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EXAMINING ECOLOGICAL CONSEQUENCES OF FERAL HORSE GRAZING USING EXCLOSURES

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

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

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

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

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

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

Exclosures

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

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

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

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

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

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

Spring Areas

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

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

METHODS

Low-elevation Study Sites: Clan Alpine Mountains

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

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

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

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

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

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

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

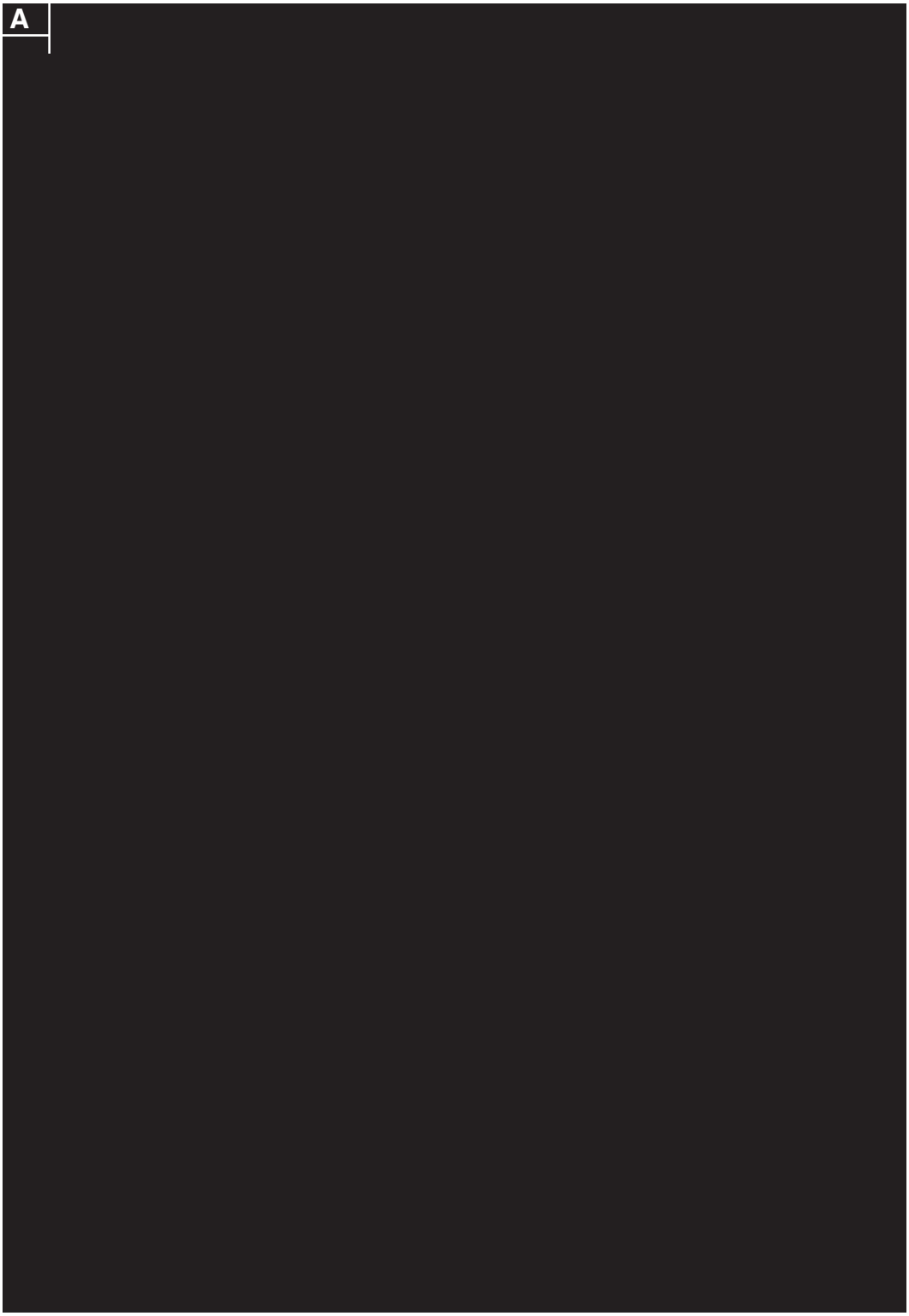
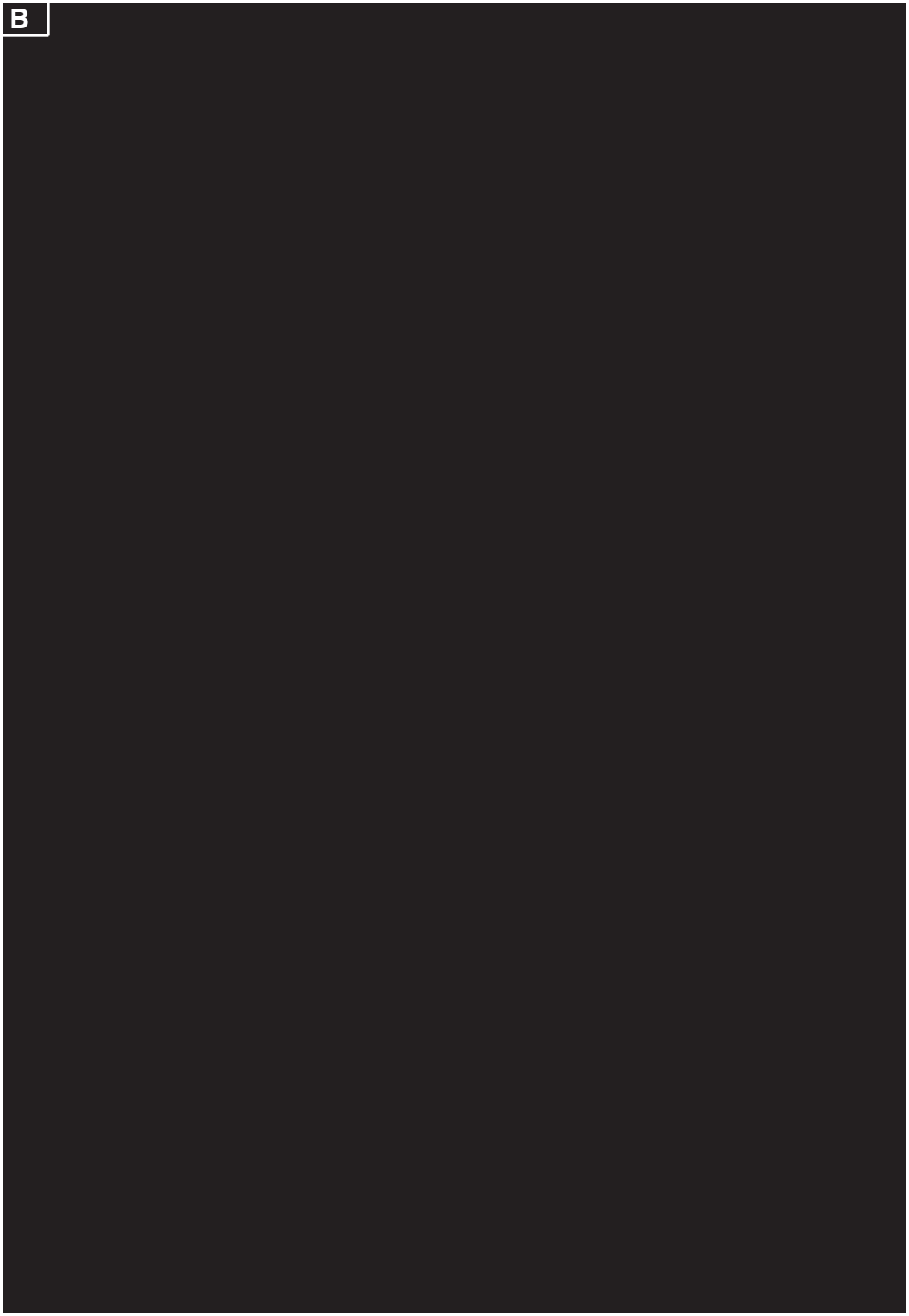


Fig. 1. Location of study plots within State of Nevada (i); within a relief map of the respective mountain range (ii); and as a small-scale schematic (iii). A, Clan Alpine Mountains; B, Seven Troughs Range.


B

High-elevation Study Site: Seven Troughs Range

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

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

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

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

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

Data Analysis

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

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

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

RESULTS

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

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

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

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

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

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

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

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

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

Clan Alpine Mountains

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

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

Seven Troughs Range

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

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

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

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

DISCUSSION

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

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

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

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

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

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

Edge Effects

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

Equivalence of Grazed and Ungrazed Plots

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

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

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

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

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

Recommendations for Future Research

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

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

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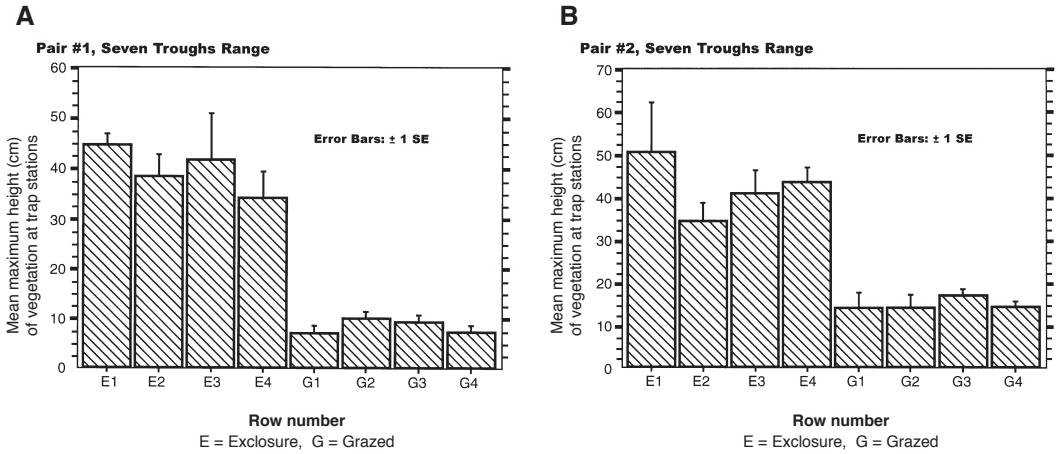

Fig. 3. Maximum height of vegetation (cm ± 1 $s_{\bar{x}}$) at trap stations by row for 2 pairs of meadow plots, Seven Troughs Range. Height at each trap station represents mean of 4 subsamples. Means for each row are obtained by considering each trap station (n = 4 per row) as replicates: A, pair #1,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

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

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

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

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

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

APPENDIX. Continued

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

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