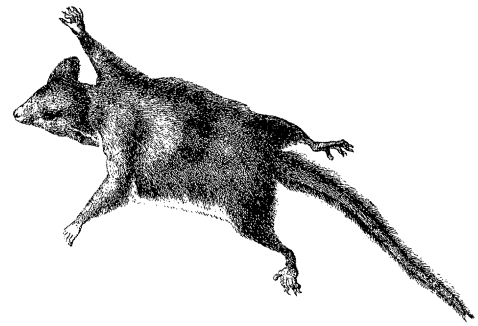

Commentary

Management implications of the ecology of free-roaming horses in semi-arid ecosystems of the western United States

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Abstract Compared to other ungulates of North America, free-roaming horses (*Equus caballus*) possess a unique evolutionary history that has given rise to a distinct suite of behavioral, morphological, and physiological traits. Because of their unique combination of cecal digestion, an elongate head with flexible lips, and non-uniform use of the landscape, horses represent a unique disturbance agent in semi-arid ecosystems of the western United States. Consequently, it is inappropriate to assume that influences of horses on the structure, composition, function, and pattern of arid and semi-arid ecosystems will mirror influences of cattle or other artiodactyls. Although management areas for free-roaming horses occupy 18.6 million ha of land across western North America, we know relatively little about how western ecosystems and their components have responded to this uniquely managed ungulate. I draw on my research of horse habitats in the western Great Basin (U.S.A.) to examine predictions of horses' unique influence, and advocate for continued research to refine our understanding of synecological relationships among horses and diverse ecosystem components in arid and semi-arid regions.

Key words *Bos taurus, Equus caballus,* life-history traits, management, semi-arid ecosystems

Management of free-roaming horses (*Equus caballus*) in western North America has proven to be an ongoing political controversy in the 20th and 21st centuries, and the management challenge has escalated in importance since passage of the Wild Free-Roaming Horse and Burro Act (1971). Local, state, and federal politicians, often using incomplete or faulty knowledge, have increasingly tried to constrain the outcomes of wild horse and burro (*E. asinus*) management (Zarn et al. 1977, Wagner 1983, Bellisle 1997, Bama 1998). Galvanization of interest groups (such as ranchers, animal-rights activists, hunters, conservationists, and horse advocates) is increasingly forcing managers to adopt more rigorous, scientifically based methods and analyses to justify management actions. Although free-roaming horses have inhabited western North America since the end of the 16th century, little synecological research has been done to quantitatively characterize how they interact with ecosystem

components there. The National Academy of Sciences recognized the importance of potential effects of free-roaming horses on native biota when they commissioned 6 studies in 1980 to address those effects. However, the database for formulating a sound management program was very limited (Wagner 1983).

This article is written in response to the perceptions of some managers, biologists, and the general public that free-roaming horses are ecologically comparable to domestic cattle (*Bos taurus*) (e.g., equivalencies used in management calculations of Animal Unit Months [AUMs]) and refill niches occupied by equids prior to the Pleistocene megafaunal extinctions (e.g., Zarn et al. 1977, Wagner 1983). Because of the former perception, their influence on structure, composition, and function of semi-arid ecosystems is explicitly or (more often) implicitly assumed to parallel cattle influences. I describe the biology of free-roaming horses in western North America, and draw from my research in 9 herd management areas of the western Great Basin (U.S.A.) to highlight ways that horses constitute a unique influence on western landscapes. To further clarify the role that horses play in disturbance regimes of western North America, I conclude that further synecological research is needed to characterize how this herbivore interacts with other ecosystem components.

History and genetics of wild horses in North America

Although equids arose and diversified in North America (Simpson 1951), they were one of 18 taxa known from the Great Basin to vanish from the continent at the end of the Pleistocene around 10,000-14,000 years ago (Grayson 1993). This wave of extinctions resulted from hunting by prehistoric humans, climate change (and resulting vegetation shifts), or a combination of the two (Martin 1984, references in Martin and Klein 1984, Grayson 1993). After equids were absent from North America for at least 10,000 years, domestic horses were brought to the southwestern United States by Spaniards near the end of the 16th century (Zarn et al. 1977, Wagner 1983, Fradkin 1989). Reductions in predator numbers, increased availability of water due to construction of "wildlife guzzlers," increased mobility facilitated by fences in disrepair, and the longstanding commensal relationship between horses and humans resulted in the number of free-roaming horses in the United States rising to an estimated peak of 2-7 million animals during the 19th century (Ryden 1978, Thomas 1979). However, numbers of horses declined steadily during the late 19th through the mid-20th century because of persecution, domestication, and other means of removal, facilitated by the Taylor Grazing Act of 1934 (Wagner 1983).

With protection afforded by the Wild Free-Roaming Horse and Burro Act of 1971, which was enacted largely in response to inhumane treatment of free-roaming horses, numbers of horses on public lands rose sharply from approximately 17,300 in 1971 to an estimated peak of 57,200 in 1978 (Wagner 1983, Anonymous 1997). Given the changes in selective forces mentioned above, many herds have exhibited annual population growth rates of 20% and higher (Wolfe 1980, Eberhardt et al. 1982, Anonymous 1997). According to a recent Bureau of Land Management (BLM) estimate (30 May 2002), free-roaming horses in the western United States currently number around 38,815 individuals on 208 herd management areas encompassing 17.5 million ha of BLM-administered lands across 10 states. In addition, lands administered by the United States Forest Service (that contain other jurisdictions) contribute an additional 1.1 million ha and approximately 1,600 animals (Anonymous 1997). In Nevada, the state with the most animals and herd areas, nearly 30% of the state's area is occupied by horse and burro herd management areas (Anonymous 1997, Hammond World Atlas Corporation 2000).

Several authors have suggested that current populations of free-roaming horses in the western United States are not the result of a single introduction 350-450 years ago but rather the amalgamation of repeated introductions of domestic horses and subsequent mixing with already established feral herds (e.g., Ryden 1978, Wagner 1983). Similarly, Beebe and Johnson (1964) suggested that due to repeated interbreeding with released or abandoned domestic horses, the free-roaming horse of the western United States differs little from other small domestic horse breeds. Ryden (1978) believed that descendants of the original Andalusian horses brought from Spain to the Americas numbered in the hundreds and had largely been removed to captivity. Bowling (1994) compared 19 polymorphic loci from blood samples of 975 free-roaming horses from 7 Great Basin sites with samples from 16 domestic horse breeds and

found no difference in either number of variants or expected heterozygote frequency. From pairwise comparisons of Nei's genetic distance measurements, Bowling (1994) concluded that Great Basin horses originated from Iberian, American saddle horse, and draft horse breeds.

Because free-roaming horses are relatively easy to study (in that they are large, easily detectable, diurnal, and found in groups), there is a relatively well-developed literature on various aspects of horse biology. These studies include descriptive studies of diet (e.g., Hansen 1976) and of partitioning of dietary and habitat niches when horses are sympatric with other native and domestic ungulates (e.g., Hubbard and Hansen 1976, Olsen and Hansen 1977, Hanley and Hanley 1982, Krysl et al. 1984, McInnis and Vavra 1987, Coates and Schemnitz 1994). Behavioral ecology research has suggested that because of their large body size and great speed and power, free-roaming horses are socially dominant when interacting with native ungulates of the Great Basin, producing effects on wildlife species different from those produced by cattle (Meeker 1979, Berger 1985).

Moreover, studies have addressed genetic questions related to herd uniqueness and concern for minimum viable populations (e.g., Bowling and Touchberry 1990, Goodloe et al. 1991, Gross 2000) as well as issues of social biology (Feist 1971, Miller 1980, Berger 1986, Turner et al. 1992) and reproductive biology (Eberhardt et al. 1982, Seal and Plotka 1983, Garrott et al. 1991). Immunocontraception has been deemed the most humane and socially acceptable method of population control, and studies have proliferated in recent years to fine-tune this technique for management (e.g., Turner et al. 1997, Powell and Monfort 2001).

Although our understanding of the autecology (i.e., the biology of organisms or populations, without regard to other elements in the ecosystem) of horses and their interactions with other ungulates has improved greatly in recent decades, understanding how free-roaming horses interact with the non-ungulate components of semi-arid ecosystems is only beginning (Crane et al. 1997, Fahnestock 1998, Fahnestock and Detling 1999, Peterson 1999). This is especially curious, given that research on grazing impacts on plant communities was given the highest priority by the Committee on Wild and Free-Roaming Horses and Burros over 2 decades ago (Wagner et al. 1980). Given the large extent of land that horse management areas occupy, an understanding of how horses affect various components of their environment seems vitally important. In studying 2 sagebrush-dominated elevational strata across 9 mountain ranges of the Great Basin during 2 wet years, I found that horse-occupied areas possessed more deer mice (*Peromyscus maniculatus*), more depauperate rodent guilds, fewer ant mounds, and more plant species, in addition to lower grass and shrub cover, than did horse-removed areas (Beever et al. 2003). This result suggests that there remains room to fine-tune both our understanding of free-roaming horses' roles in semi-arid landscapes and the determination of ecologically appropriate herd sizes.

Comparison of free-roaming horses and other large herbivores in western North America

Compared to other ungulates of North America, horses possess a unique evolutionary history that has given rise to a distinct suite of behavioral, morphological, and physiological traits (Simpson 1951, Hafez et al. 1969, Feist and McCullough 1975, Janis 1976, Berger 1986). In contrast to other large Intermountain West ungulates that are ruminants, horses are cecal digesters (Janis 1976, Hanley and Hanley 1982). Combined with their large body size, this type of digestion places more time–energy constraints on the animal, meaning that the free-roaming horse is one of the least-selective ungulate grazers across most of western North America (Hanley and Hanley 1982). Thus, fewer plant species may remain ungrazed in areas occupied by free-roaming horses compared to areas grazed by other ungulates. Although elk (*Cervus elaphus*) and feral burros can also consume a broad spectrum of food items, these species occupy only small portions of the area encompassed by the 18.6 million ha of wild-horse herd areas. This use of a lower-quality diet requires that horses consume 20–65% more forage than would a cow of equivalent body mass (Hanley 1982, Wagner 1983, Menard et al. 2002). In addition, horses possess a more elongate head and more flexible lips than cattle and, unlike cattle, have upper front incisors. Consequently, they can trim vegetation more closely to the ground than do cattle, sometimes delaying the recovery of plants (Symanski 1994, Menard et al. 2002).

Differences between free-roaming horses and cattle become more numerous and more pronounced

as one scales up to investigate how the biology of horses translates into grazing consequences at the landscape scale (i.e., within and across mountain ranges). For example, horses often segregate elevationally from sympatric cattle, using steeper slopes and occupying higher elevations (Pellegrini 1971, Ganskopp and Vavra 1986). This difference may stem in part from the fact that free-roaming horses in North America are related to the truly wild Przewalski's horse (*E. c. przewalskii*) native to the cooler Asian and European steppes (Wagner 1983, van Dierendonck and Wallis de Vries 1996). Several authors have noted horses' disproportionately high use of ridgetops and high benches (Pellegrini 1971, Miller 1980, Keiper and Berger 1982, Ganskopp and Vavra 1987). I agree with Pellegrini's (1971) premise that such behavior may be an effort to maximize the viewshed of the horse, rather than pest avoidance as suggested by Keiper and Berger (1982). This behavior may represent an evolutionary vestige of a "flight" response to predation predominantly in the past, a phenomenon not generally observed in cattle on western landscapes.

Another difference between cattle and free-roaming horses is that horses tend to use semi-arid landscapes more heterogeneously at some spatial scales than do cattle. At the smallest scales, horses will use a few trails repeatedly to cross the landscape (Figures 1*a*, 1*b*), whereas cattle more often graze all portions of an area with similar intensity (Menard et al. 2002). Horses restrict themselves to fewer pathways partly because of their territoriality—they patrol the territory boundary of the group repeatedly (Pellegrini 1971, Zarn et al. 1977). Horses also use only a few trails to travel to and from water (particularly during the driest seasons), traveling farther from water each day than do cattle (Pellegrini 1971, Green and Green 1977). In contrast, cattle tend to stay close to springs or riparian areas throughout the day and season, unless managed otherwise (review in Kauffman and Krueger 1984). Cattle also create detectable trails in some

Figure 1. Examples of heterogeneity in habitat use by free-roaming horses in semi-arid ecosystems. (*a*) Trails primarily created by horses traveling across a sagebrush-dominated hillside on Dogskin Mountain, western Nevada. (*b*) Trails created by horses in salt-scrub habitat, central Nevada.

instances, but often the number, length, and spatial extent of cattle trails are less than horse trails (personal observation). As a means of territorial establishment and boundary marking (Pellegrini 1971), free-roaming horses concentrate their defecations in dung posts and stud piles that can reach over 60 cm in height and >10 m^2 in extent (Pellegrini 1971). In contrast, unless they are near a watering source, cattle distribute themselves and their defecations more uniformly across the landscape. At the landscape scale, concentration of cattle at watering areas constitutes an exception to the generality of greater heterogeneity in habitat use by horses compared to cattle. Heterogeneous use of landscapes by free-roaming horses should translate into different effects on the processes of soil stabilization, water retention, and nutrient cycling, as well as on vegetative characteristics, than mosaics created by cattle grazing.

To test this prediction, I examined the ecosystem consequences of heterogeneous use of a landscape by free-roaming horses in field research in western Nevada at sites in high- and low-elevation big sagebrush (*Artemisia tridentata*) habitats. At the broadest (landscape) scale, sites from which horses had been removed for 10–14 years exhibited significant differences in vegetative characteristics (e.g., grass cover, shrub cover, species richness) from horse-grazed sites (Beever 1999, Beever et al. 2003). In addition, I observed trends of the same magnitude and direction when I compared, within horse-grazed sites, randomly located line-intercept transects with transects placed alongside established horse trails (25–30 cm from the trail center) (Beever 1999). Specifically, randomly located transects at horse-occupied sites exhibited an average of 1.2–9.5 times greater grass cover, lower forb cover (at all but the lowest-elevation site), 1.6–2.5 times greater shrub cover, and greater species richness of shrubs than did "horse-trail" transects. This second-level (smaller-scale, within-site) comparison corroborates the existence of heterogeneity in grazing intensity at both the landscape and site scales.

In addition, I used a handheld penetrometer to measure penetration resistance of soil surface horizons (a surrogate of soil-surface hardness) at both horse-removed and horse-grazed sites. I sampled 10 points within a 1-m-diameter circle at each of 25 locations per 1.82-ha site (see Beever et al. 2003), and hypothesized that relative variability in hardness values among locations within a site would be higher at horse-grazed sites, due to horses' heterogeneous use of the landscape. Relative variability (as measured by CV) in penetration resistance averaged 1.65 times higher at horse-occupied sites in 1997 sampling, even though resistance was 3.0 and 4.5 times higher at horse-occupied sites at high elevations and low elevations, respectively (E. Beever, unpublished data; Beever et al. 2003). Sampling in 1998 showed an even greater difference in penetration resistance, as horse-occupied sites exhibited 17.4 times higher penetration resistance than horse-removed sites at low elevations and 2.9 times higher penetration resistance at high elevations (E. Beever, unpublished data; Beever et al. 2003). The much lower means dictated that horse-removed sites in 1998 did not have greater variability in soil hardness but rather exhibited significantly lower relative variability than horse-occupied sites. Thus, the greater amount of absolute variability observed at horse-occupied sites in 1998 was overridden by the vast difference in mean hardness.

Due to the differences noted above, it is inappropriate to assume that effects of grazing by free-roaming horses are similar in nature or in magnitude to effects of grazing observed for cattle or other species. Even among the closely related African equids, Klingel (1972) noted considerable differences in social organization. Differences such as grouping behavior can affect movement patterns in horses (Berger 1986) and other ungulate populations (Bailey 1984, Feh et al. 1994). Ways in which greater heterogeneity in habitat use by horses (relative to cattle) at several spatial scales translates into effects on patch dynamics, landscape ecology, and a cumulative measure of ecosystem function remain unknown. Consequently, in light of the tremendous amount of controversy engendered by issues of horse management (Thomas 1979, Wagner 1983, Linklater et al. 2002), it is important to study both the interactions of free-roaming horses with other species and their general effects on ecosystems. Recent studies of horses in more mesic ecosystems (e.g., Levin et al. 2002, Menard et al. 2002) have provided an insightful first step in that direction. For example, in 2 wetlands in France, Menard et al. (2002) found that cattle used forbs and shrubs much more than did horses, whereas horses spent more time feeding in short-grass areas and maintained a mosaic of patches of short and tall grass. However, these ecosystems have horses present in only limited numbers and over a limited area, and their response to horse grazing is likely fundamentally different than what would be expected in

semi-arid ecosystems where thresholds and nonlinear dynamics dominate (Mack and Thompson 1982, Laycock 1991).

Just as it is questionable to extrapolate past research on grazing or browsing effects of other ungulates to horses, extrapolating results of numerous published studies on domestic horses to free-roaming populations may be problematic, particularly with respect to behavior. Since the time horses were first released into North America ca. 350-450 years ago, they may have diverged from their mixed domestic ancestry in some traits. When compared to the average generation time of free-roaming horses, approximately 3-6 years, 350-450 years translates into approximately 75-150 generations during which natural selection could have acted. However, because free-roaming herds have continued to receive immigrants from and interbred with domestic horses, differences between domestic and free-roaming animals more likely simply reflect phenotypic plasticity in horses experiencing different availability of forage, demographics, and available habitats, rather than genetic divergence. For example, eliminative behavior in free-roaming horses is often concentrated at "stud piles" along edges of territories dominated by harem-possessing stallions (Pellegrini 1971, Miller 1980). In contrast, such concentration of feces is generally not observed to the same degree in domestic horses, even in large pasture areas (Ödberg and Francis-Smith 1977). Because eliminative behavior may direct horse movements and affect nutrient cycling at various scales, spatial distribution of grazing effects may thus differ between domestic and free-roaming horses.

Another behavior that may differ between domestic and free-roaming horses is grouping. Although domestic horses may exhibit social stratification (Hafez et al. 1969), they do not appear to exhibit the full complement of associations (e.g., harem bands, multiple male and female bands, and bachelor groups) observed in free-roaming horses (Feist 1971, Berger 1977, Zarn et al. 1977, Miller 1980). However, in domestic settings the proportions of horses that are mares, yearlings, geldings, and studs will greatly influence the diversity of associations observed. Thus, knowledge of the grazing ecology of domestic horses in captive settings (Hafez et al. 1969, Reiner and Urness 1982) may not accurately predict expected consequences of free-roaming horse grazing, due to differences in their behavior. Free-roaming horses are believed by some to possess harder hooves and have ability to last for longer periods without water than some domestic horse breeds (S. Kipping, BLM, Washington D.C., personal communication), though this contention has not been demonstrated with empirical data.

In summary, because of the behavioral differences between captive and free-roaming horses (which may or may not reflect heritable traits), we cannot uncritically rely on studies of domestic horses to help us understand ecosystem response to free-roaming horses. More investigations are needed on free-roaming horse populations to predict how they will influence their surroundings.

Management considerations and conclusion

In addition to the differences noted above, a final suite of differences between horse and cattle influences on semi-arid landscapes arises from the unique management status of horses. Free-roaming horses are not managed as wild or as domestic animals; they currently occupy a unique political status among large mammals of North America. Although cattle and free-roaming horses are of similar size, cattle generally are managed more intensively (e.g., with fencing exclosures and enclosures, rotation grazing, herding, provision of salt licks and supplemental water, etc.) than are horses. In contrast, horses by law must be managed under a "minimal management strategy." For example, other than during periodic removals, many free-roaming herds of horses are not fenced. In contrast to other wild ungulates, however, hunting of horses is not permitted, as mandated by the Wild Free-Roaming Horse and Burro Act of 1971. These policies constrain possible management strategies and mean that distribution of horse grazing across semi-arid landscapes will diverge greatly from cattle distribution.

Herbivory and trampling may occur across a larger percentage of the physiographically heterogeneous Intermountain West with the addition of wild horses (*sensu* Symanski 1994), as in Australia (Symanski 1994). Other ungulates such as mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) also use upland and steep areas (Ganskopp and Vavra 1987). These ungulates are substantially lighter and possess smaller hoof-surface areas than horses (Symanski 1994); consequently, native ungulates may exert less physical impact on plants and upper soil horizons than do free-roaming horses at similar densities.

My purpose in this article has not been to argue whether horses in western North America should be considered "wild" or "feral." I refer readers to the thoughtful and well-balanced treatment of that controversy by the Committee on Wild and Free-Roaming Horses and Burros (Wagner et al. 1982). My purpose has been to highlight the uniqueness of the free-roaming horse among large herbivores of western North America, and to explore ways in which their differences from other ungulates may translate onto managed landscapes. Paleontological and other lines of evidence have suggested that large-bodied grazers existed at low densities across the Intermountain West from the Pleistocene extinctions of 10,000–14,000 years ago until >180 years ago (Mack and Thompson 1982; Milchunas et al. 1988, Grayson 1993). Relative to grassland and savannah ecosystems, ecosystems that have experienced herbivory infrequently or at low intensity over evolutionary time may be less resilient to contemporary nonnative grazing, and may require more careful monitoring of responses to grazing of both plants and other ecosystem components to avoid deterioration.

Determining whether extant free-roaming horse populations exhibit density-dependent population regulation is complicated by at least three factors, reducing the utility of this consideration in management decisions: 1) horse population levels are likely kept below the carrying capacity of landscapes by periodic removals; 2) ability of management areas to sustain horses depends on the degree of niche overlap between horses and native herbivores in the area (Wagner 1983); and 3) density-independent mortality (e.g., from catastrophes or extremely severe conditions) occurs periodically.

In closing, I acknowledge that results from ecological research on free-roaming horses will be implemented in the context of a highly complex sociopolitical arena (Wagner 1983, Boyles 1986, Linklater et al. 2002). Given current legislation, there is no question that some number of free-roaming horses will be maintained in the United States. The primary management questions are how many horses there should be, how they should be distributed, and, following these, how to control horse numbers (Wagner 1983). With a clearer understanding of horses' effects, appropriate management levels can be adapted to facilitate grazing intensities and spatial mosaics that explicitly consider all species occupying public lands.

When mandates from ≥2 types of legislation (e.g., Wild Free-Roaming Horse and Burro Act of 1971, Endangered Species Act) come into conflict, I recommend the use of directed ecological research, open communication, and varied means of compromise, achieved through education and consensus-building. Under this strategy, well-planned synecological research and monitoring may be used to direct and bound options presented to the general public. For example, public concern regarding competition between free-roaming horses and either cattle or browsing mule deer or bighorn sheep is widespread. However, conditions necessary to demonstrate ecological competition (i.e., mutually reduced fitness) are difficult to achieve in the field (Wagner 1983), and the contention could be satisfactorily assessed only through replicated factorial experiments with AUMs kept constant across treatments within large-scale enclosures. Numerous aspects of horse management have been driven by political and social forces without sufficient biological understanding (Beever and Brussard 2000, Linklater et al. 2002). Therefore, I recommend enlightening societal concerns with adequate relevant ecological data when determining appropriate management levels (Boyles 1986).

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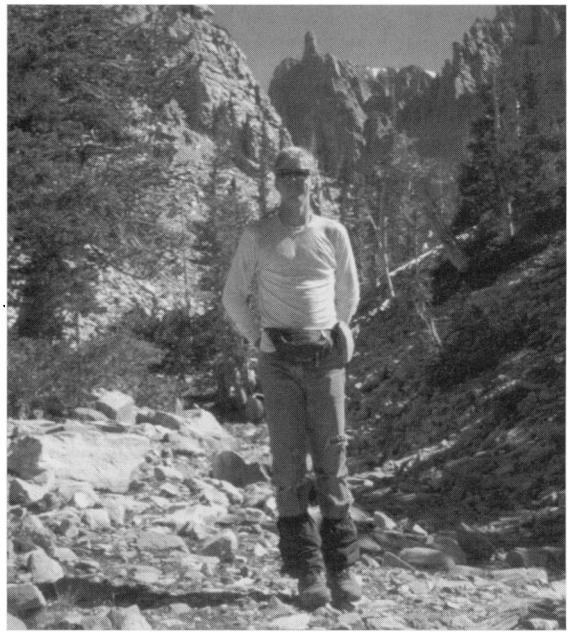

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