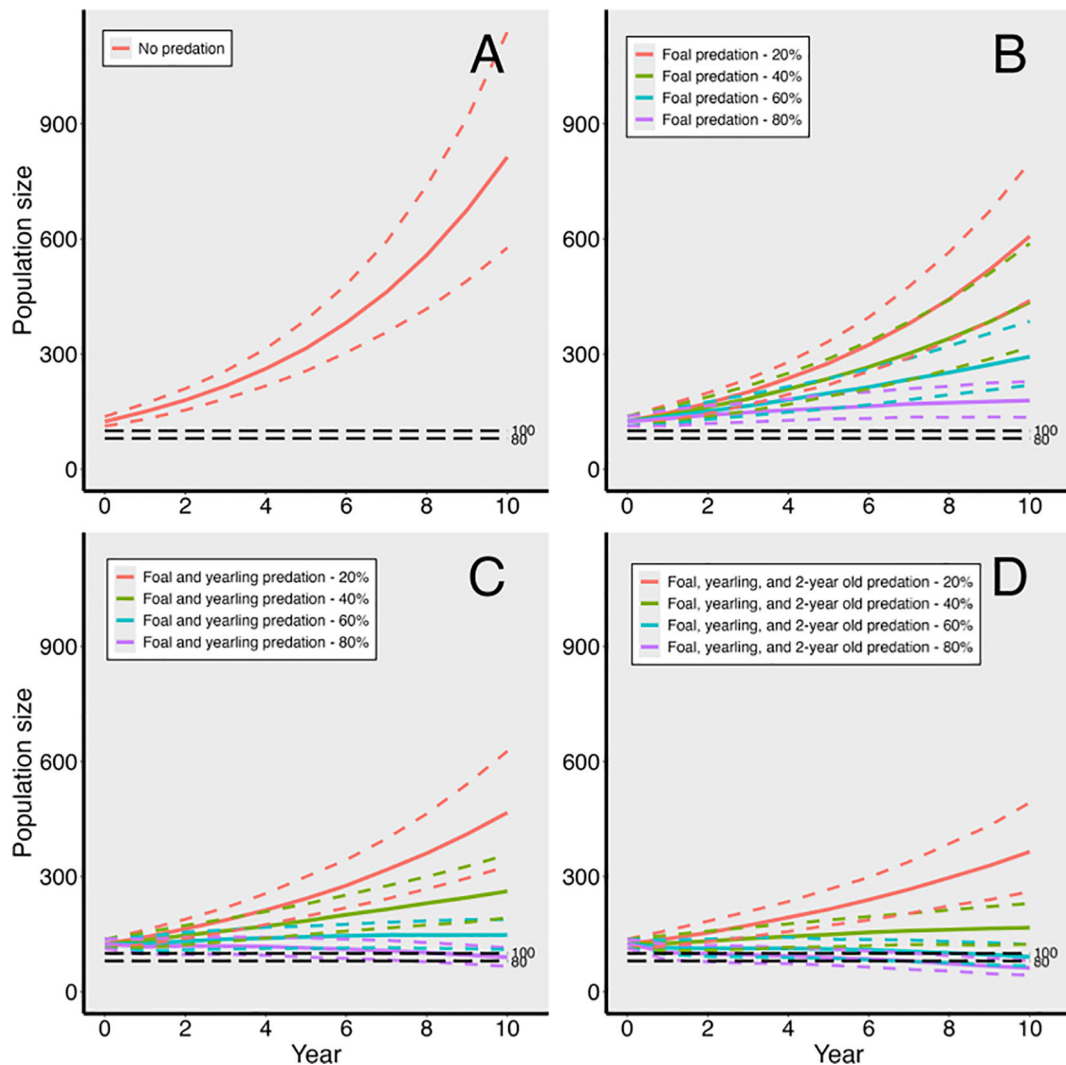


FIGURE 4

Results of a scenario analysis that projected a female-only feral horse (*Equus caballus*) population (125 individuals) with a target population size of 100 horses under scenarios varying in predation magnitude on foals, yearlings, and 2-year old horses. (A) Null model of no predation, when horse populations grew with unregulated exponential growth given survival and reproductive rates that yielded deterministic population growth rate of 1.206; (B) four scenarios with 20%, 40%, 60%, and 80% reduced survival of foals due to predation relative to the no-predation scenario; (C) scenarios of 20%, 40%, 60%, and 80% reduced survival of foal and yearling horses due to predation; (D) scenarios of 20%, 40%, 60%, and 80% reduced survival of foals, yearlings, and 2-year olds due to predation. For each panel, bold lines are means and dashed lines are 95% CL from 1,000 simulation replicates for each scenario. Black horizontal dashed lines represent the target population range desired by management (80-100 horses)

2010). Rates at the high end of this range were recorded at times or in herds with little or no evidence of predation (Berger, 1986; King et al., 2023); conversely, some of the lowest rates observed were from herds with confirmed mountain lion predation (Turner et al., 1992; Roelle et al., 2010; Schulman et al., 2024). Given empirical results suggesting predation primarily affects foals, and that adults and yearlings comprise < 30% of all horses predated (Andreasen et al., 2021; Iacono et al., 2024), our models suggest that it would be unlikely for mountain lion predation alone to yield the reductions in survival necessary to result in stable or declining population growth. All of this implies that large horse populations subjected to predation may still express positive growth rates, albeit more slowly than they would in the absence of heavy foal mortality. Horse population growth rates vary across space and through time, and so accurately calculating the proportional decrease stemming from predation will benefit from replication of field measures under a

variety of environmental conditions, including the relative abundance of alternative prey occupying the same system.

Our empirical analysis of the Delamar-Clover horse population in southeastern Nevada demonstrated that chronic mountain lion predation was insufficient to reduce growth rates to a stable dynamic, because the population continued to grow despite the presence of this chronic mortality factor. Nevertheless, our results suggest predation has the potential to induce modest reductions in λ through assumed density-independent predation. Despite experiencing a minimum of 132 predation-caused mortalities over a two-year period, this horse population continued to exhibit positive population growth, with mountain lion predation potentially reducing this growth by half, i.e. from 1.14 to 1.07 on average. These results mirror those reported by Pierce et al. (2012), in which mountain lion predation reduced the annual rate of increase in a mule deer population from a potential of 15-20%, down to an actual 10% per yr. Although our results have

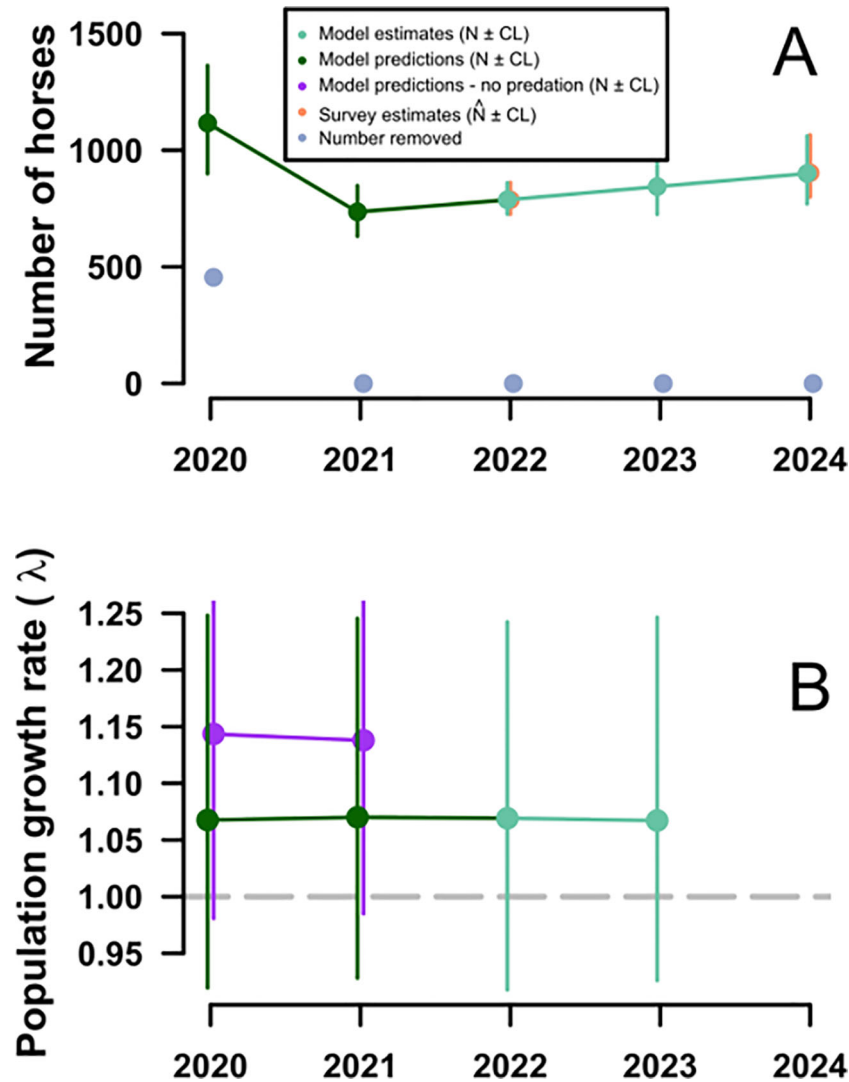


FIGURE 5

Model estimates and predictions for (A) population size, N , and (B) population growth rate, λ , from a state-space simulation model of feral horses (*Equus caballus*) in the Delamar-Clover study area in southeastern Nevada during 2020–2024. ‘Survey estimates’ refer to population estimates from double-observer aerial surveys of horse population size conducted in February of 2022 and 2024 that were used as data in the model. The model estimated N and λ during 2022–2024, and then was used to make predictions two years into the past, assuming similar λ as 2022–2024. We presented two predictions for λ during 2020–2021: with (dark green) and without predation (purple). Four-hundred-fifty-five (455) horses were removed from the population in December 2020.

considerable uncertainty due to the nature of our estimation exercise (a single population, over a two-year interval, with assumptions about parameters, etc.), they do suggest that the effect of mountain lion predation at reducing horse population growth is unlikely to be the sole mechanism regulating horse populations – at least in mixed-prey communities such as the one studied here.

The presence of alternative prey species likely influences the ability of mountain lions to influence growth rates of horses in this system. Examples of mountain lion predation having suppressive effects on survival rates or λ in mule deer have been observed in systems with an abundant, alternative prey source (Robinson et al., 2002). However, negative demographic effects have more commonly been documented in small, isolated populations, including mountain caribou and bighorn sheep (Kinley and Apps, 2001; Festa-Bianchet et al., 2006; Johnson et al., 2013), or on species with slower life histories, such as elk (Proffitt et al., 2020). In contrast, horses exhibit early sexual maturity (~ 2 yrs),

long reproductive lifespans (~ 20 yrs), no known reproductive senescence, and perhaps most importantly, weak density-dependent effects on reproduction and population dynamics (Grange et al., 2009; Roelle et al., 2010). Additionally, notwithstanding an 11-month gestation (Satué et al., 2011), horses exhibit a wide birthing season (March–September; Roelle et al., 2010; Ransom et al., 2016), and the ability to nurse a foal during gestation (Boyd and Keiper, 2005). All of these qualities combine to result in a species with exceptional fecundity and survival relative to its body mass, which yield strong population growth that native predators apparently are unable to regulate under conditions observed here.

Although deer and horses exhibit extensive distributional overlap on western rangelands (Stoner et al., 2021), there are some herd areas with sufficiently low deer densities that horses may actually serve as the primary food resource for resident mountain lions (e.g., Andreasen et al., 2021). Predation effects can be strong on small populations

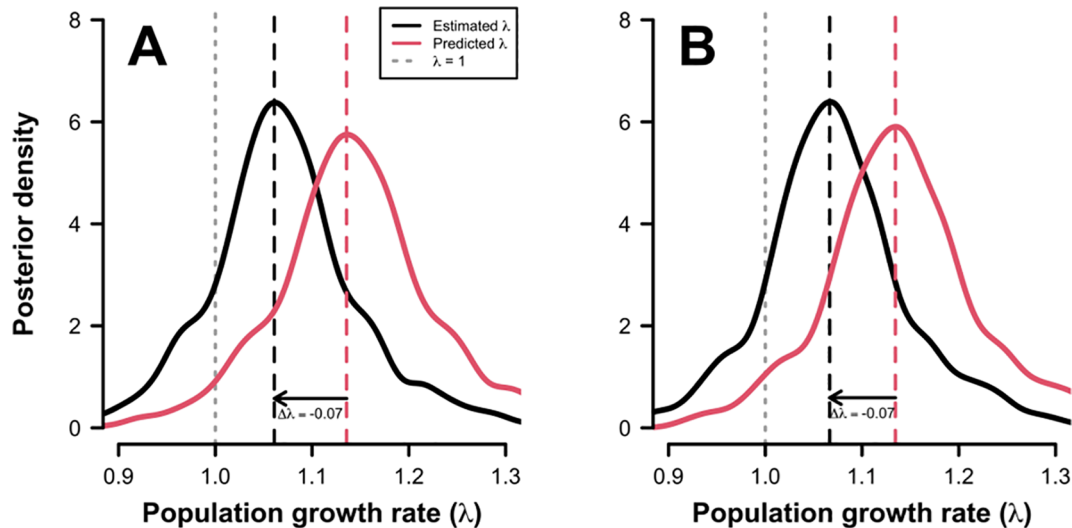


FIGURE 6

Posterior density distributions of feral horse population growth rates (λ) in the Delamar-Clover study area of southeastern Nevada during 2020 (A) and 2021 (B). Black lines indicate state-space model estimates ('Estimated λ '); red lines indicate state-space model predictions of what λ may have been in the absence of predation ('Predicted λ ') by mountain lions (*Puma concolor*). Vertical dashed lines indicate the median of the posterior density. $\Delta\lambda$ indicates the most likely predicted change in horse population growth due to mountain lion predation in each year.

(Sawyer and Lindzey, 2002), particularly when predators specialize on a certain species, they can have substantial impacts on single cohorts (e.g., Ross et al., 1997; Knopff et al., 2010). For example, of the studies that observed periods of static growth in horse populations subjected to mountain lion predation, all of them occurred in herds of < 170 animals (Turner et al., 1992; Gregor and Romney, 1999; Roelle et al., 2010). Conversely, the estimated horse population of the Delamar-Clover study area was approximately 821 animals, and mule deer comprised > 60% of the ungulates consumed by mountain lions on that site (Iacono et al., 2024). In addition to herd size, it is also possible that predation on horses could vary annually due to individual behavior (Iacono et al., 2024), in response to fluctuations in prey density (i.e., predation rate may be positively correlated with prey population size; Branch et al., 1996), or as a function of the degree of spatial overlap with preferred prey (Johnson et al., 2013). Future efforts to model these relationships might treat mountain lion predation effects as (1) non-linear or (2) dependent on horse population density and subsequent encounter rates.

Given the availability of a preferred prey resource, fluctuations in fawn production may influence the degree to which horses either subsidized, or comprised the majority of, the mountain lion diet in any specific year. Mule deer are the single most important prey species for mountain lions across their North American range (Pierce and Bleich, 2003), and availability of this species can affect mountain lion recruitment (Laundré et al., 2007; Pierce et al., 2012). In arid and semi-arid climates, annual mule deer production is closely tied to precipitation (Wasley, 2004; Heffelfinger et al., 2018). The temperate latitudes of southwestern North America are prone to multi-year droughts, which are forecasted to increase in frequency, duration, and severity in coming decades (McEvoy et al., 2020). Yet, it is unclear how horse reproduction and foal survival are influenced by precipitation and subsequent forage availability. Thus, if fawn production declines during periods of drought, but foal production remains relatively constant, then mountain lion populations could be

buoyed by the presence of an alternative but relatively abundant prey species. This scenario could plausibly result in a “predator-pit” (Clark and Hebblewhite, 2021) – a situation in which a predator population is uncorrelated with its primary prey stemming from the presence of secondary prey or food subsidies that are not subject to the same underlying drivers (e.g., density-dependent reproduction). Under these conditions it is conceivable that mountain lions would increase reliance on foals and so further negatively affect recruitment in horse populations. Evaluating how foal and fawn production co-varies with precipitation can further improve understanding and help predict total predation effects on horses.

Management implications

We present multiple lines of evidence suggesting that mountain lion predation on horses is neither a panacea nor a pipedream for management agencies: mountain lions can exert negative effects on horse population growth, but this source of mortality is insufficient to be the sole mechanism or stand-alone solution to horse abundance for natural resource agencies tasked with managing horse populations. Thus, predation might work in conjunction with other artificial reductions to survival (removals) or reproduction (fertility control treatment, e.g. Schulman et al., 2024), which may remain necessary components of horse management, either to reduce positive population growth, or to bring excessively large populations within target ranges. When accounted for in conjunction with large-scale gathers, sustained predation may be able to slow the rate at which unmanaged horse populations grow or recover from management-induced reductions. Thus, sustained predation could potentially make gathers in mountainous terrain smaller and less frequent, thereby allowing managers to focus efforts on faster-growing herds unaffected by predation, or those more prone to conflict with private landowners. To better understand how mountain lions might influence horse population management, four additional lines of inquiry could be

evaluated to inform management practices: (1) identify and map landscape features that render horses vulnerable to predation; (2) use results to identify management units where herds may be subject to some degree of predation; (3) measure and compare horse population growth in management units with and without predation; and (4) measure and compare horse population growth between areas where mule deer and horses overlap to determine how predation on horses varies with fluctuations in deer populations.

Author's note

The USGS promotes open science through policies ensuring public access to research data and publications, aligning with federal mandates to make scientific information findable, accessible, interoperable, and reusable (FAIR).

Data availability statement

Publicly available datasets were analyzed in this study. Data used in this article can be found in [Iacono et al. \(2024\)](#), and through the Bureau of Land Management web site (https://www.blm.gov/sites/default/files/docs/2025-03/2025_Wild_Horse_and_Burro_Population_Estimates.pdf).

Ethics statement

The study did not collect novel field data with animals and as such did not require institutional animal care and use ethics approval. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

DS: Conceptualization, Investigation, Project administration, Writing – original draft, Writing – review & editing. BF: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. KS: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Ackerman, B. B., Lindzey, F. G., and Hemker, T. P. (1984). Cougar food habits in southern Utah. *J. Wildlife Manage.* 48, 147–155. doi: 10.2307/3808462
- Andreasen, A. M., Stewart, K. M., Longland, W. S., and Beckmann, J. P. (2021). Prey specialization by cougars on feral horses in a desert environment. *J. Wildlife Manage.* 85, 1104–1120. doi: 10.1002/jwmg.22087
- Ashman, D., Christensen, G. C., Hess, M. L., Tsukamoto, G. K., and Wickersham, M. S. (1983). *The mountain lion in Nevada* (Carson City, Nevada, USA: Nevada Dept. of Wildlife).
- Bailey, R. G. (1983). Delineation of ecosystem regions. *Environ. Manage.* 34, Suppl. 1, S14–S26. doi: 10.1007/BF01866919
- Ballard, W. B., Lutz, D., Keegan, T., Carpenter, L. H., and deVos, J. (2001). Deer-predator relationships: a review of recent North American Studies with an emphasis on mule and black-tailed deer. *Wildlife Soc. Bull.* 29, 99–115. Available online at: <https://www.jstor.org/stable/3783986> (Accessed February 15, 2026).
- Bechert, U. S., Turner, J. W., Baker, D. L., Eckery, D. C., Bruemmer, J. E., Lyman, C. C., et al. (2022). Fertility control options for management of free-roaming horse populations. *Human-Wildlife Interact.* 16, 179–216. doi: 10.26077/3f26-5f33
- Benton, T. G., and Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *Trends Ecol. Evol.* 14, 467–471. doi: 10.1016/S0169-5347(99)01724-3
- Berger, J. (1986). *Wild horses of the Great Basin: social competition and population size* (Chicago, Ill: University of Chicago Press).
- Berger, J., and Wehausen, J. (1991). Consequences of a predator-prey disequilibrium in the Great Basin Desert. *Conserv. Biol.* 5, 243–248. doi: 10.1111/j.1523-1739.1991.tb00129.x
- Boyce, P. N., and McLoughlin, P. D. (2021). Ecological interactions involving feral horses and predators: Review with implications for biodiversity conservation. *J. Wildlife Manage.* 85, 1091–1103. doi: 10.1002/jwmg.21995
- Boyd, L., and Keiper, R. (2005). “Behavioural ecology of feral horses,” in *The Domestic Horse: The Origins, Development and Management of Its Behaviour*. Eds. D. S. Mills and S. M. McDonnell (Cambridge University Press, Cambridge, UK), 55–82.
- Branch, L. C., Pessino, M., and Villarreal, D. (1996). Response of pumas to a population decline of the plains vizcacha. *J. Mammal.* 77, 1132–1140. doi: 10.2307/1382795
- Bureau of Land Management (2010). *Wild horses and burros management handbook, H-4700-1* (Washington, D.C: Office of the Assistant Director, Renewable Resources and Planning).
- Bureau of Land Management (2022). Herd area and herd management area statistics as of March 1, 2022. Available online at: https://www.blm.gov/sites/default/files/docs/2022-04/2022_HAHMA_Stats_4.12.2022.pdf (Accessed February 27, 2026).
- Bureau of Land Management (2023). Herd area and herd management area statistics as of March 1, 2023. Available online at: https://www.blm.gov/sites/default/files/docs/2023-04/2023_HMA-HA_PopStats_4-3-2023_Final.pdf (Accessed June 16, 2025).
- Bureau of Land Management (2025). Herd area and herd management area statistics as of March 1, 2025. Available online at: https://www.blm.gov/sites/default/files/docs/2025-03/2025_Wild_Horse_and_Burro_Population_Estimates.pdf (Accessed September 2, 2025).
- Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation. 2nd edition* (Sunderland, MA: Sinauer Associates, Inc).
- Clark, T. J., and Hebblewhite, M. (2021). Predator control may not increase ungulate populations in the future: A formal meta-analysis. *J. Appl. Ecol.* 58, 812–824. doi: 10.1111/1365-2664.13810
- Cunningham, S., Gustavson, C. R., and Ballard, W. B. (1999). Diet selection of mountain lions in southeastern Arizona. *J. Range Manage.* 52, 202–207. doi: 10.2307/4003681
- de Kroon, H., van Groenendael, J., and Ehrlén, J. (2000). Elasticities: A review of methods and model limitations. *Ecology* 81, 607–618. doi: 10.1890/0012-9658(2000)081[0607:EAROMA]2.0.CO;2
- Driscoll, C. A., MacDonald, D. W., and O'Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proc. Natl. Acad. Sci. United States America* 106, 9971–9978. doi: 10.1073/pnas.0901586106
- Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J. T., and Pelletier, F. (2006). Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc B* 273, 1537–1543. doi: 10.1098/rspb.2006.3467

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcosc.2025.1603626/full#supplementary-material>

- Folt, B., Schoenecker, K. A., Ekernas, L. S., Edmunds, D. R., and Hannon, M. (2023). PopEquus: A predictive modeling tool to support management decisions for free-roaming horse populations. *Ecosphere* 14, e4632. doi: 10.1002/ecs2.4632
- Forrester, T. D., and Wittmer, H. U. (2013). A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. *Mammal Rev.* 43, 292–308. doi: 10.1111/mam.12002
- Gaillard, J. M., Festa-Bianchet, M., and Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* 13, 58–63. doi: 10.1016/S0169-5347(97)01237-8
- Garrott, R. A. (1991). Feral horse fertility control: potential and limitations. *Wildlife Soc. Bull.* 19, 52–58. Available online at: <https://www.jstor.org/stable/3782416> (Accessed February 15, 2026).
- Garrott, R. A., Eigel, T. C., and Plotka, E. D. (1991). Age-specific reproduction in feral horses. *Can. J. Zool.* 69, 738–743. doi: 10.1139/z91-106
- Garrott, R. A., and Siniff, D. B. (1992). Limitations of male-oriented contraception for controlling feral horse populations. *J. Wildlife Manage.* 56, 456–464. doi: 10.2307/3808859
- Garrott, R. A., and Taylor, L. (1990). Dynamics of a feral horse population in Montana. *J. Wildlife Manage.* 54, 603–612. doi: 10.2307/3809357
- Gering, E., Incorvaia, D., Henriksen, R., Wright, D., and Getty, T. (2019). Maladaptation in feral and domesticated animals. *Evolutionary Appl.* 12, 1274–1286. doi: 10.1111/eva.12784
- Grange, S., Duncan, P., and Gaillard, J.-M. (2009). Poor horse traders: large mammals trade survival for reproduction during the process of feralization. *Proc. R. Soc. B* 276, 1911–1919. doi: 10.1098/rspb.2008.1828
- Grange, S., Duncan, P., Gaillard, A.R.E. Sinclair, P.J.P. Gogan, J.-M., Packer, C., Hofer, H., and East, M. (2004). What limits the Serengeti zebra population? *Oecologia* 140, 523–532. doi: 10.1007/s00442-004-1567-6
- Grant, L. R., Griffin, P., Weikel, J., and Pielstick, L. (2021). High pregnancy rates in two-year-old wild horses. *Northwest Nat.* 102, 252–253. doi: 10.1898/1051-1733-102.3.252
- Greger, P. D., and Romney, E. M. (1999). High foal mortality limits growth of a desert feral horse population in Nevada. *Great Basin Nat.* 59, 374–379. Available online at: <https://www.jstor.org/stable/41713139> (Accessed February 15, 2026).
- Griffin, P. C., Ekernas, L. S., Schoenecker, K. A., and Lubow, B. C. (2020). *Standard operating procedures for wild horse and burro double-observer aerial surveys. US Geological survey techniques and methods, book 2, chapter A16* (Washington, D.C: U.S. Dept of Interior).
- Heffelfinger, L. J., Stewart, K. M., Bush, A. P., Sedinger, J. S., Darby, N. W., and Bleich, V. C. (2018). Timing of precipitation in an arid environment: Effects on population performance of a large herbivore. *Ecol. Evol.* 8, 3354–3366. doi: 10.1002/ece3.3718
- Hennig, J. D., Duchardt, C. J., Esmaceli, S., Fuhlendorf, S. D., Beck, J. L., Francisco, T. I., et al. (2023). A crossroads in the rearview mirror: the state of United States feral equid management in 2023. *BioScience* 73, 404–407. doi: 10.1093/biosci/biad033
- Hornocker, M. G. (1970). An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. *Wildlife Monogr.* 21, 3–39. Available online at: <https://www.jstor.org/stable/3830518> (Accessed February 15, 2026).
- Hurley, M., Unsworth, J. W., Zager, P., Hebblewhite, M., Garton, E. O., Montgomery, D. M., et al. (2011). Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monogr.* 178, 1–33. doi: 10.1002/wmon.4
- Iacono, P. C., Schoenecker, K. A., Manlove, K., Jackson, P. J., and Stoner, D. C. (2024). Evaluating mountain lion diet before-and-after feral horse removal in a semi-arid environment. *Ecosphere* 15, e4919. doi: 10.1002/ecs2.4919
- Jenkins, S. H. (2002). *Feral horse population model, WinEquus* (Reno, NV: University of Nevada).
- Johnson, H. E., Hebblewhite, M., Stephenson, T. R., German, D. W., Pierce, B. M., and Bleich, V. C. (2013). Evaluating apparent competition in limiting the recovery of an endangered ungulate. *Oecologia* 171, 295–307. doi: 10.1007/s00442-012-2397-6
- Keiper, R., and Houpt, K. (1984). Reproduction in feral horses: an eight year study. *Am. J. Veterinary Res.* 45, 991–995. doi: 10.2460/ajvr.1984.45.05.991
- Kellner, K. (2016). jagsUI: A wrapper around “rjags” to streamline “JAGS” analyses. Available online at: <https://cran.r-project.org/web/packages/jagsUI/jagsUI.pdf> (Accessed October 26, 2024).

- King, S. R. B., Cole, M. J., Barton, C., and Schoenecker, K. A. (2023). Proximate factors affecting mortality and maternal abandonment of young free-roaming feral horse foals. *J. Veterinary Behav.* 66, 1–10. doi: 10.1016/j.jvbeh.2023.06.006
- King, S. R. B., and Schoenecker, K. A. (2025). Effects of phylogeny and habitat on social structure and behavior of two equid species. *Behav. Ecol. Sociobiol.* 79, 1–21. doi: 10.1007/s00265-025-03602-7
- Kinley, T. A., and Apps, C. D. (2001). Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Soc. Bull.* 29, 158–164. Available online at: <https://www.jstor.org/stable/3783993> (Accessed February 15, 2026).
- Knopff, K. H., Knopff, A. A., Kortello, A., and Boyce, M. S. (2010). Cougar kill rate and prey composition in a multi-prey system. *J. Wildlife Manage.* 74, 1435–1447. doi: 10.1111/j.1937-2817.2010.tb01270.x
- Kricher, J. C., and Morrison, G. (1993). *A field guide to the ecology of western forests* (Boston, MA: Houghton-Mifflin Co.).
- Laundré, J., Hernández, L., and Clark, S. G. (2007). Numerical and demographic responses of pumas to changes in prey abundance: Testing current predictions. *J. Wildlife Manage.* 71, 345–355. doi: 10.2193/2005-627
- Leslie, P. H. (1945). On the use of matrices in certain population mathematics. *Biometrika* 33, 183–212. doi: 10.1093/biomet/33.3.183
- Logan, K. A., and Swenor, L. L. (2001). *Desert puma: Evolutionary ecology and conservation of an enduring carnivore* (Washington, DC: Island Press).
- Maehr, D. S., Belden, R. C., Land, D. E., and Wilkins, L. (1990). Food habits of panther in southwest Florida. *J. Wildlife Manage.* 54, 420–423. doi: 10.2307/3809651
- McEvoy, D. J., Pierce, D. W., Kalansky, J. F., Cayan, D. R., and Abatzoglou, J. T. (2020). Projected changes in reference evapotranspiration in California and Nevada: Implications for drought and wildland fire danger. *Earth's Future* 8, e2020EF001736. doi: 10.1029/2020EF001736
- Morris, W. F., and Doak, D. F. (2002). *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis* (Sunderland, Massachusetts, U.S.A: Sinauer Associates, Inc.).
- National Research Council [NRC] (2013). *Using science to improve the BLM Wild Horse and Burro Program: a way forward* (Washington, D.C., USA: National Academies Press).
- Neaux, D., Sansalone, G., Lecompte, F., Haruda, A., Schafberg, R., and Cucchi, T. (2020). Examining the effect of fertilization on craniomandibular morphology in pigs, *Sus scrofa* (Artiodactyla: Suidae). *Biol. J. Linn. Soc.* 131, 870–879. doi: 10.1093/biolinnean/blaa156
- Newmark, W. D., and Rickart, E. A. (2012). High-use movement pathways and habitat selection by ungulates. *Mamm. Biol.* 77, 293–298. doi: 10.1016/j.mambio.2012.03.007
- Ockenfels, R. A. (1994). Mountain lion predation on pronghorn in central Arizona. *Southwestern Nat.* 39, 305–306. doi: 10.2307/3671604
- Phillips, D. (2018). *Wild horse country: the history, myth, and future of the mustang, America's horse* (New York, NY: W.W. Norton & Co.).
- Pierce, B. M., and Bleich, V. C. (2003). "Mountain lion," in *Wild mammals of North America: biology, management, and conservation*, 2nd ed. Eds. G. A. Feldhamer, B. C. Thompson and J. A. Chapman (The Johns Hopkins University, Baltimore, MD), 744–757.
- Pierce, B. M., Bleich, V. C., Monteith, K. L., and Bowyer, R. T. (2012). Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *J. Mammal.* 93, 977–988. doi: 10.1644/12-MAMM-A-014.1
- Plummer, M. (2003). "JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling," in *Proceedings of the 3rd international workshop on distributed statistical computing*, vol. 124. Eds. K. Hornik, F. Leisch and A. Zeileis (Vienna, Austria), 1–10.
- Proffitt, K. M., Garrott, R., Gude, J. A., Hebblewhite, M., Jimenez, B., Paterson, J. T., et al. (2020). Integrated carnivore-ungulate management: a case study in west-central Montana. *Wildlife Monogr.* 206, 1–28. doi: 10.1002/wmon.1056
- Public Law 92-195 (1971). *The Wild Free-Roaming Horses and Burros Act of 1971. Authenticated U.S. Government information* (Washington, D.C., USA: United States Government Printing Office).
- Ransom, J. I., Lagos, L., Hrabar, H., Nowzari, H., Usukhjargal, D., and Spasskaya, N. (2016). "Wild and feral equid population dynamics," in *Wild equids: ecology, management and conservation*. Eds. J. Ransom and P. Kaczensky (Johns Hopkins University Press, Baltimore, MD), 68–86.
- R Core Team (2023). *R: A language and environment for statistical computing* (Vienna, Austria: R Foundation for Statistical Computing).
- Robinson, H. S., Wielgus, R. B., and Gwilliam, J. C. (2002). Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Can. J. Zool.* 80, 556–568. doi: 10.1139/z02-025
- Roelle, J. E., Singer, F. J., Zeigenfuss, L. C., Ransom, J. I., Coates-Markle, L., and Schoenecker, K. A. (2010). *Demography of the Pryor Mountain Wild Horses 1993-2007: U.S. Geological Survey Scientific Investigations Report 2010-5125* (Washington, D.C.: U.S. Dept of Interior).
- Ross, P. I., and Jalkotzy, M. G. (1996). Cougar predation on moose in southwestern Alberta. *Alces* 32, 1–8. Available online at: <https://alcesjournal.org/index.php/alces/article/view/827> (Accessed February 15, 2026).
- Ross, P. I., Jalkotzy, M. G., and Fest-Bianchet, M. (1997). Cougar predation on bighorn sheep in southwestern Alberta during winter. *Can. J. Zool.* 74, 771–775. doi: 10.1139/z97-098
- Ruprecht, J., Forrester, T. D., Clark, D. A., Wisdom, M. J., Smith, J. B., and Levi, T. (2024). Variability and correlations among vital rates and their influence on population growth in mule and black-tailed deer. *J. Wildlife Manage.* 89, 1–20, e22690. doi: 10.1101/2024.03.15.585316
- Sánchez-Villagra, M. R. (2022). *The process of animal domestication* (Princeton, NJ: Princeton University Press).
- Satué, K., Felipe, M., Mota, J., and Muñoz, A. (2011). Factors influencing gestational length in mares: A review. *Livestock Sci.* 136, 287–294. doi: 10.1016/j.livsci.2010.09.011
- Sawyer, H., and Lindzey, F. G. (2002). *A review of predation on bighorn sheep (Ovis canadensis)* (Laramie, WY: Wyoming Cooperative Fish and Wildlife Research Unit).
- Schaub, M., and Kéry, M. (2021). *Integrated population models: Theory and ecological applications with R and JAGS* (London, U.K: Elsevier. Academic Press).
- Schoenecker, K. A., King, S. R., and Messmer, T. A. (2021). The Wildlife Professions Duty in Achieving Science-Based Sustainable Management of Free-Roaming Equids. *The Journal of Wildlife Management* 85, 1057–1061.
- Schoenecker, K. A., Crabb, M., Folt, B. P., and Stoner, D. C. (2026). *Population size of horses in five Herd Areas in Nevada 2022 to 2025: U.S. Geological Survey data release* (Fort Collins, CO). doi: 10.5066/P14BABZA
- Schoenecker, K. A., Esmaili, S., and King, S. R. B. (2023). Seasonal resource selection and movement ecology of free-ranging horses in the western United States. *J. Wildlife Manage.* 87, 1–21. doi: 10.1002/jwmg.22341
- Schulman, M. L., Hayes, N. K., Wilson, T. A., and Grewar, J. D. (2024). Immunocontraceptive efficacy of native porcine Zona Pellucida (pZP) treatment of Nevada's Virginia Range free-roaming horse population. *Vaccines* 12, 1–15. doi: 10.3390/vaccines12010096
- Stoner, D. C., Anderson, M. T., Schroeder, C. A., Bleke, C. A., and Thacker, E. T. (2021). Distribution of competition potential between native ungulates and free-roaming equids on western rangelands. *J. Wildlife Manage.* 85, 1062–1073. doi: 10.1002/jwmg.21993
- Stoner, D. C., Sexton, J. O., Choate, D. M., Nagol, J., Bernales, H. H., Sims, S. A., et al. (2018). Climatically driven changes in primary production propagate through trophic levels. *Global Change Biol.* 24, 4453–4463. doi: 10.1111/gcb.14364
- Stubben, C. J., and Milligan, B. G. (2007). Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Software* 22, 11. doi: 10.18637/jss.v022.i11
- Turner, J. W., Wolfe, M. L., and Kirkpatrick, J. F. (1992). Seasonal mountain lion predation on a feral horse population. *Can. J. Zool.* 70, 929–934. doi: 10.1139/z92-132
- Van Duyn, C., Ras, E., De Vos, A. E. W., De Boer, W. F., Henkens, R. G. H. G., and Usukhjargal, D. (2009). Wolf predation among reintroduced Przewalski horses in Hustai National Park, Mongolia. *J. Wildlife Manage.* 73, 836–843. doi: 10.2193/2008-027
- Van Soest, P. J. (1994). *Nutritional Ecology of the Ruminant* (New York, NY: Cornell University Press), 488.
- Wasley, T. (2004). *Nevada's mule deer - population dynamics, issues and influences* (Reno, NV: Nevada Dept. of Wildlife, Biological Bulletin No. 14).
- Watts, A., Johnson, C. N., Carver, S., Butler, C., Harvey, A. M., and Cameron, E. Z. (2020). Maternal protectiveness in feral horses: responses to intraspecific and interspecific sources of risk. *Anim. Behav.* 159, 1–11. doi: 10.1016/j.anbehav.2019.10.018
- Wittmer, H., McLellan, B. N., Seip, D. R., Young, J. A., Kinley, T. A., Watts, G. S., et al. (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Can. J. Zool.* 83, 407–418. doi: 10.1139/z05-034
- Wolfe, M. L. (1980). Feral horse demography - a preliminary report. *J. Range Manage.* 33, 354–360. doi: 10.2307/3897882
- Wolfe, M. L. (1986). Population dynamics of feral horses in western North America. *Equine Veterinary Sci.* 6, 231–235. doi: 10.1016/S0737-0806(86)80046-6
- Wolfe, M. L., Ellis, L. C., and MacMullen, R. (1989). Reproductive rates of feral horses and burros. *J. Wildlife Manage.* 53, 916–924. doi: 10.2307/3809588