

CHARACTERIZING GRAZING DISTURBANCE IN SEMIARID ECOSYSTEMS ACROSS BROAD SCALES, USING DIVERSE INDICES

ERIK A. BEEVER,^{1,3} ROBIN J. TAUSCH,² AND PETER F. BRUSSARD¹

¹Program in Ecology, Evolution, and Conservation Biology/314, University of Nevada, Reno, Nevada 89557 USA
²USDA Forest Service, Rocky Mountain Research Station, 920 Valley Rd., Reno, Nevada 89512 USA

Abstract. Although management and conservation strategies continue to move toward broader spatial scales and consideration of many taxonomic groups simultaneously, researchers have struggled to characterize responses to disturbance at these scales. Most studies of disturbance by feral grazers investigate effects on only one or two ecosystem elements across small spatial scales, limiting their applicability to ecosystem-level management. To address this inadequacy, in 1997 and 1998 we examined disturbance created by feral horses (*Equus caballus*) in nine mountain ranges of the western Great Basin, USA, using plants, small mammals, ants, and soil compaction as indicators. Nine horse-occupied and 10 horse-removed sites were stratified into high- and low-elevation groups, and all sites at each elevation had similar vegetation type, aspect, slope gradient, and recent (≥ 15 -yr) fire and livestock-grazing histories. Using reciprocal averaging and TWINSpan analyses, we compared relationships among sites using five data sets: abiotic variables, percent cover by plant species, an index of abundance by plant species, 10 disturbance-sensitive response variables, and grass and shrub species considered "key" indicators by land managers. Although reciprocal averaging and TWINSpan analyses of percent cover, abiotic variables, and key species suggested relationships between sites influenced largely by biogeography (i.e., mountain range), disturbance-sensitive variables clearly segregated horse-occupied and horse-removed sites. These analyses suggest that the influence of feral horses on many Great Basin ecosystem attributes is not being detected by monitoring only palatable plant species. We recommend development of an expanded monitoring strategy based not only on established vegetation measurements investigating forage consumption, but also including disturbance-sensitive variables (e.g., soil surface hardness, abundance of ant mounds) that more completely reflect the suite of effects that a large-bodied grazer may impose on mountain ecosystems, independent of vegetation differences. By providing a broader-based mechanism for detection of adverse effects, this strategy would provide management agencies with defensible data in a sociopolitical arena that has been embroiled in conflict for several decades.

Key words: broad spatial scales; disturbance; *Equus caballus*; feral horses; grazing; Great Basin; landscape ecology; monitoring; Nevada; reciprocal averaging; semiarid ecosystems; TWINSpan.

INTRODUCTION

Disturbances, both natural and anthropogenic, produce changes within ecosystems that vary in spatial and temporal extent. Frequency, intensity, scale (extent), and timing (season) are all fundamental aspects of disturbance regimes (Pickett and White 1985). Recovery from disturbance in semiarid systems such as the Great Basin can be relatively slow and uncertain, or may involve systems shifting to new stable states (Laycock 1991, Tausch et al. 1993, Rietkerk and van de Koppel 1997). Several studies in western North America have reported no significant recovery of various ecosystem components after one to several decades of removal of the disturbance agent (McLean and

Tisdale 1972, Rice and Westoby 1978, West et al. 1984, Heske and Campbell 1991, Knapp 1992), but other studies from the same region have found that systems experiencing removal of disturbance can exhibit significant changes over both short and long time scales (Laycock 1967, Dormaar et al. 1994, Dobkin et al. 1998, Beever and Brussard 2000). Clearly, further research on detecting disturbance in semiarid systems can help to clarify the factors that determine response to disturbance, mechanisms by which change occurs, and how effects vary across the landscape.

Ungulates are a disturbance agent that may directly influence arid ecosystems in numerous ways, including consumption of plants, redistribution of nitrogen and plant seeds via urination and defecation, trampling of vegetation, and compaction of soils (Hobbs 1996, Belsky and Blumenthal 1997). Most studies investigating effects of grazing by large mammals, especially feral horses, have been performed at sites distributed over relatively localized regions. Areas such as the Great

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Corresponding Editor: D. P. C. Peters.

³ Present address: USGS-BRD, Forest & Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA. E-mail: erik_beever@usgs.gov

Basin, however, are physiographically very diverse, and many potentially affected taxa exhibit high degrees of local adaptation. Furthermore, response to disturbance can depend upon attributes of the disturbance, as well as on the local coevolutionary history of the species involved in the interaction (Briske 1993, DeAngelis and Huston 1993, Noy-Meir 1993). These sources of variability may severely limit ecologists' ability to extrapolate results of ecosystem response to disturbance or release from disturbance at one or a few sites to broad-scale conclusions (Westoby 1980, Mack and Thompson 1982). Although many small-scale comparisons of acute grazing vs. no grazing have been made, effects of chronic disturbance over broad areas are not well understood. In addition, although disturbance by cattle has been investigated, feral horses are only beginning to be investigated as a disturbance agent. Previous research has found that disturbance by feral horses (*Equus caballus*) can significantly influence aspects of vegetation, small mammals, ants, and soils (Beever 1999; E. A. Beever and P. F. Brussard, unpublished manuscript). Given this knowledge, we used 19 sites located in nine mountain ranges of the Great Basin of the western United States to study the ability of various response variables to detect disturbance by horses across the landscape.

Research in western North America comparing grazing-disturbed areas with protected or recovering areas often focuses attention on one or two types of response variables (e.g., Medin and Clary 1989, Schulz and Leininger 1991, Rosenstock 1996). Even when investigators examine three or more response variables, disturbance effects are frequently evaluated separately for each variable. Although ecosystem management and conservation biology are moving toward more holistic management at larger scales, it is difficult to assess whether disturbance produces a broadly detectable change in semiarid ecosystems. Although results from various studies can be compared to infer how several ecosystem components might react to a single type of disturbance (e.g., Kauffman and Krueger 1984), differences in experimental conditions among studies may confound results and prevent the creation of a unified predictive model. Whereas monitoring and much research often investigate only defoliation-related effects of grazing, we attempted to quantify the effects of numerous grazing-related disturbance processes listed at the beginning of the previous paragraph.

Because of the complex environmental gradients present within the Great Basin, a repeating sequence of more than 200 distinct mountain ranges isolated by numerous valleys (Hunt 1967, Fiero 1986, Grayson 1993), it is difficult to create a monitoring scheme appropriate for assessing disturbance across broad spatial scales. As demonstrated by Brown (1971) and subsequent researchers (e.g., Lawlor 1998), even adjacent mountain range complexes may contain different collections of montane mammal species. This differenti-

ation may be even more pronounced for plant species that have low vagility (Kartesz 1987, Charlet 1991). We therefore sought to compare the ability of different monitoring strategies to detect disturbance by feral horses amidst the clinally complex gradients of Great Basin landscapes.

In most field districts, managers are unlikely to adopt and implement assessments that are prohibitively time-intensive or costly. However, given limited agency budgets, it is important that monitoring: (1) consistently detects change; (2) is sufficiently sensitive to provide an early signal of degradation; (3) provides information across broad spatial scales; and (4) relates to the disturbance processes and mechanisms of change that may influence response variables (Noss 1990). Here we compare sites at both high and low elevations with different degrees of disturbance by feral horses. We applied two multivariate techniques, reciprocal averaging and TWINSpan analysis, to empirical field data collected in 1997 and 1998. We tested whether horse-occupied and horse-removed sites could be discriminated across broad spatial scales using data sets of plant cover (all species or only species of management concern), abiotic variables, and a set of disturbance-sensitive variables related to vegetation, soils, small mammals, and ants.

In evaluating these alternative monitoring strategies, the objectives of our research were to: (1) determine to what extent inherent site (i.e., abiotic) differences existed between selected horse-occupied and horse-removed sites; (2) determine how the composition of plant species at semiarid sites changes across broad spatial scales; (3) ascertain whether diverse disturbance-sensitive variables detect disturbance more consistently than abiotic or strictly plant-related data sets; and (4) compare characterization of horse-occupied and horse-removed sites using commonly monitored response variables ("key" plant species only) with characterization using other data sets.

METHODS

Site selection

We collected data at 17 sites in eight mountain ranges in western and central Nevada during 1997 and 19 sites in nine ranges during 1998 (Table 1, Fig. 1). During both years, sites were stratified into high (2000–2286 m) and low (1340–1700 m) elevations (hereafter, "strata"), corresponding roughly to the lower and upper sagebrush zones. Half of the sites in each elevational stratum had horses removed for the last 10–14 yr; feral horses had access to the remaining ("horse-occupied") sites since at least 1971 (Table 1). Because horses were known from aerial censuses to have used horse-occupied sites during at least some seasons in some years during the 3–8 yr before our sampling, we assumed that disturbance had occurred on these sites. Two low-elevation, horse-removed sites were added in 1998.

Sampling of all response variables occurred within the boundaries of a mammal-trapping grid (area = 1.82 ha per site).

All sites were dominated by big sagebrush (*Artemisia tridentata*), east-facing, of low (<40%) slope gradient, and located within 1.0 km of a dirt road to facilitate small-mammal trapping. Because feral horses often demonstrate a tendency for heavy use of productive mesic sites (Miller 1980, Rogers 1991, Crane et al. 1997, Detling 1998), we compared sites in scrub habitat distant from streams and springs. All sites had not been burned within at least the last 15 yr, and cattle were actively excluded or stocked at low densities (T. Seley and J. Gianola, Bureau of Land Management Horse Specialists, *personal communication*). Consequently, the ratio of horse defecations : cattle defecations across years at all horse-occupied sites exhibited a geometric mean of 10.4:1. Furthermore, fecal counts suggested that intensity of recent cattle grazing did not differ between horse-grazed and horse-removed sites during 1997 ($P = 0.71$) or 1998 ($P = 0.60$). Pellet counts of other ungulates, primarily mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*), also did not differ between horse-occupied and horse-removed areas in either year ($P > 0.20$). Although accurate site-specific data on historical grazing intensities were not available, geographic interspersal of sites, combined with lack of spatial pattern in historical grazing (Young and Sparks 1985), suggested that historical livestock use was not appreciably different between treatment groups. Simultaneously satisfying all seven of these criteria restricted us to two or three sites per mountain range; of these, we selected sites with the least cattle use.

Although many grazing studies use very small-sized plots that are often paired, we argue that larger sized plots correspond more closely with scales at which large-bodied herbivores such as horses will affect ecosystems. Thus, although at the finest scale we chose sites that exhibited maximum homogeneity of big sagebrush vegetation and avoided steep slopes (after satisfying the six other selection criteria), variability in depth to bedrock, color of soils, soil texture, and to some degree, abundance of calcium carbonate varied notably across the 1.82-ha area at many sites. Consequently, variability in soil characteristics within each site and among replicates of an elevation-treatment category rivaled variability between treatments. We collected samples of the upper 20 cm of soil horizons at sites, one from each quadrant of the trapping grid, and dug soil pits to supplement information from NRCS (Natural Resources Conservation Service) soil surveys. We also used cover of dominant shrub and grass species to further clarify which soil series occurred in our plot.

FIELD PROCEDURES

Vegetation

Sampling was conducted from May through August in 1997 and 1998. To characterize vegetation, we used

four 50-m line-intercept transects as subsamples at each site. We measured an index of abundance (the number of individuals intersected per transect; Bonham 1989) and cover (the sum of the lengths of tape intercepted by individual plants, divided by the total transect length) for each plant species encountered (Whittaker 1973). Hereafter, we refer to this index of abundance as simply "abundance." We used a random-number generator to select the mammal trap station at which to begin each transect, but forced selection of one line transect in each quadrant of the grid (Goodall 1952). From preliminary transect work, we found that four dispersed transects consistently captured variability among transects and species richness at sites.

Forbs and grasses with no evidence of current photosynthesis were excluded from measures of cover. Because dense clumping and early senescence of cheatgrass (*Bromus tectorum*) plants made it difficult to identify individuals, cheatgrass values represent the average number of stems that crossed the tape per 50-m transect.

Disturbance-sensitive response variables

We measured penetration resistance using a pocket penetrometer (Soiltest model CL-700, Evanston, Illinois, USA) that measures the pressure required to push the flat end of a 6.4 mm diameter cylindrical rod beyond a distance of 6.4 mm into the soil surface (Bradford 1986, USDA 1993). Hard soil surfaces can decrease infiltration rates, inhibit digging by burrowing mammals, limit plant establishment, and restrict root growth (USDA 1993, Belsky and Blumenthal 1997). Time constraints prevented us from measuring soil moisture and soil structure (including bulk density) directly. Instead, we measured penetration resistance at least 48 h after a precipitation event. Penetration resistance declines with increasing soil moisture and decreasing bulk density. Consequently, a reduction in penetration resistance can reflect higher infiltration, higher water-holding capacity, lower evapotranspiration in near-surface horizons, or lower bulk density. Higher infiltration, in turn, can occur as a result of changes in both soil and vegetation structure. Because penetration resistance values exhibited great variability in preliminary sampling, we adopted a two-tiered sampling strategy at each site that involved taking 10 measurements within 1 m of every fourth mammal trapping station, for a total of 250 subsampled measurements per site. Measurement locations were offset from areas sampled in previous years. All samples were taken in bare inter-spaces (>20 cm from shrub bases); values were discarded and another reading was taken if the penetrometer contacted a rock or shrub root. Although this disturbance variable is abiotic, it is distinguished from the data set of "abiotic" inherent site characteristics by being dynamic and vulnerable to trampling influences.

We trapped small mammals using a 10 × 10 trapping grid with a single 8 × 8 × 25 cm Sherman trap (Sher-

TABLE 1. Physiographic and other characteristics of 19 study sites used to compare horse-occupied and horse-excluded areas in high- and low-elevation sagebrush habitats. Sites occurred in nine mountain ranges in the western Great Basin of North America and were sampled in 1997 and 1998.

Site no.†	Mountain range	Site name	RA tag	Horse status	Elevation (m)	Soil textural classification	Average slope (%)‡
High-elevation, horse-excluded sites							
1	Pah Rah Range	Virginia Peak	P1	absent	2134	stony loam	25
2	Sonoma Range	Lake valley hillside	S1	absent	2164	stony loam	40
3	Sonoma Range	Cabin	S2	absent	2118	stony loam	25
4	Humboldt Range	Pflum Creek Mine	H1	absent	2000	gravelly loam	20
High-elevation, horse-occupied sites							
5	Dogskin Mountain	Dry Valley Creek saddle	D1	present	2060	sandy loam	20
6	Dogskin Mountain	Dry Valley Creek peak	D2	present	2200	sandy loam	30
7	Seven Troughs Range	Side road w/junipers	G1	present	2225	sandy loam	20
8	Seven Troughs Range	High saddle	G2	present	2286	sandy loam	25
Low-elevation, horse-excluded sites							
9	Pah Rah Range	Bigmouth Canyon	P2	absent	1500	sandy loam	15
10	Truckee Range	Jeep trail	T1	absent	1540	sandy loam	5
11	Truckee Range	Sage Hen Creek	T2	absent	1500	sandy loam	10
12	Humboldt Range	Low side valley	H2	absent	1433	sandy loam	25
13	Virginia Range#	Horse Spr1:Fernley view	V1	absent	1400	sandy loam	5
14	Virginia Range#	Horse Spr2:homogen. vly	V2	absent	1500	gravelly loam	5
Low-elevation, horse-occupied sites							
15	Dogskin Mountain	Winnemucca Valley spur	D3	present	1646	sandy loam	25
16	Clan Alpine Mountains	Dixie Valley vista	C1	present	1340	stony loam	10
17	Clan Alpine Mountains	Shoshone Pass	C2	present	1700	gravelly loam	15
18	Virginia Mountains	Flanigan1: Juniper saddle	F1	present	1646	stony loam	20
19	Virginia Mountains	Flanigan2: Juniper Basin	F2	present	1554	stony loam	25

† Site numbers correspond to locations shown in Fig. 1.

‡ Obtained using a handheld clinometer, averaged across the entire sampling area.

§ Subjective classification of exposure, after Wentworth (1976): 0, site somewhat protected by adjacent slopes; 1, site on open slope, unsheltered by adjacent slopes.

|| Subjective classification of disturbance, after Wentworth (1976): 1, apparently undisturbed; 2, slight disturbance; 3, moderate; 4, heavy; 5, severe.

¶ Average from four line-intercept transects performed during 1997 and 1998.

Site sampled in 1998 only.

man, Tallahassee, Florida, USA) at each station, with rows and columns separated by 15 m. Grids were located within homogeneous vegetation assemblages. Trapping occurred for three consecutive rainless nights at each site. We recorded species, sex, body mass (± 0.2 g), trap station, and reproductive status of each animal, and whether it had been captured previously.

We counted aboveground ant mounds within 2 m of an imaginary line drawn along the rows of the trapping grid, which produced a 4×1485 m undulating strip transect. Although we encountered both thatched mounds (produced by *Formica*) and pebble mounds (constructed mostly by *Pogonomyrmex*), we gave a value of 1 to each mound.

Assessment of recent grazing intensity at small spatial scales: fecal counts

At each site, we assessed relative intensity of use by cattle, horses, and all native ungulates by tallying fecal piles within 2 m of the rows of the mammal-trapping grid. To avoid overcounting instances in which an animal defecated while moving across the site, cattle-produced fecal piles < 8 cm in diameter and horse-

produced piles with < 4 pellets were not counted. Fecal counts suggested that the recent intensity of horse grazing varied little among high-elevation sites (184.5 ± 10.2 dung piles per site, mean ± 1 SE). Although one site heavily used by horses created greater variability in intensity among low-elevation sites (96.4 ± 38.8 dung piles per site), this site (C1) did not exhibit consistent differences from other low-elevation sites in RA (Fig. 2) or TWINSpan analyses.

ANALYSIS

Data sets

We characterized sites using five types of variables. The first four, abiotic characteristics (e.g., precipitation, elevation, soil erodibility), abundance by plant species, percent cover by plant species, and percent cover of plant species sampled by horse managers, are commonly used for monitoring. The fifth type included variables that have been shown by previous research (Table 2) to respond to disturbance. We did not pool samples across years because some variables exhibited significant interannual variation (Beever 1999) and because we added two sites in 1998. For each of the

TABLE 1. Extended.

Aspect	Position on slope	Exposure \S	Non-horse disturbance \parallel	Average percent bedrock \parallel	Distance to nearest same-range site (km)
ENE	upper	0	1	3.22	4.4
NE	middle	1	2	0.09	3.1
ENE	lower	0	3	3.99	3.1
NE	middle	0	3	0.68	3.4
E	upper	1	2	4.57	0.6
NE	upper	1	2	1.00	0.6
E	upper	1	2	1.78	0.8
E	middle	1	2	0.11	0.8
E	lower	0	3	0.05	4.4
NE	lower	1	1	0.13	4.1
NE	lower	0	3	0.41	4.1
SE	middle	0	3	0	3.4
ENE	lower	1	2	0	2.7
ENE	middle	0	3	0	2.7
NE	middle	0	4	3.44	2.8
NE	middle	0	1	0.66	12.3
E	middle	1	1	0.02	12.3
E	middle	1	1	0.59	1.1
ESE	middle	0	2	0.76	1.1

abiotic and disturbance data sets, we used a correlation matrix between all variables to identify multicollinearity in our variables ($r > 0.70$). In such cases, we present analyses with the abiotic or disturbance variable whose connection to response variables has been most strongly developed in previous research.

Abiotic variables: inherent site characteristics

We used data from several sources to assess the degree to which sites were distinguishable on the basis of their inherent site properties, as opposed to the more dynamic properties such as soil hardness and vegetative cover in other data sets. Because sites were not near existing weather stations, we used a PRISM model-generated 1:1 190 000 scale map based on 1961–1990 weather data to estimate average annual precipitation at each site (Daly et al. 1994). These modeled long-term averages were then multiplied by the ratio of precipitation received at the nearest weather station during 1997 or 1998 to the 30-yr average received at that station (Hungerford et al. 1989). Values for mean annual number of frost-free days, available water capacity, and erosion factors K and T (an index of susceptibility to erosion by rainfall, and the maximum rate of erosion tolerated to permit sustained crop productivity, respectively) were obtained from published and unpublished soil surveys of the Natural Resources Conservation Service (e.g., Baumer 1983, Zielinski 1994).

Soil types were mixed among high- and low-elevation strata, with horse-occupied and horse-removed sites each having five sites dominated by sandy loams, three with stony loams, and one (or two) with gravelly loams (Table 1). Because most sites contained significant heterogeneity in soil properties within the 1.82-ha area, we estimated values of variables at sites using an average weighted to reflect percentage composition occupied by each of the three soil series in the association at each site. We also recorded (Table 1) the position of the site on the slope, its exposure, non-horse disturbance, and amount of exposed bedrock, following Wentworth (1976). Non-horse disturbance was a categorical estimate, from relatively undisturbed to severely disturbed, that included evidence of human and livestock use at the site (e.g., rubbish, off-road vehicle tracks, livestock defecations). Other variables included Julian date (day 1 = 1 January) of vegetation sampling, elevation in meters, and mean slope gradient measured at numerous locations within each site with a handheld clinometer. Horse-occupied and horse-removed sites did not significantly differ (two-way ANOVAs, $P > 0.05$; $0.05 < \text{power} < 0.50$) in any of their abiotic properties previously mentioned or in their depth to bedrock when each variable was analyzed individually using published NRCS, modeled, or field-collected data (Beever 1999). Horse-removed and horse-occupied sites also did not differ systematically in their soil color,

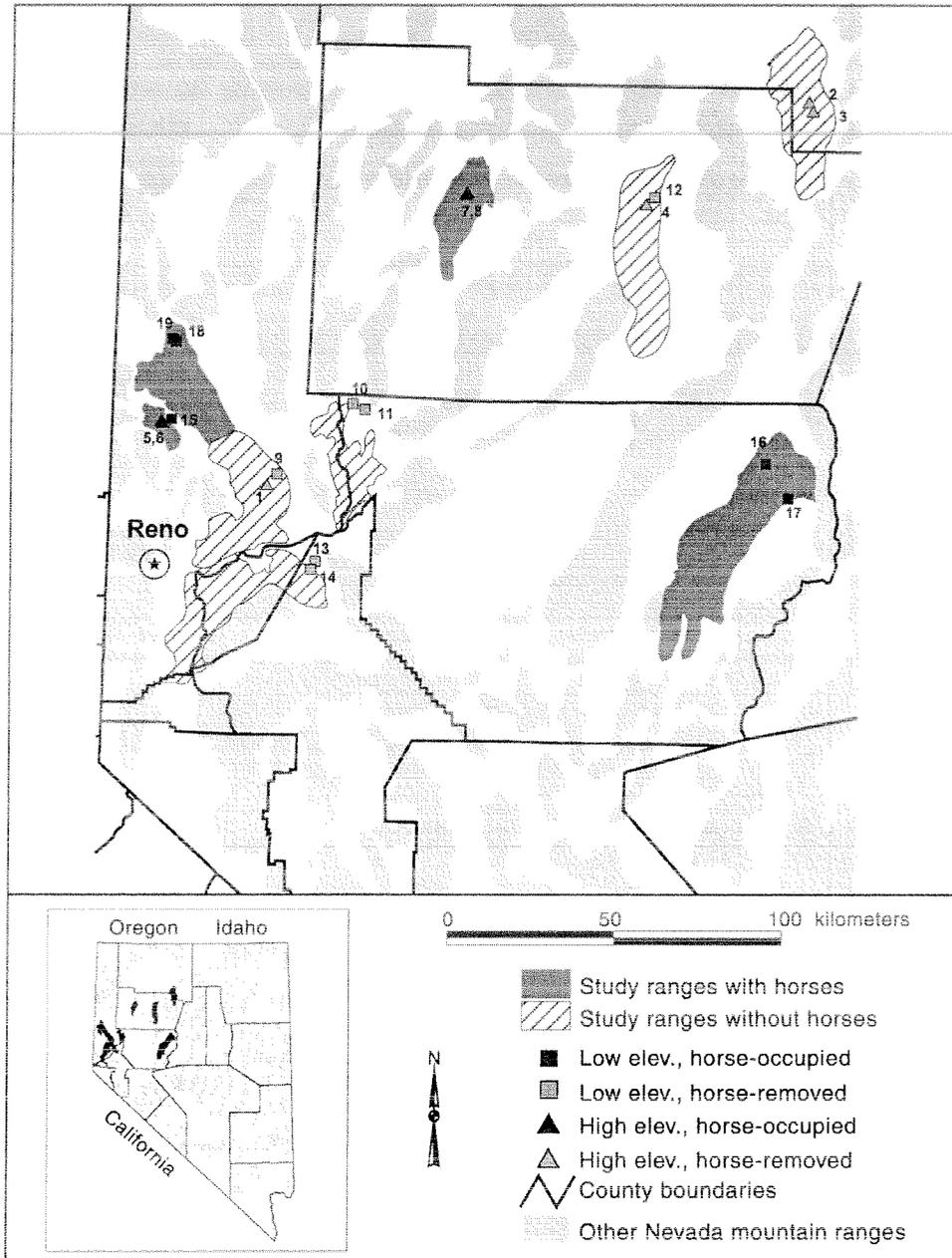


FIG. 1. Locations of 19 horse-occupied or horse-removed sites in the western Great Basin, Nevada (USA), sampled during 1997 and 1998.

permeability, structure, consistence, plasticity, or degree of calcic soils. Here we tested whether sites differed when all quantitative variables available for all sites were included.

Individual plant species data

Because most synecological research on feral horses has involved plants and because horse-monitoring

strategies currently focus exclusively on vegetation, we investigated relationships among sites using three measurements of the plant community. The first measurement included site-by-site abundance data for each plant species observed in 1997 or 1998, and the second used percent cover data. Because cover has been suggested to be more important than abundance in community dynamics (Daubenmire 1959), the final clas-

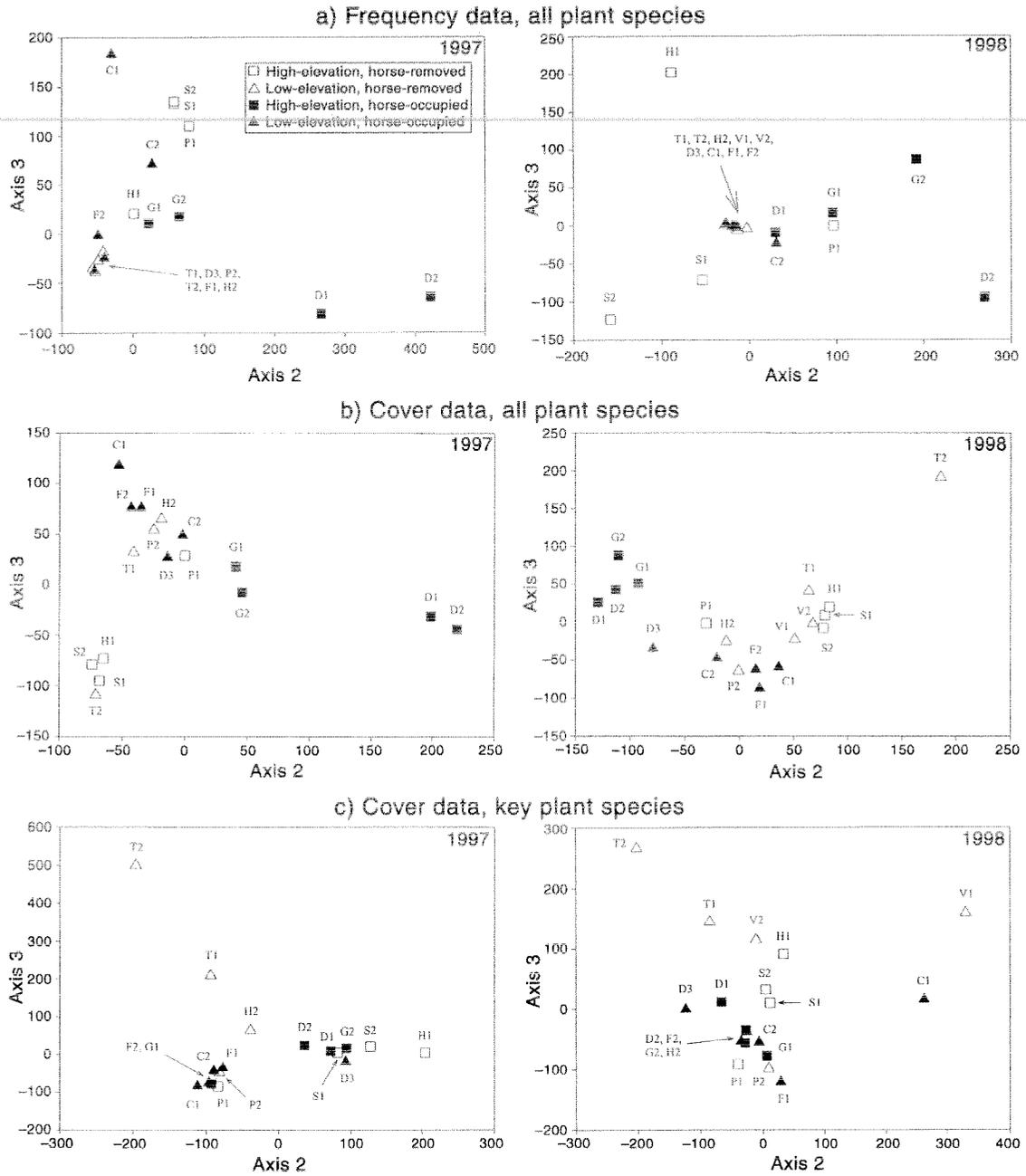


FIG. 2. Relationships between horse-removed and horse-occupied sites in two elevational strata, from reciprocal-averaging analyses with data sets composed of: (a) abundance (no. plants/transect) of all plant species; (b) percent cover of all plant species; (c) percent cover of only plant species monitored by agency managers (i.e., species dominant in horse diets from the region). All data are from sites in the western Great Basin, during summers of 1997 and 1998. The key for site "tags" (e.g., T2) is found in Table 1, column 4.

sification involved cover of only "key" grass and shrub species monitored by horse managers in the western Great Basin (listed in Appendix A). We identified species and life forms following Hickman (1993).

Disturbance variables

The final set of variables used to characterize horse-occupied and horse-removed sites was the set of 10 (of all variables measured) response variables shown pre-

TABLE 2. List of disturbance-sensitive variables used in RA and TWINSpan analyses, accompanied by references that support their connection to disturbance, based on grazing disturbance unless noted.

Variable (units)	References
Penetration resistance [\approx soil surface compaction] (MPa)	Kelly and Walker (1976), Wood et al. (1987), Wertz et al. (1989), Mahaney and Linyuan (1991), Dormaar et al. (1994), Belsky and Blumenthal (1997), van de Koppel et al. (1997)
Abundance of aboveground ant mounds in a 5940-m ² area (unitless)	Majer (1983), [‡] Rosenberg et al. (1986), [‡] Andersen and Sparling (1997), [‡] Suarez et al. (1998) [‡]
Percentage of small-mammal community (long RCR) as <i>P. maniculatus</i> (unitless) [†]	Martell (1983), [‡] Schulz and Leininger (1991), Bich et al. (1995), Songer et al. (1997), [‡] Bradley et al. (2000)
Total number of small-mammal individuals (long RCR) captured per site, three nights trapping	Reynolds and Trost (1980), Medin and Clary (1989), Heske and Campbell (1991), Rosenstock (1996), Hayward et al. (1997)
Percentage of hypothetical small-mammal species captured at a site (= long RCR; unitless) [†]	Reynolds and Trost (1980), Medin and Clary (1989), Dunstan and Fox (1996), Rosenstock (1996)
Species richness of plants at a site	Rummel (1951), Reynolds and Trost (1980), Brady et al. (1989), Knapp (1992), [‡] Rusch and Oesterheld (1997)
Mean percent cover of grasses at a site [$n = 4$ transects] (unitless) [†]	Pickford (1932), Gardner (1950), Webb and Stielstra (1979), Brady et al. (1989)
Mean percent cover of forbs at a site [$n = 4$ transects] (unitless) [†]	Pickford (1932), Shupe and Brotherson (1985), Maschinski et al. (1997), [‡] Dobkin et al. (1998), Clary (1999)
Mean percent cover of shrubs at a site [$n = 4$ transects] (unitless) [†]	Pickford (1932), Bock et al. (1984), Brady et al. (1989), Owens and Norton (1990)
Number of cheatgrass stems per 50-m transect [$n = 4$ transects] (unitless)	Pickford (1932), Gould (1951), Mack (1981), Pyke (1986), D'Antonio and Vitousek (1992), Knapp (1996)

[†] The variable was arcsine-transformed before being entered into analyses.

[‡] The variable was affected by some type of disturbance other than grazing.

viously to be potentially altered by mammalian herbivory (Table 2). We arcsine-transformed all percentage variables (Sokal and Rohlf 1995). In the few cases in which a site was not sampled for a particular variable, we estimated its value either by regressing 1998 values for the variable on 1997 values or (less frequently) by using the mean of the site's treatment-elevation category from that year (Appendix B).

Values for cheatgrass (*Bromus tectorum*) abundance and percent cover of grasses, forbs, and shrubs represent averages from four 50-m line transects (Table 2). We calculated plant species richness for sites by pooling subsamples and adding any other species observed inside or within 10 m of the trapping grid. Realized community richness of small mammals reflected the percentage of nocturnal granivorous rodent species potentially present at each site (dictated by range maps, elevation, vegetation, soil type, and microhabitat) that were actually captured during trapping. We used this relative measurement (*sensu* Cam 2000) because the pool of mammal species that we could potentially capture varied greatly across our sites.

Reciprocal averaging (RA) and TWINSpan analyses

All data matrices were analyzed in PC-ORD 2.0 (McCune and Mefford 1995) using RA (reciprocal averaging; Hill 1973) and TWINSpan (Hill 1979, Gauch and Whittaker 1981) techniques. In RA, site and species ordinations are done simultaneously, with the species scores representing averages of the site scores, and reciprocally, the site ordination scores representing av-

erages of the species ordination scores (Gauch 1982, Ludwig and Reynolds 1988). We used graphs to visually examine relationships between sites for all three axis combinations (i.e., 1–2, 1–3, and 2–3). Because elevation was the strongest determinant of many of our variables (Beever 1999) and because axis 1 carried most of the variation due to elevation, we used Axes 2 and 3 to illustrate relationships between sites after accounting for the effects of elevation.

TWINSpan analyses traditionally have been used to classify sites and plant species simultaneously, based upon compositional similarity or distinctness. However, TWINSpan may be used to divide a reciprocal ordination space for several types of ecological data (McCune and Mefford 1995). We used a minimum group size of three for division of sites, with a maximum of five indicators per division and 100 species in the final table. Indicator species in TWINSpan occur at the end of the reciprocal-averaging axes and are used to further polarize the ordination (McCune and Mefford 1995). Because each abiotic and disturbance variable exhibited a unique mean and standard deviation, we used frequency histograms of values for each variable with 15–30 equivalent divisions to assign groups into five discrete categories in TWINSpan analyses. This allowed us to calibrate diverse variables to the same scale and enter the same analysis. We used cut levels of 0, 2, 5, 10, and 20 for plant abundance analyses, cut levels of 0, 0.02, 0.05, 0.10, and 0.20 for percent cover analyses, and cut levels of 0, 1, 2, 3, and 4 for abiotic and disturbance variables. One of the most useful out-

puts of TWINSpan analyses is the ordered two-way table (McCune and Mefford 1995), which graphically represents relationships between sites and variables.

We evaluated the effectiveness of data sets for characterizing sites with RA and TWINSpan analyses by observing how closely results matched our design criteria, i.e., our designation of sites with respect to elevational stratum and presence of horses. Given our assumption that all horse-occupied sites had experienced at least *some* level of disturbance (by virtue of their occasional-to-frequent use by horses) compared to horse-removed sites, we assumed that horse-occupied sites should be more similar to each other than to horse-removed sites. RA analyses provided graphical representations of relationships among sites, and were evaluated by visual inspection. In TWINSpan analyses, we compared the four collections of sites created by the first two levels of division (hereafter, "groups") to the grouping of sites illustrated in Table 1. An "equal mix" of horse-removed and horse-occupied sites meant that numbers of sites from the two treatments were exactly equal in groups with an even number of sites, and differed by one in groups containing an odd number of sites. We defined "improvement" of classification by the third-level TWINSpan division as a perfect separation of a group of ≥ 3 horse-removed and horse-occupied sites that could not be explained by biogeographic (mountain range) patterns. For TWINSpan analyses only, we measured the effects of biogeography by tallying the number of sites from the same range that occurred in the same group.

RESULTS

In 1997, we found a total of 72 plant species at 17 sites, with an average of 15 species/site. In 1998, we recorded 182 species from 19 sites, with an average of 24 species/site. However, 78 of these 182 species were small, ephemeral forbs distinguishable as separate species, but too phenologically advanced for identification. Because we encountered many uncommon species in 1998, we analyzed these cover data with downweighting to reduce the contribution that rare species made to differentiation among sites. However, because fewer species were encountered in 1997 and downweighting of those data produced no significant change in the relationships among sites, we present 1997 cover and all "key species" results without downweighting (Fig. 2a-c).

RA analyses

Regardless of which combination of axes was used or whether downweighting of rare species occurred, sites were associated largely by mountain range in analyses of plant abundance data, due to range-to-range differences in species composition (Beever 1999). Across years and axis combinations, all low-elevation sites across mountain ranges appeared to be very similar (Fig. 2a), indicating a high level of floristic simi-

larity, especially in 1998. The lone exception was the pair of Clan Alpine sites, separated from remaining low sites along axis 1 in 1997. Using 1998 data, most lower-elevation sites (depending upon axis combination) clustered so tightly that they could not be easily discriminated. Downweighting rare species slightly reduced the association of sites by mountain range, although not consistently. All three pairs of high-elevation sites were distinguishable from other sites, except for one pair in 1998 (Fig. 2a). Sites from the same mountain range (hereafter, "pairs") but different elevational strata never associated. Overall, horse-occupied sites were not clearly distinguishable from horse-removed sites in either year.

In both 1997 and 1998, percent cover of individual plant species segregated sites by mountain range to an even greater extent than did abundance data. Both high-elevation horse-occupied pairs of sites segregated from other sites in both years, and in 1998 one low-elevation pair of sites from each treatment type (Horse Springs HMA [Horse Management Area] and Virginia Mountains) additionally segregated from other sites (Fig. 2b, 1998 data). Analyses of percent cover data suggested greater differences between sites of different ranges than did analyses of plant abundance data in both years, especially improving the differentiation of low-elevation sites (Fig. 2a-b). Data from percent cover by plant species trailed only data from disturbance variables in their ability to separate horse-occupied and horse-removed sites along the ordination axes. Percent cover data clearly separated half (four) of the horse-removed sites from occupied sites in 1997, and all but 1-3 of the horse-removed sites in 1998 (e.g., Fig. 2b). One site (T2) with the most salt-scrub influence separated strongly from other sites in both years on all axis combinations (Fig. 2b).

Analyses of the cover of "key" plant species suggested that most sites were too similar to be distinguishable, and that mountain range effects explained most of the remaining variability. Across both years and all axis combinations using key plant species cover, >50% of sites clustered tightly together, suggesting no difference between horse-occupied and horse-removed sites (Fig. 2c). The Truckee Range site (T2) again separated strongly from other sites across years and axis combinations. In spite of sometimes great distance between them (Table 1), sites within the same mountain range and elevational stratum usually possessed vegetation more similar in composition to each other than to sites from other ranges (Fig. 2c).

Reciprocal averaging of 12 inherent (abiotic) site properties suggested that relationships among sites were strongly affected by elevation, slightly affected by mountain range, and were not noticeably affected by presence of horses (Fig. 3a). In contrast to characterizations using plant species, abiotic variables grouped sites less consistently by mountain range, particularly in 1998 (Fig. 3a). Abiotic variables showed

TABLE 3. Number of sites (out of 17 or 19) that TWINSPAN analyses grouped by mountain range and sites whose classification matched experimental design criteria (i.e., presence of horses and elevation), using five types of data sets in 1997 and 1998.

Site data†	No. sites grouped with sites of the same range	Classification accuracy‡	
		Second level of division	Third level of division
1997 (n = 17 sites)			
Abiotic variables	12	8	no improvement
Frequency, all plant spp.	10	11	no improvement
Percent cover, all plant spp.	8	7	no improvement
Percent cover, eight "key" plant spp.	8	9	no improvement
Disturbance variables	10	15	no improvement
1998 (n = 19 sites)			
Abiotic variables	14	12	no improvement
Frequency, all plant spp.	15	12	no improvement
Percent cover, all plant spp.	17	13	no improvement
Percent cover, 16 "key" plant spp.	13	10	no improvement
Disturbance variables	12	14	17

† Data were collected from sites in nine mountain ranges in the western Great Basin of North America.

‡ Defined in *Methods*, expressed as number of sites grouped according to elevation stratum and presence of horses (i.e., in agreement with the organization of Table 1).

other sites of the same range (Table 3). In contrast, the two groups containing the most sites exhibited equal mixes of horse-occupied and horse-removed sites, and only 13 sites grouped according to our experimental criteria (Table 3). Greater cover of one-sided bluegrass (*Poa secunda* ssp. *secunda*) most strongly distinguished horse-occupied from horse-removed sites at low elevations in 1998.

Cover of key plant species of management concern classified sites similarly to analyses using all plant species, although mountain range effects were somewhat reduced. In 1997, three of four TWINSPAN groups possessed an equal mix of horse-removed and horse-occupied sites, and the fourth contained two high-elevation sites from the same range. Although only nine sites grouped according to experimental criteria, biogeographic tendencies were weaker yet, as only eight sites grouped according to mountain range (Table 3). Two of the four primary TWINSPAN groups in 1998 possessed an equal mix of horse-occupied and horse-removed sites, and no more than two-thirds of sites in either of the other two groups came from one treatment group.

Analyses using inherent site (abiotic) properties also exhibited strong effects of biogeography, as all but five sites, the same in both years, fell into groups with other sites from the same range (Table 3). In contrast, TWINSPAN groups classified only eight of our 17 sites in 1997 and 12 of 19 sites in 1998 according to experimental design criteria (Table 3). Across both years, all eight groups produced by the first two divisions contained both horse-occupied and horse-removed sites, and six of these groups exhibited equal mixes of sites from the two treatment types.

In contrast to the above data sets, analyses of dis-

turbance variables largely separated horse-occupied from horse-removed sites at both high and low elevations (Table 3). In 1997, all eight high-elevation sites and all but two low-elevation sites were separated into horse-removed and occupied groups. Horse-removed sites in 1997 were distinguished most strongly from occupied sites by greater shrub cover at high elevations and by higher numbers of ant mounds at low elevations. In 1998, two of the initial four TWINSPAN groups were composed exclusively of either low-elevation horse-occupied or horse-removed sites. The largest group contained seven of eight high-elevation sites. These seven sites segregated into horse-removed and horse-occupied groups with the third level of division (Table 3), which did not occur in any of 24 cases from other data sets of both years. In 1998, horse-occupied sites were distinguished from horse-removed sites at high elevations by sparser shrub cover, and at low elevations by greater dominance of deer mice.

When looking collectively at TWINSPAN analyses across years for plant species cover, plant species abundance, and abiotic variables, sites were not lumped in the same group as other sites from the same range in only 29% of 108 cases. About half (17 of 31) of those occurrences were sites that were each the lone site in the stratum and mountain range in which it was located (Table 1: P1, H1, P2, H2, or D3). Eight of those 17 occurrences, in turn, were instances in which Pah Rah Range sites were split into different groups. Of the remaining 14 (i.e., 31 minus 17) occurrences, eight were instances in which sites in the Clan Alpine Mountains were ordered in different groups. Thus, sites in a mountain range that were most distant geographically from other sites in the same range tended to dissociate themselves more frequently than did geographically

closer same-range sites when we used vegetative or abiotic variables to detect disturbance.

DISCUSSION

Although effects of grazing disturbance are probably sustained at hierarchical spatial and temporal scales (Archer and Smeins 1991), most investigations of herbivory, especially herbivory by feral horses, occur at a few closely located sites using only one or two types of disturbance indicators. Although this strategy provides greater experimental control in mensurative and manipulative field experiments, findings have low external validity and, thus, low predictive ability. We have demonstrated that grazing disturbance can be detected in semiarid environments such as the Great Basin across broad spatial scales using diverse response variables, even when treatment differences in plant communities are masked by geographic differences in species composition (Fig. 4). Thus, with careful site selection and explicit consideration to avoid possible confounding factors, it is possible to broaden the experimental domain to meaningfully investigate effects of disturbance across broad spatial scales. It is important to note, however, that multivariate statistics such as reciprocal averaging and TWINSpan have limited ability to establish cause-effect relationships, in spite of tools available to supplement these analyses and clarify their interpretation for biological systems.

Assessment of inherent site differences between horse-occupied and horse-removed sites

Abiotic inherent properties of sites showed no consistent difference between horse-occupied and horse-removed sites. For both years, TWINSpan analyses with abiotic variables suggested that physical properties of sites more closely reflected mountain range differences than presence of horses, a result consistent with the complex gradients of natural clinal variation present in the physiographically diverse Great Basin (Fig. 4). Similarly, horse-removed and occupied sites were not distinguishable in RA analyses based on abiotic properties for either 1997 or 1998 data. Relationships reflected location (i.e., mountain range) and elevation, both perhaps influenced by local climate patterns. Because plant growth in the Great Basin is often limited by water, the result that high-elevation, horse-occupied sites exhibited lower plant species richness and lower grass and shrub cover in spite of receiving on average 16–23% greater precipitation than horse-removed sites (Beever 1999) suggests that horse-related disturbances overshadow environmental influences. Segregation of high-elevation sites from different treatments in 1997 occurred only because we sampled slightly earlier at horse-occupied sites; segregation disappeared when sampling date was removed from the analysis.

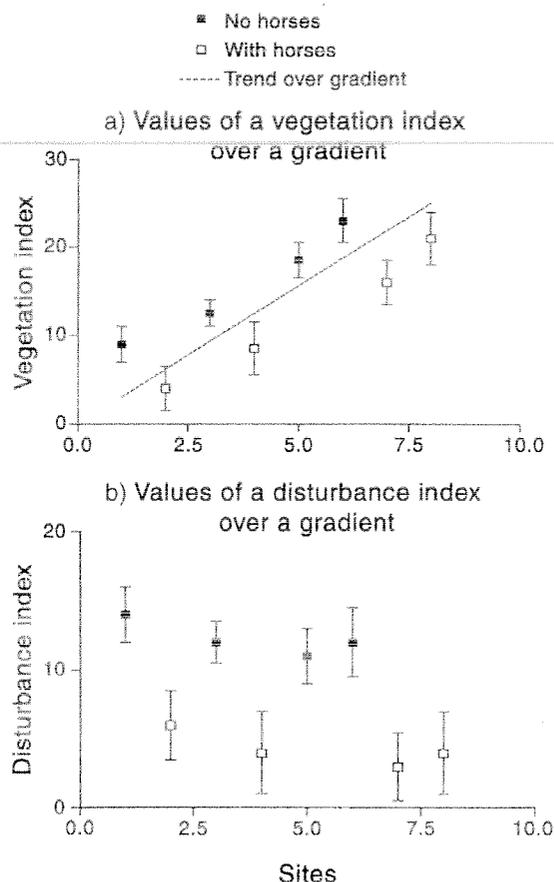


FIG. 4. Heuristic illustration of the detection of disturbance by horses on sites occurring across an environmental gradient, where pairing of sites is not sociopolitically feasible. Measurement of disturbance by a vegetation index. Even though values for horse-occupied sites are consistently below the trend line, multivariate analysis will not separate the two groups. Use of the proper disturbance index factors out the effect of the gradient (in essence, by flattening the trend line), allowing for direct assessment of the effect of horse disturbance, independent of clinal variability.

Effects of broad sampling domain on environmental assessment

The strong effect of mountain range on site relationships in both RA and TWINSpan analyses using data sets of plant cover and abundance suggests that flora of isolated ranges in the western Great Basin possess numerous distinctive species and compositional patterns, especially in their upper sagebrush zones (Grayson 1993, Charlet 1996). Thus, monitoring strategies proposed for detecting ungulate disturbance across large spatial areas must account for patterns arising from vicariance or strong abiotic differences (Fig. 4), especially when assessing less vagile organisms in heterogeneous environments. This is best accomplished by using variables that are sufficiently generic to be

appropriate for monitoring grazing disturbance at these scales across the entire sampling domain. If they are not, then managers and experimenters should use other means to stratify by, or factor out, the dominant environmental gradients. Otherwise, much larger sample sizes are needed to achieve equivalent statistical power. We suggest that the 10 disturbance variables listed in Table 2 are examples that reflect a reasonable compromise between the ideals of: (1) capturing directly or indirectly many of the components and processes in sagebrush scrub habitats of the Great Basin, especially those that relate to grazing disturbance; and (2) being concise enough to be readily implemented by land managers.

Just as samples from different ranges provided investigation of broad-scale effects of disturbance, comparing relationships among same-range sites separated by varying amounts of elevation and distance allowed investigation of the effects of elevational clines. If elevation strongly influences variables in our data sets, then TWINSpan analyses should associate sites with other same-range sites least frequently for mountain ranges having sites separated by the greatest amount of elevation. We indeed observed greater difference in floral composition and abiotic characteristics within and between elevation categories in the Clan Alpine and Pah Rah ranges, respectively, than for other ranges. Clan Alpine sites were separated by 360 m elevation, more than 2.5 times greater separation than any other same-range pair of sites in the same elevational stratum (Table 1). Perhaps also contributing to greater heterogeneity was the fact that Clan Alpine sites are horizontally separated by 12.7 km, far greater than for sites in any other range. Similarly, comparing ranges that had a site in each elevational stratum, Pah Rah sites were elevationally separated more than were Humboldt sites (Table 1). Not surprisingly, Pah Rah sites segregated in different groups twice as often as did Humboldt Range sites. These patterns of differences suggest that although grazing may be meaningfully monitored across broad spatial scales, sampling strategies should stratify locations by habitat type and elevation (or life zone), when possible, to account for naturally occurring variation.

Greater distinctness of high-elevation sites in RA and TWINSpan plant cover and abundance analyses is important for interpreting grazing disturbance both within and across ranges, and has implications for management. First, however, why did high-elevation sites exhibit greater difference among ranges as compared to low-elevation sites? Because differentiation of horse-removed from horse-occupied sites at high elevation using abiotic variables did not occur in 1998, and because differences observed in 1997 were due merely to earlier sampling of horse-occupied sites, differences in plant communities may reflect both the effects of vicariance and isolation as well as effects of weaker environmental gradients across all high-elevation

sites. Secondly, because low-elevation sites are more contiguous, dispersal of plants among ranges can occur more easily within lower-elevation than higher-elevation habitats. Finally, many plant species contributing to the significantly greater species richness of high-elevation (vs. low-elevation) sites were small, poorly dispersing forbs (Hickman 1993) observed in only one range. Because of these between-range differences, it is critical to have, within each stratum, treatment replicates from more than one mountain range; otherwise, treatment effects are confounded by mountain-range effects. In terms of management, monitoring of disturbance based on plants at higher elevations needs to account for greater effects of disjunct species distributions than does monitoring performed at low elevations.

Both increasing the *spatial* domain from one to several mountain ranges and increasing the *temporal* domain from one to two years affected the interpretation of the influence of horses. Stronger biogeographic pattern in both RA and TWINSpan in 1998 than in 1997 analyses of plant abundance and cover may be due, in part, to the greater number of species observed in 1998. Earlier sampling in 1998 (mean = 27 d earlier), leading to less senescence of plants, and 1.2 times greater precipitation across all sites in 1998 than in 1997 probably led to greater species richness. The effect of a larger sample size was especially evident in analyses of "key" plant species, because doubling the number of species (1998 vs. 1997 data) both lessened the segregation of treatment types and increased the effects of biogeography across all analyses.

Do grazing-disturbed semiarid ecosystems exhibit systematic differences from ecologically similar undisturbed (i.e., recovering) sites?

In both RA and TWINSpan analyses in both years, disturbance-sensitive variables that are relatively independent of geographic differences distinguished horse-occupied and horse-removed sites more clearly than did cover of all plant species, cover of key species, or abiotic variables. In separate analyses of each disturbance variable (Beever 1999), all variables exhibited overlap in values between treatment groups, and only some variables exhibited significant differences between horse-occupied and horse-removed sites. Because disturbance variables distinguished horse-occupied and horse-removed sites better than did data sets of exclusively plant variables, indirect effects of grazing disturbance (e.g., on small mammals or ants) may combine with direct effects (e.g., vegetation removal) to shape the dynamics of mountain ecosystems in the Great Basin (Hobbs 1996, Keesing 1998). Because RA and TWINSpan analyses give the strongest representations on the first axis (McCune and Mefford 1995), the ability of disturbance variables to distinguish horse-occupied from horse-removed sites, even in the presence of dominating effects of elevation (Beever 1999),

suggests that there are broadly detectable differences in multiple ecosystem components between these types of sites. Furthermore, because diverse ecosystem components may respond differently to grazing disturbance, monitoring only certain components does not necessarily capture the dynamics of other taxa and processes (Simberloff 1998). Consequently, we suggest that a multifaceted set of disturbance variables may be more appropriate for assessing disturbance than the single-component monitoring strategies previously advocated (Majer 1983, Auble et al. 1994, Bradford et al. 1998, Warwick and Clarke 1998).

Although horse-occupied sites at high elevation received greater horse use than did occupied sites at low elevation (mean = 208.5 vs. 96.8 defecations/site), disturbance variables did not always discriminate sites more clearly at high elevations. Although separation of horse-occupied from horse-removed sites was nearly equal at high and low elevations in 1997, sites of different treatments were more distinct at low elevations in 1998 (especially for site S2; see next paragraph). However, a comparison of the response to disturbance of high- and low-elevation sites with different levels of use by horses is confounded by elevation.

Although we explicitly chose sites with minimal cattle use, horse-removed sites with relatively greater cattle presence more frequently dissociated from other horse-removed sites in analyses of disturbance variables. The only horse-removed site that associated with horse-occupied sites in TWINSpan disturbance analyses of both years exhibited higher cattle use than any other horse-removed area, based on standardized scat counts averaged across years. Furthermore, in 1997, this site's count of cattle defecations was twice as high as that of any other horse-removed site at high or low elevation. Similarly, the site with the second highest average cattle scat count was one of only two other misclassified horse-removed sites. Thus, although we were largely interested in investigating feral horse disturbance and there was little variability in amount of cattle grazing among sites, our suite of variables may also have utility in detecting disturbance imposed by other grazers.

Comparing characterizations of sites using key plant species and other data sets

Although ecologists increasingly realize the importance of including several ecosystem components in research, management, and monitoring (Archer and Smeins 1991, Franklin 1993, Christensen et al. 1996), management and research of feral horses in the western United States have often assessed disturbance using only vegetative data. In TWINSpan analyses, cover data of only "key" plant species correctly classified 4–6 fewer sites than did our data set of diverse disturbance variables. Furthermore, in 1998, the year in which we encountered the most plant species, key species data performed the most poorly of all five data

sets in discriminating horse-occupied and horse-removed sites. Selecting only key plant species to characterize sites also appeared to reduce biogeographic affinity compared to other data sets; TWINSpan analyses of cover of key species grouped the fewest sites by mountain range of any data set in both 1997 and 1998. Because variables such as ant mounds, number of deer mice, and (at high elevations) shrub cover were indicator variables in first divisions in TWINSpan analyses of disturbance-sensitive variables, they may contribute to differences between horse-occupied and horse-removed sites. Thus, the current practice of monitoring grasses and low-elevation shrubs may not capture important interactions that affect the composition and function of mountain ecosystems, at least for the range of vegetative values typically encountered. Another potential problem of monitoring only vegetation is that the utility of vegetation for monitoring response to herbivory is likely to vary across ranges and years with changes in precipitation (Detling 1998, Fahnestock 1998).

A wide range of alternative strategies has been proposed for monitoring programs to detect grazing disturbance. Counts of hoofprints or dung patches provide an easily implemented means to index disturbance. Unfortunately, fecal counts can be sensitive to relative digestibility of forage, and in feral horses, concentration of defecations into "studpiles" complicates quantification. Similarly, hoofprints are not well preserved and thus cannot be indexed in many soil types of the Great Basin and other semiarid regions. More importantly, neither index includes variables that relate directly to ecosystem function or processes, which are crucial for future site potential and response to management activities. Although collection of remotely sensed data allows assessment over broad spatial scales, to date, unfortunately, it has not achieved fine-scale detection of disturbance, especially in semiarid ecosystems. For example, only one or two of our 10 disturbance variables (shrub cover, cheatgrass abundance) could be reliably censused remotely, underscoring the continued importance of empirical field monitoring. It should be noted that it is possible (although difficult to test) that only our measurements of these disturbance indicators are more sensitive in detecting disturbance than are plant-related variables, rather than the ecosystem components themselves being more sensitive to disturbance.

Because current management budgets may not be able to implement monitoring across numerous sites for all of the disturbance-sensitive variables that we censused, we reanalyzed reduced versions of this data set in RA and TWINSpan analyses, without the plant-related, mammal-related, soil-related, or ant variables. We used this as a crude cost-benefit analysis, in that we sought to see how much extra discriminatory sensitivity ("bang") one could get from given amounts of monitoring effort "bucks" expended by adding more

indicators to the pool of variables. Removal of the ant variable suggested that among our sites this variable contributed least to discriminating sites, as RA analyses without ants separated horse-occupied from horse-removed sites about as well as the full disturbance data set. TWINSPAN analyses of both years were equal to the full data set at the second level of division and, in fact, were *better* than the full data set at the third level. Removal of penetration resistance of soils from the disturbance data set reduced the ability to discriminate sites only marginally in RA analyses compared to the full data set, and TWINSPAN analyses of this reduced data set classified 15 sites according to experimental design criteria in both years.

In contrast, removal of either the five plant-related variables or the three small-mammal variables from the disturbance data set noticeably blurred the distinction between horse-occupied and horse-removed sites. For the data set without mammal variables, in both years, high-elevation horse-occupied and horse-removed sites remained well discriminated in RA analyses; however, lower elevation sites of the two treatment groups appeared more similar than in analyses of the complete disturbance data set. In TWINSPAN analyses of 1997 data, the nonmammal disturbance data set classified 14 sites according to design criteria, whereas nonplant disturbance variables classified only 11 sites this way. In 1998 analyses, nonplant disturbance variables classified 14 sites according to experimental design criteria, whereas nonmammal variables discriminated only 13 sites according to design criteria. Thus, the data set without either mammal or plant variables classified from one to four fewer sites according to design criteria than did the full disturbance data set. We cannot exclude the possibility that relative importance of the five plant-related variables occurred simply because they occupied half of all disturbance-sensitive variables in the data set. Such an argument may also apply, to a lesser degree, to the importance of small-mammal variables. Given that inclusion of small-mammal trapping increased by 20–35% the time necessary to sample a pair of sites, researchers and managers must balance budgetary constraints with how sensitive and clear they desire their sampling strategy to be in order to detect disturbance. Extensiveness of the list of components monitored will vary with the number of sites to be sampled, available monitoring resources, and costs of Type II errors.

CONCLUSIONS

Perspectives on disturbance and monitoring of systems depend critically upon the scale at which the disturbance is measured (Brown and Allen 1989). For example, disturbed areas of small spatial extent are generally able to recover more quickly than larger areas. Moreover, results of monitoring to detect disturbance will depend upon which types of ecosystem components are investigated. In our landscape-scale research

in the western Great Basin, USA, strikingly different relationships between sites were obtained using data only from key species, using all plant species, and using a suite of disturbance-sensitive variables. In both RA and TWINSPAN analyses, abiotic factors, plant cover, and key plant species cover characterized sites more strongly by mountain range than by presence of horses. Abiotic factors can strongly influence the results of monitoring, and need to be accounted for in any monitoring schemes performed over broad areas. Consequently, if monitoring involves measuring percent cover of only a few or all plant species, sites within mountain ranges will appear most similar to each other, due, in part, to the occurrence of narrowly distributed plant species. In contrast to the other data sets, disturbance-related variables separated all but one or two sites according to the presence of horses in analyses of both 1997 and 1998 data. Of the other four data sets, those of percent cover of all plant species were best able to distinguish horse-occupied from horse-removed sites in both years. Table 2 lists variables potentially useful for monitoring grazing disturbance within the Great Basin, and should be considered an example of a comparatively easy research program to implement, with the exception of mammal trapping.

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APPENDIX A

A list of plant species of management interest is available in ESA's Electronic Data Archive: *Ecological Archives* A013-003-A1.

APPENDIX B

Means and standard errors for response variables of different data sets (plant abundance, plant cover, abiotic variables, and disturbance-sensitive variables) are available in ESA's Electronic Data Archive: *Ecological Archives* A013-003-A2.