

Managers' Summary- Ecological Studies of the Pryor Mountain Wild Horse Range, 1992-1997



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Managers' Summary – Ecological Studies of the Pryor Mountain Wild Horse Range, 1992–1997

Ecological Studies of the Pryor Mountain Wild Horse Range, 1992–1997 provides a synthesis of key findings of landscape-scale, interdisciplinary studies of the effects of wild horses and native ungulates on a rugged, mountain ecosystem. This is perhaps the most comprehensive study of a wild horse herd conducted. This was a complex study and one involving a truly interagency approach. Six agencies either provided input to research priority setting, funding, or both. The agencies included the Bureau of Land Management, National Park Service, U.S. Geological Survey, Montana Department of Fish, Wildlife and Parks, Wyoming Game and Fish Department, and U.S. Forest Service. The major research direction and effort came from the U.S. Geological Survey and Natural Resources Ecology Lab, Colorado State University with Montana State University and the University of Kentucky also participating. Ungulate monitoring was conducted by the U.S. Geological Survey, Biological Resources Division, Bureau of Land Management, Billings Field Office and the Montana Fish Wildlife and Parks, with funding by Bighorn Canyon National Recreation Area. Many other individuals and groups were involved and deserve credit. The report printing was made possible with funds from the Bureau of Land Management, Wild Horse and Burro Program, Washington Office. This report was prepared by the Information Management Project, Midcontinent Ecological Science Center, U.S. Geological Survey.

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of the Pryor Mountain Wild Horse
Range, 1992-1997**

Compiled by

Francis J. Singer and Kathryn A. Schoenecker

Report to the Bureau of Land Management, National Park Service, Montana Department of Fish,
Wildlife and Parks, and Wyoming Game and Fish Department on research studies
conducted from 1992 to 1997

A cooperative research effort conducted by the U.S. Geological Survey, Midcontinent Ecological Science Center and the Natural Resources Ecology Lab of Colorado State University. Funding was provided by the U.S. Geological Survey, Bureau of Land Management, National Park Service, Montana Department of Fish, Wildlife and Parks, and Wyoming Game and Fish Department.

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This report is being produced solely for the immediate needs of managers. This report is preliminary and has not been peer-reviewed nor reviewed for conformity with U.S. Geological Survey editorial standards, except for two of the reports that have been published in peer-reviewed journals and are reprinted with permission here. The remainder are currently in preparation for submission to peer review by journals. Field research by the USGS continued in 1998 and 1999 with additional work planned through 2002. The unpublished findings and conclusions reported here should be considered preliminary, subject to updating and revision.

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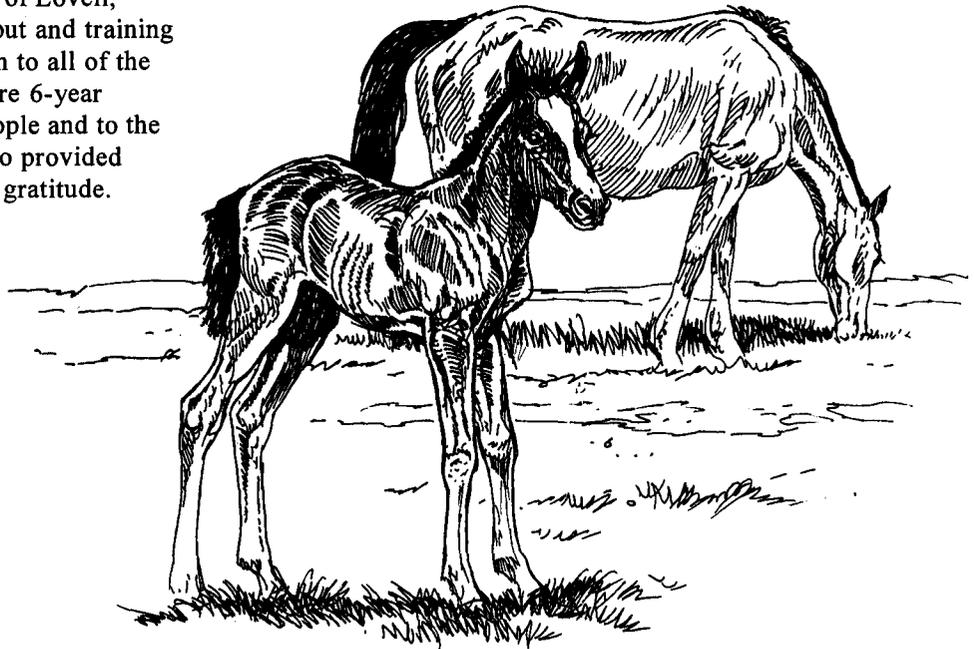
Foreword

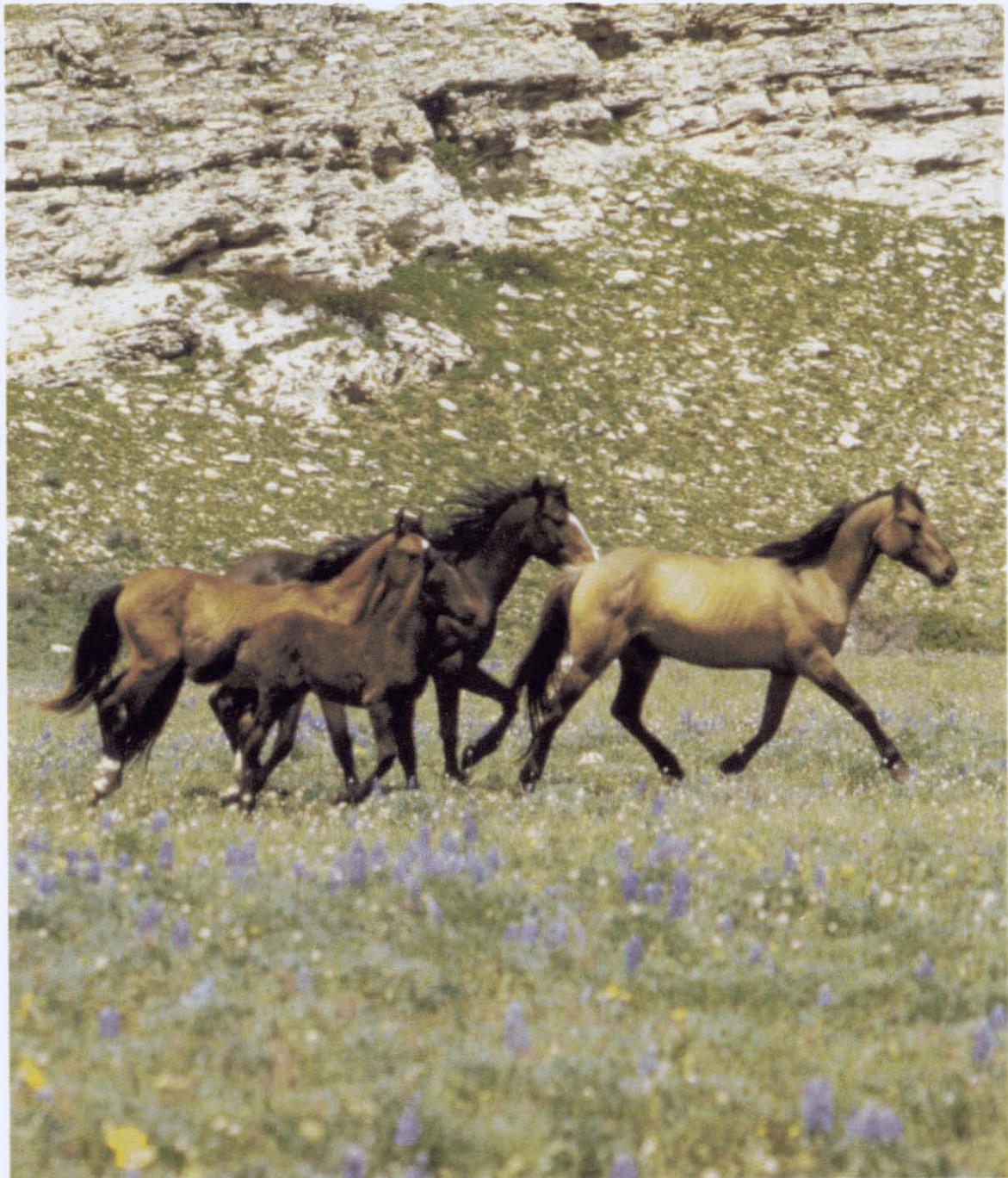
The Pryor Mountain Wild Horse Range was designated in 1968 by U.S. Department of the Interior Secretarial Order. The area encompassed by the range includes lands managed by three different agencies, the Bureau of Land Management, National Park Service, and U.S. Forest Service. Two state wildlife agencies have primary responsibilities for wildlife and fishing and hunting regulations in the area. This presents a complexity of different management philosophies. The diverse, rugged, and remote grazing ecosystem currently supports 100–200 wild horses, over 100 bighorn sheep, and several hundred mule deer.

The management of wild horses and native ungulates in the Pryor Mountains has been controversial. This controversy and debate was the topic of an interagency public meeting in early 1990. In February of 1991, Francis Singer was requested by the National Park Service to conduct a scientific problem analysis of the research needs for the area. Needs that were identified included a study of the competitive interactions between the three ungulates inhabiting the area, a study of the effects of all ungulates on the vegetation, a study of conservation genetics of the wild horses, and simulations of the predicted effects of different management scenarios. This resulted in several funding requests and eventually in an interagency funding effort. All agencies met twice a year, 1991 through 1994, to provide guidance and input on priorities. Initially the funding was principally by the National Park Service and Bureau of Land Management with Montana Fish Wildlife and Parks providing aerial, logistic and equipment support. In more recent years (since 1995) funding has been primarily by the newly designated National Biological Service, now the Biological Resources Division of the U.S. Geological Survey. Key participants in the initial funding and priority setting process were Dan Bricco, Jay Parks and David Jaynes of the Bureau of Land Management, Dan Huff, Robert Schiller and Terry Peters of the National Park Service, Charlie Eustace, and Shawn Stewart of Montana Fish Wildlife and Parks, and Tom Easterly and Jerry Radse from the Wyoming Game and Fish Department. Since 1994, Linda Coates-Markle of the Billings Field Office, Bureau of Land Management has provided considerable research direction and also support in the form of both ground and aerial monitoring of the wild horses. Shawn Stewart assisted with funding and participated as an observer during winter aerial surveys of the mule deer and bighorn sheep since 1995. Darrell Cook, Robert Byrne, and Rick Lasko provided housing for field staff and funding support of the sheep and deer surveys in recent years.

Research direction has been provided primarily by Francis Singer and the U.S. Geological Survey. The various principal investigators of each study; James Detling, John Gross, Michael Coughenour, Gus Cothran, and Lynn Irby also provided research direction and input to the studies. Two significant public presentations of the findings have occurred, both organized by Linda Coates-Markle and the Billings Field Office. One was a Public Forum in May 1997 in Billings and the second a Population Viability Analysis Forum in April 1999 held in Fort Collins.

Reverend Floyd Schwieger of Lovell, Wyoming has provided input and training on wild horse identification to all of the researchers during the entire 6-year process. To all of these people and to the many other individuals who provided assistance, we express our gratitude.





SECTION I.

VEGETATION STUDIES

Summary of Vegetation Dynamics at the Pryor Mountain Wild Horse Range, 1992–1996

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Executive Summary

The effects of management practices on federally managed and national park ecosystems, and particularly the effects of ungulate populations, have received much recent attention (Wagner et al. 1995; Detling 1998; Singer et al. 1998a,b; Huff and Varley 1999; Porter and Underwood 1999; Wright 1999). The Pryor Mountain Wild Horse Range (PMWHR) was created in 1968 and has as a long-term management goal the maintenance of balance within the entire ecosystem (Bureau of Land Management 1997). In 1992, two studies designed to provide insight into the ungulate-vegetation system were initiated in the PMWHR. This report reviews relevant findings from these studies (Peterson et al. 1997; Gerhardt and Detling 1998), and further analyzes data collected in the studies. The goal of these additional analyses was to provide general conclusions about vegetation dynamics in the PMWHR. We used two different types of analyses. Step-wise general linear models (GLM) were used to determine which factors best explained the trends and differences in each of 11 vegetation variables across all 12 exclosure sites and across 5 years (1992–1996). Principal components analyses (PCA) were performed for each monitored site to assess how overall vegetation compares between years and between exclosed and control plots.

Reports from the two studies showed that offtake by ungulates was variable across sites and years, but that significant offtake of grasses and forbs could be detected (Peterson et al. 1997). Lower herbaceous plant

biomass was detected outside exclosures at a number of sites within the PMWHR (Peterson et al. 1997; Gerhardt and Detling 1998). However, significant reductions were not consistent across sites or years. Exclosure effects on plant cover and C₃ grass nitrogen concentration were also detectable but variable (Peterson et al. 1997; Gerhardt and Detling 1998).

Part of our additional analyses focused on selecting the spatial and temporal factors most related to vegetation dynamics. A step-wise GLM was used on 11 vegetation variables: herbaceous biomass, species richness, total plant cover, absolute grass cover, absolute forb cover, relative grass cover, absolute forb cover, litter cover, bare ground cover, biomass difference, and percent biomass difference. For each variable, we determined which environmental factors best explained the variance. Ten environmental factors were considered for inclusion in the models: plot (exclosed vs. control), year (1992–1996), mean site annual precipitation, current growing season precipitation (March to July), soil, previous winter horse population, current summer horse population, east (UTM coordinate), north (UTM coordinate), and elevation. A second part of our analyses focused on comparing the overall vegetation condition in exclosed and grazed plots at each site. We used principal components analyses to show the variability in vegetation in both plot types over a number of years.

Results from these analyses show that, across sites and years, only some vegetation variables measured are significantly different inside and outside exclosures. Significant overall differences were detected for grass

cover and near significant differences were shown for biomass and litter. However, factors related to the location of sites and/or the time of measurement explained most of the variability for each vegetation variable.

Previous analyses of biomass data from 1992–1996 demonstrated that although herbivory effects were detectable, they were generally localized and not consistent across years. Averaged across location and years, herbaceous plant biomass in our GLM analysis was not significantly different inside and outside of exclosures (inside: mean = 86.2 g m⁻², SE = 11.0; outside: mean = 76.6 g m⁻², SE = 10.2; $P = 0.078$). Although the absolute difference inside and outside exclosures was not affected by any temporal factors, the relative difference (%) did vary between years and the magnitude of this variation was related to the east-west location of sites.

Across all sites, exclosures do not appear to have a consistent or strong interactive effect with environmental variables. As revealed in the PCA graphs, there were exceptions to this, but in general, interannual changes which occurred in the control plots appear to be mirrored in the exclosed plots. This observation is in agreement with the results of the general linear models in which plot x temporal environmental factor interactions were relatively weak.

Although the difference between exclosed and control plots showed variation between years, no sites showed a trend for increasing convergence. Although we did not perform ordination analyses using individual species data, the suite of vegetation variables used (biomass, richness, and cover) may contain enough information to detect changes in the state of the vegetation system. If rapid and directional transitions were occurring in either plot type, that plot might be expected to follow a relatively consistent trajectory across years. The lack of strong linear changes is corroborated by the GLM results which did not detect a significant trend for the exclosure effects to be cumulative over time. However, changes in the plant community may not be linear, and vegetation models emphasizing multiple states and transitions may be more relevant (Allen-Diaz and Bartolome 1998; Augustine et al. 1998). These models assume that changes may not be consistently directional, but instead are influenced by numerous factors which may result in multiple future states, each dependent on a transition threshold (Westoby et al. 1989; Friedel 1991; Laycock 1991).

Averaged across years and locations, the main effect of exclosures was significant only for relative grass cover ($P < 0.001$), although the effect was nearly significant for several other vegetation variables: absolute grass cover ($P = 0.052$), litter ($P = 0.066$), and biomass ($P = 0.078$). Although previous analyses (Peterson et al. 1997) showed that exclosure effects could vary between years and across sites, we found no strong interactions between exclosures and either spatial or temporal factors for any vegetation variable. The only statistical indication of a location- or time-specific effect of the exclosures is in the GLM analyses of the two composite variables: absolute (g m⁻²) and relative (%) biomass difference.

Neither winter nor summer horse herd size had a detectable influence on the exclosure effect. In addition, neither growing season nor annual precipitation had detectable influences on the exclosure effect. This suggests that over the range of herd sizes present from 1992–1996, the effect (or lack of effect) of the exclosures was consistent.

Introduction

The effects of management practices on national park ecosystems have received a great deal of attention recently (Wagner et al. 1995; Detling 1998; Singer et al. 1998a,b; Huff and Varley 1999; Porter and Underwood 1999; Wright 1999). Of particular concern has been the effect of ungulates on the parks' vegetation and the relative effects of herbivores and abiotic factors on both the vegetation and other system properties or functions (Frank and McNaughton 1992; Detling 1998; Frank et al. 1998; Pastor et al. 1998; Singer et al. 1998a,b; Fahnestock and Detling 1999). Early management practices generally encouraged high populations of ungulates (Wright 1999). Only later was it realized that a singular goal of protecting ungulates may lead to instability in ecosystem functioning [references in Huff and Varley (1999), Porter and Underwood (1999), Wright (1999)].

The PMWHR was created in 1968 and has as a long-term management goal the maintenance of balance within the entire ecosystem (BLM 1997). In 1992, two studies designed to provide insight into the ungulate-vegetation system were initiated in the Pryor Mountain Wild Horse Range. One study focused on providing an assessment of habitat and dietary overlap between the PMWHR's ungulate populations (horses,

bighorn sheep, and mule deer). Kissell et al. (1996) evaluated overlap and competition among ungulates by determining seasonal food and diet habits, interspecific behaviors, and population dynamics in a three-year study. The second study focused on detecting the impacts of herbivores on the PMWHR vegetation (Peterson et al. 1997). Permanent and moveable exclosures were used to estimate offtake and to compare vegetation dynamics (biomass, cover, nitrogen concentration) in exclosed and unexclosed plots over 3 years. In 1994, an additional vegetation study began with the goal of monitoring vegetation in a wider range of vegetation communities (Gerhardt and Detling 1998). Data from these projects has been incorporated into a simulation modeling project (Coughenour, in preparation) which, it is anticipated, will be used to assess vegetation conditions under a variety of environmental and management scenarios.

In addition to concern over ungulate effects, the effect of culling and population size on the genetic, reproductive, and social health of the PMWHR horse herd has recently been assessed. This research has focused on establishing the genetic and phenotypic uniqueness of the herd, assessing the reproductive and social health of the herd, and determining the reproductive health of individual horses. Future horse management plans must evaluate both the estimates of herd sizes required for a viable long-term horse population and the effect of these populations on the vegetation.

Our goal in this report was to: (1) summarize the previous reports on vegetation dynamics (Peterson et al. 1997; Gerhardt and Detling 1998); and (2) further analyze previously reported data in order to provide results that allow for general conclusions about vegetation dynamics in the PMWHR. We used two different types of analyses. Step-wise general linear models were used to determine which factors best explained the trends and differences in each of 11 vegetation variables: herbaceous biomass, species richness, total cover, bare ground cover, litter cover, absolute and relative grass cover, absolute and relative forb cover, and two composite variables, absolute and percent biomass difference between exclosed and control plots. In addition, we used principal components analysis, a multivariate technique, for each monitored site to assess how overall vegetation compares between years and between exclosed and control plots.

Methods

Study Site

All vegetation sampling was conducted from 1992–1996 in the PMWHR. Created in 1968, the PMWHR is located along the border of Montana and Wyoming (Carbon County, Montana, and Big Horn County, Wyoming) and encompasses approximately 38,000 acres of Bureau of Land Management (BLM), Custer National Forest, Bighorn Canyon National Recreation Area, and private lands. Elevations within the range vary from approximately 3,500 to 8,000 feet and annual rainfall varies from approximately 5 to 20 inches depending on location.

Data Review from Prior Reports

We reviewed the relevant findings presented in the two final reports (Peterson et al. 1997; Gerhardt and Detling 1998). Details of the sampling methods and statistical analyses are not repeated here, but can be found in those references. In reviewing these two reports, we highlighted only those results which dealt with the effects of grazing at permanent exclosure sites.

Data Sources

Vegetation data were obtained from two related studies. From both studies, we used aboveground herbaceous biomass and plant cover estimates from July sampling periods, approximately the time of peak standing crop. The first study lasted from 1992 to 1994 and measured herbaceous vegetation at five permanent exclosure sites inside the PMWHR (Forest Service, Penns Cabin, Sykes Ridge, North Horse, South Horse). Details on sampling design and data collection during this study can be found in Peterson et al. (1997), Fahnestock (1998), Peterson (1999), and Fahnestock and Detling (1999). The second study lasted from 1994–1996 and measured vegetation at the five exclosure sites sampled from 1992–1994 and at an additional seven permanent exclosure sites (Yellowhill, North Bay, Peninsula, Turkey Flats, RAWS, Subalpine, Bat Cave). Sampling methods for cover and herbaceous biomass followed those designed in the first study; details of these methods can be found in Gerhardt and Detling (1998).

Environmental data were collected from three sources. For each site, we used UTM coordinates, elevation, mean annual precipitation at each site, and soil type data from Coughenour (in preparation; Table 1). Data on post-cull and summer horse population size (1991–1996) were obtained from the BLM (Coates-Markle, personal communication, BLM; Fig. 1). Growing season precipitation data (March–July) from 1992–1996 was obtained for the Lovell weather station (site ID = 485770) from the National Climatic Data Center of the National Oceanic and Atmospheric Administration (Fig. 2).

Statistical Analyses

Vegetation data were analyzed in two different ways. All analyses were performed with S-Plus 4.5. The first type of analysis was designed to detect trends in vegetation on a large spatial scale. We used general linear models on the pooled data from all sites and years to analyze the effects of 10 environmental variables on each of 11 vegetation variables. In the

second type of analysis we focused on a smaller spatial scale and used multivariate analyses to detect overall trends in vegetation dynamics at each site.

For the GLM analyses, data from all sites and years were pooled and each dependent variable was analyzed separately to detect the effects of environmental variables. Each of the following vegetation variables was analyzed with a separate GLM: herbaceous biomass, species richness, total plant cover, absolute grass cover, absolute forb cover, relative grass cover, absolute forb cover, litter cover, bare ground cover, biomass difference, and percent biomass difference. For each variable, we determined which environmental factors best explained the variance by using a step-wise (forward and backward) model building process. Ten environmental factors were considered for inclusion in GLMs: plot (exclosed vs. control), year (1992–1996), mean site annual precipitation, current growing season precipitation (March–July), soil, previous winter horse population, current summer horse population, east (UTM coordinate), north (UTM coordinate), and elevation.

Table 1. Location, soil, and mean annual precipitation data for each site. Data were provided by Coughenour (1999).

Site	UTM coordinates			Soil	Mean precipitation (mm)
	East	North	Elevation (m)		
Bat Cave	713239	4989779	1,540	LH2	200
Forest Service	709042	5001156	2,490	HD	495
North Bay	716437	4984732	1,175	SA1	205
North Dryhead	715368	4994476	1,320	Hk2	300
Peninsula	717136	4992480	1,275	Hk2	260
Penns Cabin	710300	5002000	2,540	HE	510
RAWS	709459	5005097	2,670	LH2	510
South Dryhead	715360	4992896	1,340	Hk2	300
Subalpine	708760	5004936	2,650	TX	510
Sykes Ridge	712499	4995456	2,000	HD	414
Turkey Flats	710597	4987887	1,290	Hf	260
Yellowhill	715257	4989259	1,410	LH2	280

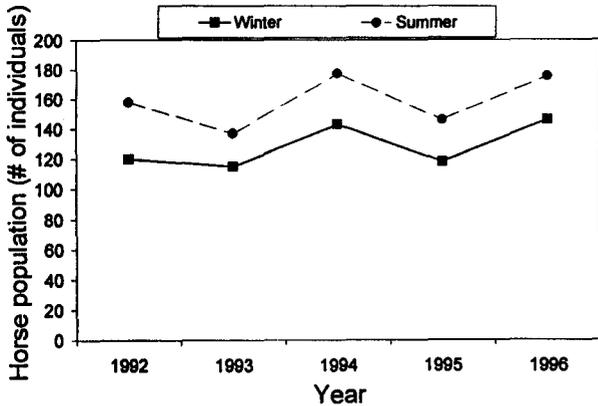


Fig. 1. Wild horse population from 1992 to 1996. For each year, the post-cull population size of the previous winter (fall-spring) and the post-foaling population of the given year (summer) are plotted. The distance between points for a given year represents births.

Because of the large number of potential factors that could be included in the model, we used a step-wise process based on the Akaike Information Criterion (AIC). The AIC value provides a quantitative method for suggesting which of the possible factors should be included in the final model. Using the AIC, inclusion in the model is based on both the additional information gained by adding a factor and a penalty for the increased complexity of the model. The model building process started with an intercept-only model and terms were added or deleted one at a time. Potential models ranged from intercept models to models including any combination of the following terms: all main effects, all two-way interactions, and all three-way interactions. At each step in model building, all potential models were evaluated. If the addition of any main effect or interaction would result in a model with a lower AIC, the term which resulted in a model with the lowest AIC was added. If the deletion of any term would result in a model with a lower AIC, that term was deleted. Because high order interaction terms are difficult to interpret biologically, we restricted interactions to three-way or lower.

In most cases, the plot variable (exclosed vs. control) was not included in the best model. However, because we were interested in the effect of this factor, we calculated an additional GLM for each dependent

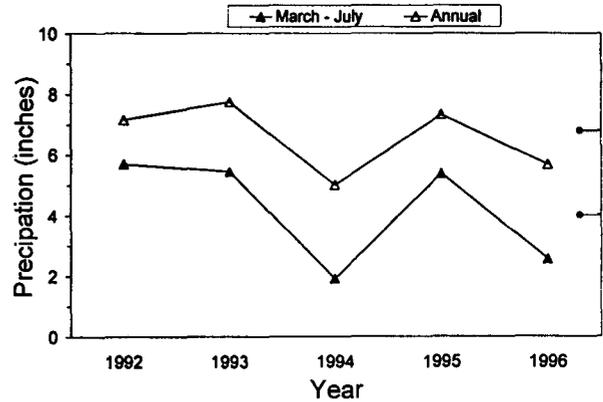


Fig. 2. Growing season and annual precipitation from 1992 to 1996 at the Lovell, Wyoming weather station. Weather data was not measured at each exclosure site. The 30-year average (1961–1990) for the growing season (March–July) and year are indicated along the right border of the plot.

variable which included the factors selected for the best model, plus the plot factor.

In a second type of analysis, we used a multivariate ordination approach (Principal Components Analysis, PCA) to follow changes over time in the overall vegetation at each site. The goal of ordination analysis is to represent samples which are similar with points which are closely spaced on the ordination axes (Gauch 1982; ter Braak 1987). Although PCA assumes that vegetation responses are linearly related to environmental factors, we selected it over other ordination techniques because the response variables were not species cover data, and we assumed that at a given site, vegetation responses would be approximately linear over a narrow environmental range. Because we were interested in determining both differences between plots (exclosed vs. control) and between years, we used data from each year and plot as a sample. We conducted a PCA for each site with the following variables: herbaceous biomass, species richness, total plant cover, absolute grass cover, absolute forb cover, relative grass cover, absolute forb cover, litter cover, and bare ground cover. Analyses for each site included only those years in which all vegetation characteristics were estimated. Because vegetation variables were measured on different scales, PCA was performed using a correlation matrix of the standardized values for each variable.

Results

Summary of Findings in Previous PMWHR Vegetation Projects: 1992–1994

A 3-year project provided intensive studies into vegetation dynamics from 1992 to 1994 at five permanent exclosure sites [Forest Service, North Dryhead, Penns Cabin, South Dryhead, Sykes Ridge; Peterson et al. (1997); Fahnestock (1998); Peterson (1999) Fahnestock and Detling (1999)]. Findings from the project are presented in the National Park Service report (Peterson et al. 1997). Results and discussions on biomass, offtake, production, nitrogen concentration, and other aspects are also presented by Peterson (1999), and the results and discussions of species composition and cover analyses are provided by Fahnestock (1998) and Fahnestock and Detling (1999). Detailed and complete methods, results, and discussions can be found in these sources.

Small moveable exclosures were used to estimate offtake of grass and forbs/shrubs during three growing seasons (1992, 1993, and 1994). Because of a large variance in the samples, detecting offtake proved difficult. Over the 3 years, significant grass offtake was found at three sites, and significant forb/shrub offtake was found at another two (Peterson 1999; Peterson et al. 1997).

Despite the difficulty of measuring growing season offtake, significant differences in biomass and plant/species cover were found at some sites during some years. Data on herbaceous plant biomass were analyzed separately for each of the five permanent exclosure sites to detect the effects of year (1993 vs. 1994) and plot (exclosed vs. control). Total biomass (grass + forbs + dwarf shrubs) was significantly affected by exclosures at all sites, and was higher inside than outside except at Penns Cabin where the opposite was true (Peterson 1999; Peterson et al. 1997). The effect of year on total biomass was not consistent across sites, with significant changes between 1993 and 1994 detected at only two of the five sites. When total biomass was separated into component categories, three subcomponents (live grass biomass, dead grass biomass, total grass) were significantly higher inside exclosures, except at Penns Cabin where the exclosure had no effect. The remaining component, forbs and dwarf shrubs, was different inside and outside the

exclosure only at the Penns Cabin site. Like its effect on total biomass, the effect of year on biomass components varied between sites (see Table 1 in Peterson et al. 1997).

Forage quality at each site was estimated by determining the nitrogen concentration of the live C₃ grass component. Analyses of this data to detect the effects of year and exclosures were performed separately for each site. Nitrogen concentration differed between years only at the North Dryhead site, and differed inside and outside of exclosures at three sites. Grass at two of these sites had higher nitrogen concentrations outside the exclosures, while an opposite effect was found at the third site.

Differences in plant cover between 1993 and 1994 were greater than those between exclosed and control plots. Averaged across years and sites, total cover in control and exclosed plots was 56% and 59%; averaged across sites, total plant cover decreased over 40% between 1993 and 1994 (71% to 40%; Fahnestock 1998; Fahnestock and Detling 1999). This decrease in cover was consistent across elevations and paralleled a reduction in growing season precipitation which was twice as high in 1993 as 1994 (Peterson et al. 1997; Fahnestock 1998; Fahnestock and Detling 1999). Not all functional groups and species changed similarly between years. At low elevation sites, most of the change on total plant cover was attributed to decreases in absolute grass cover with corresponding increases in relative forb cover (Fahnestock 1998; Fahnestock and Detling 1999). At higher elevation sites (Penns Cabin and Forest Service), the absolute covers of both grasses and forbs decreased between years. Although cover did not differ inside and outside exclosures consistently at any site, it was affected by exclosures at the two higher elevation sites in one year (1993). However, the exclosed plot at the Forest Service site had higher cover than the adjacent control plot, while the exclosed plot at Penns Cabin had lower cover than the control plot, similar to the plot comparisons of biomass.

Summary of Findings in Previous PMWHR Vegetation Projects: 1995–1996

A study started in 1994 was designed to extend the work just described by estimating biomass and cover at 12 permanent exclosure sites. Five of these sites were sampled from 1992–1994, and the additional seven

were established in 1994 (Bat Cave, North Bay, Peninsula, RAWS, Subalpine, Turkey Flats, Yellowhill). Details of the sampling and full results can be found in Gerhardt and Detling (1998).

July herbaceous biomass was analyzed by pooling data across all 12 sites from 1995 and 1996. After accounting for the variation due to site differences, mean biomass differed between years. However, the decrease from 1995 to 1996 was greater at some sites than others. Similar to the effect of year, the exclosures had a general effect averaged across sites and years, but the effect of the exclosure varied across sites, ranging from no effect to relatively strong effects (Gerhardt and Detling 1998).

Plant cover was analyzed separately for lower and upper elevation sites. At the four upper elevation sites (Forest Service, Penns Cabin, RAWS, Subalpine), mean total plant cover was not significantly affected by the exclosures, and did not change significantly between 1995 and 1996.

This result was consistent across all functional groups. At the remaining eight lower elevation sites, mean total cover was unaffected by exclosures, but did vary across years, decreasing from 34% in 1995 to 27% in 1996 (Gerhardt and Detling 1998). This decrease between years could not be attributed to any single functional group.

In addition to comparing herbaceous biomass, Gerhardt and Detling (1998) compared shrub production inside and outside exclosures at two exclosure sites (Bat Cave and Yellowhill) which are located in curl-leaf mountain mahogany (*Cercocarpus ledifolius*) communities. Current annual growth (g/shrub) of *Cercocarpus* differed significantly between the two sites, but not between years, and was not affected by the exclosures.

General Linear Models

For each dependent variable, we found the model which best fit the data by using the AIC criteria and a step-wise GLM. Because this technique selects factors based on the AIC, the factors selected for each dependent variable differed. The selected model for each vegetation variable is presented below. Many of the selected models did not include the plot factor (exclosed vs. control). However, because we were

interested in the amount of influence this factor had on the vegetation, we added plot to each selected model if it was not included based on AIC selection methods (Appendix A). This allowed us to demonstrate the effect or lack of effect of the exclosures.

Biomass

Three factors had strong effects on aboveground herbaceous biomass: soil, year, and east coordinate (soil: $F = 33.8$, $P < 0.001$; year: $F = 22.8$, $P < 0.001$; east: $F = 148.2$, $P < 0.001$; Fig. 3a-c). Mean biomass was highest on TX soils and lowest on SA1 soils. In addition to the biomass differences due to soil type, there was a trend for biomass to increase from the eastern side of the PMWHR to the western side. Averaged across soil types and location, biomass differed significantly between years. When added to the model, the effect of plot type was not significant at the $\alpha = 0.05$ level ($F = 3.2$, $P = 0.078$; Fig. 4a), indicating that averaged across all sites and years, biomass did not differ significantly inside and outside exclosures.

Richness

Species richness was significantly higher on certain soil types ($F = 18.1$, $P < 0.001$) and increased with site elevation ($F = 210.2$, $P < 0.001$; Fig. 5a,b). The effect of the exclosures on richness was not significant ($F = 0.7$, $P = 0.393$; Fig. 4b).

Total Plant Cover

The main effects of elevation and summer horse population were significant (elevation: $P < 0.001$; summer population: $P < 0.001$) and the interaction between these terms was significant (summer x elevation: $P = 0.001$). The significance of the elevation term and the summer population term indicates that total cover increased with increasing site elevation (Fig. 6a), and decreased with increasing summer horse population size (Fig. 6b). However, the significant interaction between these two terms suggests that the effect of elevation on plant cover varied depending on summer herd size (Fig. 6c). The exclosures had no effect on total cover ($P = 0.852$; Fig. 4c).

Bare Ground

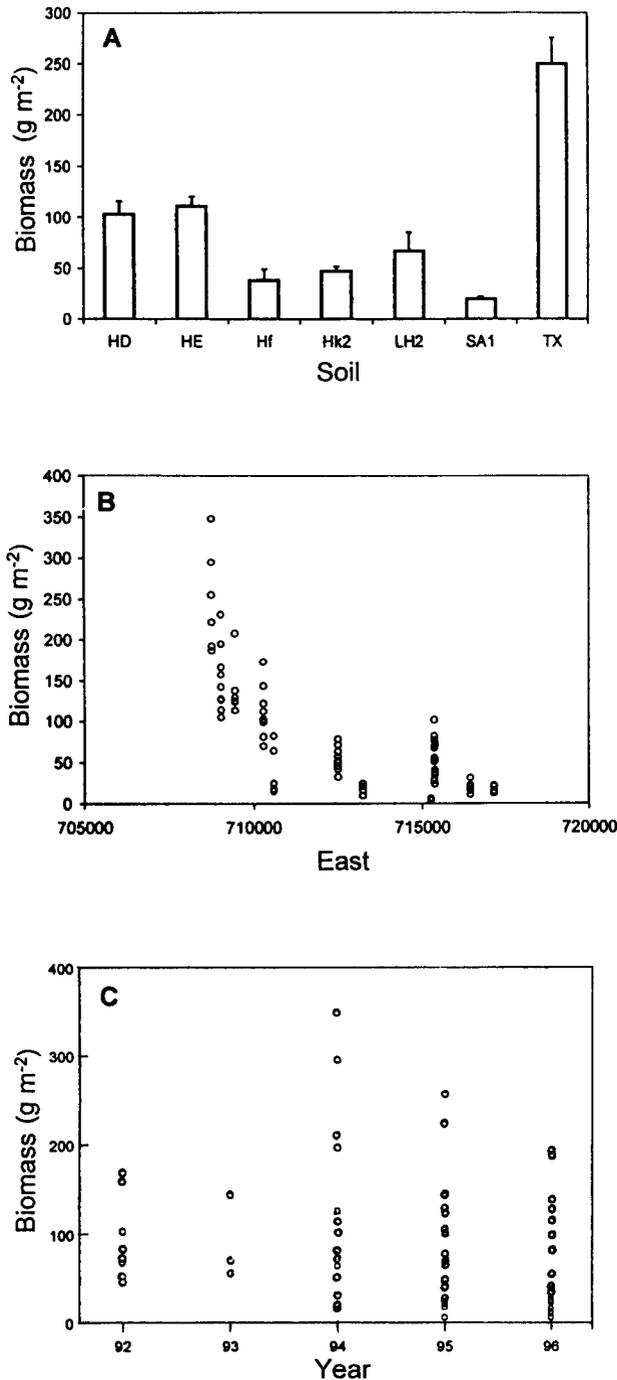


Fig. 3. Aboveground biomass plotted against factors from step-wise GLM analysis: Soil type, east coordinate, and year. The plot of biomass vs. soil shows the mean and standard error.

The percentage of bare ground was affected by location (east: $P < 0.001$; north: $P = 0.003$), increasing towards the east and decreasing towards the north (Fig. 7a,b). In addition to location, the percentage of bare ground depended on the soil type of the sites, being lowest on TX soils and highest on Hf soils ($P < 0.001$; Fig. 7c). Averaged across all sites, there was also a significant tendency for higher summer horse populations to be correlated with a higher percentage of bare ground ($P = 0.003$; Fig. 7d). Exclosures did not have a significant effect on bare ground ($P = 0.575$; Fig. 4d).

Litter

The model selected to explain the cover of litter included four terms: east, growing season precipitation, winter horse population, and plot. Litter cover decreased significantly from west to east ($P < 0.001$; Fig. 8a), and increased significantly with growing season precipitation ($P = 0.002$; Fig. 8b). Litter cover also varied significantly with winter horse populations ($P = 0.007$; Fig. 8c). Based on AIC criteria, plot type was included in the selected model, but the effect of plot was not significant at the $\alpha = 0.05$ level ($P = 0.066$; Fig. 4e).

Absolute Grass Cover

The absolute cover of grass was significantly influenced by mean site precipitation ($P < 0.001$; Fig. 9a) and by the current year's growing season precipitation ($P < 0.001$; Fig. 9b). The main effect of summer herd size was significant ($P < 0.001$; Fig. 9c). However, the interaction between summer herd size and current year's growing season precipitation was also significant ($P = 0.002$) indicating that the effect of summer herd size on grass cover depended on recent precipitation. Although plot was not selected based on AIC criteria, the exclosures did have a nearly significant effect ($P = 0.052$; Fig. 4f).

Relative Grass Cover

The selected model for relative cover of grass included seven significant factors: east ($P < 0.001$; Fig. 10a), north ($P = 0.002$; Fig. 10b), elevation ($P < 0.001$; Fig. 10c), year ($P < 0.001$; Fig. 10d), soil ($P < 0.001$; Fig. 10e), the interaction between soil and

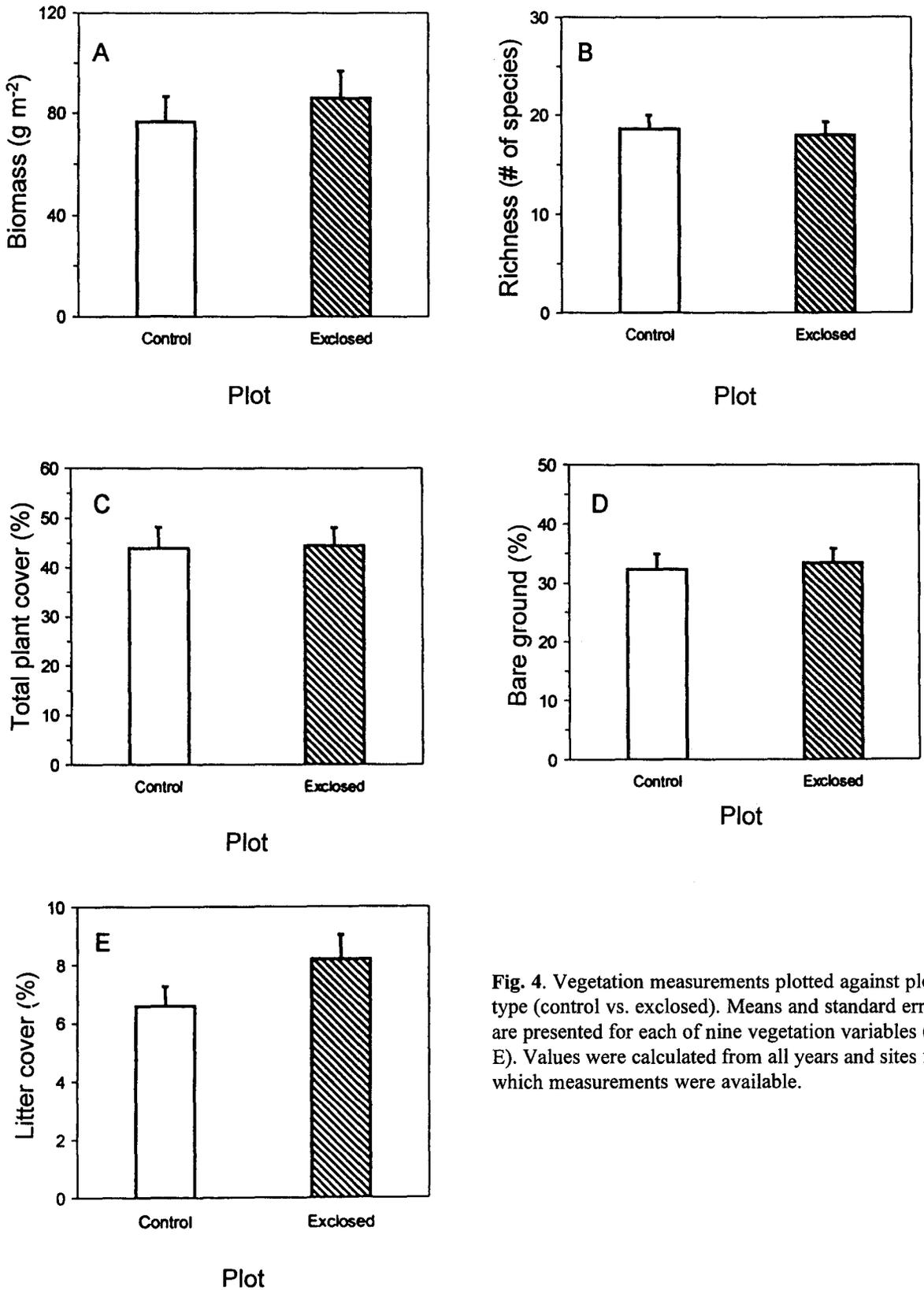


Fig. 4. Vegetation measurements plotted against plot type (control vs. exclosed). Means and standard errors are presented for each of nine vegetation variables (A–E). Values were calculated from all years and sites for which measurements were available.

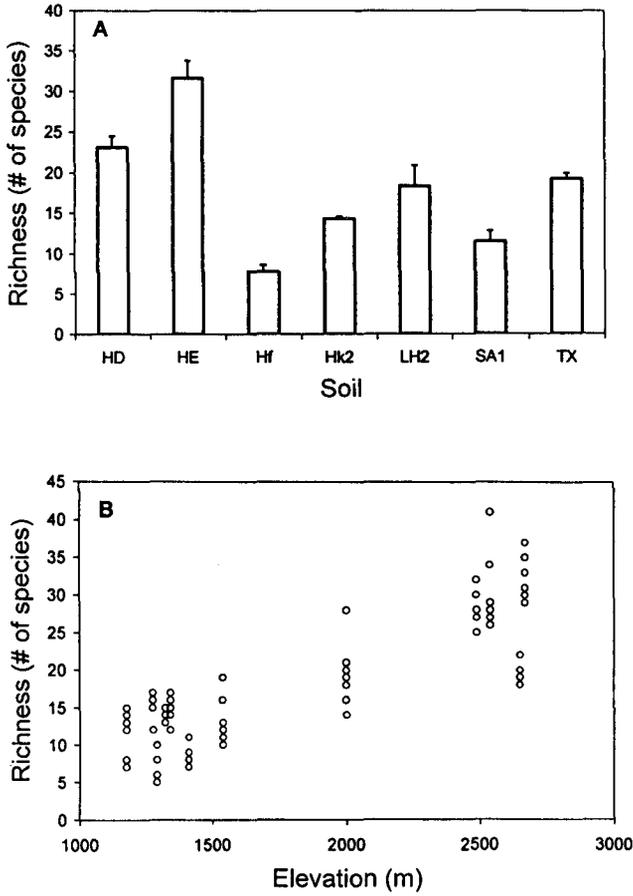


Fig. 5. Richness plotted against factors selected from step-wise GLM analysis: Soil type and elevation. The plot of richness vs. soil shows the mean and standard error.

north ($P < 0.001$), and plot ($P < 0.001$). Although it is not readily apparent from Fig. 10a–c, there was a linear trend for slightly increasing relative cover from west to east, and a slight decreasing linear trend from south to north and from lower to higher elevation. The linear trend over years (Fig. 10d) was decreasing from 1993 to 1996, and overall, relative grass cover was slightly higher inside exclosures than outside (Fig. 4g).

Absolute Forb Cover

The model for the absolute forb cover included only the elevation factor. Forb cover increased strongly with increasing elevation ($P < 0.001$), showing a slight

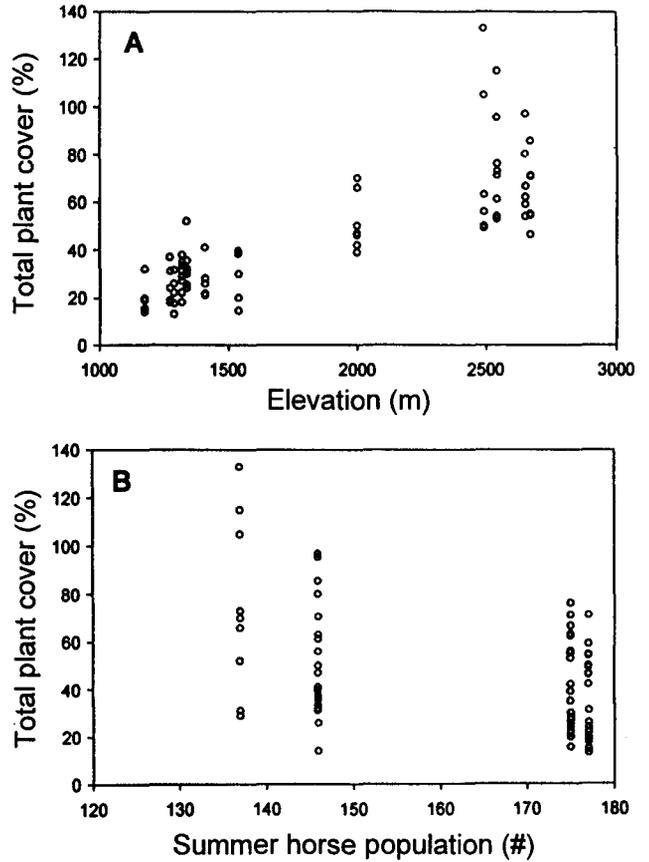


Fig. 6. Total cover plotted for factors selected from step-wise GLM analysis: Elevation (A), summer horse population (B), and the interaction between these two factors (C). In graph C, individual panels present total cover vs. elevation for the summer horse population indicated at the top of the panel.

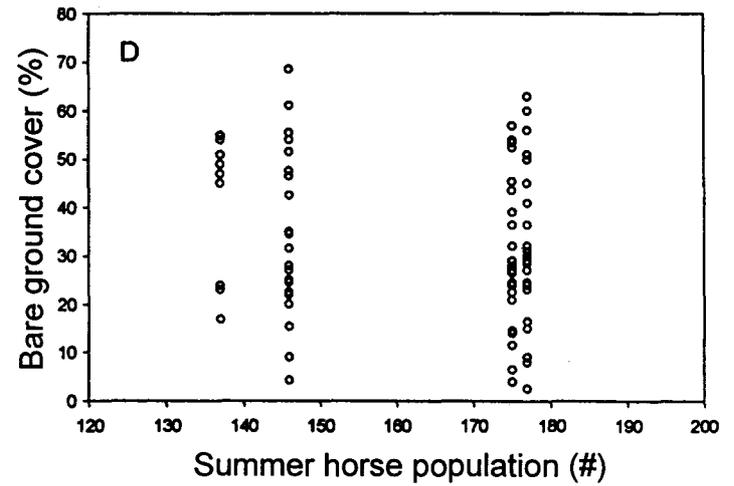
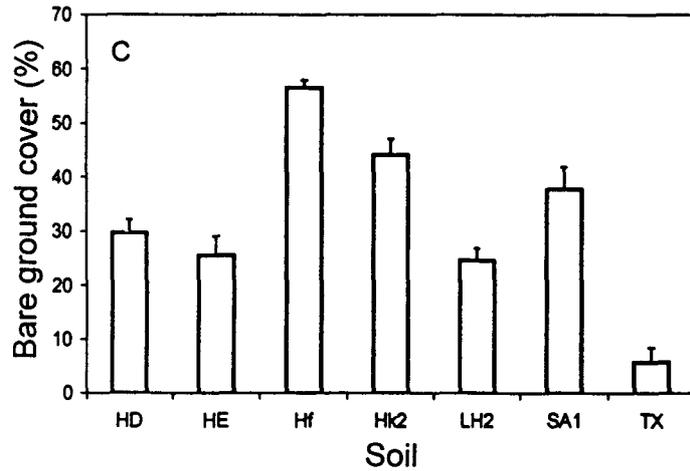
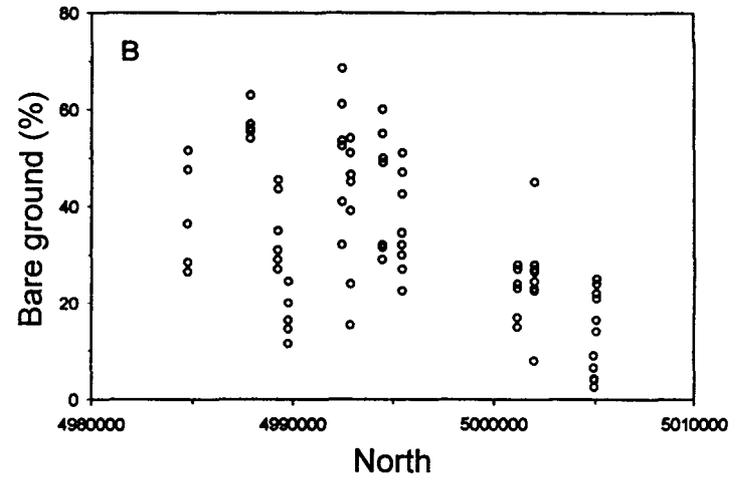
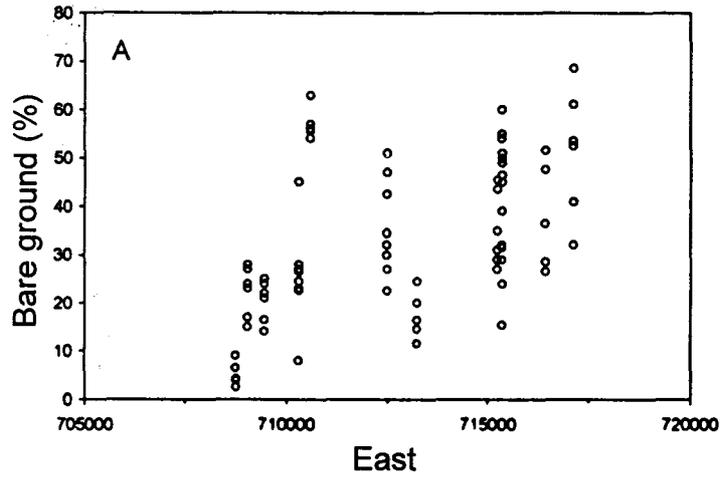


Fig. 7. Total cover plotted for factors selected from step-wise GLM analysis: East coordinate (A), north coordinate (B), soil (C), and summer horse population (D). Means and standard errors are presented for each soil type (C).

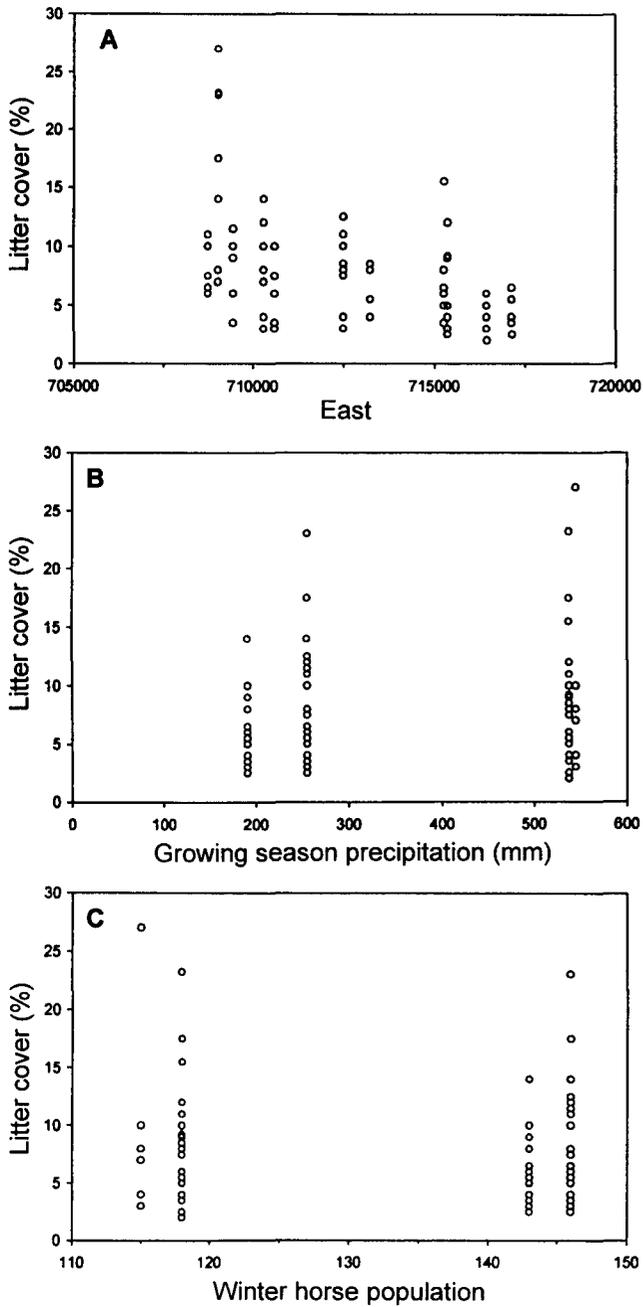


Fig. 8. Litter cover plotted for factors selected from step-wise GLM analysis: East coordinate (A), growing season precipitation (B), and winter horse population (C).

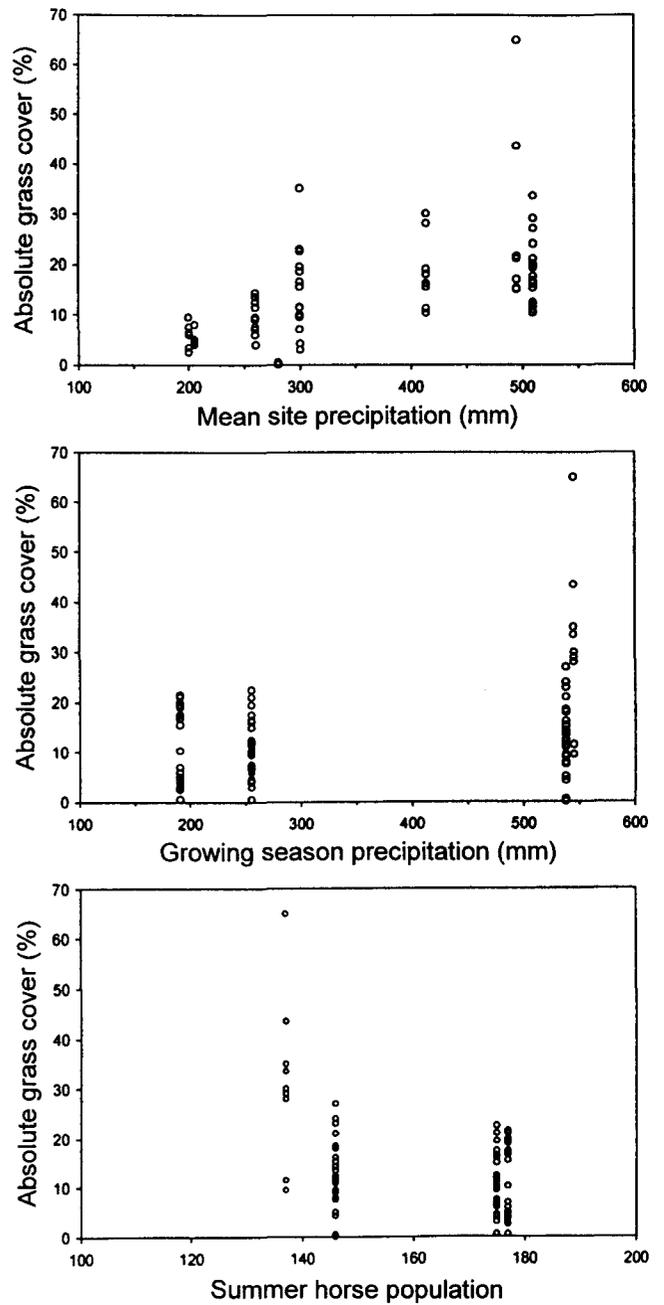


Fig. 9. Absolute grass cover plotted for factors selected from step-wise GLM analysis: Mean site precipitation (A), growing season precipitation (B), and summer horse population (C).

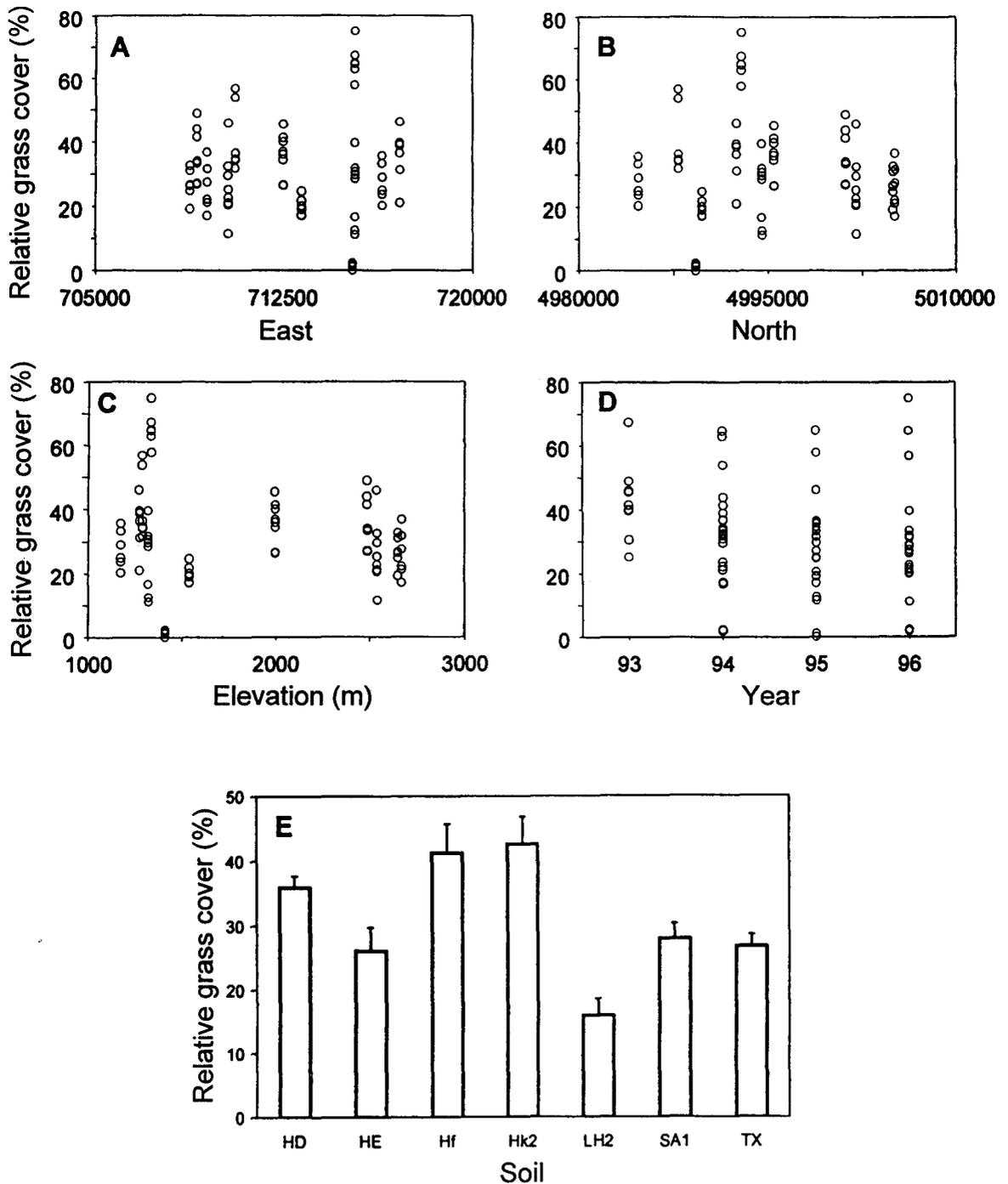


Fig. 10. Relative grass cover plotted for factors selected from step-wise GLM analysis: East coordinate (A), north coordinate (B), elevation (C), year (D), and soil (E). The x axes in A and B are UTM coordinates. Means and standard errors are shown in E.

increase up to 2,000 m and then a sharper increase from 2,000 m to higher elevations (Fig. 11). Exlosures did not significantly affect forb cover ($P = 0.291$; Fig. 4h).

Relative Forb Cover

Although relative forb cover also tended to vary with elevation, the effect of elevation on relative cover of forbs was not quite significant ($P = 0.098$; Fig. 12a). The main effect of north-south location had a significant effect ($P < 0.001$; Fig. 12b). However, the interaction between north-south location and elevation was significant (north x elevation: $P < 0.001$), suggesting that the effect of a similar shift north depended on elevation and whether elevation changed with north-south location (for example, moving north in the Dryhead vs. moving north up Sykes Ridge). Exlosures did not have a significant effect on relative forb cover ($P = 0.123$; Fig. 4i).

Biomass Difference

Although the difference in biomass inside and outside exclosures was not constant over time or space (Figs. 13 and 14), the only factor selected in the step-wise analysis was soil type ($P = 0.007$; Fig. 15).

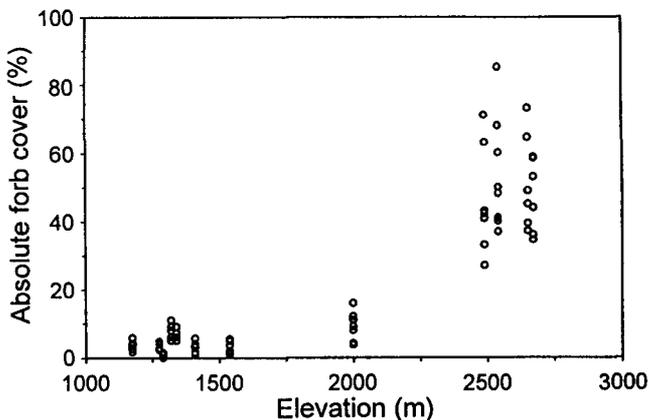


Fig. 11. Absolute forb cover plotted for factor selected from step-wise GLM analysis: East coordinate.

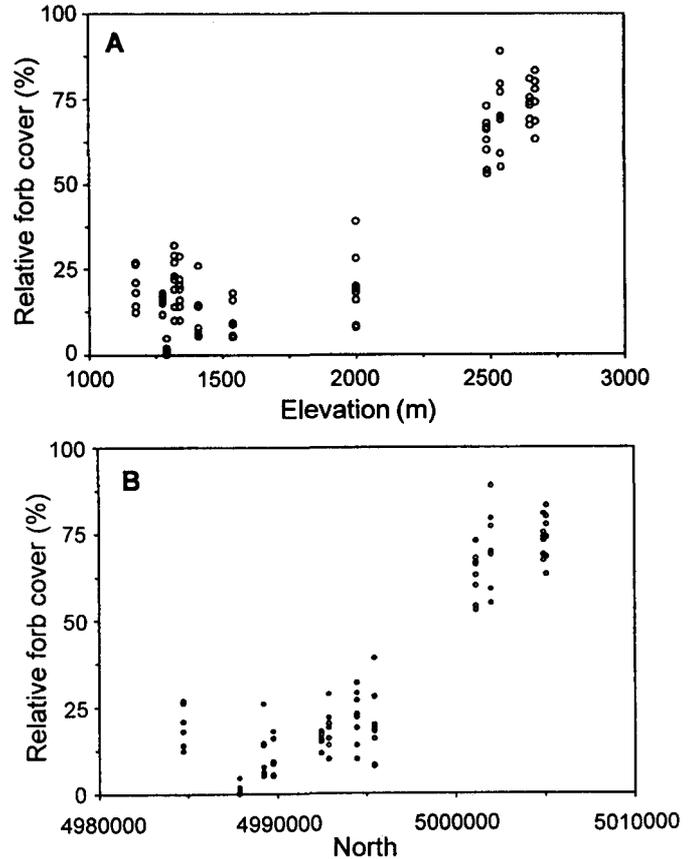


Fig. 12. Relative forb cover plotted for factors selected from step-wise GLM analysis: Elevation (A) and north coordinate (B).

Percent Biomass Difference

The percent difference in biomass inside and outside exclosures also varied temporally and spatially (Fig. 16), and was significantly affected by five factors. Percent difference in biomass depended on soil type ($P = 0.001$; Fig. 17a), elevation ($P = 0.003$; Fig. 17b), and year ($P = 0.043$; Fig. 18a). The percent difference decreased from west to east (east: $P = 0.020$; Fig. 18b), but this east-west trend varied between years (east x year: $P = 0.003$; Fig. 18c).

Principal Components Analyses

PCA was performed on data from each site for all years in which all vegetation variables were measured.

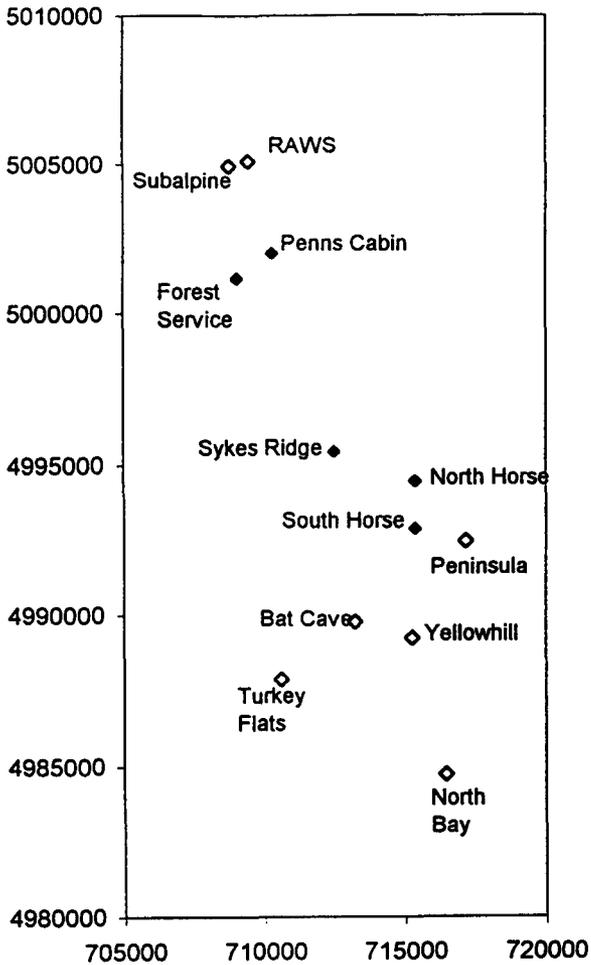


Fig. 13. Map of exclusion sites in PMWHR with site name indicated. Sites were GPS located and the x and y axes represent UTM coordinates. Vegetation at five sites (◆) was measured for 5 years (1992–1996). At the remaining seven sites (◇), vegetation was measured from 1994–1996.

The time span was 4 years (1993–1996) for five sites (Forest Service, Penns Cabin, Sykes Ridge, North Horse, South Horse), 3 years for another five sites (Subalpine, RAWS, Peninsula, Turkey Flats, North Bay), and 2 years for two sites (Bat Cave and Yellowhill). For each site, nine vegetation variables were included in the PCA: herbaceous biomass, species richness, total plant cover, absolute and relative grass cover, absolute and relative forb cover, litter cover, bare ground cover. The analyses allows visual comparisons

of overall vegetation differences between plot types (excluded vs. control) and across years, but does not produce significance tests.

We provide PCA graphical output from each site separately and discuss overall trends in the Discussion. The axes in each PCA plot (Fig. 19) are composites of the nine vegetation variables, and are statistically derived to best separate the sample points. For a detailed description of each plot's axes, review the eigenvalues and loadings presented in Appendix B. In general, vegetation variables which load highly on an axis help separate points along that axis; for variables that have low loadings on an axis, differences in that variable between samples have a small effect on the spread of points. While significance tests are not provided in a PCA, the value of the technique for these data is in providing a way to compare the effects of plot type vs. yearly trends on overall vegetation characteristics, and to determine whether trends in vegetation change across years are similar inside and outside exclosures, or whether exclosures have larger overall effects in certain years. In addition, it can suggest whether vegetation inside and/or outside exclosures is following a trend which may indicate successional changes over time.

Discussion

Two studies conducted from 1992 to 1996 reported a variety of vegetation responses to exclosures and suggested that PMWHR vegetation responds to interannual biotic and abiotic variation. A 3-year intensive investigation (1992–1994) into vegetation dynamics at five permanent exclosure sites demonstrated significant vegetation changes between years, but few consistent effects of exclosures across years or sites (Peterson et al. 1997; Fahnestock 1998; Peterson 1998). In general, their study focused on detecting vegetation differences at smaller, site-specific spatial scales and many of the statistical analyses selected were chosen to pinpoint the effects of herbivory. Data were analyzed by individual site or by pooling data from sites located geographically close. The second 3-year study (1994–1996) monitored vegetation less intensively while attempting to expand the spatial scale by sampling at 12 permanent exclosure sites (Gerhardt and Detling 1998). Although the analyses used in the second study addressed larger areas of the PMWHR, they required that strict statistical conclusions be limited to those areas actually sampled.

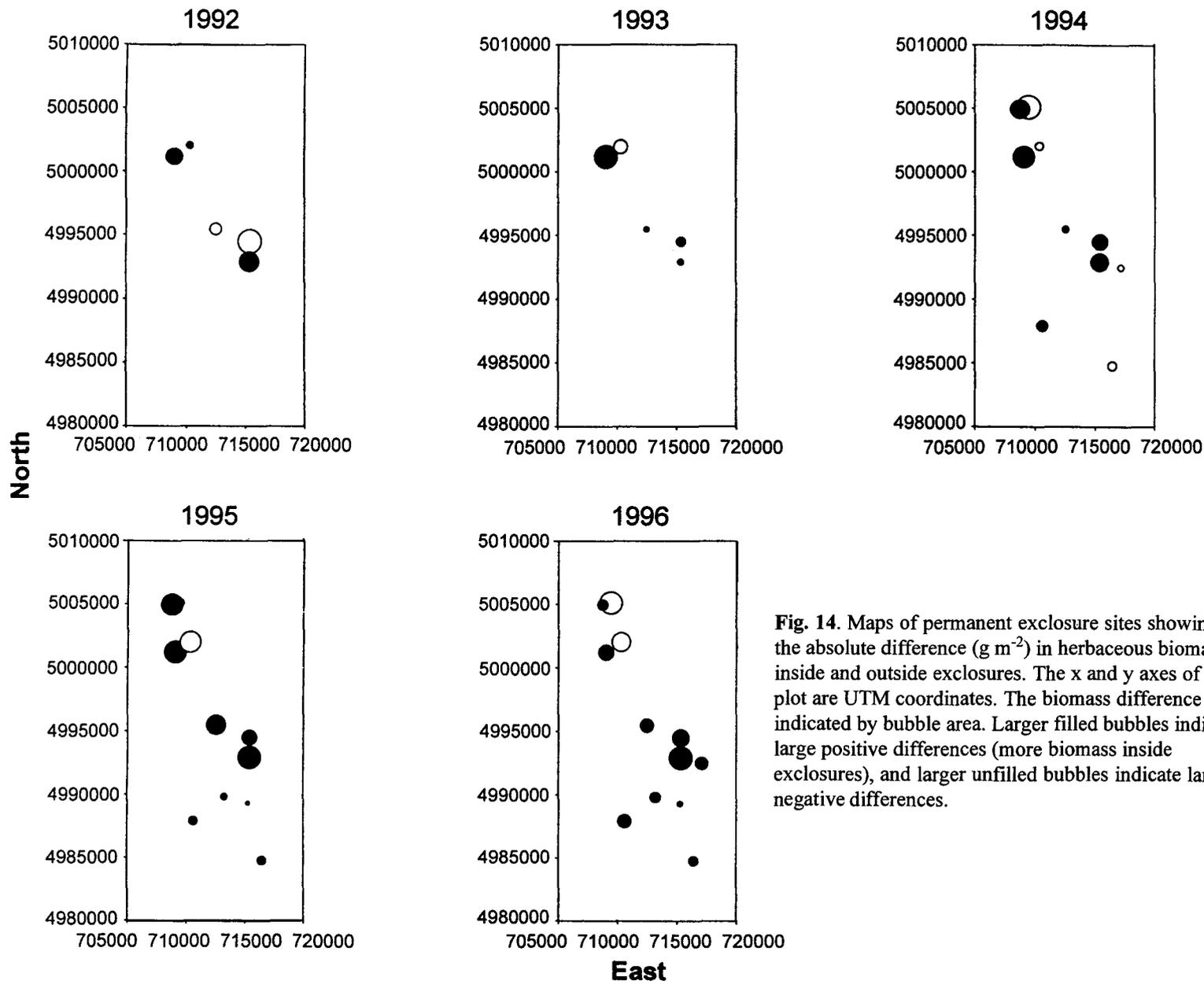


Fig. 14. Maps of permanent exclosure sites showing the absolute difference (g m^{-2}) in herbaceous biomass inside and outside exclosures. The x and y axes of each plot are UTM coordinates. The biomass difference is indicated by bubble area. Larger filled bubbles indicate large positive differences (more biomass inside exclosures), and larger unfilled bubbles indicate large negative differences.

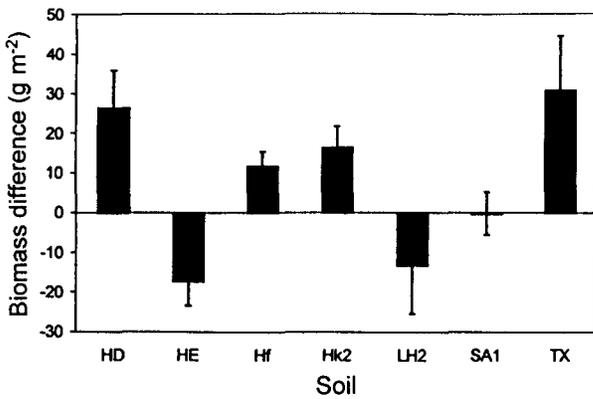


Fig. 15. Biomass difference (exclosed-control) plotted for factor selected from step-wise GLM analysis: Soil.

Based on fecal analysis, Kissell et al. (1996) found that the diet of PMWHR horses was 60% to 90% grass, with forbs and shrubs increasing or decreasing in dietary importance with year and season. This compares with feral horse diets in New Mexico, which consisted of 91% grass and a small shrub and forb component (Smith et al. 1998). The Peterson et al. (1997) study was the only PMWHR study in which growing season offtake was directly estimated by using small moveable exclosures. Offtake of both grasses and forbs was detected. Depending on year and site, estimates of offtake by grazers ranged from 0 to 43% of current year's aboveground herbaceous biomass and (Peterson 1999; Peterson et al. 1997). As reviewed by Peterson et al. (1997), these estimates fall within the middle of the ranges of offtake found in other grazed systems (Coppock et al. 1983; Cargill and Jeffries 1984; McNaughton 1985; Whicker and Detling 1988; 1988; see also Frank and McNaughton (1992); Singer et al. (1998a), and, averaged across sites in the PMWHR, compare with those reported for feral horses in other systems [3% to 20% offtake; Keiper (1981); Duncan 1992]).

Although significant offtake was not detected at all sites, both studies reported significant vegetation differences inside and outside permanent exclosures (Peterson et al. 1997; Gerhardt and Detling 1998). However, many differences between exclosed and control plots were detected only at some sites and even then, only in one or a few years. For example, the Penns Cabin site tended to show different vegetational trends than the remaining sites. From 1993–1994,

herbaceous biomass inside four permanent exclosures ranged from 67% to 80% of that found outside exclosures, while the Penns Cabin site had approximately 20% more biomass outside the exclosure (Peterson et al. 1997). A similar result was found for total plant cover: greater cover outside the exclosure at the Penns Cabin site, but the opposite result at other sites. As a second example of site/area specific effects, total plant cover showed significant decreases from 1993 to 1994, paralleling a decrease in growing season precipitation. Although this between-year effect was much stronger than the average effect of the exclosures, differences between locations were evident.

In addition to testing for a landscape-wide effect of plot, our GLM analyses were designed to detect the locations or times when any plot effects were significant. Both the grazing patterns of ungulates and the effects of grazing on vegetation are known to be influenced by multiple factors. The distribution and foraging patterns of ungulates are patchy and depend on vegetation characteristics as well as abiotic factors which act directly on the herbivore (e.g. slope, distance to water) or indirectly on the vegetation (e.g., soil, precipitation, etc.; McNaughton 1985, Senft et al. 1987; Coughenour 1991; Wallis de Vries and Daleboudt 1994; Bailey et al. 1996; Moen et al. 1997; Detling 1998; Frank et al. 1998). The effects of grazing are also determined by multiple factors and, therefore, are linked both to the distribution of ungulates in time and space and the distribution of resources (McNaughton 1985; Whicker and Detling 1988; Pastor and Naiman 1992; Hobbs 1996; Pastor et al. 1998; Singer et al. 1998b).

Both previous reports indicate that vegetation dynamics varied over time and space. In order to provide conclusions at a landscape level, we used GLM analyses on data from all sites and years, and accounted for spatial and temporal effects by including these in the model building process. Because factors which influence system states and processes operate on a number of scales (Hansson et al. 1995) and it is useful to know at what scales these factors are influential (Underwood and Chapman 1998), we tried to include variables that addressed multiple scales. In addition, we included a number of temporal factors. Each of these was allowed to interact with spatial variables to detect interannual effects that were significant only in certain locations, or localized effects that occurred only in certain years.

The model selection process began with only the overall mean for each variable and selected factors that

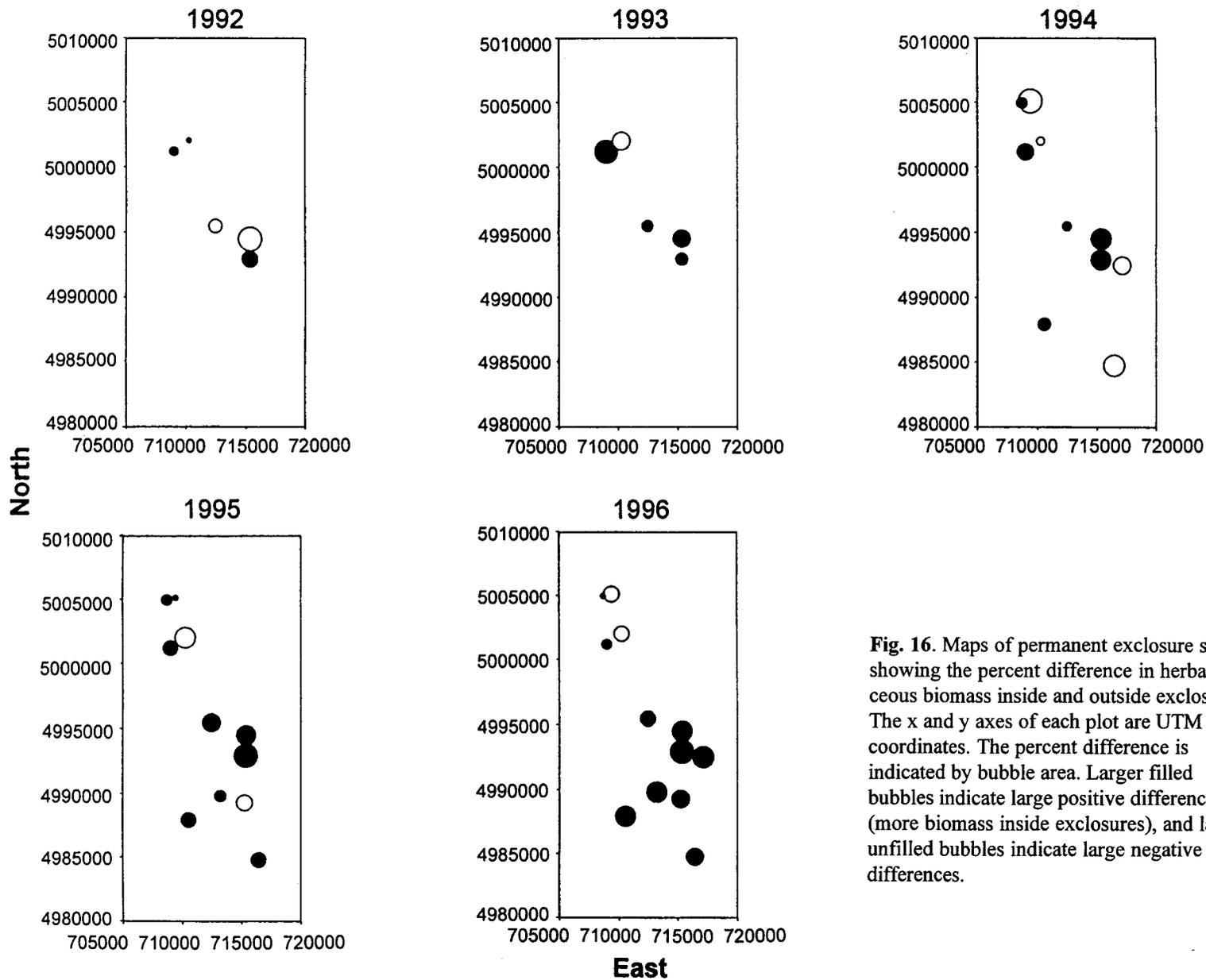


Fig. 16. Maps of permanent exclosure sites showing the percent difference in herbage biomass inside and outside exclosures. The x and y axes of each plot are UTM coordinates. The percent difference is indicated by bubble area. Larger filled bubbles indicate large positive differences (more biomass inside exclosures), and larger unfilled bubbles indicate large negative differences.

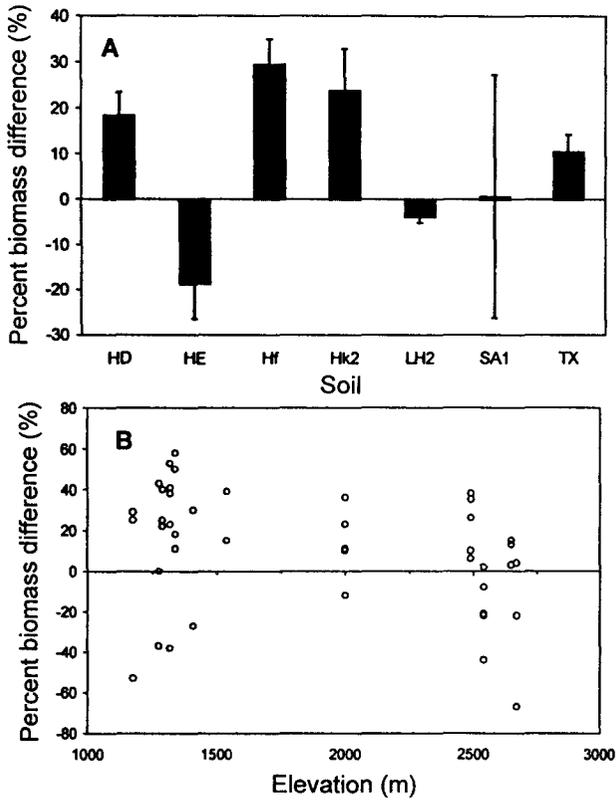


Fig. 17. Percent biomass difference (exclosed-control/exclosed) plotted for factors selected from step-wise GLM analysis: Soil (A) and elevation (B).

best explained the variation in the data. Because selecting which factors to include subjectively may lead to the omission of critical factors or the inclusion of trivial factors, we used an information criterion (AIC) to select models. The concept behind the AIC is that adding an additional independent variable can always explain some variation, but this can lead to the inclusion of too many variables which explain trivial trends or differences. The AIC rates each potential model based on both the variation and differences explained as well as the number of factors. A model which explains a similar amount of variation with fewer factors is preferred. All potential models are rated before omitting or including additional factors.

Several overall trends are evident in the models. First, of the total number of potential factors that could have been selected (175 first, second, and third-order factors), only 15 were chosen (Table 2; Appendix A). Although different factors were included for different

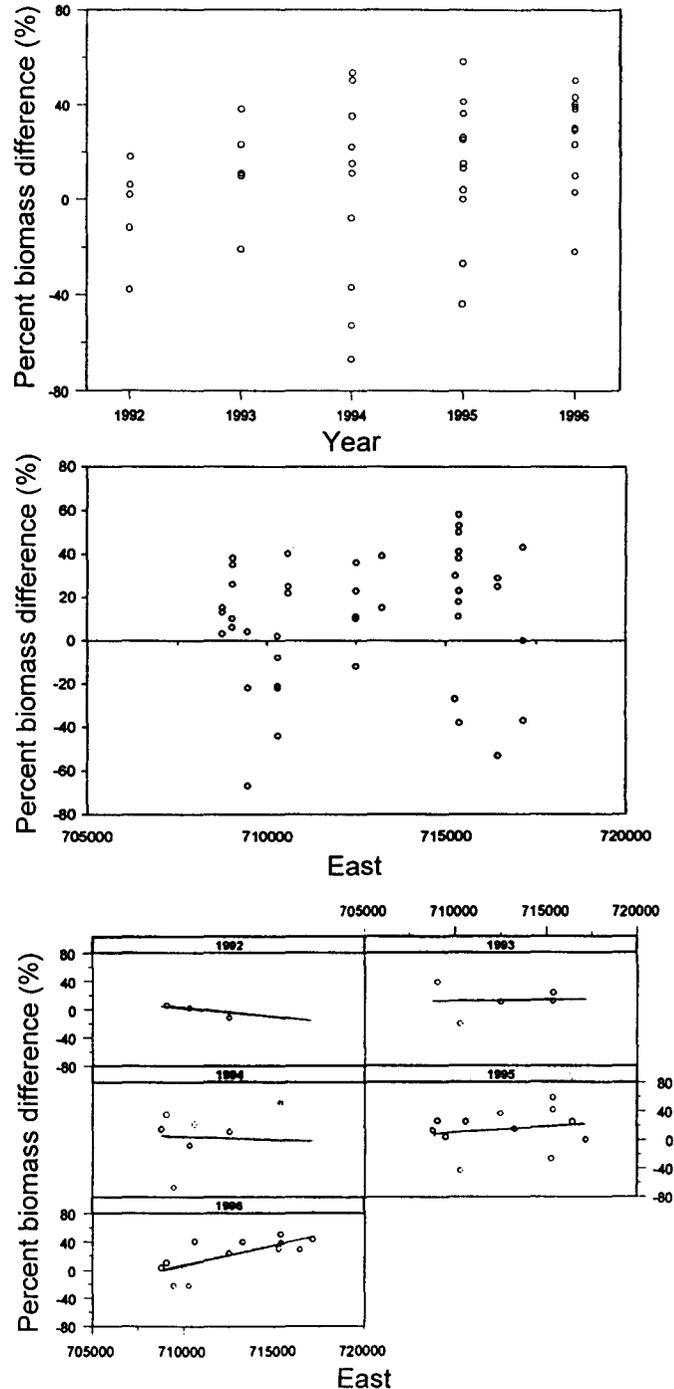


Fig. 18. Percent biomass difference plotted for factors selected from step-wise GLM analysis: Year, east coordinate, and the interaction between these two factors. In the last graph, individual panels present percent biomass difference vs. east coordinate (including the linear trend) for the year indicated at the top of the panel.

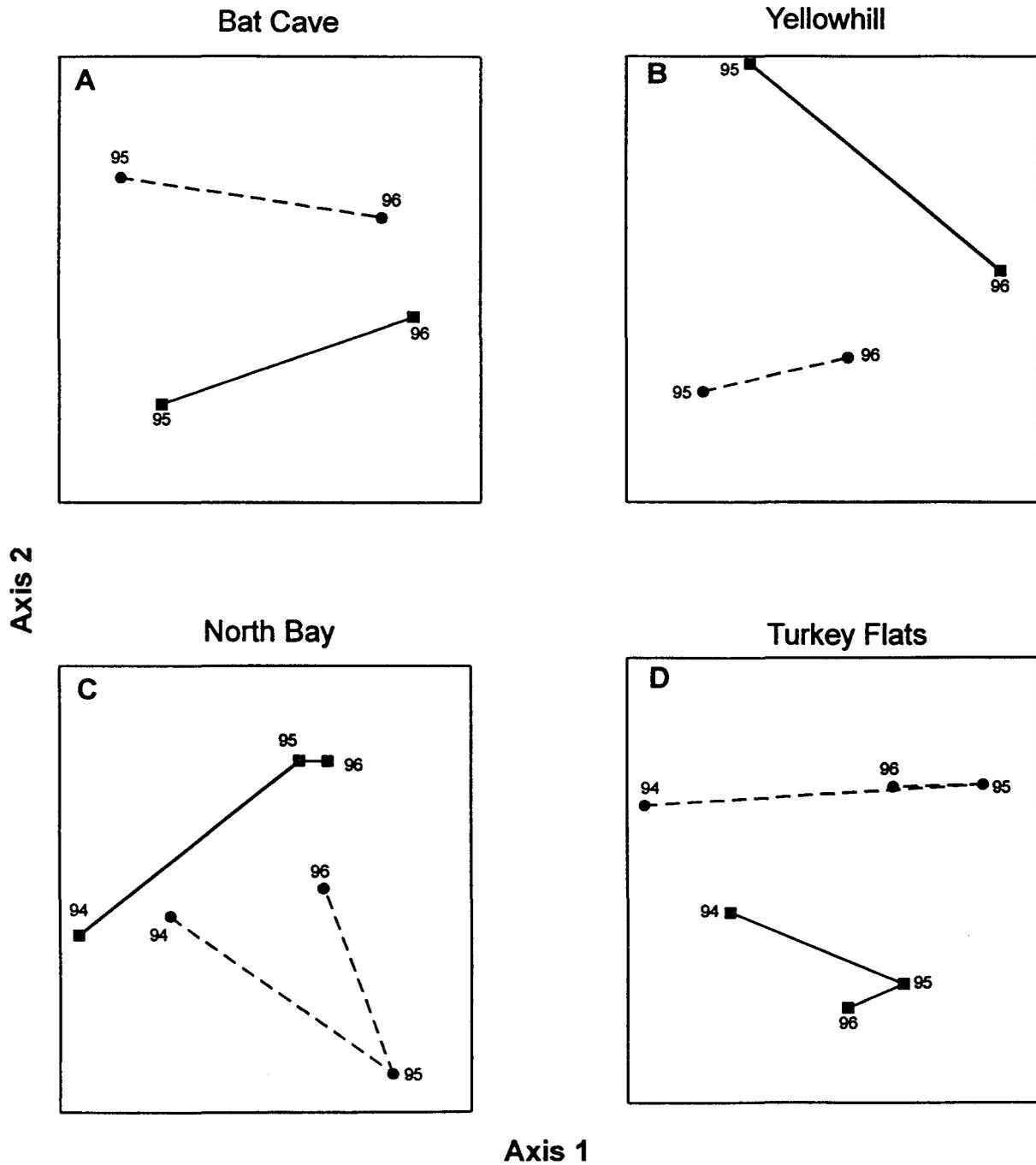


Fig. 19. Plots of samples from each site along PCA axes 1 and 2. Differences along each axis represent differences in a suite of vegetation characteristics. Points are plotted for each year in which biomass and cover measurements were made. The year of each measurement is indicated (1993–1996). Control plots (solid line) and exclosed plots (dashed line) are connected sequentially across years. PCA statistics can be found in Appendix B.

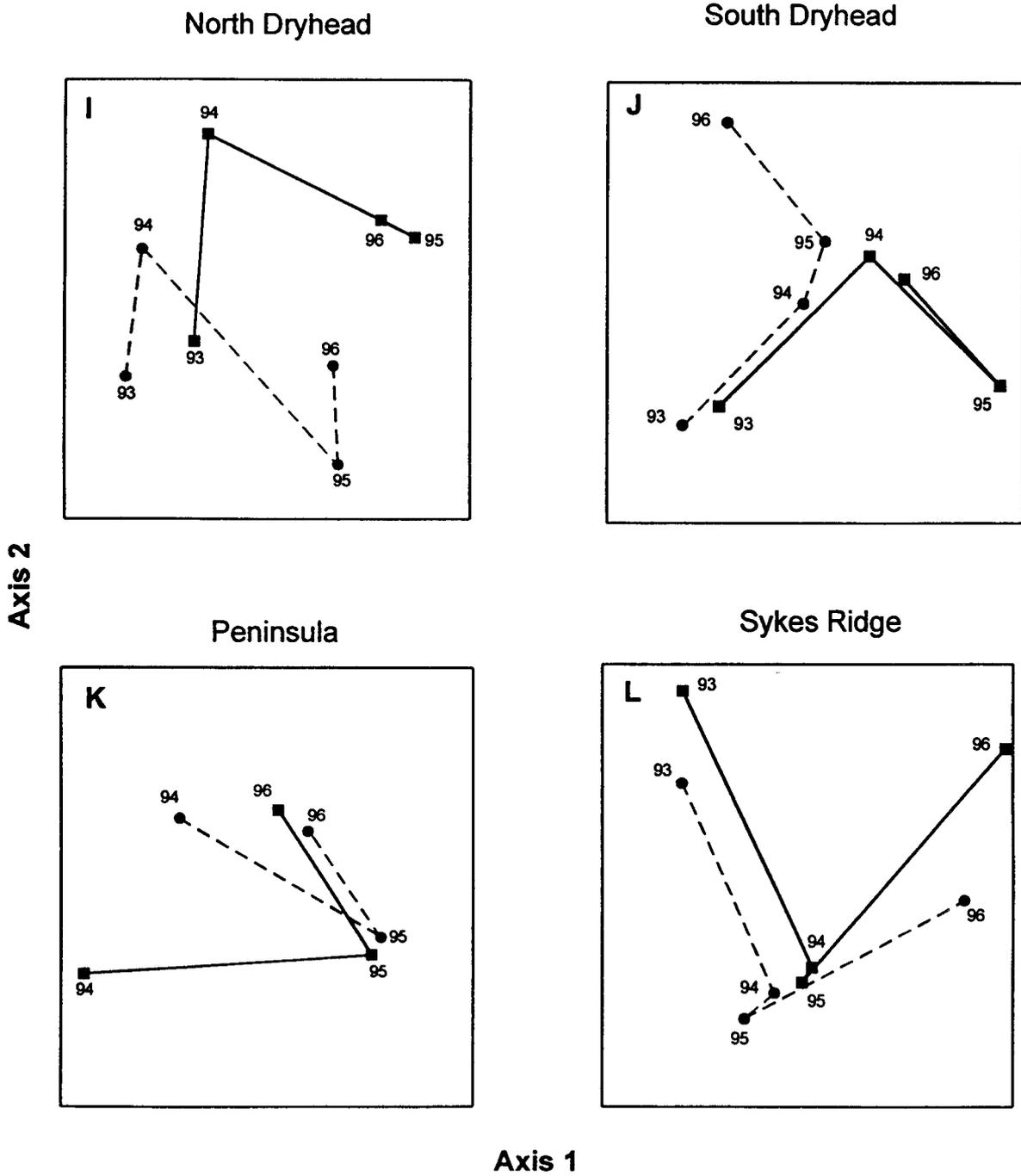


Fig. 19. Continued.

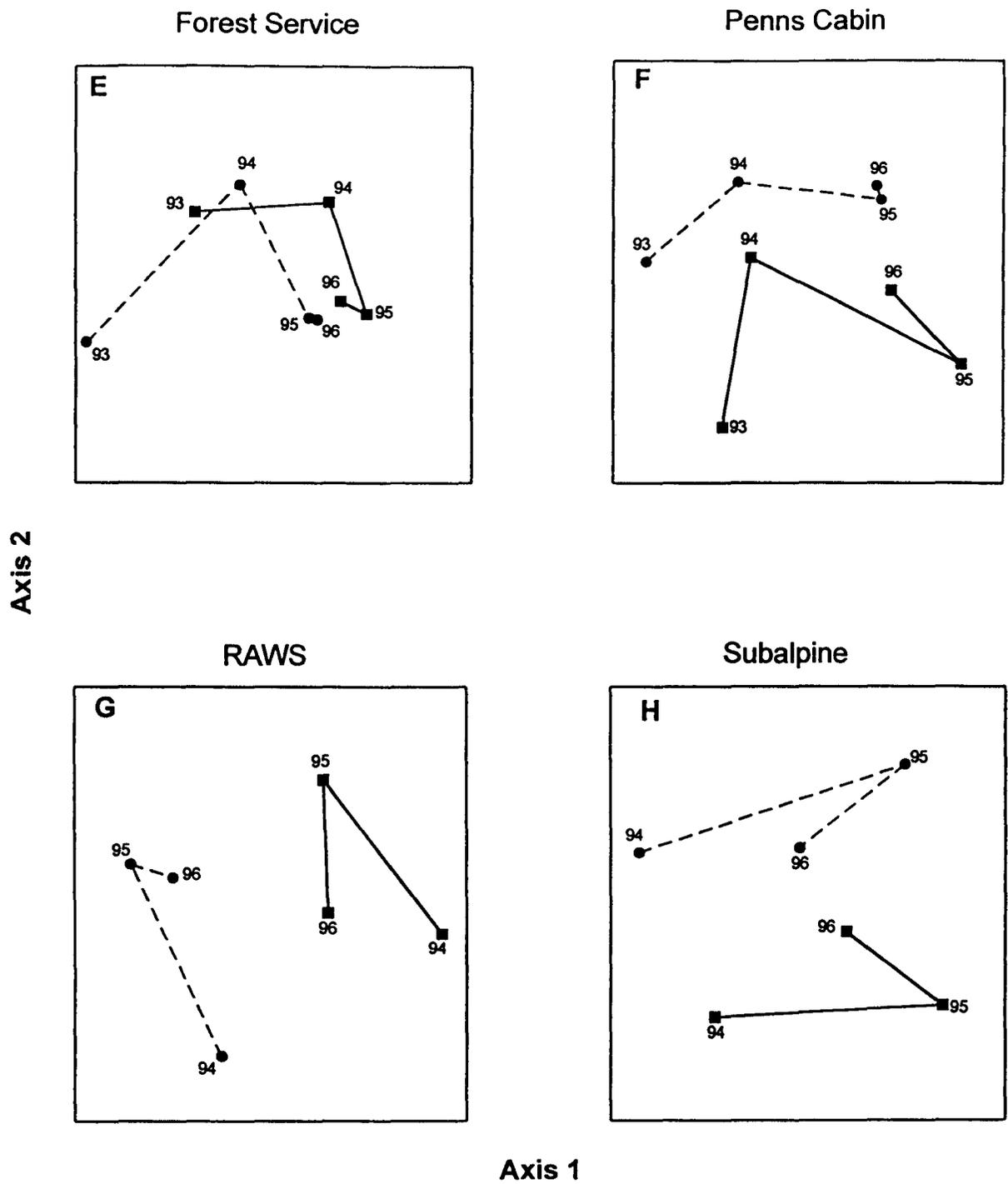


Fig. 19. Concluded.

dependent vegetation variables, the small number of independent variables selected suggests that the main trends and differences in vegetation variables were explained by relatively few factors.

Second, the main factors are grouped into two categories: those describing generally spatial differences between samples and those related to temporal differences. Spatial factors include: east; north; elevation; soil and mean site precipitation, both combinations of spatial and abiotic factors; and plot, the treatment factor which is a spatial variable on a relatively small scale. Temporal factors include: year, growing season precipitation, summer horse population, and winter horse population. Factors related to location (east, north, elevation, soil) tended to have strong effects on relatively many vegetation variables (Table 2). These results compare to those in the previous reports which suggested that vegetation responses varied between sites (Peterson et al. 1997; Fahnestock 1998; Gerhardt and Detling 1998; Peterson 1999). Those factors which showed interannual variation (year, growing season precipitation, summer and winter horse populations) explained less of the overall vegetation dynamics, but still had significant effects. This was especially true for absolute grass cover which was significantly affected by three temporal factors and one spatial/abiotic factor (Table 2). Third, the number of significant factors, and thus the complexity of the explanatory models, varied among vegetation variables. Of the 11 vegetation variables, seven were explained by three or fewer factors (Table 2). Relative grass cover (7 factors), absolute grass cover (5 factors), and relative biomass difference (5 factors) were the variables with the most complex models. The main effects of all environmental factors were strongly significant for at least one vegetation variable. Of the main effects, elevation and soil were selected for the most models (six each), and winter horse population (1 model), mean site precipitation (1), growing season precipitation (2), and plot (2) were selected least often. Of the over 100 interaction terms possible, only 5 had strong significant effects (Table 2).

Plot was a selected factor only for grass cover. Although absolute grass cover was not significantly different at the $\alpha = 0.05$ level ($P = 0.052$), mean grass cover inside exclosures was 16%, and cover outside was 13%. For relative grass cover, plot was highly significant, with average cover outside exclosures about 83% of that inside (Fig. 4f,g). Neither absolute nor relative forb cover differed inside and outside

exclosures, and the effect of the exclosures on total plant cover and bare ground was very weak ($P = 0.851$; $P = 0.575$; Appendix A). These results may differ from those in 1993–1994 (Peterson et al. 1997; Fahnestock 1998) because of the smaller spatial scales which were addressed in that study and because the current analyses included sites where shrubs were a significant component of the vegetation.

Although not selected in the model building process, plot had nearly significant effects on two other vegetation variables: litter and biomass. Averaged across all years and sites, mean litter was 8.2% inside and 6.6% outside ($P = 0.066$). The near significance of this difference indicates a tendency for litter to accumulate inside exclosures, but suggests that this accumulation may occur only over short timespans. This supposition is strengthened by several facts. First, litter decreased slightly but significantly with higher previous winter horse populations (Fig. 8c), and increased slightly with growing season precipitation (Fig. 8b). Second, plot did not interact with year, suggesting that the effects of the exclosure on litter did not build up over the course of the studies.

Both previous reports indicate that exclosures had significant effects on herbaceous biomass. In this analysis, although average biomass tended to be lower outside exclosures (77 g m^{-2} vs. 86 g m^{-2}), this difference was not significant ($P = 0.078$). The difference in results may be explained by the fact that both previous studies used sampled plots as replicates. In Peterson et al. (1997), sites were then analyzed separately. In Gerhardt and Detling (1998) plots were then pooled across sites and years. In the first case, variability due to site is not included in the analyses, and detected effects are restricted to individual sites. In the second case, variability due to site is included, but replication is increased. While both replication schemes are relevant to analyze the sites measured, neither is best suited to extrapolating general trends across studies and the entire PMWHR. The current analysis suggests that across years and sites there is a general and nearly significant trend for biomass to be higher inside exclosures.

Similar to litter, any biomass differences between exclosed and control plots did not seem to vary greatly over time. No temporal factors which interacted significantly with plot were selected for the biomass model, suggesting that the effects of grazing on biomass did not accumulate over the sampling period (1992–1996). In other words, we found no trend for the amount of biomass difference to increase over time of

the enclosure treatment. This is supported by the fact that when we analyzed the actual biomass difference (g m^{-2}), no temporal factors were included in the model (Table 2). However, when analyzed as percent biomass difference, a relative effect, changes in the enclosure affect over time were apparent. Year had a significant effect on percent biomass difference ($P = 0.043$), but the interaction between year and east coordinate was a much stronger effect ($P = 0.002$; Appendix A). This indicates that the interannual changes in the percent difference of biomass between control and enclosed plots depended on location in the PMWHR. Because biomass followed a decreasing trend from west to east (Fig. 3b), and is therefore correlated with the east coordinate, the effect of location on percent biomass difference may be related to the annual distribution of biomass, and presumably horses, in the PMWHR. It appears that there may be a trend for relative differences in biomass to vary more in the eastern portion of the PMWHR (Fig. 18c), where mean biomass is low (Fig. 3b). Figure 18c also suggests that percent biomass difference was greatest, especially towards the east, in 1996, a year in which precipitation was low (Fig. 2) and horse populations were relatively high (Fig. 1). The interannual trend of percent differences in biomass is also shown in the maps (Fig. 16). It is evident that north-south location and elevation also affect relative biomass differences significantly (Table 2).

In previous analyses of the PMWHR vegetation data, the only factor which varied over time was year (Peterson et al. 1997; Gerhardt and Detling 1998). In this analysis, calendar year was included as a potential factor, but several other factors also varied over time (growing season precipitation, summer horse population, winter horse population, and interactions involving these terms). In reviewing Table 2, it is evident that while certain vegetation variables differed between years, the temporal factor most related to these changes was not consistent. For example, calendar year had a strong effect on biomass, but seasonal precipitation and horse populations did not. Interpreting why certain temporal factors or interactions had or failed to have an effect on vegetation variables is somewhat complicated by the fact that these temporal factors are correlated with each other (growing season precipitation and summer horse population; $r = -0.879$; growing season precipitation and winter horse population, $r = -0.966$; Figs. 1 and 2).

Variation in growing season precipitation had a significant effect on litter cover and absolute grass

cover, a finding reported and discussed in Peterson et al. (1997) and Fahnestock (1998). Like litter, absolute grass cover tended to increase with higher seasonal precipitation (Fig. 9b). It is interesting that absolute grass cover was lower in 1995 than in 1993, two years in which seasonal precipitation was nearly equally high (Fig. 2). It seems possible that because summer horse populations also had a significant effect on absolute grass cover ($P < 0.001$), the difference between 1993 and 1995 could be a result of different summer populations. However, this does not appear to be true because summer horse populations were nearly the same in both years. Although not statistically addressed, Figs. 1 and 2 indicate the possibility that variation in either horse populations during the previous year or precipitation in the previous year may have effects on the current year's grass cover.

Total plant cover and bare ground both decreased significantly with summer horse population (Table 2). The results for total plant cover indicate that lower plant cover tended to occur when horse populations were higher. However, the fact that the interaction between plot and summer populations was not significant suggests the decreases in total plant cover at higher horse populations were similar inside and outside the enclosures. Although it is not obvious why bare ground also decreased with increasing summer herd size, the decreases, again, were similar inside and outside the enclosures.

Neither of the previous reports indicate either yearly differences or differences due to enclosure for species composition or richness. Our results indicate that richness did not vary over time and was similar inside and outside of enclosures (Fig. 4b). Richness depended on soil and elevation (Fig. 5a,b), and showed a consistent linear increase with elevation. Reviews of grazing impacts on richness in a wide range of systems found that grazing effects on species richness depend on the system's nutrient richness (Proulx and Mazumder 1998). The effect of grazing in nutrient-poor systems was a decrease in richness; the effect on nutrient-rich systems was the opposite. If abiotic resource levels in the PMWHR vary sufficiently across space or years, any effects of grazers on richness may also depend on location or precipitation. A study of Rocky Mountain grasslands (including the PMWHR) found no significant effects of grazers on the richness of either native or exotic plant species, or on the cover of plant functional groups (grass, forbs, shrubs; Stohlgren et al. 1999). Although their study was conducted at a much larger spatial scale, including

enclosure sites in four states, their results were similar to ours in finding a strong correlation between richness and both soil and elevation. They conclude that grazing effects are localized and are probably weak at the landscape scale, with richness being determined primarily by abiotic factors (Stohlgren et al. 1999).

The principal components analysis performed on vegetation data from each site reveal the local but overall similarity or dissimilarity of vegetation in the enclosed and control plots, and how vegetation in each plot changed between years. Each axis in the PCA plots (Fig. 19) represents a suite of the nine vegetation variables, so the score of a plot along each axis provides information on a number of vegetation characteristics. Because each axis is a composite, shifts along the axes represent correlated changes in multiple original, vegetation variables; similar scores on either axis represent similarities in a number of the original variables. In interpreting the plots (Fig. 19), it may be informative to compare the relative effects of plot versus year. A consistent separation based on plot type indicates that control and enclosed plots differed each year. Greater separation of plots in certain years indicates divergence in some components of overall vegetation; less separation indicates convergence.

Plots of PCA scores for each site indicate several general trends. First, few sites exhibited a consistent trend toward divergence of plots. Although the separation was greater in some years than others, the overall difference between control and enclosed plots did not appear to increase consistently each year. Similarly, there was little indication that enclosed plots changed less between years than control plots. With a few exceptions (e.g., South Horse 1994–1995, Fig. 19f), vegetation in both enclosed and control plots appear to have responded similarly to interannual differences in environmental factors, maintaining a relatively consistent vegetation difference between plots. For example, at Forest Service, enclosed and control plots were most dissimilar in 1993 when the enclosed plot had more biomass as well as higher absolute covers of total plants, grass, forbs, and litter. While the plots differed in the following years, the overall difference was smaller and the plots moved in the same direction along both axes between years (Fig. 19e). In other words, the effect of environmental factors appears to have been similar inside and outside the enclosure. At South Horse, plots shifted similarly between years except between 1994 and 1995 when the control plot had more forb cover but less litter and relative grass cover (Fig. 19l). A general comparison of

all plots also suggests that site location has an effect on interannual differences (Fig. 19). Vegetation was similar between 1995 and 1996 at several sites (e.g., Forest Service, Penns Cabin, Turkey Flats), but showed changes at these sites between 1994 and 1995. On the other hand, vegetation at Sykes Ridge was very similar from 1994 to 1995 but showed strong changes from 1995 to 1996.

Conclusions and Management Implications

The projects and data reviewed in this report represent the most complete analyses of vegetation dynamics conducted in the PMWHR. As a result of the two field projects (Peterson et al. 1997; Gerhardt and Detling 1998), 10 new permanent enclosures were erected in the Horse Range, allowing vegetation dynamics inside and outside of enclosures to be monitored and compared at a total of 12 sites.

1. Previous analyses of biomass data from 1992–1996 demonstrated that although herbivory effects were detectable, they were generally localized and not consistent across years. Averaged across location and years, herbaceous plant biomass in our GLM analysis was not significantly different inside and outside of enclosures (inside: mean = 86.2 g m^{-2} , s.e. = 11.0; outside: mean = 76.6 g m^{-2} , s.e. = 10.2; $P = 0.078$). Although the absolute difference inside and outside enclosures was not affected by any temporal factors, the relative difference (%) did vary between years and the magnitude of this variation was related to the east-west location of sites.
2. Across all sites, enclosures do not appear to have a consistent or strong interactive effect with environmental variables. As revealed in the PCA graphs (Fig. 19), there were exceptions to this, but in general, interannual changes which occur in the control plots appear to be mirrored in the enclosed plots. This observation is in agreement with the results of the general linear models in which plot \times temporal environmental factor interactions were relatively weak.
3. Although the difference between enclosed and control plots showed variation between years, no sites showed a trend for increasing convergence. Although we did not perform

ordination analyses using individual species data, the suite of vegetation variables used (biomass, richness, and cover) may contain enough information to detect changes in the state of the vegetation system. If rapid and directional transitions were occurring in either plot type, that plot may be expected to follow a relatively consistent trajectory across years. The lack of strong linear changes is corroborated by the GLM results which did not detect a significant trend for the enclosure effects to be cumulative over time. However, changes in the plant community may not be linear, and vegetation models emphasizing multiple states and transitions may be more relevant (Allen-Diaz and Bartolome 1998; Augustine et al. 1998). These models assume that changes may not be consistently directional, but instead are influenced by numerous factors which may result in multiple future states, each dependent on a transition threshold (Westoby et al. 1989; Friedel 1991; Laycock 1991).

4. Averaged across years and locations, the main effect of enclosures was significant only for relative grass cover ($P < 0.001$), although the effect was nearly significant for several other vegetation variables: absolute grass cover ($P = 0.052$), litter ($P = 0.066$), biomass ($P = 0.078$). Although previous analyses (Peterson et al. 1997) showed that enclosure effects could vary between years and across sites, we found no strong interactions between enclosures and either spatial or temporal factors for any vegetation variable (Table 2). The only statistical indication of a location- or time-specific effect of the enclosures is in the GLM analyses of the two composite variables: absolute (g m^{-2}) and relative (%) biomass difference.
5. Related to the previous conclusion, neither winter nor summer horse herd size had a detectable influence on the enclosure effect. In addition, neither growing season nor annual precipitation had detectable influences on the enclosure effect. This suggests that over the range of herd sizes present from 1992–1996, the effect (or lack of effect) of the enclosures was consistent.

Literature Cited

- Allen-Diaz, B., and J. W. Bartolome. 1998. Sagebrush-grass vegetation dynamics: Comparing classical and state-transition models. *Ecological Applications* 8:795–804.
- Augustine, D. J., L. E. Frelich, and P. A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. *Ecological Applications* 8:1260–1269.
- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49:386–400.
- Bureau of Land Management. 1997. Pryor Mountain Wild Horse Range Wild Horse Removal Plan. Bureau of Land Management, Billings, Mont.
- Cargill, S. M., and R. L. Jeffries. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology* 21:669–689.
- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1–9.
- Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44:530–542.
- Coughenour, M. B. In preparation. Carrying capacity of the Pryor Mountain Wild Horse Range - an ecosystem modeling approach. Completion report to the U.S. Geological Survey, Fort Collins, CO. 194 pp.
- Detling, J. K. 1998. Mammalian herbivores: Ecosystem level effects in two grassland national parks. *Wildlife Society Bulletin* 26:438–448.
- Duncan, P. 1992. Horses and grasses: The nutritional ecology of equids and their impact on the Camargue. Springer-Verlag, New York. 287 pp.
- Fahnestock, J. 1998. Vegetation responses to herbivory and resource supplementation in the Pryor Mountain Wild Horse Range. Ph.D. dissertation. Colorado State University, Fort Collins. 125 pp.
- Fahnestock, J., and J. K. Detling. 1999. The influence of herbivory on plant cover and species composition

- in the Pryor Mountain Wild Horse Range, USA. *Plant Ecology* 144:145–157.
- Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* 73:2043–2058.
- Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the earth's grazing ecosystems. *BioScience* 48:513–521.
- Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: A viewpoint. *Journal of Range Management* 44:422–426.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge. 298 pp.
- Gerhardt, T. D., and J. K. Detling. 1998. Monitoring vegetation in the Pryor Mountain Wild Horse Range. Addendum report. 46 pp.
- Hansson, L., L. Fahrig, and G. Merriam, editors. 1995. *Mosaic landscapes and ecological processes*. Chapman & Hall, New York. 356 pp.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. *Ecological Applications* 9:17–29.
- Keiper, R. R. 1981. *Ecological impact and carrying capacity of ponies*. U.S. Fish and Wildlife Service, Chincoteague National Wildlife Refuge, Va.
- Kissell, R. E., Jr., L. R. Irby, and R. J. Mackie. 1996. Competitive interactions among bighorn sheep, feral horses, and mule deer in Bighorn Canyon National Recreation Area and Pryor Mountain Wild Horse Range. Completion report. 152 pp.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management* 44:427–433.
- McNaughton, S. J. 1985. Ecology of a grazing system: The Serengeti. *Ecological Monographs* 55:259–294.
- Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. *Ecology* 78:505–521.
- Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690–705.
- Pastor, J., B. Dewey, R. Moen, D. J. Mladenoff, M. White, and Y. Cohen. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. *Ecological Applications* 8:411–424.
- Peterson, J., J. Fahnestock, and J. K. Detling. 1997. Ungulate/vegetation interactions at the Pryor Mountain Wild Horse Range. Completion report on Agreement No. 1268-1-9002. 154 pp.
- Peterson, J. 1999. *Ungulate/vegetation dynamics in the Pryor Mountain Wild Horse Range*. Ph.D. dissertation. Colorado State University, Fort Collins. 155 pp.
- Porter, W. F., and H. B. Underwood. 1999. Of elephants and blind men: Deer management in the U.S. national parks. *Ecological Applications* 9:3–9.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.
- Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998a. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–1993. *Wildlife Society Bulletin* 26:375–390.
- Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. *Wildlife Society Bulletin* 26:419–428.
- Smith, C., R. Valdez, J. L. Holecheck, P. L. Zwank, and M. Cardenas. 1998. Diets of native and non-native ungulates in south-central New Mexico. *Southwestern Naturalist* 43:163–169.
- Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9:45–64.
- ter Braak, C. J. F. 1987. Chapter 5. Ordination. Data analysis in community and landscape ecology. Pages 91–173 in R. H. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, editors. *Pudoc Wageningen*. 299 pp.
- Underwood, A. J., and M. G. Chapman. 1998. A method for analyzing spatial scales of variation in composition of assemblages. *Oecologia* 117:570–578.
- Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. *Wildlife policies in the U.S. national parks*. Island Press, Washington, D.C. 242 pp.

- Wallis de Vries, M. F., and C. Daleboudt. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* 100:98–106.
- Westoby, M., B. H. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–784.
- Wright, R. G. 1999. Wildlife management in the national parks: Questions in search of answers. *Ecological Applications* 9:30–36.

Appendix A. Summary statistics for GLM analyses on vegetation variables. Factors included are those selected using AIC criteria in a step-wise GLM procedure. In addition, the plot factor (exclosed vs. control) was added to each model. Type III sums of squares are presented.

Biomass					
	Df	SS	MS	F	P
Year	1	14,524	14.524	22.81	0.000008
Soil	6	127,251	21,208	33.30	0.000000
East	1	94,356	94,356	148.17	0.000000
Plot	1	2,028	2,028	3.18	0.078256
Residuals	78	49,671	637		

Richness					
	Df	SS	MS	F	P
Soil	6	1,112.9	185.5	18.01	0.00000
Elevation	1	2,165.3	2,165.3	210.24	0.00000
Plot	1	7.6	7.6	0.74	0.39246
Residuals	73	751.8	10.3		

Total Cover					
	Df	SS	MS	F	P
Elevation	1	32,462	32,462	300.98	0.00000
Summer	1	7,312	7,312	67.79	0.00000
Plot	1	4	4	0.04	0.85121
Elevation x summer	1	1,357	1,357	12.58	0.00067
Residuals	77	8,305	108		

Bare Ground					
	Df	SS	MS	F	P
East	1	1,573.4	1,573.4	20.706	0.00002
North	1	696.2	696.2	9.162	0.00344
Summer horse	1	702.5	702.5	9.245	0.00331
Soil	6	7,193.5	1,198.9	15.778	0.00000
Plot	1	24.1	24.1	0.318	0.57470
Residuals	71	5,395.1	76.0		

Litter					
	Df	SS	MS	F	P
East	1	526.0	526.02	34.628	0.000000
G-season precipitation	1	159.4	159.4	10.493	0.001770
Winter horse	1	115.3	115.29	7.590	0.007323
Plot	1	53.0	52.96	3.486	0.065679
Residuals	77	1,169.7	15.19		

Appendix A. Continued.

Absolute Grass					
	Df	SS	MS	F	P
Mean site precipitation	1	1,981.5	1,981.5	45.240	0.000000
G-season precipitation	1	797.6	797.6	18.210	0.000056
Summer horse	1	980.5	980.5	22.387	0.000010
Plot	1	171.0	171.0	3.903	0.051825
Summer horse x G-season precipitation	1	479.4	479.4	10.944	0.001437
Residuals	76	3,328.8	43.8		
Relative Grass					
	Df	SS	MS	F	P
Elevation	1	721.4	721.4	18.351	0.0000592
East	1	1,107.3	1,107.3	28.167	0.0000013
North	1	422.8	422.8	10.756	0.0016411
Soil	6	9,078.2	1,513.0	38.487	0.0000000
Year	1	598.9	598.9	15.233	0.0002206
Plot	1	694.9	694.9	17.677	0.0000782
Soil x north	2	2,539.7	1,269.8	32.301	0.0000000
Residuals	68	2,673.3	39.3		
Absolute Forbs					
	Df	SS	MS	F	P
Elevation	1	33,263	33,263	293.95	0.000
Plot	1	128	128	1.13	0.291
Residuals	79	8,940	113		
Relative Forbs					
	Df	SS	MS	F	P
Elevation	1	239.5	239.5	2.777	0.09968
North	1	2,713.5	2,713.5	31.469	0.00000
Plot	1	209.9	209.9	2.435	0.12279
North x elevation	1	3,402.4	3,402.4	39.459	0.00000
Residuals	77	6,639.4	86.2		
Biomass Difference					
	Df	SS	MS	F	P
Soil	6	12,234	2,039.1	3.536	0.0072355
Residuals	37	21,36	576.7		

Appendix A. Concluded.

	Percent Biomass Difference				
	Df	SS	MS	F	P
Elevation	1	0.428182	0.4281824	10.25903	0.00300935
East	1	0.248675	0.2486745	5.95811	0.02018158
Year	1	0.184130	0.1841304	4.41167	0.04341733
East x year	1	0.448985	0.4489853	10.75746	0.00245421
Residuals	33	1.377325	0.0417371		

Appendix B. Statistics for PCA axes 1 and 2 by site. For each axis, eigenvalues and percent of variance explained are listed. Factor loading columns for each vegetation variable contain the loading (-1 to 1) of the variable for that axis. High absolute loadings indicate that a variable changes strongly along a PCA axis, with sign (+ or -) indicating the direction of change.

	PCA axis	Eigenvalue	Variance explained	Biomass	Richness	Total cover	Bare ground	Litter	Grass (absolute)	Grass (relative)	Forbs (absolute)	Forbs (relative)
Bat Cave	1	6.0	66.8	-0.50	0.29	-0.44	-0.46		-0.12		0.12	0.48
	2	2.5	27.6	0.44	0.26	-0.18	0.19	0.36	0.17	0.56	0.15	0.42
			94.3									
Yellowhill	1	4.6	50.7	-0.19	-0.22	-0.36	0.41	-0.23	0.18	0.36	0.46	0.44
	2	3.2	35.5	0.18	-0.47	-0.31		0.47	-0.52	-0.36	0.10	0.17
			86.3									
North Bay	1	3.3	36.6	-0.38	0.45	0.29	0.26		0.22	-0.17	0.53	0.38
	2	2.9	31.8	-0.36	0.25	-0.50	-0.10	-0.31	-0.42	0.26	-0.16	0.42
			68.4									
Turkey Flats	1	4.9	54.1	-0.41	0.43	0.44	-0.33	0.42	0.34	-0.13		0.22
	2	2.8	30.7	0.21	0.13		0.37		0.34	0.44	0.54	0.45
			84.8									
Forest Service	1	4.9	54.5	-0.40		-0.40	0.22		-0.43	-0.42	-0.36	0.38
	2	2.0	22.4		0.26	-0.20	-0.59	-0.62	-0.13	0.17	-0.29	-0.20
			76.9									
Penns Cabin	1	4.3	48.1	-0.36	-0.27		-0.15	0.35	-0.43	-0.44	0.25	0.46
	2	2.4	26.9	-0.42		-0.64	0.11	-0.17	-0.23	0.17	-0.53	
			75.0									
RAWS	1	4.6	51.2	0.36	0.34	-0.36		-0.45	-0.43	-0.32	-0.22	0.30
	2	2.8	26.3	-0.12		0.39	0.31		-0.45	-0.45	0.57	0.45
			77.5									

The Influence of Herbivory on Plant Cover and Species Composition in the Pryor Mountain Wild Horse Range, USA¹

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Abstract. We investigated the effects of short- and long-term ungulate grazing on plant species cover and composition in arid lowland and more mesic upland communities of the Pryor Mountain Wild Horse Range (PMWHR). Measurements were taken over two years which differed significantly in growing season precipitation. Interannual differences in plant cover were significantly greater than differences between grazed and ungrazed communities. In the arid lowlands total plant cover decreased from 47% in 1993, a relatively wet year, to 29% in 1994, a relatively dry year. In the more mesic uplands total plant cover decreased from 107% in 1993 to 56% in 1994. The magnitude of change in cover was greatest in the grasses, especially for *Pseudoroegneria spicata*, the most abundant species in the lowland communities, which decreased from 21% cover in 1993 to 11% in 1994. There was not a consistent effect of herbivory on plant cover across sites, but its effects, particularly on the dominant perennial grasses, were conspicuous at some sites. For instance, in the lowlands cover of *P. spicata* was 3% to 12% in long-term grazed sites and 9% to 28% in short- to long-term ungrazed sites. Our study indicates that abiotic factors (e.g., precipitation) are more likely than grazing to affect abundances of key plant species, and hence ecosystem dynamics, in the PMWHR, and that the effects of herbivory are more localized and more prevalent in the lowland grasses than in the other plant functional groups.

Keywords: Grazing, horses, plant species composition, Pryor Mountains, *Pseudoroegneria spicata*.

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Introduction

Botanical composition of grassland communities is controlled by many factors such as climate, soils, topography, fire, and biotic influences. Grazing is a biotic influence of particular interest since grasslands and large herbivores have a long coevolutionary history (Stebbins 1981; Mack and Thompson 1982; Coughenour 1985). Mammalian herbivores can substantially influence the dynamics of plant communities by altering primary production, decomposition of organic matter, the cycling and distribution of nutrients, and competitive relationships among plant species (Cumming 1982; Crawley 1983; McNaughton 1985; Seastedt 1985; Detling 1987; McNaughton et al. 1988; Sala 1988; Whicker and Detling 1988). Plant responses to herbivory, however, are highly variable and depend on the type of herbivory, its timing, intensity, and frequency, and the availability of environmental resources for growth (Coughenour 1985; McNaughton 1986; Belsky 1987).

Precipitation in grassland ecosystems is an environmental resource that is highly variable in time and space (Ripley 1979), and there is a strong correlation between plant production and precipitation in many grasslands (e.g., Webb et al. 1978; Lauenroth 1979; Lauenroth and Sala 1992). Intermittent water deficits in these systems often alter plant growth and reproduction; hence, community structure and composition, as species with different tolerances and competitive abilities are variously affected (e.g., Coupland 1958; Knapp 1984; Burke et al. 1991). Both water and grazing stresses can affect plant species diversity (both richness and relative abundance) in grassland communities. In communities with a range of plant growth forms, responses to intermittent water deficits and to the direct and indirect effects of grazing may differ, so that the relative advantage of one growth form over another may change over time (e.g., Jameson 1963; Archer and Detling 1984; Wallace et al. 1984; Fahnestock and Knapp 1994; O'Connor and Roux 1995). The persistence of plant species in grassland ecosystems, therefore, largely depends on the ability of individuals to cope with complex and dynamic interactions between herbivory and limitations of water and other environmental resources (McNaughton et al. 1982; Coughenour 1985; Chapin and McNaughton 1989).

Wild horses (*Equus caballus*) occur over large areas of arid and semi-arid rangelands in the western United States where they may potentially compete with

livestock and native ungulates for forage (Berger 1986; Boyce et al. 1990). Because their populations may grow rapidly and potentially cause range degradation (Fisher 1983; Bastian et al. 1999), wild horse populations are now controlled in most areas. The Pryor Mountain Wild Horse Range (PMWHR) was established in Montana and Wyoming in 1968 to preserve a population which had unique physical characteristics reminiscent of the original Spanish breeds brought to North America in the 1500s (BLM 1984). A management conflict has arisen as a result of native bighorn sheep (*Ovis canadensis*) recolonizing formerly used areas of the PMWHR beginning in the 1970s (BLM 1984; Boyce et al. 1990). In calling for additional information to use in managing horse and sheep populations, Boyce et al. (1990) stressed the need for research aimed at quantifying the effects these herbivores are having on plant communities in the PMWHR.

Presently, little is known about the effects of grazing on plant community composition in the PMWHR, whose flora contains both Great Basin and Rocky Mountain elements (Lichvar et al. 1985). Therefore, the main focus of this study was to evaluate the effects of short- and long-term ungulate (wild horses, bighorn sheep, and mule deer) herbivory on plant species composition and abundance of key species in the PMWHR. Measurements were taken within and outside of several grazing exclosures in arid lowland communities, where the Great Basin element is the major component of the flora, and more mesic upland communities, where the Rocky Mountain element is predominant. Since grasses are important components of horse diets, we hypothesized that grass cover would increase following release from long-term grazing, while forb and dwarf shrub abundance would decrease. Vegetation measurements were made in 1993, a relatively wet year, and 1994, a relatively dry year, allowing us to also evaluate the relative influence of interannual differences in precipitation and associated abiotic factors on vegetation dynamics.

Study Area

The PMWHR consists of about 18,000 ha of rangeland in southern Montana and northern Wyoming, USA. Of this, only about 60% is considered suitable for grazing by wild horses, with the remainder having sparse vegetation with a preponderance of rock outcrop and bare soil (BLM 1984). The PMWHR partially overlaps the southern portion of the Bighorn Canyon

National Recreation Area (BCNRA), portions of Custer National Forest, and other state and private lands (Fig. 1). Elevation ranges from 1,190 m in the southeastern lowlands to over 2,400 m in the northern portions of the PMWHR, and much of the area is characterized by deep, steep-walled canyons, isolated grassy plateaus, foothill slopes, and karst topography (BLM 1984; Knight et al. 1987). Annual precipitation ranges from 130 mm in the most arid lowlands to over 500 mm at upper elevations (BLM 1984), and is likely the primary factor controlling the productivity gradient from the desert-shrubland and grassland communities in the lowlands to the coniferous woodlands interspersed with montane meadows in the uplands.

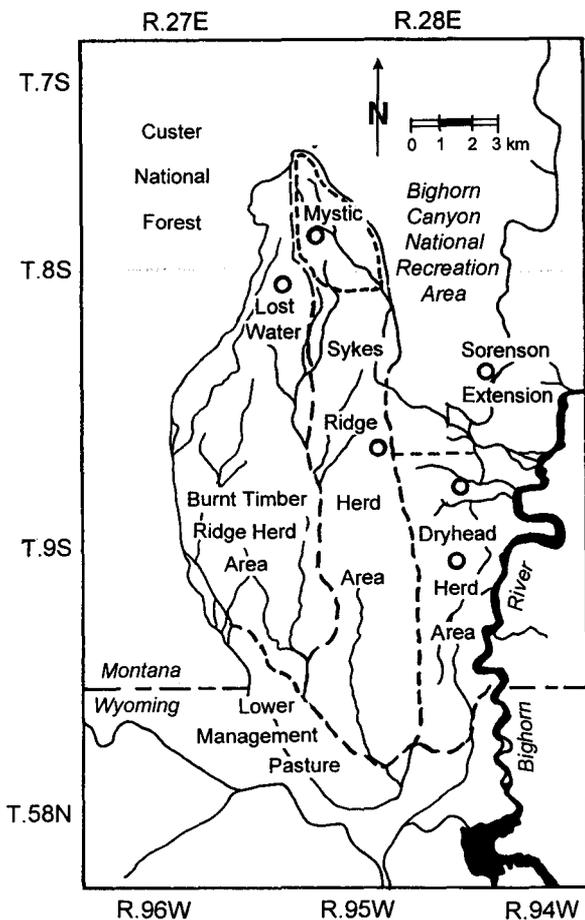


Fig. 1. Location of the Pryor Mountain Wild Horse Range and approximate location of study sites (circles). See text for additional details. Figure adapted from BLM (1984).

It is not known exactly how long wild horses have inhabited the Pryor Mountains. Although there is speculation that they may have occupied the areas as early as the 1700s, the earliest records date to 1910 (BLM 1984; Boyce et al. 1990). The Pryor Mountains were also grazed by livestock before the official designation of the area as a horse range in 1968, and in some areas, this grazing may have been quite substantial. Nevertheless, horses have been one of the primary grazers in this system for the last century and today there are three main herd areas within the PMWHR: Tillet and Sykes Ridges, which run from the lowlands to the top of east Pryor Mountain, and the Dryhead, which is entirely in the lowlands of the BCNRA (Fig. 1). The Sorensen Extension is a 1,076 ha lowland that borders the north boundary of the Dryhead herd area (Fig. 1). It was used from 1980 to 1992 to provide additional range for wild horses and to ease grazing pressure on the arid Dryhead herd area. Although the stocking goal for the PMWHR is to maintain the herd at 121 horses, the population has fluctuated between 70 and 200 individuals since the designation of the horse range in 1968. At the time of this study there were about 150 horses, 175 bighorn sheep, and 500 mule deer occupying the PMWHR (Kissell 1996).

Methods

Plant species composition and cover estimates were made in the arid lowland communities by sampling vegetation in sites with different histories of grazing, and within and outside of grazing exclosures. All lowland sites were at an elevation of ca. 1,300 m that received similar annual precipitation (233 mm yr^{-1}) and were in plant communities dominated by grasses, herbaceous dicots (forbs), cushion plants, and dwarf shrubs [Fahnestock (1998); nomenclature follows Kartesz (1994)]. Two 50 m x 50 m exclosures were built in June 1992 in the Dryhead herd area (Fig. 1), and each exclosure was paired with an adjacent or nearby unfenced (50 x 50 m) site to which animals had unlimited access. Two additional 50 m x 50 m ungrazed sites were delineated in June 1992 in the Sorensen Extension (Fig. 1). These sites were located within an area that had been fenced from wild horse herbivory since before 1980. These sites were paired with adjacent 50 m x 50 m unfenced sites that had been grazed from 1980 to 1992. Thus, our lowland grazing treatments consisted of two plant communities with long histories (>100 years) of horse and other ungulate grazing (Dryhead unfenced

sites), two sites that were recently (1–2 years) released from shorter-term (ca. 12 years) grazing (Sorenson unfenced sites), two plant communities with long histories of protection from wild horse grazing (Sorenson exclosures), and two sites recently (1–2 years) released from long-term grazing (Dryhead exclosures).

In the more mesic upland plant communities, vegetation patterns were monitored in two long-term exclosures (Fig. 1) previously erected in the northern part of the Tillett Ridge herd area and in adjacent, similarly sized areas to which wild horses had unlimited access. These exclosures were established decades ago in areas representative of two of the dominant grassland community types in the uplands of the PMWHR. The Forest Service exclosure is about 35 m x 50 m, was erected in the 1950s, while the Penn's Cabin exclosure is about 100 m x 50 m, and was built in 1963. The Forest Service site was built in an area with deeper soils than the Penn's Cabin site. Both exclosures were established in areas dominated by grasses, sedges, and forbs. Although these exclosures were not adequately replicated, they are valuable for examining the response of vegetation to the long-term effects of ungulate grazing.

Plant species composition and cover were estimated inside and outside each exclosure during 1993, a year with above average growing season precipitation and 1994, a year with below average growing season precipitation. At the lowland sites, plant communities were sampled in May, June, and July, and at the upland sites, measurements were made in July to correspond with the approximate time of peak aboveground biomass accumulation. Precipitation data from 1982 to 1994 for the lowland sites were obtained from a weather station located between the Sorenson Extension and the Dryhead herd area sites. An automated weather station installed in 1991 near the Kruger "Mystic" area (Fig. 1) provided growing season precipitation data for the two upland sites.

In each site sampled, a 0.10 m² quadrat was placed every 2.5 m along the diagonal of the site and live and standing dead canopy coverage was estimated for each species (Daubenmire 1959). Twenty replicate quadrats were used in each site, except in 1993 when only 15 quadrats were used at the two upland sites. This method was not sensitive to detecting the presence of rare species in each community (Stohlgren et al. 1998), but did enable us to monitor trends in cover of the dominant plant species. Plant community parameters,

including litter cover, plant species richness, relative cover, and Shannon diversity (H' ; Zar 1984), were calculated for each fenced (hereafter called "ungrazed") and adjacent unfenced (hereafter called "grazed") site.

Plant cover patterns in the lowland communities were compared using general linear models procedures (SAS 1989), with site (i.e., Dryhead vs. Sorenson; related to differences in grazing history), herbivory (i.e., differences between inside and outside exclosures), year (i.e., 1993 vs. 1994; related to differences in precipitation), and month within year as main variables. Few consistent differences in total plant cover were detected between months in the lowland sites, so to simplify interpretation we used the mean cover of each species averaged over the growing season each year for additional analyses. Similar analyses were performed on the data from the upland sites, with the exception of month as a main variable since data were only collected in July at these sites. Cover data for all sites were transformed for analysis as: $\text{cover} = \arcsin[\sqrt{\% \text{ cover of the individual species}}]$ (Zar 1984). Comparisons of species cover patterns between grazed and ungrazed sites and between years were further assessed using the Tukey test (Zar 1984). We used *t*-test procedures to compare diversity information from grazed and ungrazed sites and between years (Hutcheson 1970).

Results

Mean annual precipitation (1982–1994) in the lowland sites of the PMWHR was 233 mm yr⁻¹. Both years of this study had annual precipitation close to this mean, 257 mm in 1993 and 210 mm in 1994. There were large differences, however, in growing season rainfall between 1993 and 1994. Growing season (March to July in the lowlands) rainfall in 1993 was 202 mm, well above the long-term average of 143 mm, while in 1994 it was only 101 mm (Fig. 2a). Annual precipitation in the upland sites was also considerably different between years, with 507 mm in 1993 and 374 mm in 1994. Growing season (April to August in the uplands) rainfall was 399 mm in 1993, but only 193 mm in 1994 (Fig. 2b). Much of the interannual variation in precipitation in both the lowlands and uplands was the result of differences in June and July rainfall.

Interannual differences (i.e., 1993 vs. 1994) in plant cover patterns were substantially greater than between grazed and ungrazed sites in both the lowland and upland communities. Total plant cover (live and current year's dead) averaged across all lowland sites was 47%

in 1993, the wet year, and 29% in 1994, the dry year ($P < 0.01$; Tables 1 and 2). Across all upland sites, total plant cover was 107% in 1993, but only 56% in 1994 ($P < 0.05$; Tables 1 and 3). In contrast, total plant cover was not significantly ($P > 0.05$) different across all lowland grazed (47%) and ungrazed (48%) sites in 1993. In 1994, these values decreased to 28% and 29% in grazed and ungrazed sites, respectively (Tables 1 and 2). In the uplands, total plant cover was also similar ($P > 0.05$) in grazed and ungrazed sites (110% and 103%, respectively, in 1993; 61% and 52%, respectively, in 1994; Tables 1 and 3).

While lower total plant cover was measured at all sites in 1994, the dry year, than in 1993, the magnitude of change in cover between years was not the same for all species or functional groups. Interannual changes in cover of the grasses were particularly evident in both the lowland and upland plant communities. In the lowland communities, cover of the grasses decreased from 26% in 1993 to 14% in 1994 ($P < 0.05$; Table 2). Much of this reduction in grass cover was the result of changes in cover of *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), the most abundant grass in the lowland plant communities (Table 2). Cover of the forbs, on the other hand, remained relatively constant between 1993 (8%) and 1994 (6%), as did cover of the other plant functional groups at the lowland sites (Table 2).

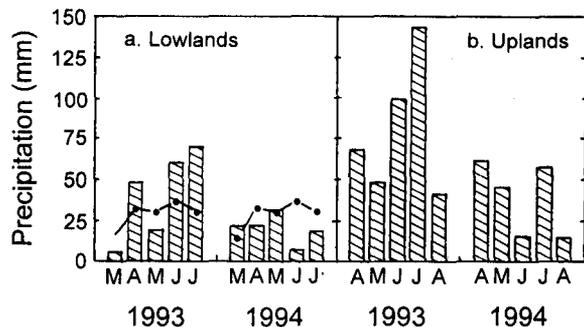


Fig. 2. Growing season precipitation patterns for 1993 and 1994 in the: (a) lowlands, and (b) uplands of the Pryor Mountain Wild Horse Range. Vertical bars indicate cumulative monthly precipitation (mm). Circles indicate long-term (1982–1994) mean precipitation (cm) in the lowlands (long-term data not available for the uplands).

In the uplands, the magnitude of change in cover between years was relatively large in both the graminoids and forbs. Cover of the graminoids averaged across all upland sites decreased from 46% in 1993 to 20% in 1994, and cover of the forbs decreased from 54% in 1993 to 31% in 1994 ($P < 0.05$; Tables 1 and 3). Cover of the other plant functional groups generally remained similar between years at the upland sites (Table 3).

Differences in plant cover and species composition patterns inside and outside exclosures were not as consistent across sites as those associated with abiotic variables (e.g., precipitation). However, there were significant differences in cover at some sites that correlated with grazing history. For instance, total plant cover in the Dryhead sites averaged 35% in 1993 and 1994, while at the Sorenson sites it was 41% ($P < 0.01$; Table 2). Cover of the grasses was consistently lower in long-term grazed (i.e., Dryhead sites) lowland sites than in short- (Dryhead exclosures) and long-term (Sorenson exclosures) ungrazed sites ($P < 0.05$; Table 2). Cover of live and recent dead grass in 1993 was 21% in long-term grazed lowland sites and 28% in ungrazed sites, while in 1994 it was 11% in grazed sites and 14% in ungrazed sites (Table 2). Most of this difference was the result of cover differences in *P. spicata*, the dominant grass in these lowland communities. Cover of *P. spicata* in grazed sites was 12% in 1993 and 3% in 1994 (Table 2). In contrast, cover of *P. spicata* in ungrazed sites was 24% and 12% in 1993 and 1994, respectively ($P < 0.05$; Table 2).

There were also some differences in species composition between the Dryhead (historically and currently grazed by horses) and Sorenson (short- to long-term ungrazed by horses) sites. For instance, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama) and *Stipa comata* Trin. and Rupr. (needle-and-thread) comprised 11% and 9%, respectively, of the total plant cover in the Dryhead sites, but were nearly absent from the Sorenson sites (Table 2). Species composition and forb cover, cushion plants, and dwarf shrubs were not significantly different between the Sorenson and Dryhead sites. In contrast, some cactus [(e.g., *Opuntia polyacantha*) (pricklypear) and *Pediocactus simposinii* (nipple cactus)] and shrub species *Artemisia* spp. (sagebrush)] were present in relatively low amounts in the Dryhead sites but were not found at the Sorenson sites (Table 2). Similar changes in plant species composition were measured at other grazed lowland sites in the PMWHR suggesting that these changes were likely the result of grazing and not simply due to landscape variation (Fahnestock 1998).

Table 1. Analysis of variance results for the effects of year (corresponding to interannual precipitation variability), site, and herbivory on total live plant and live grass cover for the lowland and upland communities in the Pryor Mountain Wild Horse Range. Mean square errors (MS) are from Type III sums of squares (SAS 1989). Cover = arcsine [sqrt (% cover of the individual species)].

Source	df	MS	F	df	MS	F
	Total live plant cover			Live grass cover		
<u>Lowland Communities</u>						
Year	1	1,369.00	27.09 ^b	1	567.63	7.82 ^a
Site	1	114.49	2.27	1	66.83	0.92
Herbivory	1	14.82	0.29	1	17.02	0.23
Year X site	1	9.30	0.18	1	0.11	0.01
Year X herbivory	1	3.24	0.06	1	5.64	0.08
Site X herbivory	1	27.04	0.54	1	13.51	0.19
Error	9	50.53		9	72.60	
<u>Upland Communities</u>						
Year	1	1,585.79	3,171.57 ^a	1	412.57	22.92
Site	1	423.50	847.00 ^a	1	240.29	13.35
Herbivory	1	30.25	60.50	1	72.25	4.01
Year X site	1	37.79	75.57	1	4.57	0.25
Year X herbivory	1	156.25	312.50 ^a	1	25.00	1.39
Site X herbivory	1	1,225.00	2,450.00 ^a	1	306.25	17.01
Error	1	0.50		1	18.00	

^a $P < 0.05$

^b $P < 0.01$

Some differences in plant community attributes between grazed and long-term ungrazed areas were also evident in the more mesic uplands. For instance, total plant cover at the Forest Service site was significantly lower outside than inside the enclosure in 1993, the wetter year, but not in 1994 ($P < 0.05$; Table 3). Grass cover was 42% outside and 63% inside this enclosure in 1993 ($P < 0.05$; Table 3). In 1994, the dry year, grass cover was much lower than in 1993, but the differences between grazed and ungrazed areas were not significantly different. *Elymus lanceolatus* (Scribn. and J. G. Sm.) (Gould thickspike wheatgrass) was the grass most reduced by grazing at this site. By contrast, cover of *Poa secunda* J. Presl. (Sandberg bluegrass) increased slightly with grazing at this site in 1993 ($P < 0.05$; Table 3), as well as at Penn's Cabin site. However, there were large reductions in cover of *P. secunda* at both of these sites in 1994, the dry year. At the Penn's Cabin site, cover of *Koeleria macrantha* (Lebed.) J.A. Schultes (Junegrass) was reduced by grazing in 1993,

but not in 1994 (Table 3). Cover of *Carex filifolia* Nutt. (threadleaf sedge) was not significantly affected by grazing either year at the Penn's Cabin site, although its cover was significantly reduced in 1994 compared to 1993 (Table 3). In contrast to the Forest Service site, total plant cover at the Penn's Cabin site was higher outside than inside the enclosure in both years. Forb cover was greater ($P < 0.05$) outside the enclosure both years, while cover of grasses was greater outside the enclosure only in 1993. Cushion plants and succulents together made up less than 10% of the total plant cover at the two upland sites, and neither differed significantly inside and outside the enclosures (Table 3).

While total plant cover was consistently lower in 1994, the dry year, than in 1993, plant species richness and diversity did not exhibit similar trends. At the Sorenson sites, plant species richness was greater in 1994 than in 1993 in the grazed treatment, but was not significantly different between years in the Dryhead sites. Collectively, plant species diversity (H') at all

Table 2. Percent cover of live and current year's dead material of the dominant species and plant functional groups, and other community characteristics, in the lowland study sites of the Pryor Mountain Wild Horse Range. Measurements are growing season means from outside (Out) and inside (In) grazing exclosures in 1993 (wet year) and 1994 (dry year). Significant ($P < 0.05$) differences between sites, years, or grazing treatment are shown by different letters. The absence of letters indicates no statistical tests were performed.

	<u>Sorenson Extension sites</u>				<u>Dryhead herd area sites</u>			
	<u>1993</u>		<u>1994</u>		<u>1993</u>		<u>1994</u>	
	Out	In	Out	In	Out	In	Out	In
<u>Grasses</u>								
<i>Pseudoroegneria spicata</i>	26 ^a	28 ^a	15 ^b	15 ^b	12 ^b	19 ^a	3 ^c	9 ^b
<i>Stipa comata</i>	<1	<1	<1	<1	5	4	2	2
<i>Poa secunda</i>	0	<1	0	<1	<1	<1	<1	<1
<i>Bouteloua gracilis</i>	<1	0	<1	0	4 ^a	3 ^a	6 ^a	1 ^a
Total grasses	27 ^a	29 ^a	16 ^b	16 ^b	21 ^a	26 ^a	11 ^b	12 ^b
<u>Forbs</u>								
<i>Tetranneuris acaulis</i>	4	2	2	1	2	<1	<1	<1
<i>Lesquerella alpina</i>	2	2	2	2	2	2	2	2
<i>Erigeron</i> spp.	2	1	<1	<1	<1	<1	<1	<1
15 others*	3	3	4	4	2	2	3	3
Total forbs	11 ^a	8 ^a	8 ^a	7 ^a	6 ^a	5 ^a	5 ^a	5 ^a
<u>Cushion Plants</u>								
<i>Phlox hoodii</i>	7	6	2	3	3	4	2	4
<i>Leptodactylon caespitosum</i>	2	2	3	2	6	4	1	2
Total cushion plants	9 ^a	8 ^a	5 ^a	5 ^a	9 ^a	8 ^a	3 ^a	6 ^a
<u>Dwarf Shrubs and Shrubs</u>								
<i>Gutierrezia sarothrae</i>	3 ^a	4 ^a	3 ^a	3 ^a	6 ^a	9 ^a	3 ^a	4 ^a
<i>Krascheninnikovia lanata</i>	0	<1	<1	<1	<1	<1	<1	<1
<i>Artemisia frigida</i>	0	0	0	0	<1	<1	<1	0
<i>Artemisia nova</i>	0	0	0	0	<1	0	<1	0
Total dwarf shrubs	3 ^a	4 ^a	3 ^a	3 ^a	7 ^a	9 ^a	4 ^a	4 ^a
<u>Succulents</u>								
<i>Opuntia polyacantha</i>	0	0	0	0	<1	<1	<1	<1
<i>Pediocactus simpsonii</i>	0	0	0	0	<1	<1	0	0
Total succulents	0	0	0	0	<1 ^a	<1 ^a	<1 ^a	<1 ^a
<u>Total Plant Cover</u>	50 ^a	48 ^a	33 ^b	31 ^b	43 ^a	48 ^a	23 ^b	27 ^b
Litter cover	10 ^a	11 ^a	3 ^b	4 ^b	8 ^a	6 ^a	3 ^a	3 ^a
Richness (total no. of species)	14 ^b	15 ^b	18 ^a	17 ^{a,b}	16 ^{ab}	14 ^b	20 ^a	17 ^{a,b}
Diversity (H')	0.78 ^b	0.73 ^b	0.9 ^a	0.90 ^a	0.99 ^b	0.87 ^c	1.16 ^a	1.00 ^b

*Not all species represented on each sampling date, grazing treatment, or site.

Table 3. Percent cover of live and current year's dead plant material of the dominant species and plant functional groups, and other community characteristics, in the upland study sites of the Pryor Mountain Wild Horse Range. Measurements are from outside (Out) and inside (In) grazing exclosures in July 1993 (wet year) and July 1994 (dry year). Significant ($P < 0.05$) differences between years or grazing treatment are shown by different letters within each site. The absence of letters indicates no statistical tests were performed.

	Forest Service site				Penn's Cabin site			
	1993		1994		1993		1994	
	Out	In	Out	In	Out	In	Out	In
Graminoids								
<i>Elymus lanceolatus</i>	14 ^b	36 ^a	9 ^b	14 ^b	0 ^b	0 ^b	2 ^a	5 ^a
<i>Festuca idahoensis</i>	12 ^a	10 ^a	5 ^b	4 ^b	4 ^a	<1 ^a	3 ^a	2 ^a
<i>Poa secunda</i>	8 ^a	4 ^b	2 ^b	<1 ^b	16 ^a	2 ^b	0 ^b	0 ^b
<i>Carex filifolia</i>	7	4	0	1	19 ^a	18 ^a	9 ^b	6 ^b
<i>Koeleria macrantha</i>	0	0	0	0	8 ^b	13 ^a	7 ^b	4 ^b
3 others*	1	9	1	3	0	0	1	<1
Total graminoids	42 ^b	63 ^a	17 ^c	23 ^c	47 ^a	33 ^b	21 ^c	17 ^c
Forbs								
<i>Arenaria congesta</i>	10	7	3	2	1	0	<1	0
<i>Antennaria</i> spp.	7	8	2	3	3	<1	2	<1
<i>Phlox longifolia</i>	5	12	<1	2	<1	0	3	<1
<i>Astragalus miser</i>	6	5	2	<1	4	0	2	1
<i>Zigadenus venenosus</i>	5	2	2	<1	1	2	3	2
<i>Cerastium arvense</i>	2	2	3	3	15	<1	2	1
<i>Draba</i> spp.	0	0	0	0	7	5	0	0
<i>Erigeron</i> spp.	3	3	2	1	1	5	3	3
<i>Gilia roseata</i>	0	0	<1	0	5	4	2	1
<i>Astragalus drummondii</i>	<1	0	1	<1	3	4	2	2
29 others*	16	20	12	10	26	17	23	22
Total forbs	54 ^a	59 ^a	28 ^b	22 ^b	66 ^a	38 ^{b,c}	42 ^b	33 ^c
Cushion Plants								
<i>Leptodactylon caespitosum</i>	9 ^a	12 ^a	5 ^a	5 ^a	<1 ^a	<1 ^a	6 ^a	3 ^a
Succulents								
<i>Sedum lanceolatum</i>	<1 ^a	0 ^a	0 ^a	0 ^a	2 ^a	2 ^a	2 ^a	2 ^a
Total Plant Cover	105 ^b	133 ^a	50 ^c	49 ^c	115 ^a	73 ^b	71 ^b	54 ^c
Litter cover	7 ^c	27 ^a	8 ^c	14 ^b	7 ^a	7 ^a	3 ^a	4 ^a
Richness (total no. of species)	30	27	31	24	34	29	41	41
Diversity (H')	1.22	1.16	1.26	1.14	1.25	1.15	1.45	.47

*Not all species represented on each sampling date, grazing treatment, or site.

sampling dates in the lowland sites tended to be slightly higher in grazed than in ungrazed sites (0.96 vs. 0.88, respectively; $P < 0.10$), and higher in 1994 than in 1993 (0.99 vs. 0.84, respectively; $P < 0.05$). Lack of site replication precluded statistical testing of richness and diversity patterns in upland communities, and there were no significant differences in either richness or species diversity in response to grazing or year when examining the upland sites collectively.

Discussion

Differences in plant cover patterns in the PMWHR were substantially greater between years than between grazed and ungrazed sites. Plant cover across all lowland and upland sites was over 45% lower in the drier year, 1994, than in 1993 (42% vs. 77%, respectively). In a companion study, Peterson et al. (1997) also detected lower aboveground net primary production in the dry year compared to the wet year. In contrast to these differences between years, plant cover across all grazed sites (61%) was not significantly different from plant cover at ungrazed sites (58%). While these results do not preclude the possibility of a grazing effect in ungrazed sites prior to the erection of exclosures, they do suggest that plant community dynamics in the PMWHR are influenced more by abiotic variables, especially by interannual differences in growing season precipitation, than by wild horse grazing [see also Fahnestock and Detling (1999)].

Fluctuation in precipitation has been found to be the principal cause of variability in ecosystems ranging from deserts to highly productive grasslands (Coupland 1958; Webb et al. 1978, 1983; Lauenroth 1979; McNaughton et al. 1982; Milchunas and Lauenroth 1993). The results of Webb et al. (1978, 1983) and Lauenroth (1979) suggest that control of vegetation dynamics by precipitation is much more likely in arid and semiarid regions, such as grasslands, while interactions with other environmental resources (e.g., light, nutrients) become increasingly important in more mesic ecosystems. Mean annual precipitation in the PMWHR, especially in the lowlands, is closer to the dry end of the precipitation range in the above studies, and the responses of plants in both the lowland and upland communities of this study suggest a tighter coupling of these communities to abiotic factors, such as growing season precipitation, than to herbivory at the ungulate densities encountered in the PMWHR.

These results are consistent with studies from several other grassland ecosystems with large herbivores. Milchunas et al. (1994) analyzed long-term forage production data across 50 years of cattle grazing treatments in the semiarid shortgrass steppe of North America. They concluded that productivity was most sensitive to precipitation and least sensitive to grazing intensity, especially during the cool-season. Likewise, O'Connor and Roux (1995) concluded that community change over 23 years in the grassy dwarf shrubland of Karoo, South Africa, was mostly driven by rainfall variation, and that the effects of sheep grazing were more likely to be small in any one year. In the Serengeti, McNaughton (1979) also found rainfall to be the principal extrinsic variable driving ecosystem productivity. Since rainfall was extremely variable in time and space, however, grazing by large native ungulates was also an important factor contributing to grassland productivity and community composition in the Serengeti.

The substantive differences in cover between 1993 and 1994 were not accompanied by large changes in species composition, most likely because of the short-term nature of this study. Rather, there was a significantly lower absolute abundance of the dominant perennial grasses in 1994, the drier year, compared to 1993. This decrease in grasses was generally accompanied by an increase in the relative, but not absolute, abundance of forb species, especially in the more arid lowlands. Cover of the cushion plants and dwarf shrubs did not change significantly between years in either the lowland or upland sites, perhaps owing to their inherently slower growth rates. Collectively, these results suggest that plant functional groups respond differently to interannual variations in precipitation in the PMWHR, and that the dominant perennial grasses are most sensitive to changes related to growing season precipitation [see also Fahnestock and Detling (1999)].

In the upland sites, the reduction in grass cover in 1994, the dry year, was evenly distributed among several codominant species. In contrast, *P. spicata*, the most prevalent lowland species, accounted for almost all of the reduction in grass cover in the lowland sites and most of the reduction in total plant cover between 1993 and 1994. *P. spicata* comprises 40% of the total plant cover in these lowland study sites and 84% of the graminoid cover, and is generally considered to be the dominant species in undisturbed lowlands of these northern grasslands (Fisser 1964). The 50% reduction in

cover of this species across all lowland sites in 1994 compared to 1993 suggests that *P. spicata* may be an important determinant of ecosystem carrying capacity in the lowlands of the PMWHR. This has important potential implications for the management of wild horses in these arid lowlands, especially given the low productivity of these areas and the potential for high habitat overlap between horses, bighorn sheep, and mule deer in these areas during winter. Since grasses are important components of horse diets (Berger 1986), comprising over 70% of their annual diet in the PMWHR (Coates and Schemnitz 1988, 1989; Kissell 1996), variation in the productivity of grasses as a result of annual precipitation variability may affect horse productivity and health in the PMWHR. To compensate for this reduction in the abundance of grasses, horses and other grazers may have to increase the intake of non-graminoid species, move to more productive areas (e.g., uplands and riparian areas), and/or use stored body reserves.

Greater species diversity (H') in the lowlands in the dry year was partly attributable to an increase in the number of species in these sites, and to a reduction in the absolute abundance of the dominant grasses, thereby allowing subordinate species to increase in relative abundance (i.e., greater species evenness). Although there was not an overall effect of grazing on species richness or diversity across all sites in the PMWHR, our study suggest that diversity and richness may be increased in at least some sites as a result of grazing. Studies in a variety of grasslands have examined the effects of large grazers on plant species diversity (Heady 1966; Hansen and Gold 1977; Coppock et al. 1983; McNaughton 1985; Noy-Meir et al. 1989; Hartnett et al. 1996; Collins et al. 1998). These and other studies have shown that plant species diversity may increase, decrease, or remain unchanged as a result of grazing activity (Olf and Ritchie 1998). In many grasslands the dominant species, if palatable, decline with increasing intensities of grazing, and the reduction in competitive dominance allows for the coexistence of a greater diversity of species at moderate grazing levels (Milchunas et al. 1988). Results from other recent studies suggest that increased diversity in grasslands may confer greater ecological stability in these systems, including greater interannual stability in productivity and species composition in response to drought and other stresses (Frank and McNaughton 1991; Tilman and Downing 1994; Tilman et al. 1996).

Differences in plant cover patterns as a result of herbivory were not as numerous or as consistent as interannual differences in cover, further supporting the hypothesis that abiotic factors exert primary control on plant community dynamics in the PMWHR. In the uplands, substantial differences in plant cover existed inside and outside the Forest Service and Penn's Cabin enclosures, the two oldest enclosures studied. However, there were contrasting patterns at these sites. For example, total plant cover was greater inside the Forest Service enclosure than outside the enclosure in 1993, but greater outside than inside Penn's Cabin enclosure in both years. Likewise, the absolute and relative abundance of some grass species was greater outside than inside these enclosures, while the opposite was true for other grass species. Since similar patterns were not detected at these two sites, it is not clear whether these patterns are attributable to different responses to herbivory, different grazing pressures at these sites, or to other underlying site attributes. It is clear, however, that the effects of herbivory are not consistent across the uplands of the PMWHR, and that plant community responses to abiotic variables (e.g., precipitation) are more often significant.

In the lowlands, the effects of herbivory on plant cover patterns were more uniform than in the upland sites. For instance, total plant cover in 1993 and 1994 combined was 12% lower in long-term grazed sites than in sites recently (1–2 years) protected from grazers (Dryhead enclosures). Lower cover in grazed sites was almost entirely attributable to a reduction in the abundance of *P. spicata*, consistent with its classification as a decreaser under increasing grazing pressure (Williams 1963).

Comparison of long-term grazed sites (Dryhead unfenced sites) in the lowlands with nearby (ca. 2 km north) long-term ungrazed sites (Sorenson enclosure sites) suggests that long-term grazing in the PMWHR has also resulted in some shifts in species composition. In the grazed sites, cover of *P. spicata* was lower than in the ungrazed sites. This lower cover of the dominant lowland grass presumably has allowed several subordinate grasses to increase in cover in grazed sites. For instance, the grasses *Stipa comata*, *Poa secunda*, and *B. gracilis*, make up a larger percentage of the total plant cover in the Dryhead sites than in the Sorenson sites. *B. gracilis* is commonly considered to be an increaser in many grazed rangelands (Fisser 1964;

Milchunas et al. 1989). Additionally, in the long-term grazed sites, *Artemisia* spp. and cactus, also common increasers in grasslands (Fisser 1964), were present, whereas these species were absent in the Sorenson Extension sites. Consistent with other studies in dry climates (e.g., Austin et al. 1981; Coppock et al. 1983; O'Connor and Roux 1995), these results suggest that the influence of grazing on plant species composition may become more important over longer time periods.

Collectively, the results of this study suggest that abiotic environmental variables, particularly growing season precipitation, are more likely to affect overall vegetation dynamics in the PMWHR than herbivory by horses and other ungulates. Nevertheless, long-term ungulate herbivory has significantly reduced grass cover and increased plant species diversity at some sites, especially in the lowlands. Therefore, grazing by large ungulates may also have a potentially important, longer-term influence on grassland dynamics in the PMWHR.

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Literature Cited

- Archer, S., and J. K. Detling. 1984. The effects of defoliation and competition on regrowth of tillers of two North American mixed-grass prairie graminoids. *Oikos* 43:351–357.
- Austin, M. P., O. B. Williams, and L. Belbin. 1981. Grassland dynamics under sheep grazing in Australian Mediterranean type climate. *Vegetatio* 47:201–211.
- Bastian, C. T., L. W. Van Tassell, A. C. Cotton, and M. A. Smith. 1999. Opportunity costs related to feral horses: A Wyoming case study. *Journal of Range Management* 52:104–112.
- Belsky, A. J. 1987. The effects of grazing: Confounding of ecosystem, community, and organism scales. *American Naturalist* 129:777–783.
- Berger, J. 1986. *Wild horses of the Great Basin*. University of Chicago Press, Chicago.
- BLM. 1984. Herd management area plan: Pryor Mountain Wild Horse Range. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.
- Boyce, M. S., L. H. Metzgar, and J. T. Peters. 1990. Bighorn sheep and horses on the Bighorn Canyon National Recreation Area: Wilderness or pasture? Pages 51–67 in S. I. Zeveloff and C. M. McKell, editors. *Wilderness issues in arid lands of the western United States*. University of New Mexico Press, Albuquerque.
- Burke, I. C., T. G. F. Kittel, W. K. Lauenroth, P. Snook, C. M. Yonker, and W. J. Parton. 1991. Regional analysis of the central Great Plains. *BioScience* 41:685–692.
- Chapin, F. S., III, and S. J. McNaughton. 1989. Lack of compensatory growth under phosphorus deficiency in grazing-adapted grasses from the Serengeti plains. *Oecologia* 79:551–557.
- Coates, K. P., and S. D. Schemnitz. 1988. Habitat utilization, interspecific interactions, and status of a recolonized population of bighorn sheep at a wild horse range. Completion report to the University of Wyoming - National Park Service Research Center and Bighorn Canyon National Recreation Area.
- Coates, K. P., and S. D. Schemnitz. 1989. The bighorn sheep of Bighorn Canyon National Recreation Area and Pryor Mountain Wild Horse Range: Ecological relationships and management recommendations. Completion report to the National Park Service and the Bureau of Land Management.
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280:745–747.
- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1–9.
- Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: Adaptations, exceptions, and interacting processes. *Annals of the Missouri Botanical Garden* 72:852–863.
- Coupland, R. T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. *Botanical Review* 24:273–317.

- Crawley, M. J. 1983. *Herbivory: The dynamics of animal-plant interactions*. University of California Press, Berkeley.
- Cumming, D. H. M. 1982. The influence of large herbivores in savanna structure in Africa. Pages 217–245 in B. J. Huntley and B. H. Walker, editors. *Ecology of tropical savannas*. Springer-Verlag, Berlin.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43–64.
- Detling, J. K. 1987. Grass response to herbivory. Pages 56–68 in J. L. Capinera, editor. *Integrated pest management on rangeland: A shortgrass prairie perspective*. Westview Press, Boulder.
- Fahnestock, J. T. 1998. *Vegetation responses to herbivory and resource supplementation in the Pryor Mountain Wild Horse Range*. Ph.D. dissertation. Colorado State University, Fort Collins.
- Fahnestock, J. T., and J. K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. *Journal of Range Management* 52:263–270.
- Fahnestock, J. T., and A. K. Knapp. 1994. Plant responses to selective grazing by bison: Interactions between light, herbivory, and water stress. *Vegetatio* 115:123–131.
- Fisher, C. 1983. The wild horse dilemma: background, prospective, and action. *Rangelands* 5:164–166.
- Fisser, H. G. 1964. Range survey in Wyoming's Big Horn Basin. *Wyoming Agricultural Experiment Station Bulletin* 424R.
- Frank, D. A., and S. J. McNaughton. 1991. Stability increases with diversity in plant communities: Empirical evidence from the 1988 Yellowstone drought. *Oikos* 62:360–362.
- Hansen, R. M., and I. K. Gold. 1977. Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. *Journal of Range Management* 30:210–213.
- Hartnett, D. C., K. R. Hickman, and L. E. F. Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in the tallgrass prairie. *Journal of Range Management* 49:413–420.
- Heady, H. F. 1966. Influence of grazing on composition of *Themeda triandra* grassland, east Africa. *Journal of Ecology* 54:705–728.
- Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. *Journal of Theoretical Biology* 29:151–154.
- Jameson, D. A. 1963. Responses of individual plants to harvesting. *Botanical Review* 29:532–594.
- Kartesz, J. T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland*. Timber Press, Portland.
- Kissell, R. J., Jr. 1996. *Competitive interactions among bighorn sheep, feral horses, and mule deer in Bighorn Canyon National Recreation Area and the Pryor Mountain Wild Horse Range*. Ph.D. dissertation. Montana State University, Bozeman. 148 pp.
- Knapp, A. K. 1984. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. *Oecologia* 65:35–43.
- Knight, D. H., G. P. Jones, Y. Akashi, and R. W. Myers. 1987. *Vegetation ecology in the Bighorn Canyon National Recreation Area*. A final report submitted to the U.S. National Park Service and the University of Wyoming - National Park Service Research Center.
- Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective. Pages 3–24 in N. R. French, editor. *Perspectives in grassland ecology*. Springer-Verlag, New York.
- Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2:397–403.
- Lichvar, R. W., E. I. Collins, and D. H. Knight. 1985. Checklist of vascular plants for the Bighorn Canyon National Recreation Area, Wyoming and Montana. *Great Basin Naturalist* 45: 734–746.
- Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hoofed mammals. *American Naturalist* 119:757–773.
- McNaughton, S. J. 1979. Grassland-herbivore dynamics. Pages 46–81 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti, dynamics of an ecosystem*. University of Chicago Press, Chicago.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* 55:259–294.
- McNaughton, S. J. 1986. On plants and herbivores. *American Naturalist* 128:765–770.
- McNaughton, S. J., M. B. Coughenour, and L. L. Wallace. 1982. Interactive processes in grassland ecosystems. Pages 167–193 in J. R. Estes, E. R. Tylr, and J. N. Brunken, editors. *Grasses and grasslands*. University of Oklahoma Press, Norman.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* 38:794–800.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327–366.

- Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87–106.
- Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11–23.
- Milchunas, D. G., J. R. Forwood, and W. K. Lauenroth. 1994. Forage production across fifty years of grazing intensity treatments in the shortgrass steppe. *Journal of Range Management* 47:33–139.
- Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77:290–310.
- O'Connor, T. G., and P. W. Roux. 1995. Vegetation changes (1949–71) in a semi-arid, grassy dwarf shrubland in Karoo, South Africa: Influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology* 32:612–626.
- Olf, M., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13:261–265.
- Peterson, J., J. Fahnestock, and J. K. Detling. 1997. Ungulate/vegetation interactions at the Pryor Mountain Wild Horse Range. Completion report on Cooperative Agreement No. 1268-1-9002 to the National Park Service and the Bureau of Land Management. 154 pp.
- Ripley, E. A. 1979. Grassland climate. Pages 7–24 in R. T. Coupland, editor. *Grassland ecosystems of the world*. Cambridge University Press, Cambridge.
- Sala, O. E. 1988. The effect of herbivory on vegetation structure. Pages 317–330 in M. J. A. Werger, P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven, editors. *Plant form and vegetation structure*. SPB Academic Publishing, The Hague.
- SAS Institute. 1989. *SAS/STAT User's Guide*. Fourth edition. SAS Institute Inc., Cary, N.C. 479 pp.
- Seastedt, T. R. 1985. Maximization of primary and secondary productivity by grazers. *American Naturalist* 126:559–564.
- Stebbins, G. L. 1981. Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden* 68:75–86.
- Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *Journal of Range Management* 51:164–172.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–365.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720.
- Wallace, L. L., S. J. McNaughton, and M. B. Coughenour. 1984. Compensatory photosynthetic responses of three African graminoids to different fertilization, watering and clipping regimes. *Botanical Gazette* 145:151–156.
- Webb, W., S. Szarek, W. Lauenroth, R. Kinerson, and M. Smith. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology* 59:1239–1247.
- Webb, W. L., W. K. Lauenroth, S. R. Szarek, and R. S. Kinerson. 1983. Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. *Ecology* 64:134–151.
- Whicker, A. D., and J. K. Detling. 1988. Modification of vegetation structure and ecosystem processes by North American grassland mammals. Pages 301–316 in M. J. A. Werger, P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven, editors. *Plant form and vegetation structure*. SPB Academic Publishing, The Hague.
- Williams, C. S. 1963. *Ecology of bluebunch wheatgrass in northwestern Wyoming*. Ph.D. dissertation. University of Wyoming, Laramie.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice Hall, Englewood Cliffs.

Appendix. Species of the functional groups for the lowland and upland plant communities of the Pryor Mountain Wild Horse Range. All grasses are C₃ unless otherwise indicated. Nomenclature follows Kartesz (1994).

Lowland Plant Communities

Graminoids: *Bouteloua gracilis* (C₄), *Carex filifolia*, *Poa secunda*, *Pseudoroegneria spicata*, *Stipa comata*

Forbs: *Astragalus spatulatus*, *Castilleja* spp., *Chaenactis douglasii*, *Cryptantha flavoculata*, *Erigeron* spp., *Eriogonum brevicaulis*, *Gaura coccinea*, *Geum* spp., *Hymenopappus filifolius*, *Lesquerella alpina*, *Linum lewisii*, *Lithospermum incisum*, *Penstemon eriantherus*, *P. laricifolius*, *Sphaeralcea coccinea*, *Stanleya pinnata*, *Tetraneuris acaulis*, *Verbascum thapsus*

Cushion plants: *Leptodactylon caespitosum*, *Phlox hoodii*

Dwarf shrubs and shrubs: *Artemisia frigida*, *A. nova*, *Gutierrezia sarothrae*, *Krascheninnikovia lanata*

Succulents: *Opuntia polyacantha*, *Pediocactus simpsonii*

Upland Plant Communities

Graminoids: *Carex filifolia*, *Danthonia unispicata*, *Elymus lanceolatus*, *Festuca idahoensis*, *Koeleria macrantha*, *Nassella viridula*, *Poa secunda*, *Stipa comata*

Forbs: *Achillea millefolium*, *Agoseris glauca*, *Allium* spp., *Anemone multifida*, *Antennaria* spp., *Arenaria congesta*, *Astragalus drummondii*, *A. miser*, *Besseyia wyomingensis*, *Calochortus nuttallii*, *C. occidentalis*, *Cerastium arvense*, *Comandra umbellata*, *Crepis runcinata*, *Cusickiella douglasii*, *Descurainia pinnata*, *Draba* spp., *Erigeron* spp., *Frasera speciosa*, *Gentian* spp., *Geum rossii*, *G. triflorum*, *Gilia roseata*, *Ipomopsis roseata*, *Lappula occidentalis*, *Lesquerella alpina*, *Linum lewisii*, *Orthocarpus luteus*, *Oxytropis* spp., *Pedicularis parryi*, *Phlox longifolia*, *Polygonum bistortoides*, *Saxifraga rhomboidea*, *Senecio canus*, *Solidago multiradiata*, *Taraxacum officinale*, *Tetraneuris acaulis*, *Tragopogon dubius*, *Zigadenus venenosus*

Cushion plants: *Leptodactylon caespitosum*

Succulents: *Sedum lanceolatum*

Plant Responses to Defoliation and Resource Supplementation in the Pryor Mountains¹

By

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and

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Abstract. Field studies were conducted in two types of grasslands in the Pryor Mountain Wild Horse Range of northern Wyoming and southern Montana to examine plant biomass production and nitrogen responses to the separate and combined effects of graminoid defoliation and increased environmental resource (water or nutrients) supply. Short-term plant responses were monitored over 2 years, which differed substantially in growing season precipitation. In the arid, low elevation grassland, total grass biomass was significantly lower in the dry year than the wet year in all treatments. Defoliation of the grasses did not reduce their aboveground biomass production in the wet year, but severely reduced it in the dry year, primarily because of a decrease in tiller density. Mass of remaining individual tillers increased with clipping in the dry year, and nitrogen concentrations of the grasses increased with clipping in both years. Irrigation alone increased total belowground biomass compared to the other treatments, but did not increase the aboveground biomass production of any plant functional group. Clipping plus irrigation resulted in greater total aboveground biomass production and higher nitrogen concentrations of the grasses than control or irrigated treatments. Clipping graminoids in the more mesic montane grassland did not decrease their biomass production in either year, but did increase their nitrogen concentrations and increase the collective aboveground biomass production of the other plant functional groups. Fertilization and fertilization plus clipping significantly increased total aboveground biomass production in both years, and total belowground biomass was greatest in fertilized plots.

Keywords: Nitrogen, primary production, Pryor Mountain Wild Horse Range, *Pseudoroegneria spicata*, wild horses.

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Introduction

Many large ungulate herbivores preferentially consume grasses relative to their proportion in the plant community (Schwartz and Ellis 1981; Vinton et al. 1993). This not only changes the relative ability of grasses to acquire resources, but also alters the competitive interactions within the community as plant species or functional groups are differentially affected by the direct and indirect effects of selective herbivory. For example, selective grazing of dominant grasses by bison in tallgrass prairie can increase photosynthesis and growth of neighboring ungrazed plants of the same and other species (Fahnestock and Knapp 1993, 1994).

The ability of grasses to compensate for biomass consumed by large herbivores is controlled in part by the availability of environmental resources that can readily be acquired by the plants (Chapin and McNaughton 1989). When resources such as water, light, and mineral nutrients are abundant and readily available to plants, increased aboveground productivity of grasses in response to moderate grazing levels is possible (Archer and Tieszen 1980; McNaughton 1985; Seastedt 1985; Hik and Jeffries 1990; Pandey and Singh 1992; Frank and McNaughton 1993). Conversely, when environmental resources are limited, the ability of grasses to replace tissue lost to grazers is reduced. The persistence of plants in grassland ecosystems, therefore, largely depends on the ability of individuals to cope with complex and dynamic interactions between herbivory and limitations of environmental resources.

The environmental resources that most frequently limit the growth of plants and their ability to recover from grazing and other disturbances often differ with the type of grassland being studied. In arid and semi-arid grasslands, water availability most often limits plant growth (Lauenroth 1979; Sala et al. 1988), while in more humid grasslands, or in wet years, light and nutrients, especially nitrogen availability, are more likely to limit plant growth (Knapp and Seastedt 1986; Burke et al. 1991). The response of plants to grazing may also differ between and within species, depending on the nutrient and water stress tolerance of the species present, and on the type of herbivory and its intensity and frequency (Crawley 1983; Wallace et al. 1984; Coughenour et al. 1985a,b; Polley and Detling 1989).

In the Pryor Mountain Wild Horse Range (PMWHR) in southern Montana and northern Wyoming, grasses comprise over 70% of the wild horses'

annual diet (Kissell 1996). Little is known, however, about the ability of the grasses in this system to maintain production in response to this potentially substantial grazing pressure, or about the interaction of herbivory with water or nutrient availability in the Pryor Mountains. The principal objective of this research, therefore, was to determine if the dominant grasses in the PMWHR could acquire the resources necessary to maintain biomass and nitrogen production in response to selective grass defoliation, or whether there were environmental resource limitations (i.e., water or nutrient limitations) to growth following defoliation. Because the relative competitive ability of other plants may be differentially affected by selective grass herbivory, we also investigated whether selective defoliation of the grasses would result in increased biomass production or nitrogen content of other plant functional groups, particularly forbs. We hypothesized that biomass production and nitrogen concentrations would increase in plants with additional resource supply, and that the potential negative effects of defoliation on grass growth would be ameliorated with increased resource supply.

Materials and Methods

Site Description

The experiments took place during the summers of 1993, a year with above average growing season precipitation, and 1994, a relatively dry year, in the PMWHR, an 18,000 ha refuge located 80 km south of Billings, Montana. Elevation ranges from 1,190 m to 2,440 m in the Pryor Mountains, and annual precipitation varies from about 130 mm in some lowland areas to over 500 mm at upper elevations. Our research was carried out in two types of grasslands in the Pryor Mountains – a low elevation arid grassland and a more mesic montane grassland – in which plant growth was presumed to be limited, respectively, by water and nutrient availability. To control for grazing, both experiments were established in long-term (>20 years) fenced areas that precluded wild horse use but were similar in botanical composition as those currently grazed by wild horses (Fahnestock 1998).

The first experiment was conducted in an arid lowland community at 1,300 m above sea level that receives only ca. 230 mm of precipitation annually. Precipitation data (1982 to 1994) for this community were obtained from a weather station located about 1 km south of our study site. Aboveground biomass in

this community averages about 128 g m^{-2} (Fahnestock 1998) and is dominated by perennial grasses (51% of total plant cover) and forbs (26% of total plant cover), with lesser quantities of cushion plants, dwarf shrubs and succulents. *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) is the most abundant plant in these lowland communities, accounting for nearly 50% of the total herbaceous plant cover and over 90% of the total grass cover (Fahnestock 1998). Since water presumably limits plant growth in these lowlands, a grass defoliation and water supplementation experiment was carried out in this community.

The second experiment was conducted in a more mesic, montane meadow at 2,400 m above sea level that receives over 500 mm of precipitation annually. This site is located approximately 4 km northwest of the lowland site. Precipitation data for this community were obtained from a weather station located about 1 km north of this site. Vegetation in this community is more abundant than in the lowlands, averaging about 177 g m^{-2} , and consists primarily of grasses and sedges (44% of total plant cover) and forbs (51% of total plant cover). Much of the precipitation at this site comes from frequent summer showers. Thus, the availability of nutrients, rather than water, presumably limits plant growth here. We carried out a graminoid (grasses and sedges) defoliation and nutrient supplementation experiment at this site.

Experimental Design and Treatments

A completely randomized 2 x 2 factorial design with 20 replicate plots was utilized for each experiment. Each experiment was established in a representative area of the upland or lowland grassland community at that site. Plots that were relatively uniform in terms of plant cover and species composition to control for differences within and between plots were selected. Each 3.2 m x 3.2 m plot was subdivided into four equal subplots to which a particular treatment was randomly assigned. In the arid lowlands the treatments were grass defoliation (D), irrigation (W), grass defoliation plus irrigation (DW), or untreated control (C). In the more mesic uplands, the treatments were graminoid defoliation (D), fertilization (F), graminoid defoliation plus fertilization (DF), or control (C).

Vegetation was sampled in each subplot with 0.25 m^2 circular quadrats that were randomly placed in one of four possible locations in each subplot. No vegetation sample was collected within 20 cm of the edge of each subplot to avoid edge effects. To simulate

recurrent, selective ungulate herbivory, all graminoid biomass in entire defoliated and defoliated plus irrigated or defoliated plus fertilized subplots of each experiment was clipped to a height of 2 cm once a month in May, June, July, and August of 1993 and 1994, and clipped biomass within the 0.25 m^2 quadrats of each treatment was retained. This level of defoliation was equivalent to 60–70% utilization of the graminoids over the course of the growing season. Additionally, at the lowland site, tillers of *P. spicata* were counted in the 0.25 m^2 quadrats of each plot, and individual tiller mass was quantified by weighing 100 tillers from each treatment in August (i.e., 5 randomly selected tillers from each of the 20 plots).

All aboveground biomass in the 0.25 m^2 quadrats of each treatment was harvested to ground level in August of both years and oven-dried at 60° C for 48 hours. Because all aboveground biomass was harvested to ground level in 1993, alternate 0.25 m^2 quadrats within each subplot were sampled in 1994. These alternate plots had received the same treatments except for the ground level harvest in 1993. Biomass and total offtake values for each treatment were sorted by functional group (e.g., live and dead graminoids, forbs, etc.) and weighed. Pooled biomass samples ($n = 5$) of each functional group were ground through an $850 \mu\text{m}$ (20-mesh) screen in a Wiley mill, subsampled, and nitrogen concentrations determined by coupled combustion/reduction and gas chromatography (CHN-1000, LECO Corporation, St. Joseph, Michigan). Aboveground N yield was calculated by multiplying the N concentration by the aboveground biomass of each functional group. Root biomass was estimated at the time of final harvest in 1994 by excavating five alternate 0.25 m^2 quadrats to the depth of 30 cm for each treatment. Soils were air-dried and roots and rhizomes were separated from soil by sieving.

In the lowland experiment, irrigated subplots were watered with hand-held sprinklers with water obtained from a nearby well. A 26.6 mm rainfall event was simulated in May, June, and July of each year, approximating a small increase in the number of large rainfall events this lowland area receives during the growing season. A total of 80 mm of water was added to irrigated plots during each growing season, resulting in a near doubling of the long-term average precipitation received at this site in May to July. Each watering event was applied over a 30-hour span so that there was no significant puddling or runoff, and water appeared to uniformly infiltrate the soil to a depth of at least 25 cm (personal observation based on

excavations). This irrigation scheme appeared to increase the availability of soil water to irrigated plants by nearly 3 weeks during the growing season (i.e., irrigated soils were appreciably more moist at 20 cm than non-irrigated soils for about 1 week following each watering event). In the upland experiment, a moderate level (39 g m⁻²) of slow-release fertilizer (20-10-5 of N-P-K) was surface-broadcast applied to the appropriate randomly selected subplots once near the beginning (late-May) of the 1993 and 1994 growing seasons. Soils were moist at the time of fertilization and rain fell on the site within 10 days of fertilization. All fertilizer was dissolved into the soil within 4 weeks of application.

Statistical Analyses

In each experiment, total biomass (i.e., May to August clipped biomass plus final August harvest biomass) and nitrogen responses to each treatment were compared using the general linear models procedure of the Statistical Analysis System (SAS 1989). Models included the main effects of treatment by functional group and the interaction of treatments. Type III sums-of-squares were used for significance ($P < 0.05$) testing, and least square methods were used to examine associations between treatments by functional group. We used *t*-test procedures to compare biomass and nitrogen responses of each functional group to treatments between years.

Results

Biomass Responses

Growing season (ca. March–July) precipitation in the lowland site was 202 mm in 1993, well above the long-term average of 143 mm, while in 1994 it was only 101 mm. Live grass biomass and live plus dead grass biomass were significantly lower in all lowland treatments in 1994 than 1993 (Table 1). However, forb and total aboveground biomass were not significantly lower in 1994 than 1993 in any treatment. In the lowland experiment, there was not a significant effect of any of the treatments (defoliated, irrigated, or defoliated plus irrigated) on biomass production of any plant functional group in 1993, the wet year (Table 1). This was not the case, however, in 1994, where grass biomass production was much lower in defoliated plots (9 g m⁻²) than in control plots (23 g m⁻²; Table 1).

Much of the lower live grass biomass production in 1994, the dry year, was the result of lower mass of individual live grass tillers. In control plots, mass was 32 mg tiller⁻¹ in 1993 but only 14 mg tiller⁻¹ in 1994 (Fig. 1a). A similar reduction in tiller mass was seen in grasses that were irrigated. In contrast, individual mass of grass tillers that were defoliated (both defoliated and defoliated plus irrigated treatments) were not reduced, but defoliation did reduce tiller density in the dry year (Fig. 1b). Grass tiller density in control plots was about 270 tillers m⁻² in both years. In defoliated treatments, density averaged 260 tillers m⁻² in 1993, but only 140 tillers m⁻² in 1994 (Fig. 1b).

Irrigation did not increase aboveground biomass production of any plant functional group in either year (Table 1). Total belowground biomass, however, was greatest in irrigated plots by the end of the experiment (Fig. 2a). Total belowground biomass in irrigated plots was 158 g m⁻², while that in control, defoliated, and defoliated plus irrigated plots averaged 98 g m⁻² (Fig. 2a). Irrigation apparently also enabled the grasses to compensate, at least in part, for tissue lost to clipping during the dry year; that is, in the dry year defoliation alone reduced live and dead aboveground grass biomass, but biomass of grasses in defoliated plus irrigated plots was not different from that of control plots (Table 1). The combined effects of defoliation and irrigation did not significantly alter aboveground biomass of any individual plant functional groups, but did result in greater total aboveground biomass production than control and defoliated treatments by the end of the experiment in 1994.

In the upland study site, growing season (ca. April to August) precipitation was also lower in 1994 (193 mm) than in 1993 (399 mm). Nevertheless, we found no interannual differences in aboveground biomass production of any plant functional group in control plots (Table 2). Selective defoliation of the graminoids also did not significantly reduce their biomass production in either year. However, defoliated plots did have greater total aboveground biomass than control plots by the end of the experiment (Table 2).

Fertilization increased live graminoid biomass in both years, and total live and dead graminoid biomass was highest in fertilized plots by the end of the experiment in 1994. At that time, live (58 g m⁻²) and dead (48 g m⁻²) graminoid biomass in fertilized plots was more than twice that in control or defoliated plots (Table 2). Aboveground biomass production of all plant functional groups was higher in fertilized plots in 1994 than in 1993 (Table 2). Total belowground

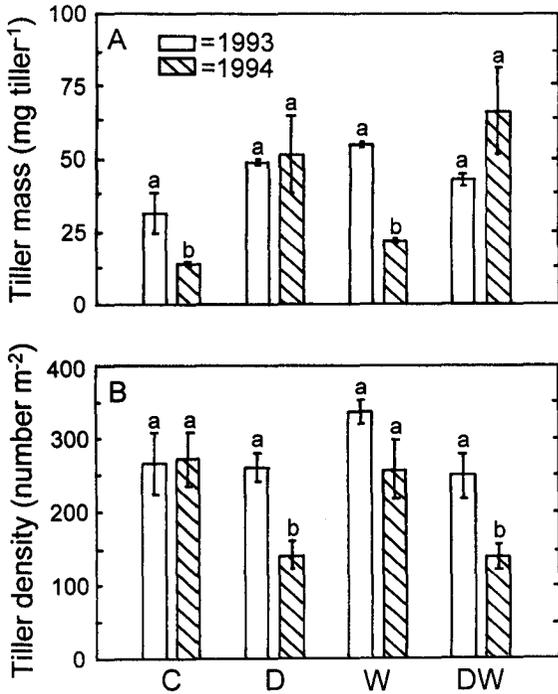


Fig. 1. (A) Individual grass tiller mass (mg tiller⁻¹) and (B) tiller density (no. m⁻²) in 1993, a wet year, and 1994, a dry year, in the lowland experimental site of the PMWHR. Measurements were made on *Pseudoroegneria spicata*, the dominant grass in these lowlands. Different letters above bars indicate significant ($P < 0.05$) differences in means between treatments and years. Treatments are control (C), grasses defoliated (D), irrigated (W), and defoliated plus irrigated (DW).

biomass in fertilized plots (620 g m⁻²) was greater than that of control (391 g m⁻²) or defoliated (306 g m⁻²) plots by the end of the experiment, but was not significantly different from defoliated plus fertilized plots (453 g m⁻²; Fig. 2b). The defoliation plus fertilization treatment increased live graminoid biomass in 1993 compared to control plots, but total grass biomass was not significantly changed by this treatment (Table 2). Additionally, total aboveground biomass was significantly higher in defoliated plus fertilized plots than in control plots in both years.

Nitrogen Responses

In the arid lowland grassland, N concentrations of both live and dead grass in defoliated and defoliated plus irrigated plots were higher in both years than those in either control or irrigated plots (Table 3). The N concentration of live grasses was significantly lower in all treatments in 1994, the dry year, than in 1993, the wet year (Table 3). In contrast, the N concentration of dead grasses was higher in all treatments in 1994 than in 1993. The N concentrations of the forbs were not significantly affected by selective grass defoliation in either year.

In the more mesic montane grassland, all treatments (defoliated, fertilized, and defoliated plus fertilized) resulted in increased N concentrations in the live graminoids, and defoliated and defoliated plus fertilized increased the N concentration of the dead graminoids, in both years (Table 4). As in the lowland site, N concentrations of live graminoids were higher in all treatments in 1993 than in 1994, and N concentrations of the forbs were not affected by any treatment in either year.

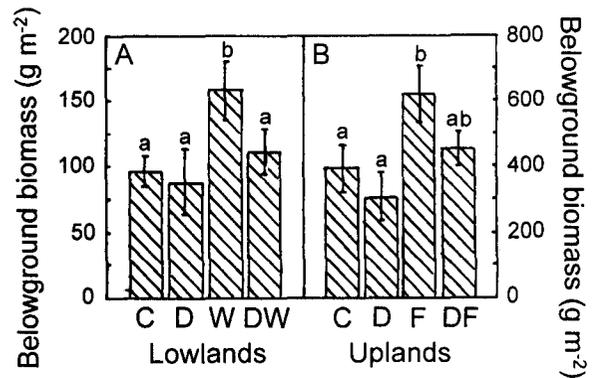


Fig. 2. Total belowground biomass (g m⁻²) in the (A) lowland and (B) upland experimental sites at the conclusion of the experiment in August, 1994. Columns headed by different letters indicate significant ($P < 0.05$) differences between treatments. Treatments are control (C), graminoids defoliated (D), irrigation (W), or fertilization (F), and graminoids defoliated plus irrigation (DW) or graminoids defoliated plus fertilization (DF). Note different scales for the two sites.

Table 1. Mean aboveground biomass (g m^{-2}) \pm 1 SE of grasses, forbs, and total biomass in control plots and defoliated, irrigated, and defoliated plus irrigated treatments from arid lowland sites ($n = 20$ for each functional group \times treatment). Values shown are for final harvest in August 1993 and 1994 and include clipped grass biomass from May through August (see text for additional details).

	Control	Defoliated	Irrigated	Defoliated and irrigated
1993				
Grasses	31.8 \pm 1.0 ^{a*} ‡	33.3 \pm 1.1 ^{a*}	33.4 \pm 1.0 ^{a*}	27.5 \pm 0.8 ^{a*}
Live	10.5 \pm 1.1 ^{a*}	13.2 \pm 1.4 ^{a*}	12.5 \pm 1.4 ^{a*}	11.8 \pm 1.2 ^{a*}
Dead	21.3 \pm 0.8 ^a	20.1 \pm 3.3 ^{a*}	20.9 \pm 2.8 ^{a*}	15.7 \pm 2.0 ^a
Forbs	25.8 \pm 2.9 ^a	33.3 \pm 3.4 ^a	30.0 \pm 2.6 ^a	27.2 \pm 3.2 ^a
Total aboveground biomass	137.2 \pm 4.5 ^a	135.6 \pm 4.7 ^a	135.4 \pm 4.5 ^a	126.8 \pm 5.2 ^a
1994				
Grasses	22.7 \pm 1.0 ^{a*}	8.6 \pm 0.4 ^{b*}	19.0 \pm 0.6 ^{a*}	14.2 \pm 0.7 ^{a,b*}
Live	6.2 \pm 1.1 ^{a*}	3.1 \pm 0.3 ^{b*}	5.6 \pm 0.7 ^{a,b*}	4.4 \pm 0.6 ^{ab*}
Dead	16.6 \pm 3.0 ^a	5.5 \pm 1.2 ^{b*}	13.4 \pm 1.9 ^{a*}	9.8 \pm 2.3 ^{a,b}
Forbs	21.0 \pm 2.8 ^a	24.4 \pm 3.7 ^a	30.3 \pm 4.5 ^a	29.8 \pm 3.4 ^a
Total aboveground biomass	119.2 \pm 7.2 ^a	123.3 \pm 12.2 ^a	134.6 \pm 10.2 ^{a,b}	149.5 \pm 8.5 ^b

‡Columns with different letters within a functional group indicate significant differences ($P < 0.05$) between treatment means. Asterisks indicate significant differences ($P < 0.05$) between 1993 and 1994 values.

Total aboveground nitrogen yield (g N m^{-2}) of the lowland and upland graminoids was increased by defoliation only in 1993, the wetter year (Fig. 3). Aboveground N yield of all lowland plants combined was increased in the defoliated plus irrigated treatment by the end of the experiment in 1994, and in the upland experiment, fertilization and defoliation and fertilization increased the aboveground N yield of the graminoids and of all plants combined in both years.

Discussion and Conclusions

In the wet year, 1993, selective defoliation of the lowland grasses, primarily *P. spicata*, had no effect on their aboveground biomass production. That is, the grasses fully compensated for the shoot biomass removed. In the dry year, however, defoliation in the absence of water supplementation severely reduced

grass biomass production. Irrigation in that year enabled *P. spicata* to compensate for shoot biomass lost to clipping. Consistent with our hypothesis, these data suggest that in the arid lowlands of the PMWHR, regrowth following grazing is closely linked to water availability.

Similar reductions in grass biomass production in response to the simultaneous pressures of clipping and water stress have also been found in other studies (e.g., Toft et al. 1987; Georgiadis et al. 1989; Simoes and Baruch 1991; Busso and Richards 1995). This response, however, is in contrast to the prediction of Hilbert et al. (1981) that plants which are stressed in some way, and consequently growing slowly compared to their potential rates, are most likely to increase production following grazing. The response of the lowland grasses in the Pryor Mountains was also not consistent with those of McNaughton et al. (1983) and

Table 2. Mean aboveground biomass (g m^{-2}) \pm 1 SE of grasses, forbs, and total biomass in control plots and defoliated, fertilized, and defoliated plus fertilized treatments from montane sites ($n = 20$ for each functional group \times treatment). Values shown are for final harvest in August 1993 and 1994 and include clipped graminoid biomass from May through August (see text for additional details).

	Control	Defoliated	Fertilized	Defoliated and fertilized
	-----(g m^{-2})-----			
1993				
Graminoids	48.5 \pm 6.4 ^{a†}	54.2 \pm 5.0 ^a	61.7 \pm 7.2 ^{a*}	65.4 \pm 6.6 ^a
Live	25.4 \pm 2.9 ^a	30.9 \pm 2.6 ^a	42.0 \pm 4.8 ^{b*}	45.2 \pm 4.6 ^b
Dead	23.0 \pm 4.2 ^a	23.2 \pm 2.7 ^a	19.7 \pm 4.1 ^{a*}	20.1 \pm 3.1 ^a
Forbs	82.0 \pm 10.7 ^a	84.0 \pm 7.0 ^a	93.6 \pm 11.3 ^{a*}	110.3 \pm 17.9 ^a
Total aboveground biomass	175.6 \pm 11.1 ^a	193.1 \pm 13.1 ^{a,b}	234.9 \pm 17.4 ^{b,c*}	234.5 \pm 15.2 ^{b,c*}
1994				
Graminoids	49.7 \pm 6.0 ^a	41.2 \pm 6.2 ^a	105.6 \pm 8.1 ^{b*}	59.6 \pm 6.5 ^a
Live	27.8 \pm 3.1 ^{a,b}	21.8 \pm 2.4 ^a	57.5 \pm 4.9 ^{c*}	36.1 \pm 4.4 ^b
Dead	21.9 \pm 3.2 ^a	19.4 \pm 3.5 ^a	48.1 \pm 6.3 ^{b*}	23.5 \pm 2.5 ^a
Forbs	90.1 \pm 12.0 ^a	101.2 \pm 12.8 ^{a,b}	146.8 \pm 16.8 ^{c*}	137.4 \pm 13.7 ^{b,c}
Total aboveground biomass	177.7 \pm 18.2 ^a	211.7 \pm 22.5 ^b	338.3 \pm 19.8 ^{c*}	282.8 \pm 17.4 ^{c*}

[†]Columns with different letters within a functional group indicate significant differences ($P < 0.05$) between treatment means. Asterisks indicate significant differences ($P < 0.05$) between 1993 and 1994 values.

Table 3. Nitrogen concentrations (%) of live and dead grass and forbs in 1993, a wet year, and 1994, a dry year, from the lowland experimental site ($n = 5$ for each functional group \times treatment).

	Control	Defoliated	Irrigated	Defoliated and irrigated
	-----(%)-----			
1993				
Live grass	0.81 \pm 0.01 ^{a†}	1.26 \pm 0.05 ^{b*}	0.85 \pm 0.04 ^{a*}	1.25 \pm 0.03 ^{b*}
Dead grass	0.45 \pm 0.01 ^{a*}	0.62 \pm 0.02 ^{b*}	0.46 \pm 0.02 ^{a*}	0.61 \pm 0.03 ^{b*}
Forbs	0.78 \pm 0.03 ^a	0.84 \pm 0.03 ^a	0.82 \pm 0.02 ^a	0.95 \pm 0.04 ^a
1994				
Live grass	0.66 \pm 0.02 ^{a*}	0.80 \pm 0.02 ^{b*}	0.62 \pm 0.02 ^{a*}	0.78 \pm 0.02 ^{b*}
Dead grass	0.53 \pm 0.03 ^{a*}	0.76 \pm 0.01 ^{b*}	0.55 \pm 0.04 ^{a*}	0.75 \pm 0.01 ^{b*}
Forbs	0.80 \pm 0.03 ^a	0.95 \pm 0.19 ^a	0.79 \pm 0.04 ^a	0.81 \pm 0.03 ^a

[†]Columns with different letters within a functional group indicate significant differences ($P < 0.05$) between treatment means. Asterisks indicate significant differences ($P < 0.05$) between 1993 and 1994 values.

Table 4. Nitrogen concentrations (%) of live and dead graminoids and forbs in 1993, a wet year, and 1994, a dry year, from the montane experimental site (n = 5 for each functional group X treatment).

	Control	Defoliated	Fertilized	Defoliated and Fertilized
------(%)-----				
1993				
Live graminoids	1.37 ± 0.04 ^{a*}	1.50 ± 0.02 ^{b*}	1.72 ± 0.02 ^{c*}	1.76 ± 0.06 ^{c*}
Dead graminoids	0.90 ± 0.03 ^{a*}	1.08 ± 0.05 ^b	1.04 ± 0.05 ^{a,b*}	1.17 ± 0.05 ^b
Forbs	1.47 ± 0.05 ^a	1.56 ± 0.03 ^a	1.58 ± 0.07 ^a	1.59 ± 0.06 ^a
1994				
Live graminoids	1.13 ± 0.02 ^{a*†}	1.27 ± 0.05 ^{b,c*}	1.24 ± 0.02 ^{b*}	1.37 ± 0.06 ^{c*}
Dead graminoids	0.70 ± 0.07 ^{a*}	0.94 ± 0.08 ^b	0.55 ± 0.01 ^{a*}	1.00 ± 0.10 ^b
Forbs	1.27 ± 0.03 ^a	1.33 ± 0.08 ^a	1.35 ± 0.05 ^a	1.25 ± 0.06 ^a

†Columns with different letters within a functional group indicate significant differences ($P < 0.05$) between treatment means. Asterisks indicate significant differences ($P < 0.05$) between 1993 and 1994 values.

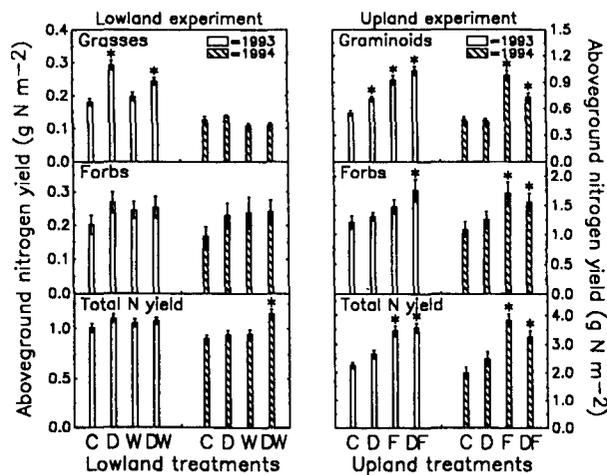


Fig. 3. Aboveground nitrogen yield (g N m^{-2} ; n = 5 for each vertical bar) for graminoids, forbs, and total N yield in the lowland and upland experiments in August, 1993 and August 1994. Treatments as in Fig. 2. Asterisks denote significantly higher N yields (calculated as N concentration multiplied by aboveground biomass) in treatment than control. Note different scales for each graph.

Coughenour et al. (1985 a,b, 1990). In their studies, the effects of water stress and defoliation were found to often act singly and one factor could reduce or ameliorate the negative effect of the other. In our study, additional water supply ameliorated the negative effects of defoliation in the dry year. In the semiarid shortgrass steppe, Milchunas et al. (1994) have found that long-term primary production across 50 years of cattle grazing treatments was most sensitive to precipitation and least sensitive to grazing intensity.

In the dry year, decreased live grass biomass in the lowland control plots was the result of lower individual tiller mass, not tiller density. Busso and Richards (1995) similarly found that mass of individual unclipped tillers of *P. spicata* was severely reduced under drought conditions compared to more average precipitation levels. They also found that plants that were irrigated showed lower tiller height, leaf area, and mass compared to plants under more average precipitation conditions. Our levels of irrigation did not increase individual grass tiller mass of *P. spicata* in either the dry or wet year. Why *P. spicata* failed to increase its aboveground biomass production in response to artificially increased water supply is not known. Although bare ground evaporation was undoubtedly high, soil excavations showed that soil

moisture was appreciably higher in irrigated compared to non-irrigated plots for at least 1 week following each watering event. It is possible that the grasses in these arid lowlands are rather insensitive to large pulses of increased water availability, such as those simulated in this study, and that frequent, smaller rainfall events may be more important to their growth [e.g., Sala and Lauenroth (1982), but see Weaver (1985)]. Additionally, the overall environment in these lowlands was still arid, which may have negated the effects of our irrigation treatment. Nevertheless, total root biomass was significantly higher in the lowland irrigated plots than in the other treatments by the end of the experiment, indicating that plant growth responses to our levels of irrigation may have been belowground only.

In the lowland site, the reduction in grass biomass with clipping that was measured in the dry year was the result of a decrease in grass tiller density and not individual tiller mass, which was much higher in clipped than control plots that year. Bluebunch wheatgrass, the dominant grass in these lowlands, has been shown to be a decreaser under increasing grazing pressure (Williams 1963). A decrease in tiller number resulting from grazing has frequently been reported (Branson 1956; Ellison 1960; Caldwell et al. 1981; Carman and Briske 1985; Polley and Detling 1988), although an increase in tiller production (Richards et al. 1988; Zhang and Romo 1995) and increased regrowth of surviving tillers (Branson 1956; Caldwell et al. 1981; McNaughton et al. 1983; Carman and Briske 1985), has also been observed. In this system, there appears to be an inverse relationship between tiller size and density, as is generally the case (Risser 1969; Gorham 1979; Christiansen and Svejcar 1988). The simultaneous pressures of clipping and water stress reduced tiller density of *P. spicata*, but increased the mass of the surviving tillers relative to those of unclipped plants. Additions of water to clipped plots in the dry year did not prevent a reduction in tiller density following clipping, providing further evidence to suggest that *P. spicata* is not very responsive to the large, infrequent rainfall events simulated in this short-term study.

In the upland defoliation-fertilization experiment, the decrease in growing season precipitation in 1994 compared to 1993 did not result in a decrease in aboveground biomass production of any plant functional group, suggesting that water did not limit plant growth at this site during the study. This was not true at all upland sites in the PMWHR, however, since decreases in plant cover and biomass were measured at

some sites in the dry year (Peterson et al. 1997; Fahnestock 1998). At this site, our finding that defoliation did not reduce live or total graminoid biomass production in either year indicates that the graminoids are apparently able to compensate for biomass lost to grazers without additional resource supply.

Fertilization increased the growth of most plant functional groups such that total above- and belowground biomass production were higher in fertilized plots than unfertilized plots by the end of the experiment. In individual plants, nutrient limitation is recognized by an increase in growth in response to an addition of the limiting nutrient. The analogous response at the community level is an increase in total community production in response to fertilization (Chapin et al. 1986). In this experiment only, the upland graminoids increased their aboveground biomass production in response to fertilization in the first year, but by the second year all plant functional groups had increased biomass production. These results suggest that species or functional groups differed in their ability to respond to increased nutrient supply or that nutrient limitations were not the same for all plants (Chapin 1980; Jaramillo and Detling 1992). Fertilization also resulted in defoliated graminoids producing more live, but not dead, biomass in 1993, than unclipped, unfertilized plants. Therefore, the effect of increased nutrient supply on defoliated graminoids in the uplands may be to decrease their rate of senescence, and increase their belowground biomass production (see above).

Our results suggest that the dominant graminoids in the Pryor Mountains are able to withstand fairly heavy levels of defoliation through compensatory growth. In the uplands, the graminoids are able to compensate for tissue lost to grazers without additional resource supply. In the lowlands, however, their ability to fully regrow following grazing is only possible when water availability is not too low. Increased water availability in the lowlands of the Pryor Mountains will most likely stimulate belowground growth in these plant communities, and will increase the nitrogen concentrations of all plants except perhaps the forbs.

In both the lowland and upland communities, selective graminoid defoliation increased the N concentrations of graminoids in both years, and increased total aboveground N yield of graminoids in the wet year. This may have resulted from increased N uptake by defoliated grasses, increased allocation of N to aboveground plant tissue, or both. Nitrogen uptake,

N concentration, and physiological activity are often higher in plants that have been grazed or otherwise defoliated than in plants from ungrazed areas (e.g., Jameson 1963; Detling et al. 1979; McNaughton 1979; Coppock et al. 1983; McNaughton et al. 1983; Ruess et al. 1983; Detling and Painter 1983; Polley and Detling 1988; Jaramillo and Detling 1988). Increased N concentrations in grazed graminoids result in higher quality forage available to herbivores. This may have important consequences for subsequent food preference by herbivores in the Pryor Mountain Wild Horse Range. In addition, the higher N-yield of defoliated graminoids suggests that herbivores may, via their grazing activities, increase not only the quality of their forage but also the quantity of crude protein subsequently available to them when they regrow the same patch. Defoliation of the graminoids did not change the aboveground biomass production or nitrogen concentrations of the other plant functional groups in the Pryor Mountains, indicating that the relative competitive abilities of plants in the upland and lowland communities are not greatly, or at least rapidly, altered by selective graminoid defoliation.

Literature Cited

- Archer, S., and L. L. Tieszen. 1990. Growth and physiological responses of tundra plants to defoliation. *Arctic and Alpine Research* 12:531–552.
- Branson, F. A. 1956. Quantitative effects of clipping treatments on five range grasses. *Journal of Range Management* 9:86–88.
- Burke, I. C., T. G. F. Kittel, W. K. Lauenroth, P. Snook, C. M. Yonker, and W. J. Parton. 1991. Regional analysis of the central Great Plains. *BioScience* 41:685–692.
- Busso, C. A., and J. H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. *Journal of Arid Environment* 29:239–251.
- Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14–24.
- Carman, J. G., and D. D. Briske. 1985. Morphologic and allozymic variation between long-term grazed and non-grazed populations of the bunchgrass *Schizachyrium scoparium* var. *frequens*. *Oecologia* 66:332–337.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233–260.
- Chapin, F. S., III, and S. J. McNaughton. 1989. Lack of compensatory growth under phosphorus deficiency in grazing-adapted grasses from the Serengeti plains. *Oecologia* 79:551–557.
- Chapin, F. S., III, P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* 127:48–58.
- Christiansen, S., and T. Svejcar. 1988. Grazing effects on shoot and root dynamics and above- and below-ground nonstructural carbohydrates in Caucasian bluestem. *Grass and Forage Science* 43:111–119.
- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1–9.
- Coughenour, M. B., S. J. McNaughton, and L. L. Wallace. 1985a. Responses of an African tall-grass (*Hyparrhenia filipendula* stapf.) to defoliation and limitation of water and nitrogen. *Oecologia* 68:80–86.
- Coughenour, M. B., S. J. McNaughton, and L. L. Wallace. 1985b. Responses of an African graminoid (*Themeda triandra* Forsk.) to frequent defoliation, nitrogen, and water: A limit of adaptation to herbivory. *Oecologia* 68:105–110.
- Coughenour, M. B., J. K. Detling, I. E. Bamberg, and M. M. Mugambi. 1990. Production and nitrogen responses of the African dwarf shrub *Indigofera spinosa* to defoliation and water limitation. *Oecologia* 83:546–552.
- Crawley, M. J. 1983. *Herbivory: The dynamics of animal-plant interactions*. University of California Press, Berkeley, Calif.
- Detling, J. K., and E. L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* 57:65–71.
- Detling, J. K., M. I. Dyer, and D. T. Winn. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* 41:127–134.

- Ellison, L. 1960. Influence of grazing on plant succession of rangelands. *Botanical Review* 26:1–78.
- Fahnestock, J. T. 1998. Vegetation responses to herbivory and resource supplementation in the Pryor Mountain Wild Horse Range. Ph.D. dissertation. Colorado State University, Fort Collins. 125 pp.
- Fahnestock, J. T., and A. K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective grass herbivory by bison. *International Journal of Plant Science* 154:432–440.
- Fahnestock, J. T., and A. K. Knapp. 1994. Plant responses to selective grazing by bison: Interactions between light, herbivory and water stress. *Vegetatio* 115:123–131.
- Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* 96:157–161.
- Georgiadis, N. J., R. W. Ruess, S. J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81:316–322.
- Gorham, E. 1979. Shoot height, weight, and standing crop in relation to density of monospecific stands. *Nature* 279:148–150.
- Hik, D. S., and R. L. Jeffries. 1990. Increases in the net aboveground primary production of salt-marsh forage grass: A test of the predictions of the herbivore-optimization model. *Journal of Ecology* 78:180–195.
- Hilbert, D. W., D. M. Swift, J. K. Detling, and M. I. Dyer. 1981. Relative growth rates and the grazing optimization hypothesis. *Oecologia* 51:14–18.
- Jameson, D. A. 1963. Responses of individual plants to harvesting. *Botanical Review* 29:532–594.
- Jaramillo, V. J., and J. K. Detling. 1988. Grazing history, defoliation, and competition: Effects on shortgrass production and nitrogen accumulation. *Ecology* 69:1599–1608.
- Jaramillo, V. J., and J. K. Detling. 1992. Small scale heterogeneity in a semi-arid North American grassland. I. Tillering, N uptake and retranslocation in simulated urine patches. *Journal of Applied Ecology* 29:1–8.
- Kissell, R. J., Jr. 1996. Competitive interactions among bighorn sheep, feral horses, and mule deer in Bighorn Canyon National Recreation area and Pryor Mountain Wild Horse Range. Ph.D. dissertation. Montana State University, Bozeman. 148 pp.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36:662–668.
- Laurenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective. Pages 3–24 in N. R. French, editor. *Perspectives in grassland ecology*. Springer-Verlag, New York, N.Y.
- McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. *American Naturalist* 113:691–703.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* 55:259–294.
- McNaughton, S. J., L. L. Wallace, and M. B. Coughenour. 1983. Plant adaptation in an ecosystem context: Effects of defoliation, nitrogen, and water on growth of an African C₄ sedge. *Ecology* 64:307–318.
- Milchunas, D. G., J. R. Forwood, and W. K. Lauenroth. 1994. Forage production across fifty years of grazing intensity treatments in the short-grass steppe. *Journal of Range Management* 47:133–139.
- Pandey, C. B., and J. S. Singh. 1992. Rainfall and grazing effects on net primary productivity in a tropical savanna, India. *Ecology* 73:2007–2021.
- Peterson, J., J. T. Fahnestock, and J. K. Detling. 1997. Ungulate/vegetation interactions at the Pryor Mountain Wild Horse Range. Completion report on Cooperative Agreement No. 1268-1-9002, to the National Park Service and Bureau of Land Management. 154 pp.
- Polley, H. W., and J. K. Detling. 1989. Herbivory tolerance of *Agropyron smithii* populations with different grazing histories. *Oecologia* 77:261–267.
- Richards, J. H., R. J. Mueller, and J. J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. *Annals of Botany* 62:173–179.
- Risser, P. G. 1969. Competitive relationships among herbaceous grassland plants. *Botanical Review* 35:251–284.
- Ruess, R. W., S. J. McNaughton, and M. B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth

- responses and nitrogen uptake of an East African sedge. *Oecologia* 59:253–261.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia* 53:301–304.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.
- SAS Institute. 1989. SAS/STAT User's Guide. Fourth edition. SAS Institute Inc., Cary, N.C. 479 pp.
- Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology* 18:343–353.
- Seastedt, T. R. 1985. Maximization of primary and secondary productivity by grazers. *American Naturalist* 126:559–564.
- Simoes, M., and Z. Baruch. 1991. Responses to simulated herbivory and water stress in two tropical C₄ grasses. *Oecologia* 88:173–180.
- Toft, N. L., S. J. McNaughton, and N. J. Georgiadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. *Australian Journal of Plant Physiology* 14:211–226.
- Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community production in tallgrass prairie. *American Midland Naturalist* 129:10–18.
- Wallace, L. L., S. J. McNaughton, and M. B. Coughenour. 1984. Compensatory photosynthetic responses of three African graminoids to different fertilization, watering and clipping regimes. *Botanical Gazette* 145:151–156.
- Weaver, T. 1985. Summer showers: Their sizes and interception by surface soils. *American Midland Naturalist* 114:409–413.
- Williams, C. S. 1963. Ecology of bluebunch wheatgrass in northwestern Wyoming. Ph.D. dissertation. University of Wyoming, Laramie.
- Zhang, J., and J. T. Romo. 1995. Impacts of defoliation on tiller production and survival of northern wheatgrass. *Journal of Range Management* 48:115–120.

Plant Cover Species Richness in the Pryor Mountain Wild Horse Range – 1998

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Summary

In 1998, plant cover and richness were measured at six enclosure sites in the Pryor Mountain Wild Horse Range (PMWHR). Enclosures were established between 1992 and 1994 and had been sampled as part of previous projects. This report summarizes the 1998 data, providing the results of statistical comparisons between vegetation inside and outside of permanent enclosures. Twelve vegetation variables were analyzed, including species richness and percent cover of 11 components: total plant, bare ground, litter, grass, relative grass, forbs, relative forbs, shrubs, relative shrubs, cushion plants, and relative cushion plants. Paired *t*-tests found no significant differences inside and outside enclosures for any of these variables ($P > 0.05$). These results are consistent with previous measurements taken at those enclosures, suggesting weak to no effects of enclosures on richness and plant cover.

Introduction

In 1992, two studies of the ungulate-vegetation system were initiated in the PMWHR. One focused on ungulate populations and interspecific competition (Kissell et al. 1996), the other focused on the impacts of herbivory on PMWHR vegetation (Peterson et al. 1997). As part of the latter project, permanent enclosures were established within the PMWHR and vegetation sampling began at these and previously erected enclosures. Vegetation monitoring at the enclosure sites continued through 1996, with additional enclosures established in 1994 (Gerhardt and Detling 1998).

In 1998, plant cover and richness were measured at six enclosure sites which were established and sampled previously (Fahnestock 1998; Gerhardt and Detling 1998; Peterson 1999; Peterson et al. 1997; Fahnestock and Detling 1999). This report summarizes the data from 1998 and provides the results of statistical comparisons between vegetation inside and outside of permanent enclosures. In addition, cover and species richness in previous years are compared to results from 1998.

Methods

Site Description

The PMWHR was created in 1968 along the border of Montana and Wyoming (Carbon County, Montana, and Big Horn County, Wyoming) and encompasses approximately 38,000 acres of Bureau of Land Management, Custer National Forest, Bighorn Canyon National Recreation Area, and private lands. Elevations within the PMWHR range from approximately 3,500 to 8,000 feet, and annual rainfall varies from approximately 5 to 20 inches, depending on location.

The six enclosure sites sampled in 1998 are located at lower elevations in the eastern and southern portions of the PMWHR (Fig. 1). All were established in 1992 or 1996: North Dryhead (1992), South Dryhead (1992), Sykes Ridge (1992), Bat Cave (1994), Peninsula (1994), and Turkey Flats (1994).

Sampling

Cover was estimated for each plant species from September 1–3, 1998 using Daubenmire frames. Cover

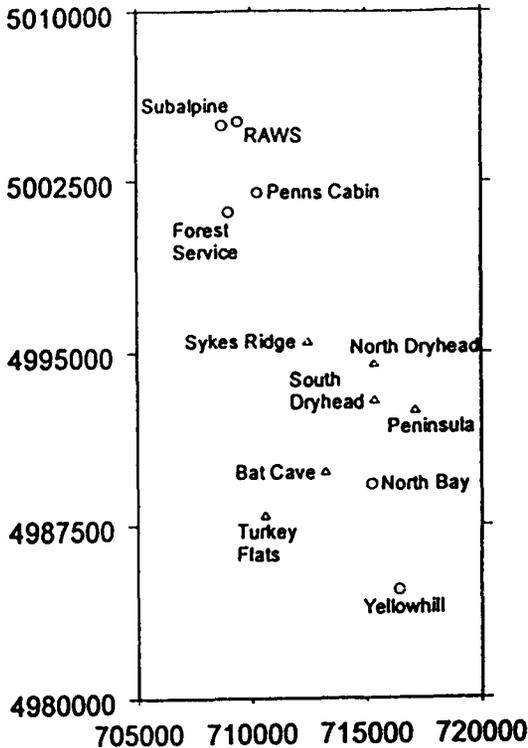


Fig. 1. Locations of permanent exclosure sites in the PMWHR. The six sites sampled in 1998 (indicated by a Δ) were located in the eastern and southern parts of the PMWHR and were established in either 1992 or 1994. The remaining six sites (O) were not sampled in 1998 and are shown only for reference. The x and y axes indicate UTM coordinates and have the same scale.

was also estimated for percent litter, bare ground, and rock. Estimates were made in the exclosed and control plots at each of six exclosure sites: Bat Cave, North Dryhead, South Dryhead, Peninsula, Sykes Ridge, and Turkey Flats. Sixteen frames were read across the diagonal of each plot except in the exclosed plot at the Bat Cave site where 15 frames were read. Measurements were made by the BLM under the supervision of Larry Padden.

Cover data from 1994–1996 were collected similarly. At each plot, cover was estimated in 15 to 20 Daubenmire frames. Sampling dates from 1994 to 1996 ranged from early July to early August and were generally at the time of peak standing crop (for details

see Peterson et al. 1997; Fahnestock 1998; Gerhardt and Detling 1998; Fahnestock and Detling 1999). Although cover was estimated at 10 to 12 exclosure sites from 1994–1996, data from only six of those sites are presented.

Analyses

Analyses were made only on data collected in 1998. For analyses, species data were pooled into five categories: grasses (including any grasses or sedges), forbs, cushion plants, *Cercocarpus*, and shrubs (including *Juniperus*, *Artemisia tridentata*, *Artemisia nova*, and *Atriplex confertifolia*). Relative cover was calculated by dividing the absolute cover of each plant group by the total plant cover. Paired *t*-tests were used to test for differences between exclosed and control plots for each of 12 variables: total plant, bare ground, litter, grass, relative grass, forbs, relative forbs, cushion plants, relative cushion plant, shrub, relative shrub, and species richness. Cover of *Cercocarpus* was not statistically compared because data were from only one exclosure site. Percent cover data was arcsine transformed before analyses, and the square root of richness data were used. Statistics were performed with SYSTAT 7.0.1 (SPSS, Inc. 1997).

Although cover data were collected in 1993 (Peterson et al. 1997) only data from 1994–1996 and 1998 are presented. Of the six sites sampled in 1998, only three of these were sampled in 1993. Statistical tests were not run on data from the 1994–1996 growing seasons for two reasons. First, these data have been analyzed in previous literature (Peterson et al. 1997; Fahnestock 1998; Gerhardt and Detling 1998; Fahnestock and Detling 1999), and second, the sampling in 1998 was done in September, 30–60 days later than sampling periods in previous years. Only means and standard errors are presented for these data.

Results

Averaged across the six sites sampled in 1998, paired *t*-tests indicated no significant differences inside and outside exclosures for any variables ($P > 0.05$, Fig. 2). Trends in richness and cover for each plot are shown (Fig. 3). Between control and exclosed plots, there were no significant trends over time for six variables.

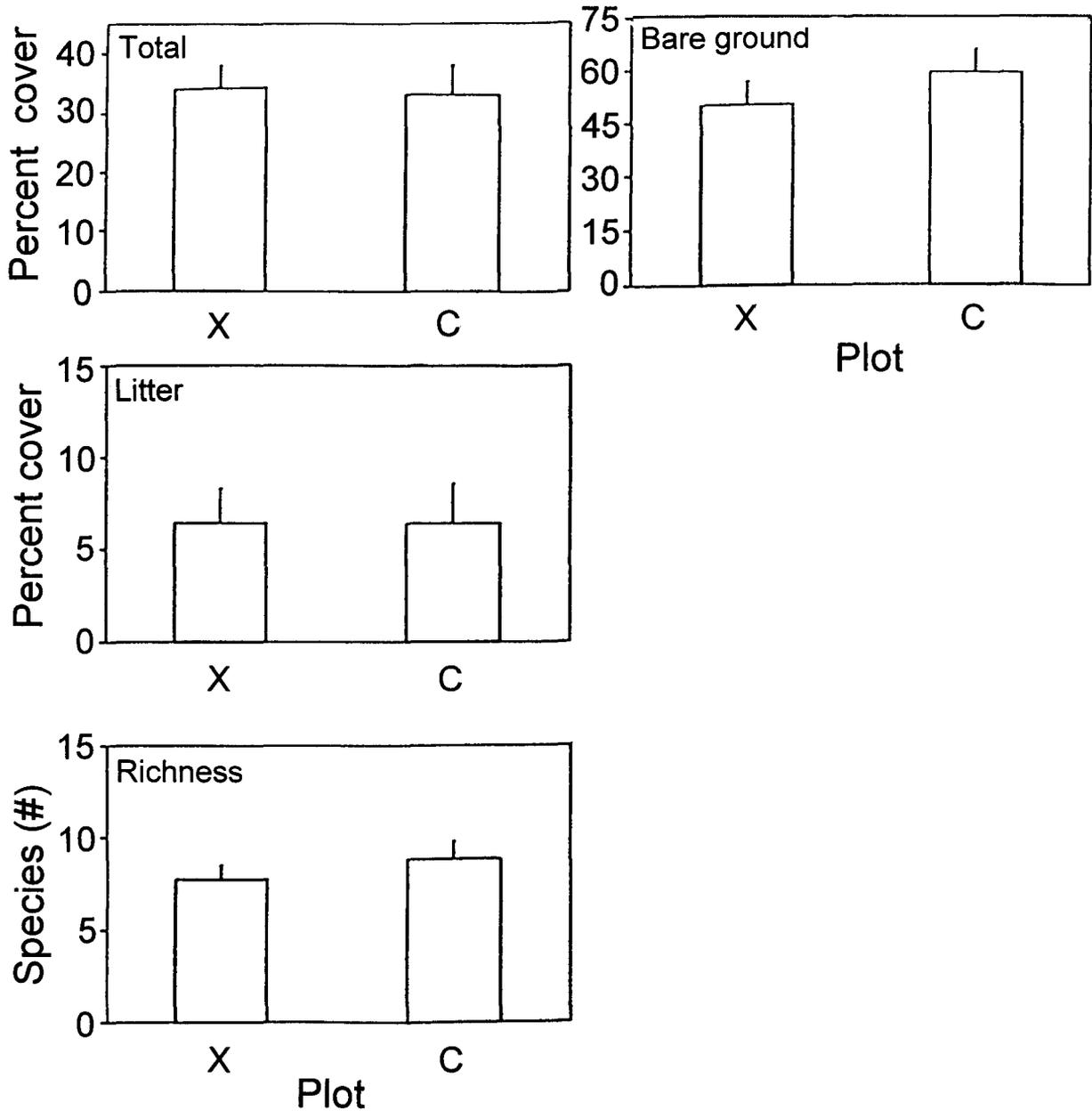


Fig. 2. Comparison of excluded (X) and control (C) plots with 12 vegetation variables. Bars indicate means and standard errors of data from plots located at six permanent exclusion sites. Notice that the scale of the y axis varies. No variable differed significantly between plots.

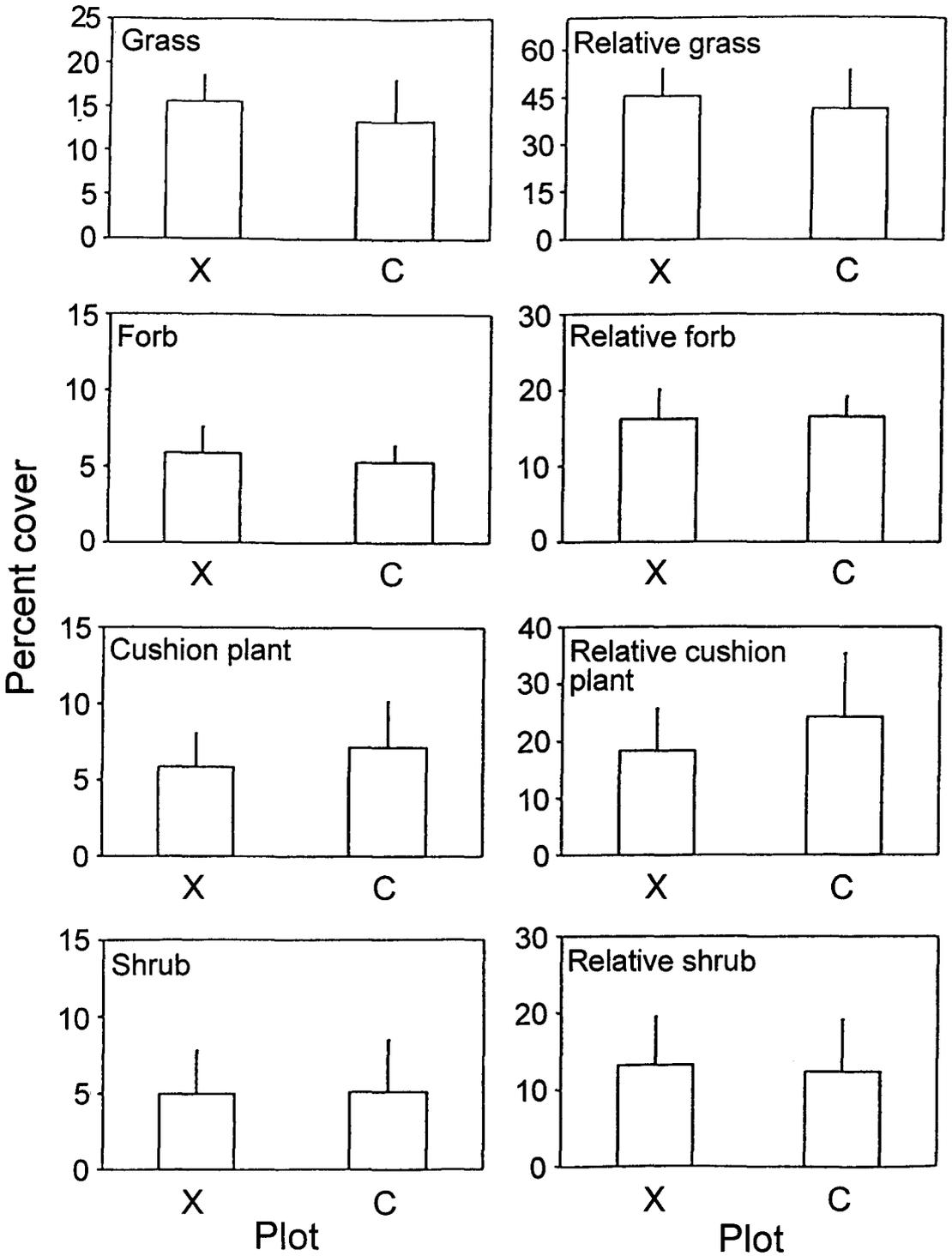


Fig. 2. Concluded.

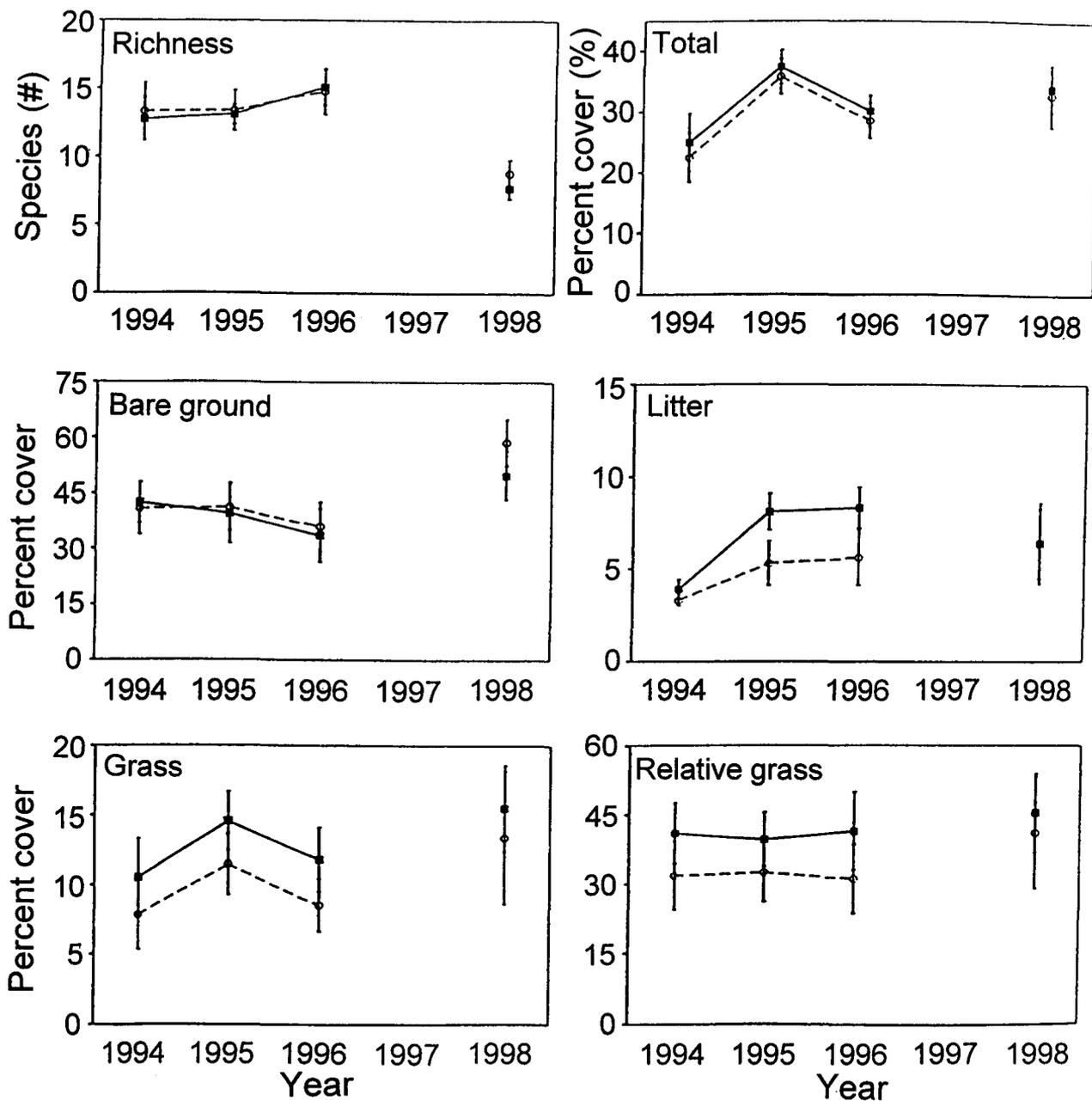


Fig. 3. Means and standard errors of species richness (#) and cover data (%) in control (O) and excluded (■) plots in 1994, 1995, 1996, and 1998. Data is from six exclosure sites and is presented for species richness (richness), % plant cover (total), % bare ground (bare ground), % litter (litter), % grass cover (grass), and % relative grass cover (relative grass).

Discussion

Of the 12 vegetation variables analyzed, none showed significant differences inside and outside of permanent exclosures (Table 1, Fig. 2). Data in 1998 was collected 30–60 days later than in previous years and at only the lower elevation exclosure sites. However, results from 1998 data are consistent with those found previously which suggested few significant differences in cover and richness between exclosed and control plots.

At the time of sampling, vegetation in the exclosed plots at each site had been protected from grazing by horses for 4 to 6 years. Exclosures at three of the six sites were established in 1992, the remaining three in 1994. Although data from prior years was not statistically reanalyzed for this report, trends in richness and cover over time are presented (Fig. 3). The graphs indicate that in all years, richness and cover of five variables (total plant, bare ground, litter, grass, relative grass) were similar in exclosed and control plots. Additionally, any changes across years appear to be similar inside and outside of exclosures. Of the six variables plotted, only species richness is noticeably different in 1998 than in previous years. This may be a result of the later sampling date in 1998 (early September vs. early July to early August from 1994–1996), with fewer species being present or recognizable after the growing season.

Previous work has suggested that interannual differences in cover patterns are greater than those between exclosed and control plots. Cover data collected in 1993 and 1994 indicated a much greater effect of year than exclosure (Fahnestock 1998; Peterson et al. 1997; Fahnestock and Detling 1999). Data from 1995 and 1996 suggested a similar trend, particularly at lower elevation exclosure sites

(Gerhardt and Detling 1998). When analyzed across several years, temporal variables (e.g., year, annual precipitation, horse population) also had stronger effects than plot on most vegetation variables (Gerhardt and Detling 1999).

Literature Cited

- Gerhardt, T. D., and J. K. Detling. 1998. Monitoring vegetation in the Pryor Mountain Wild Horse Range. Addendum report. 46 pp.
- Gerhardt, T. D., and J. K. Detling. 1999. Summary of vegetation dynamics at the Pryor Mountain Wild Horse Range (1992–1996).
- Fahnestock, J. 1998. Vegetation responses to herbivory and resource supplementation in the Pryor Mountain Wild Horse Range. Ph.D. dissertation. Colorado State University, Fort Collins. 125 pp.
- Fahnestock, J., and J. K. Detling. 1999. The influence of herbivory on plant cover and species composition in the Pryor Mountain Wild Horse Range, USA. *Plant Ecology* 144:145–157.
- Kissell, R. E., Jr., L. R. Irby, and R. J. Mackie. 1996. Competitive interactions among bighorn sheep, feral horses, and mule deer in Bighorn Canyon National Recreation Area and Pryor Mountain Wild Horse Range. Completion report. 152 pp.
- Peterson, J. 1999. Ungulate/vegetation dynamics in the Pryor Mountain Wild Horse Range. Ph.D. dissertation. Colorado State University, Fort Collins. 155 pp.
- Peterson, J., J. Fahnestock, and J. K. Detling. 1997. Ungulate/vegetation interactions at the Pryor Mountain Wild Horse Range. Completion report. 154 pp.

Table 1. Statistics for each vegetation variable. Means of control (C) and exclosed (X) plots indicate percent cover (%) and are from six sites sampled in September 1998. Statistics are shown from paired *t*-tests run on each variable.

Variable	Mean	df	<i>t</i>	<i>P</i>
Total	C = 34.0 X = 32.8	5	-0.459	0.665
Grass	C = 15.5 X = 13.4	5	-0.935	0.393
Relative grass	C = 45.5 X = 41.2	5	-0.818	0.450
Forbs	C = 5.9 X = 5.3	5	-0.021	0.984
Relative forbs	C = 16.2 X = 16.5	5	0.245	0.816
Shrubs	C = 5.0 X = 5.1	5	-0.349	0.742
Relative shrubs	C = 13.2 X = 12.5	5	-0.622	0.561
Cushion plants	C = 5.9 X = 7.2	5	0.261	0.805
Relative cushion plants	C = 18.4 X = 24.2	5	0.431	0.684
Bare ground	C = 49.9 X = 58.8	5	1.787	0.134
Litter	C = 6.4 X = 6.4	5	-0.362	0.732
Richness	C = 7.7 X = 8.8	5	1.083	0.328



SECTION II.

***CONSERVATION GENETICS
OF THE PRYOR MOUNTAIN
WILD HORSES***

A Demographic Analysis, Group Dynamics, and Genetic Effective Number in the Pryor Mountain Wild Horse Population, 1992–1997

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Introduction

The Pryor Mountain Wild Horse Range (PMWHR) was established in 1968 by the U.S. Congress to include lands administered by the Bureau of Land Management (hereafter BLM), National Park Service (hereafter NPS) and the U.S. Forest Service. The purpose of the designation was to protect the unique population of wild horses of Spanish ancestry and protect native wildlife, watershed, recreation, archeological, and scenic values. From the day of the designation of the wild horse range, the appropriate number of wild horses has been a controversial subject. Current appropriate management levels have been set at 100 adults plus the foal crop. This equates to about 130 animals. Round ups and removals occur every 2 to 3 years; thus, in recent years the population averaged

about 149 animals but with considerable fluctuations due to the increases between the removals.

In 1991, a series of research projects was started by the BLM, NPS, Forest Service, and the states of Montana and Wyoming. The purpose of those studies was to determine effects of the wild horses and native ungulates on the vegetation, soil, and any negative effects of competition between the ungulate species. In 1994, the Biological Resources Division of the U.S. Geological Survey (then the National Biological Service) initiated a series of studies on genetic conservation of wild horses.

The study of genetic conservation in the Pryor Mountain wild horse herd has been a team effort involving agency biologists and managers and scientists from four universities. The overall objectives of the study were to: (1) evaluate any losses of genetic heterozygosity in the herd and any selection for high heterozygosity; (2) determine reproductive success of mares and stallions and to conduct demographic analyses from data on the population; (3) eventually sample lifetime reproductive success of both mares and stallions; and (4) estimate genetic effective size (N_e) for

This report contains unpublished information that has not been peer-reviewed. This material will be submitted to a scientific journal in 2000 at which time some of the conclusions may be revised.

the herd, and to simulate the effects of different management actions on both N_e and the predicted loss of genetic heterozygosity over time.

The management for minimum viable population sizes of wild horses has recently become a major concern for the U.S. Department of the Interior, Bureau of Land Management. The allowable management levels for many herds have been set as low as 40 to 70 animals. There are a number of large herds in Nevada and a few large herds occur in the Intermountain West. For example, the Sulfur, Utah herd exceeds 500 animals, but most of the remaining Intermountain herds number less than 200, and many less than 100. Thus, the PMWHR is an excellent example for case studies of conservation genetics in a population that, similar to many other herds, has numbered mostly between 100 and 200 individuals for the past three decades.

The major management issues on the PMWHR include: What are the most appropriate number of wild horses to protect soil and vegetation? What are the most appropriate methods of management of horses to conserve wild horse genetics? What effect will allow a higher ratio of males in the population, or use of contraceptives have on genetic conservation? How should managers selectively remove animals? Should removals focus on the youngest animals, the least fit, the oldest animals, the least Spanish in phenotype, or should removals be random?

Most genetic variability loss from small populations is attributed to genetic drift. Genetic drift is the difference or loss in genetic frequencies between the parents and their next generation of offspring due to chance events alone. These chance events might include:

- a. in small populations, there is a greater probability of a disparity from one generation to the next in genetic variation (i.e., there is "sampling error");
- b. the lower the frequency of an allele in the parent generation, as occurs in small populations over time, the more likely it will be lost in the subsequent generations; and
- c. a high frequency of parental alleles can become fixed in small populations in the progeny generation.

Genetic effective number, or that portion of the total population (N) that actually contributes genetically to the next generation, permits an estimate of the losses in genetic variation due to genetic drift. Genetic effective number is usually characterized by the symbol N_e . The loss of genetic heterozygosity over time in a population of size N can be determined by the following formula, where H is the estimated loss of

heterozygosity per generation interval. Thus, after N_e is calculated using this formula:

$$H = \frac{1}{2N_e}$$

the manager of a small population can estimate the loss of heterozygosity over some specific period of time and assess whether or not that loss falls within some acceptable limit.

N_e is a complex number to calculate. It is at a maximum when the sex ratio of breeding adults is 1:1, when there is 0 variance in reproductive success of the adults, when the generations are non-overlapping, and when there are no fluctuations in population sizes. But these conditions are rarely met for mammals, and certainly not for wild horses. In fact, wild horses depart from these ideal conditions more than most large mammals. Breeding sex ratios are typically 1 male:2–5 females, due to a relatively stable harem organization where males >7 years hold 2–5 mares. Stallions (especially) and mares vary in their reproductive success, the generations overlap, and populations fluctuate widely, often 20–35% every 2–3 years, as rapid herd growth rates of 12–20% per year are controlled through frequent gathers and removal. Because of this complexity, N_e is typically calculated in a series of steps, each of which reduces the ratio of genetic number to total population size, N_e/N . Also, there is no single, uniformly accepted method to calculate N_e . Harris and Allendorf (1989) provide a review of different formulas that have been used to calculate N_e . We selected five of those for calculations of the N_e of the 1990s Pryor Mountain wild horse population, plus two other formulas specifically developed by Nunney (1993) for polygynous species where males hold harems.

Calculations of N_e typically involve as one major component the sex ratio of breeding adults. The effect of sex ratio on N_e is most typically stated as:

$$N_e \text{ (sex ratio)} = \frac{4NmNf}{Nm + Nf}$$

where Nm = number of breeding males, and Nf = number of breeding females. To demonstrate the effect of breeding sex ratio we take two examples of isolated herds of wild horses. In the first example, where there are five breeding females and five breeding males, the calculated N_e (sex ratio) = 10, and the ratio of $N_e/$

census $N = 1.0$ is at a maximum possible. But wild horses are polygynous and breeding is typically restricted to dominant males in a harem structure. Thus, in the second example, the breeding sex ratio is greatly biased to females (9 females:1 male). In this case, $N_e = 3.6$ and the ratio of $N_e/\text{census } N = 0.36$. In the most extreme example, when there is only one male and an infinite number of females, N_e can never exceed four. Figure 1 shows the effect of the declining ratio of breeding males:breeding females which might occur in wild horses.

Variance in reproductive success is a second major component of the estimation of N_e . The lifetime contribution of progeny by each individual who survives to reproductive age is the single most important variable in calculations of N_e [Fig. 2; Hill (1972); Ryman et al. (1981); Lemkuhl (1984); Reed et al. (1986)]. This level of demographic detail is rarely available for populations of wild animals.

Other factors that may act to significantly reduce N_e in comparison to census N include: (1) large population fluctuations; and (2) older age of first reproduction (typically, 3 years in mares and 7 years in wild horse stallions). Conversely, factors which would act to mitigate a low ratio of $N_e/\text{census } N$ in a herd might include high rates of dispersal between populations and a strong avoidance of extreme inbreeding by close relatives.

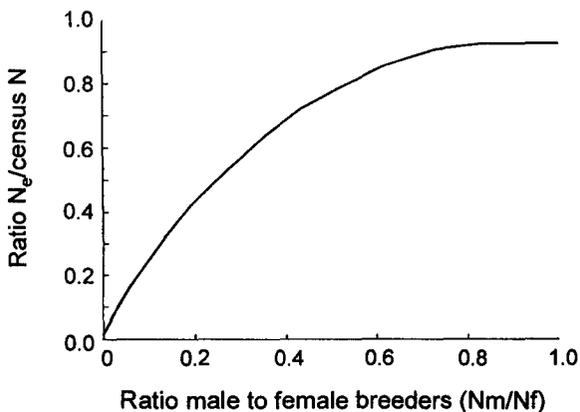


Fig. 1. The relationship of the number male to female breeders on the $N_e/\text{census } N$ ratio. Most wild horse populations have far fewer male than female breeders (e.g., 0.55 males to females [Feist and McCullough (1975)] which reduces the $N_e/\text{census } N$ ratio.

The negative biological consequences of a reduction of genetic variability, over time, in small populations include inbreeding depression. Inbreeding depression is typically demonstrated through reduced juvenile survival (Ralls et al. 1988; Jimenez et al. 1994), reduced fitness (Milton 1993; Thornhill 1993), increased asymmetry of bilateral features (Sarre and Georges 1993), and the general loss of certain alleles that may be more favorable under certain changing environmental conditions (Pemberton et al. 1992). Not all inbreeding, however, is deleterious. At moderate levels of inbreeding (but not breeding of close relatives, which is referred to as extreme inbreeding), the population may be better adapted to local environments. Negative consequences of inbreeding has proven difficult to verify in wild populations. Caughley and Gunn (1996) cite several examples of apparently inbred animals that show excellent survival of offspring. These examples include the European bison, European ibex, and African lions. The effects of extreme inbreeding, however, are always deleterious (Lacy 1987).

Study Area and Population History

The PMWHR was established in 1968 to include BLM, NPS, and U.S. National Forest lands. The PMWHR consists of about 38,000 acres of rugged canyons, rocky slopes, and gentle flats at the lower

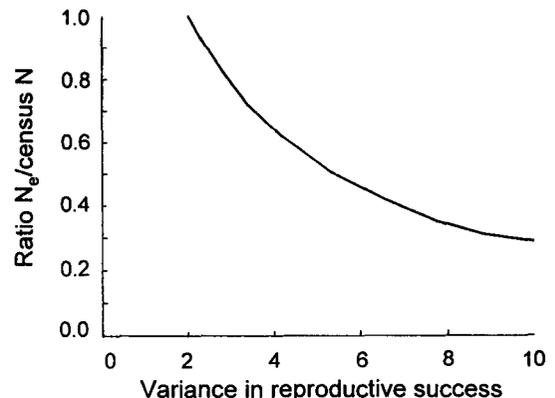


Fig. 2. The influence of variance in reproductive success on the ratio of N_e/N census N .

(1,300–1,600 m) elevations [dominated by big sagebrush (*Artemisia tridentata*); rubber rabbitbrush (*Chrysothamnus nauseosus*); shrubby cinquefoil (*Potentilla fruticosa*), and a variety of grasses and forbs (*Pseudoroegneria spicata*, *Artisida feudleeriana*, and *Stipa comata*)], and with mostly long, narrow steep-sided ridges and larger plateaus also with steep sides at mid (1,600–2,000 m) elevations [dominated by (*Cercocarpus ledifolius*, *Juniperus osteosperma*, bluebunch wheatgrass, and *Bouteloua gracilis*), and subalpine meadows at higher (2,000–2,600 m) elevations [(dominated by limber pine (*Pinus flexilis*), subalpine fir (*Abies lasiocarpa*), alpine timothy (*Phleum octoflora*), alpine bluegrass (*Poa alpinum*), Ross sedge (*Carex rossii*), and silky lupine (*Lupinus sericeus*)].

The rainfall ranges from 12–15 cm at lower elevations to 50 cm at the higher elevations. The wild horses are strongly migratory and winter in the lower and mid-elevations where typical snowdepths range from 0–25 cm. The mid-elevation ridges and plateaus are nearly always snowfree or <10 cm of snow accumulates because of wind and south and west aspects that are exposed to winter sunshine. Wild horses do not spend the winters on mountain tops where snowdepths typically exceed 1.0 m nearly all winter, except in a few rare instances. The wild horse distribution is unrestricted during winter when they eat snow for water (they may travel 2–5 km or more daily to visit snowbanks), but mid- and late-summer distributions are severely restricted by the small number of free water sources.

The wild horses occur in three possible subpopulations (west to east: Burnt Timber Ridge, Sykes Ridge, Dry Head) that are separated by one deep impassable canyon (Big Coulee), and one very long, vertical cliff face. However, they may move between the ridges on top of the mountain and below Big Coulee Canyon. At least three trails allow wild horses to occasionally cross the vertical cliff face.

The BLM seeks to manage the wild horses at about 130 head (BLM 1984, 1997) through periodic gathers and removals that occur at 1–3 year intervals.

Several distinct periods were recognized, based on management and population characteristics:

Period 1: 1970–1986

Demographics of this period were summarized by Feist and McCullough (1975), Perkins et al. (1979), and Garrott and Taylor (1990). The population was much

larger prior to 1971 ($n = 270$ horses), although completion of the PMWHR boundary fence in 1970, which excluded 40 horses and a large winter kill and starvation losses (51%) in 1977–1978 reduced the herd. Management removals maintained the herd at 120–150 horses during most of this period. Several management actions occurred during the mid-1980s to preserve forages on the winter range for use during winter only. Managers forced the migration of wild horses to the higher elevations each summer by: (1) closing one low elevation and two mid-elevation water holes; (2) improving about five water catchments at higher elevations; and (3) herding and driving the horses to the higher elevations each summer. The exception was the nonmigratory Dryhead segment, but here managers sought to limit horse numbers to <35 animals to protect soil and vegetation. Adult male to female ratios were very low during this period, typically 0.5 males:1.0 females, as a result of removals that concentrated on bachelor males and other younger animals (Garrott and Taylor 1990).

Period 2: 1992–1994

Nearly all of the wild horse population migrated to the higher elevations each summer during this period as a result of the earlier management action (only 1–2 harems remained at lower elevations near two isolated water sources). Male:female ratios were still maintained at <1 male:1 female, but there was a gradual increase in male ratios that started during this period due to a higher removal of females in 1991 and a high male birth ratio. Individuals were selected for removal during this period on the basis of selection for a more Spanish phenotype and to balance the sex ratio.

Period 3: 1995–1997

The trend toward increasing adult male:adult female ratios (1.4:1.0) continued due to a balanced removal of sexes and a higher male birth ratio.

Methods

Population Dynamics

Wild horses were intensely observed 30 person-days per year in Period 2 by Reverend F. Schwieger and G. Good (G. Ortiz). The observations increased to about 125 person-days per year during Period 3 by a combination of efforts of F. Schwieger, BLM and BRD

employees, and volunteers. Daily observations were made during the peak of foaling/breeding Period I May–30 August, while semi-weekly observations were conducted March–April and September–November. Few wild horse observations were made during the mid-winter periods, December–February. Observations were made from the ground during systematic surveys along 4wd road and trail systems that traverse the three subpopulations during those person days. The observations from foot and vehicle were augmented with two helicopter flights each fall–winter, and approximately 110–150 km of horseback surveys each year. The wild horses were approachable by humans and could be observed for periods of 2–6 hours with no apparent influence on their behaviors. Photos of each horse were taken at close distances and catalogued with any other identifying characteristics, although all behavioral observations were made at distances of 100–250 m in order not to interfere with normal wild horse behavior. The basic color of each horse was recorded, as well as any potentially identifying marks such as white marks on the head (star, snip, strip, blaze) or legs (stocking, sock, fetlock, pastern, coronet) of the horses following descriptions in Sponenberg and Beaver (1983). We identified basic body colors of palomino, white dun, sabino, cremello, sorrel, chestnut, red dun, dun, blue roan, red roan, bay, grullo, brown, brown/black, and black in the population. Every horse was individually recognizable on the basis of sex, basic body color, and face and leg markings, with the exception of five unmarked grullo stallions, and three dun stallions with stars. In these cases, the number of wither stripes and shapes of stars differentiated the animals. In 1996, 1997, and 1998, our familiarity with individual markings allowed two of us (F. Singer and L. Coates-Markle) to also identify all individual harems and nearly all individual horses even during the helicopter surveys.

Each horse was assigned a unique number during our study, based on the year and birth date of the horse. For example, the first foal born in 1996 was assigned the number 96-01, the second foal was 96-02, the third was 96-03, etc. We recorded all individually recognizable stallions, mares, yearlings, and foals observed in harems, groups, or alone. Each harem was observed for 2–6 hours, when we identified the lead harem stallion and any satellite stallions, based on dominance behavior as described in Feist and McCullough (1975), MarOom and Reis (1985), and Berger (1986). Any interchanges by mares or stallions between harems

were recorded, as well as any returns to the original harem.

We identified three levels of probability that a particular stallion sired an offspring, listed in decreasing order: (1) DNA markers of the parent (this work is still in progress); (2) if the stallion was seen copulating with the mare; or (3) if the mare was observed in the harem with the stallion at the approximate time of conception, about 340 days prior to the approximate birth date of the foal.

Data collection in 1997 included observations of harem sizes, composition, foals, stallion-stallion agonistic interactions, scars on males in August, stallion agonistic behavior, apparent stallion dominance, and reproductive success of mares and stallions as described in Singer et al. (1997). Locations of all harems were plotted on maps during systematic ground surveys of the range during summer (vehicle, saddle horse, short hikes) and during winter from two helicopter surveys. All of the demographic data, 1992–1997, were entered in QUATTRO PRO data files and analyzed using SAS data programs. This analysis was made available to J. Gross, research contractor, for use in computer simulations of genetic conservation.

Survivorship was calculated from the number of known age animals alive in year t ÷ number alive in year $t-1$. The sample of known age of animals included 144 foals born during 1992–1997, 12 (of 20) other recognizable foals born in 1991, and 6 animals born prior to 1991 whose ages were known from BLM or Rev. Schwiieger's records. Ages of the remaining 110 horses were estimated in two manners: (1) in 1994, Rev. Schwiieger estimated the ages of all adults based on their size and characteristics and his recollection of their birth; and (2) in 1997, ages were estimated from tooth patterns and wear inspected by G. Bennett (BLM) during the capture and handling for removal. Regression analysis of estimated (tooth patterns) ages and known ages for 54 animals of known age, suggested the estimated ages by tooth wear were reasonably accurate ($P = 0.0001$, $r^2 = 0.95$) (Figs. 3 and 4). The 1994 age estimates, however, were less well correlated to tooth wear estimates ($P = 0.0001$, $r^2 = 0.47$). However, the 1994 body size/morphology estimates were better for females ($P = 0.0017$, $r^2 = 0.68$) than for males ($P = 0.0146$, $r^2 = 0.43$). Following Garrott and Taylor (1990), we assumed a wild horse was dead if it was not observed for one full year. We calculated survival rates from mid-summer to mid-summer of each year (see Table 1 for definitions of demographic parameters).

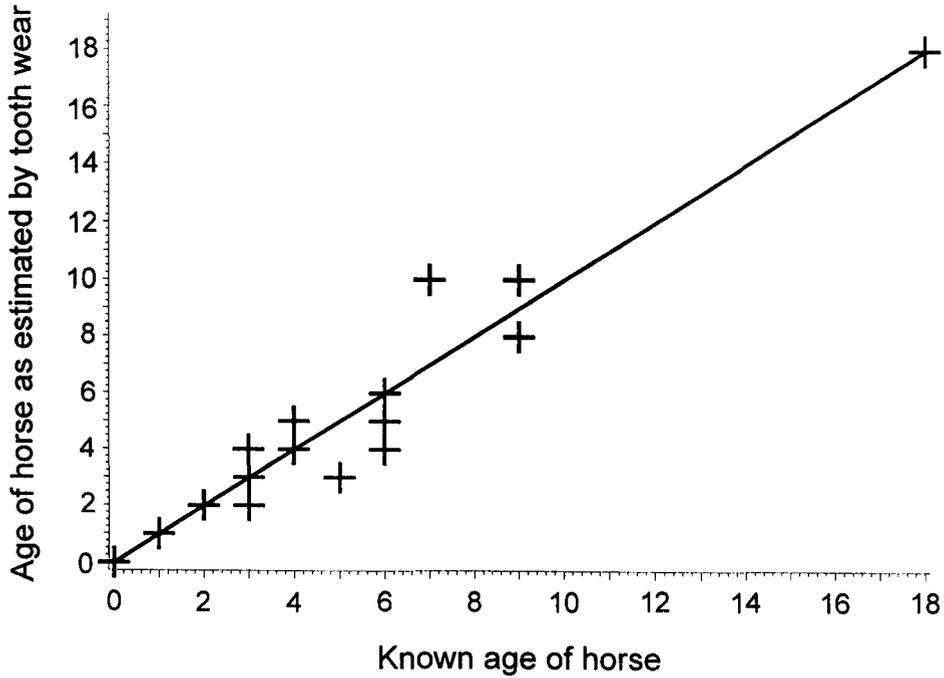


Fig. 3. The relationship between ages estimated by tooth wear and ages known for documented birth year were significant ($P = 0.001$, $r^2 = 0.95$).

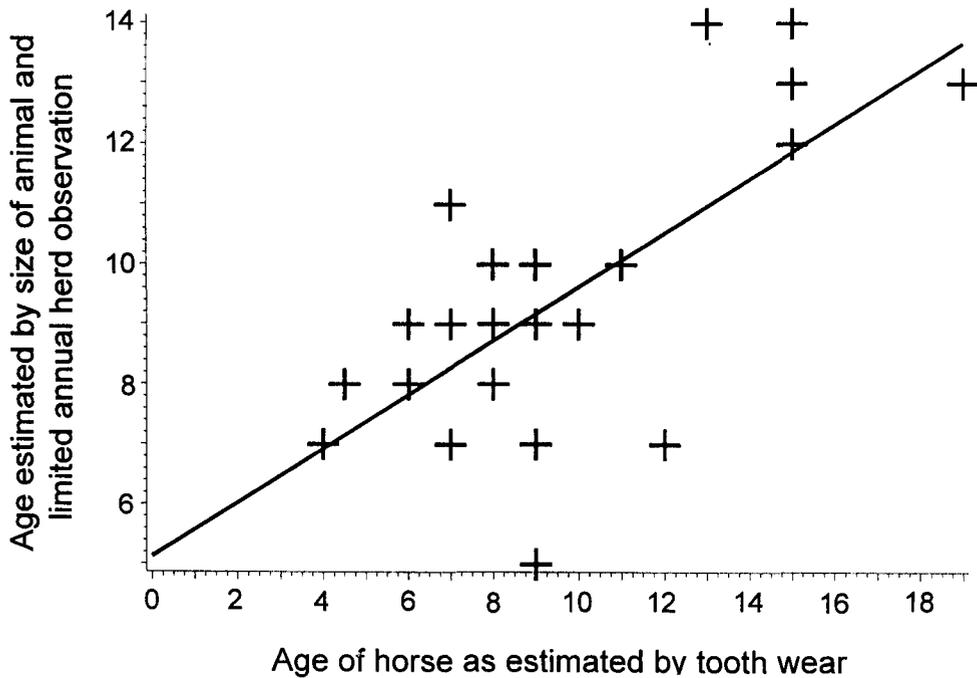


Fig. 4. The relationship between ages estimated by animal size and observation history versus age estimate by tooth wear was significant ($P = 0.001$). However, this correlation was not strong ($r^2 = 0.47$) and may indicate that body size and morphology may not be the most effective means of aging the horses.

Table 1. Definitions of demographic parameters for wild horses used in this report.

Pregnancy rate = no information.

Early mare foaling rate = age-specific foaling rates observed throughout the peak foal season during April-June.

Midsummer mare foaling rate = age-specific foaling rate observed in June-August after the peak foaling season.

Breeding age for mares = age of first reproduction for mares.

Breeding age for stallions = age stallions first observed to hold harems and sire foals.

Harem stallion foaling success rate = average siring rate of surviving live foals attributed to all harem stallions each year.

Age-specific survival rates = number of animals alive in each age class during midsummer year $t+1$ /number alive midsummer t .

Mare interchange rate between harems = the probability of a mare changing harems during each year-long period.

The number of observed interchanges or moves between harems by individually recognizable breeding age mares. Does not include the first dispersal from the natal harem.

Subadult dispersal from natal harem = The first interchange when 1-2 year old mares and stallions leave their natal harem.

Lifetime reproductive success of stallions and mares = Estimated (not observed) from the annual foaling rate for males and females X the average duration of breeding years. True values for lifetime reproductive success would require another 6-7 years of observations, since individual horses are long-lived.

Generation time (T) = calculated following Nunney (1993) as the average longevity of adults (A), corrected for maturation time, where $T = (M + A - 1)$.

Density dependence = Any influence that varies in direct proportion to population density.

Nearly all wild horse mortalities occurred in winter, with the exception of the foal class where some neonatal mortalities occurred prior to July 1 each year.

We estimated population rate of increase as:

$$\lambda = \frac{N_{(t+1)}}{N_t}$$

where N is the number of horses alive in year t, R_{t-1} the number of horses removed during the reduction programs. Thus, λ is the rate of growth of the population if horses had not been removed.

Calculations of N_e

We calculated N_e using the formulas described in Harris and Allendorf (1989) and Nunney (1993).

Harris and Allendorf (1989) compared formulas to "known" values of N_e for grizzly bears in the Greater Yellowstone Area using pedigree analysis.

The formulas we used include:

(1) LaCava and Hughes (1984):

$$\frac{1}{N_e} = \frac{1}{(4Nm)} + \frac{1}{(4Nf)}$$

where Nm = number of breeding males, Nf = number of breeding females.

(2) Ryman et al. (1981):

$$\hat{N}_e = (N \wedge L) / \{1 + 3h_2\}(VKa/K_{2a}) + (1/Ka)\}$$

where \hat{N} = annual recruitment of females to breeding age, L = mean age of mothers, h = heritability of fertility, and K_a and V_{K_a} = mean and variance of individual lifetime reproductive success of offspring who themselves survive to reproductive age.

(3) Lacy and Clark (1989), to adjust for fluctuating population size:

$$N_e = N_e / (1 + cv_2) \text{ (adjusted)}$$

where N_e = effective population size calculated assuming constant population size, and cv = coefficient of variation of breeding adults years.

(4) Reed et al. (1986):

$$\frac{1}{N_e} = \frac{1}{(4L_m M_b K_m l_m)} + \frac{1}{(4L_f F_b K_f l_f)}$$

where L = generation length, M_b and F_b = number of breeding males and females, respectively, K = number of young sired by each sex each year, l = probability that a newborn survives and reproduces.

(5) Lemkuhl (1984) who suggests four steps, to account for (respectively):

$$N_1 = (2N_e V_{K_a} + 1) / K_2$$

$$N_2 = N_1 * \{ [4N_m N_f / N_m + N_f] / N \} \text{ (imbalanced sex ratio)}$$

$$N_3 = N_2 * 2 \text{ (overlapping generations)}$$

$$N_4 = N_3 * (N_{\max} / N_{\min}) \text{ (population fluctuations)}$$

where the symbols are as above.

(6) Nunney (1993), who suggested a formula (a) for N_e specific for harem polygyny as occurs in wild horses:

$$N_e = \frac{2N}{2(V_m + V_f) + (1 - v_f)(h + 1)}$$

where V_m , V_f = variance in reproductive success of males and females, respectively, and h = number of breeding females per harem.

(7) Nunney (1993) also suggested another formula (b) specifically for harem polygyny when there is a sex difference in recruitment (as is the case for PMWHR):

$$N_e / N = \frac{4r(1 - r)R}{[2 - (1 - (h + 1)r - 1/hA^{-1})]}$$

where generation time (T) equals the average longevity of adults (A) corrected by the average maturation time (M), that is $T = (M + A - 1)$. The parameter R is the ratio of (T/A). R is the proportion of breeding males and h = harem size of breeding females.

Estimated Loss of Heterozygosity

We estimated loss of heterozygosity for the PMWHR using the formula for loss of selectively neutral heterozygosity (F) per generation (about 10 years for horses):

$$F = 1/2N_e$$

We assumed $N_e = 50$, under ideal conditions, would be the lowest population and the highest level of inbreeding that would be allowed in a population by managers, based on the recommendations of Frankel and Soule' (1981) made nearly 20 years ago during the early years of the developing field of conservation biology. This "golden rule" number of 50 for N_e has been criticized for its possible low generality, possible low applicability to wild animals, and uncertainties if this genetic population size would allow for long-term adaptation to any radical changes in the environment (Lacy 1987). Many authors recommend N_e goals much larger (e.g., a population goal of 500 was recommended for the Siberian tiger). Obviously, a goal larger than 50 is desirable, whenever feasible.

We obtained single number estimates of N_e and subsequent estimates for loss of heterozygosity for the following management scenarios: (1) no change in current management that prevailed during the 1990s; (2) if the allowable number and the average number of wild horses on the range is increased by 1.5 times; (3) an increase in horses of 2.0 times; (4) management removals of more males and few, large harems (as occurred in Period 2); and (5) if immunocontraceptives are applied to adult females. Our goal was to estimate N_e and loss of heterozygosity for the average population and the simplest of management options in order to provide conceptual insights into the effects of the options. These one-moment-in-time estimates in no way provide estimates of the population variability, environmental stochasticity, and uncertainties that might occur in the real world that can be simulated by the models. We refer the reader to Gross (1999) for more realistic and dynamic model scenarios.

Results

1992–1997 Demographics

Population size averaged 161 ± 11 (mean \pm standard error) horses during our study period, 1992–1997. The population grew at an average rate of 17% per year during this period ($\lambda = 1.176 \pm 0.017$). Management removals occurred twice during this period and a third removal had occurred in 1991 just prior to the study. The late 1991 removal was focused on adult females. The average population during this period consisted of 161 individuals, including: 25 harem stallions, 31 bachelor stallions, 52 breeding age mares, 24 yearlings, and 29 foals of the year. The average population exceeds the animal management level most years because removals occurred only every 2–3 years.

Dramatic changes occurred in the population during the study period. These changes were detailed in last years' report and included:

1. Management removals were more balanced with regard to the sexes starting in 1991, and that, combined with a higher birth rate of males, increased the ratio of adult males:females in the population.
2. A number of older males died, or their dominance status and vigor waned.
3. Because of the changes described above, by 1994 and 1995, a number of new, young, vigorous

stallions reached the age of 5–7 when they first acquired harems.

4. The fall 1994 removal may have also altered key relationships within several harems of middle-aged and older stallions aged 10–15 years, resulting in declines in harem size of several of these established harems. In particular, the harems of Blackie, King, Flash, Crow, and Herpes were reduced during the removal, and further declined during the first year following the removal. None of these older stallions regained their former large harems, although several new, young harem stallions gained large harems.

As a consequence of these trends, the number of harems increased from Period 2 to Period 3 from about 18 to 28–31, and the number of mares per harem decreased from about 4 to about 2 (Singer et al. 1997). The declining status of the oldest harem stallions (12–19 years), the increasing recruitment of a number of aggressive young stallions, and the generally larger proportion of stallions of all ages in Period 3 contributed to a greatly increased interchange rate of mares between established harems or into new harems. The harem interchange rate for mares per year increased from 0.099 in Period 2 to 0.477 in Period 3 ($P = 0.049$).

We found no difference in male versus female survivorship ($P \geq 0.22$; males = 0.965, females = 0.975). Survivorship for both sexes in the population was very high. Survivorship following mid-summer observations was 0.96 for the remainder of age class 1, 1.00 in age class 2, and about 0.98 in each year thereafter until age 16, at which time survivorship of both sexes dropped off markedly. In those years ($n = 3$) when early foaling rates were observed, first year survivorship was 0.87.

Mid-summer foaling rates were moderate, 0.63 ± 0.028 for mares of breeding age (≥ 3 years of age). Very few females first bred as yearlings and produced foals as 2-year-olds (mid-summer foal success rate for 2-year-old mares = 0.107), but 3-year-old mares produced foals at the rate of 0.54. Foal rate was highest for mares aged 4–11 years (0.67), after which time the foaling rate declined to 0.46 for mares aged 12–17. Mares recruited 0.53 individuals that would potentially reach breeding age each year (breeding age = 3 for females, 7 for males). Assuming a 1:1 sex ratio, which is the theoretical norm for most wild horse populations (Garrott et al. 1991), adult mares in the average population in the 1990s produced 0.287 ± 0.015 female progeny and $0.248 \pm$ male progeny per year that would

be recruited into the breeding population, on the average. Information on reproductive success for at least part of the 6-year study was available for 57 mares, but complete foaling information for all 6 years was only available for 38 mares. One (3%) of these 38 mares produced a foal in all 6 years, 8 (21%) produced foals in 5 of 6 years, 13 (34%) produced foals in 4 of 6 years, 11 (29%) produced foals in 3 of 6 years, and 5 (13%) produced foals in only 2 of 6 years (no mares produced 1 or 0 foals during the period).

Apparent reproductive success of 46 harem and harem satellite stallions was observed during the 1992–1997 study period (Fig. 5). Stallions first gained harems at 4–8.5 years of age (\bar{x} = 6 years), and held harems an average of 8 years. Harem stallions sired an average of 1.088 ± 0.027 surviving foals per year, of which 0.943 potentially would be recruited to breeding age. We estimate each harem stallion recruited an average of 0.505 ± 0.125 female foals and 0.438 ± 0.109 male foals per year that would survive into the breeding population. Sex ratio of surviving foals greatly favored males (1.40 males:1.00 females) during the 1990s. Not all maturing stallions acquired harems in this population, but by age 10, the probability of any stallion holding a harem increased to 0.92.

Population demographics of the PMWHR changed in the 1990s, apparently in response to the more consistent management, the more equal removal of males and females, and a higher birth rate of male foals between Period 1 (1970–1986) and Periods 2 and 3 (1992–1997 combined) (Fig. 6). Population growth rates did not differ statistically between the periods ($P = 0.528$), but numerical growth rates were higher ($\lambda = 1.176$) in the 1990s (Periods 2 and 3 pooled) than Period 1 ($\lambda = 1.119$) and the coefficient of variation (CV) was less ($CV = 3.21$) in the 1990s than during Period 1 ($CV = 17.09$). Survival did not differ between the periods ($P = 0.122$), but foal rates for young mares were higher in the 1990s. Mid-summer foaling rates for 3–5 year-old mares were 0.608 ± 0.108 in the 1990s (Periods 2 and 3) but 0.392 in Period 1 ($P = 0.048$). However, foal rates for 5–10-year-old mares ($P = 0.388$) and 10–17-year-old mares ($P = 0.084$) did not differ.

Population size varied greatly from 270 to 86 during the entire 27-year period, 1970–1997, thus providing an opportunity to investigate the possibility of density dependence or the negative relation between population size and any growth parameter in the population. We found no negative relationship between foal rate and population size ($P = 0.664$), nor survival

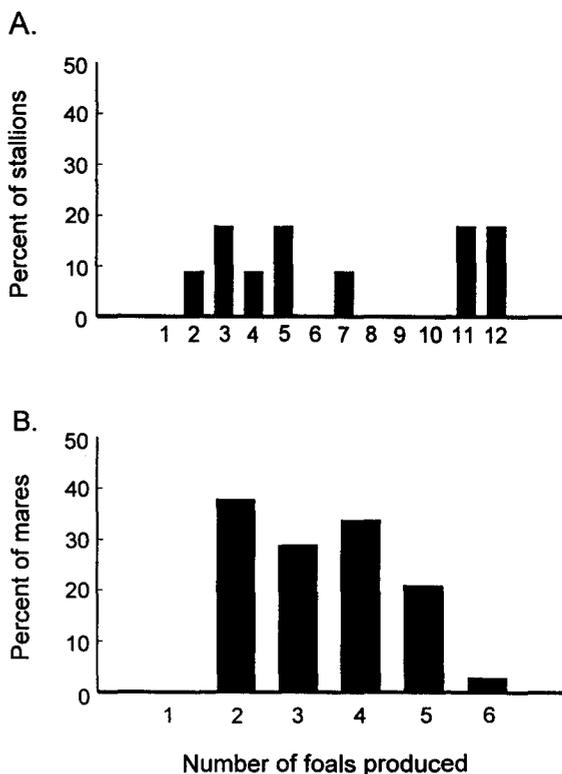


Fig. 5. Total number of foals produced by 11 harem stallions (a) and 38 mares (b) for which there were 6 years of data on reproductive performance, 1992–1997.

and population size ($P = 0.701$). However, population growth rate was negatively correlated with population size ($P = 0.010$) (Fig. 7).

Population growth rates did not vary between Period 2 and Period 3 ($P = 0.615$), the foaling rate did not vary ($P = 0.943$), nor the sex ratio of foals born ($P = 0.689$), but the sex ratio of adult breeding age animals increased from 1.0 males:1.0 females in Period 2 to 1.18:1.0 in Period 3 (prior to the late 1997 removal) (Fig. 6; $P = 0.035$). The number of harems increased from 18 in Period 2 to 31 in Period 3 ($P = 0.019$). The probability of maturing, young harem stallions (5–7 years) siring a foal increased 7-fold from Period 2 to Period 3 ($P = 0.019$), but the probability of older harem stallions (8–19 years) siring a foal decreased about 21% ($P = 0.048$).

Moderate natural gene flow occurred between the three potential subpopulations of wild horses. This gene flow was of sufficient magnitude to indicate the PMWHR supports one panmictic population of wild horses (Table 2). Panmixia is generally defined as one

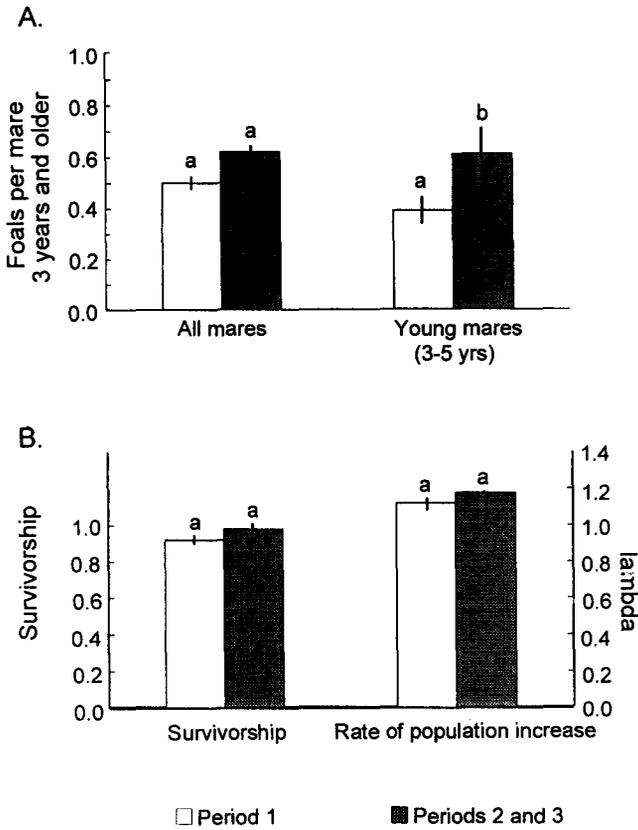


Fig. 6. Comparison in foaling rates (a), survivorship (b), and population rates of increase (λ) (b) for the Pryor Mountain wild horse herd between 1970–86 period (Period 1, Garrott and Taylor 1990) and 1992–97 (Periods 2 and 3). Different letters (a, b) denote significant differences between periods.

to five migrants (that successfully breed) between any subpopulations per generation. A wild horse generation in this case is every 9–11 years. Artificial movements of horses by managers during the study period increased panmixia (Table 1).

Genetic Effective Number

Estimates of the genetic effective number of the 1990s PMWHR population ranged widely from 16–57, but the most reliable estimators, according to the review of Harris and Allendorf (1989), averaged 43 ± 4 for the few, large harem scenario (observed in 1992–1994) and 58 ± 4 for the many, small harem scenario

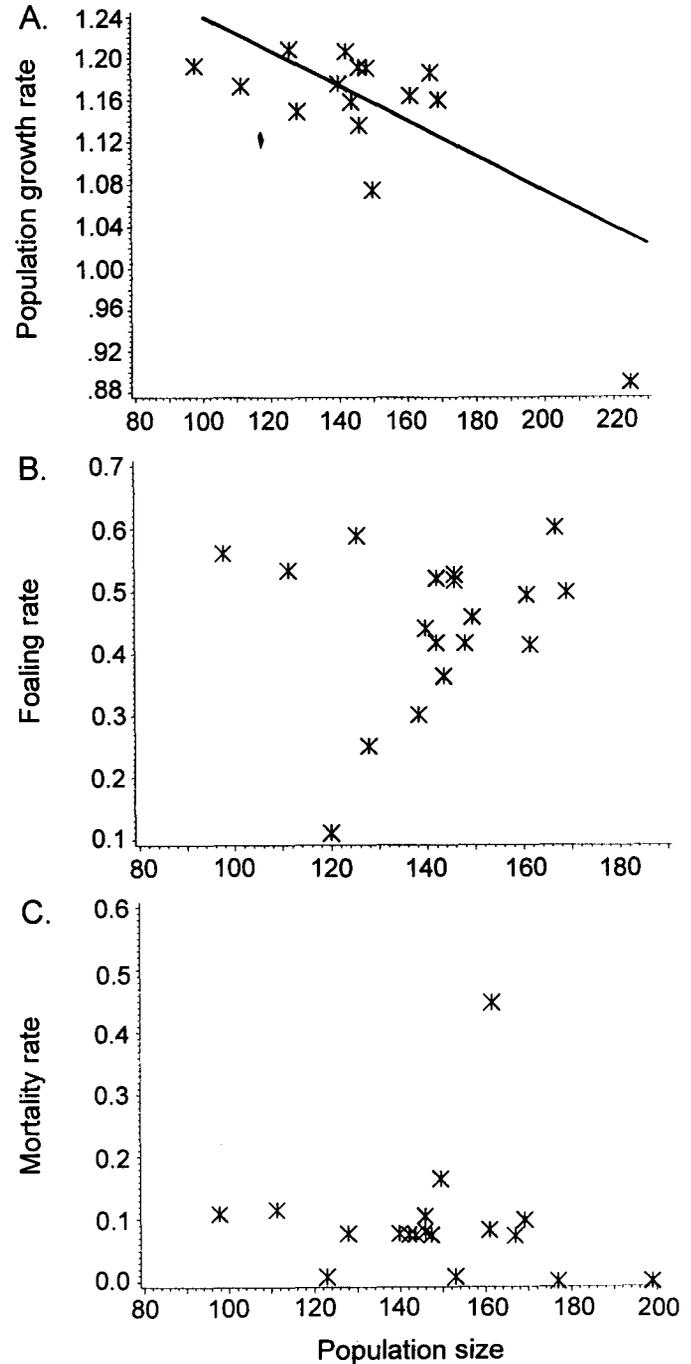


Fig. 7. Density dependence was slightly evident in the Pryor Mountain wild horse herd from the correlations of population growth rate to population size (a), $P = 0.0104$, $r^2 = 0.41$. However, no density dependence was evident when foaling rate (b) or mortality rate (c) were compared with overall population size ($P = 0.6642$ and $P = 0.7007$, respectively).

Table 2. Annual gene flow between subpopulations of Pryor horses described as proportion of population moving per generation (10 years).

Age	Mares			Stallions		
	Natural	Artificial	Total	Natural	Artificial	Total
Foal to 2-year old	0.026	0.031	0.051	0.011	0.000	0.011
3–7 year old	0.025	0.005	0.031	0.029	0.006	0.035
8+ year old	0.000	0.000	0.000	0.043	0.000	0.043

Table 3. Calculations of genetic effective number (N_e) and the ratio of N_e to total census population size (N) for the “average” population of Pryor Mountain wild horses in the 1990s.

Formula	Estimated accuracy	Reference	Few, large harems		Many, small harems	
			N_e	N_e/N	N_e	N_e/N
1	+0.54	LaCava and Hughes (1984)	54 ^a	0.34	78	0.48
2	+0.4	Ryman et al. (1981)	45*	0.28	53*	0.33
3	n.a.	Lacy and Clark (1989)	40*	0.25	47*	0.29
4	+0.20	Reed et al. (1986)	59*	0.37	78*	0.48
5	-0.27	Lemkuhl (1984)	15 ^b	0.09	17 ^b	0.18
6	n.a.	Nunney (1993)(a)	32	0.20	62	0.39
7	n.a.	Nunney (1993)(b)	39	0.24	51	0.32
		Mean	43 ± 4	0.27	58 ± 4	0.36

^aA known overestimate (Harris and Allendorf 1989).

^bA known underestimate according to the review by Harris and Allendorf (1989).

*Best estimates according to Harris and Allendorf (1989).

(observed in 1995–1997) (Table 3). We excluded formulas 1 and 5 from calculations of means because of the critical comments on those formulas by Harris and Allendorf (1989).

Our simple calculations suggested that a hypothetical scenario of permanent contraception of mares that were never allowed to breed reduced N_e substantially (-17%), but more innovative contraceptive programs that allowed mares to breed all years except for a 3-year period of contraception apparently reduced N_e only a minor amount (Table 4). Removals that were concentrated on only the oldest animals also reduced N_e substantially (-22%). As expected, increasing total population size with no other change in any demographic variable (which would not be the case) increased N_e by +50% and +100%.

Discussion

Population Dynamics

The rate of increase of 17% for the PMWHR population is high, but other workers have reported rates of increase of 18–20% in wild horses (Keiper 1976; Wolfe et al. 1989). The foaling rate of 62% for PMWHR is also only moderate when compared to foal rates of 75–89% reported for many herds (Keiper 1976; Eberhardt et al. 1982; Berger 1986; Garrott et al. 1991). Survivorship rate for the PMWHR in the 1990s period (0.98) is the highest ever reported for wild horses, although a few other populations had high survival rates of 0.94–0.97 (Eberhardt et al. 1982; Berger 1986; Siniff et al. 1986). Few yearling mares bred and produced foals as 2-year-olds in 1992–1997 (10%), similar to the reports of a low breeding rate by yearling females in the 1970s or 1980s in the PMWHR (Feist and McCullough 1975; Garrott and Taylor 1990), but higher foaling rates by 2-year-olds of 22–41% were reported from Nevada (Berger 1986; Wolfe et al. 1989; Garrott et al. 1991).

The vast majority of wild horse populations have a 1:1 sex ratio (Klingel 1975; Tyler 1972; Welsh 1975; McCort 1979). In only 4 of 148 populations reviewed by Garrott et al. (1991) were there more males than females in the <1-year-old category. Foal sex ratios did not differ from 1:1 in the population in the 1970–1986 period (Garrott and Taylor 1990). The tendency towards greater production of male foals in the PMWHR in the 1990s has a number of significant implications. A higher proportion of males will result in

smaller harems, increased competition among males for mares, a larger number of harems, and a higher interchange rate of mares between harems. A positive genetic consequence of a higher male:female ratio will be a larger number of males that produce progeny, a larger ratio of genetic effective to total population size (N_e/N), and thus, given the same wild horse population size, a lower rate of predicted loss of genetic heterozygosity.

Various ecological and evolutionary theories have been proposed to explain the expression of fetal sex ratios in mammals. The most parsimonious theory consistent with the observations on the PMWHR is that females in better condition will invest more in male progeny than female progeny. Any mechanisms that promote production and survival of large male progeny in polygamous species would be selected since such a male might in turn produce a large number of young (Trivers and Willard 1973; Clutton-Brock et al. 1982). There is field evidence from red deer (*Cervus elaphus*) and wild horses that more male progeny were born and/or surviving to dams in good condition and favorable years (Clutton-Brock et al. 1982; Monard et al. 1997). But, male offspring were more costly to produce due to higher investments in gestation and lactation and mares were less likely to produce male offspring in subsequent years (Monard et al. 1997).

We propose that wild horses are also likely in better body condition now and mares are producing more male foals than during the 1970–1986 period. A number of management actions were implemented in the 1980s that improved range conditions. Water holes on the winter range were closed off and horses were driven each year to the summer range to “rest” the winter range, and generally fewer horses have been allowed on the range, especially since 1980. Several early managers of the area who visited the area in 1997 commented on a significant visual improvement of plant condition, especially on the lower and mid-elevations (R. Hall, T. Voss, personal correspondence, October 1997). A slightly higher population growth rate, a higher numeric survival rate, and a higher foaling rate by young mares in the 1990s versus the 1970–1986 period, support our contention that the wild horses are presently in better body condition.

Many mammals exhibit density dependence relations. Jenkins and Ashley (1994) found some evidence of density dependence in a number of wild horse populations as we did in the PMWHR, but the evidence did not involve all parameters inspected. One

Table 4. Effect of census scenarios on estimates of genetic effective population size using the 1995–1997 average census population size for the Pryor Mountain wild horses as an example.

	Permanent immuno- contraception of mares to stabilize the population	Temporary (3-year) contraception of mares	Removals of oldest animals only during gathers	Increase population 1.5 fold	Increase population 2.0 fold
% change in N_e	-10	-2	-13	+29	+58
Change in the proportion of N_e/N	-0.06	-0.01	-0.08	No change	No change

explanation for the lack of density dependence in all parameters is that habitat conditions may have significantly improved in the 1992–1997 period. By including data from two periods with different range conditions, any density dependence might have been obscured. Also, there were only a few years with large population sizes and high variances, thus limiting the opportunity to document density dependence. However, the negative relationship between population growth rate and population size provides some evidence of density dependence in the PMWHR.

The comparisons between Period 1 to Periods 2 and 3 pooled suggest that the herd's body condition is improved and quite likely the range is in better condition in the 1990s. While the increase in population rate of increase was not significantly different, it was numerically higher in the 1990s, and perhaps more significantly, the variance in annual rate of increase was less in the 1990s. Populations that are on better range and/or at population levels below ecological carrying capacity (ECC), will be less influenced by weather and their populations will fluctuate less. The evidence is that the wild horse population is less influenced by annual variation in weather in the 1990s. The increase in foaling rate of the youngest breeding age mares is also interpreted as a suggestion of a trend to better conditions, since this youngest age class of breeding ungulates is most sensitive to range conditions. For example, the pregnancy rate of the youngest age class of female elk cows to breed (yearlings) varies more with relation to elk density than does older age classes of cows (Clutton-Brock et al. 1982; Houston 1982).

We attribute several recent demographic changes in the wild horse population to the higher ratio of adult males. The higher interchange rate of mares between harems appears to be a recent phenomenon that may be attributed to the greater ratio of adult males since the early 1990s. The mare interchange rate increased about 3-fold since 1994. Feist and McCullough (1975) also reported a rate in 1970 that was similar to the 1992–1994 rate, or about 15% per year (they actually observed a 7.6% rate in a 6 month period). The adult breeding sex ratio of males during their study was also low, 0.56 males:1.0 females (Feist and McCullough 1975).

We were unable to calculate an exact number for genetically effective population size for the PMWHR, but rather a general range of numbers. Our calculations suggest that, at the very best, the genetically effective population size of the herd was slightly below $N_e = 50$ in the early 1990s, but slightly above $N_e = 50$ in the 1995–1997 period. We stress that these are maximal estimates of N_e , as if no removals were occurring and if no breeding occurs between related individuals, neither of which apply. Actual N_e will be less than our calculations. It was not our goal to indicate any single most appropriate number for N_e , but rather to demonstrate the effects of different management scenarios on N_e . We concluded any increase in the allowable population size would increase total N_e . We also concluded that the following management actions tend to increase the relationship of N_e to population size:

1. Any high adult male sex ratio, approximating 1 male:1 female adult sex ratio and a consequent large number of smaller harems.

2. Population removal scenarios that concentrate only on young animals.

3. Any purposeful translocation by managers of migrants from another large population with similar alleles and higher heterozygosity, even at rates as low as three migrants every 9–12 years that would successfully breed in the PMWHR. The exact rate of migrants needed has not been precisely quantified for the PMWHR. These suggestions are based on general analyses conducted by Allendorf (1983) and Lacy (1987). Allendorf (1983) recommended managers move a small number of migrants per generation to isolated nature reserves as a compromise that:

(a) prevents loss of alleles from the local population, while (b) not preventing any (natural) adaptive genetic divergence by the population in the reserve. This is referred to as supportive breeding or the “One-Migrant-Per-Generation Rule.” This management option would achieve the goal of not losing alleles without increasing the population size limits.

4. Population subdivision might also tend to maintain a higher proportion of the genetic variability present in the original population, although each subpopulation would have a higher rate of inbreeding and a greater divergence genetically from the original source population (Lacy 1987). The three hypothetical subpopulations in the Pryor Mountains proved not to be true subpopulations, since the number of migrants per generation makes them a panmixing population. However, during the planning for any new additions to the range, the advantages of any new, true subdivision might be considered. To accomplish this, the rate of migrants should be <1 per generation between any new subpopulations and the PMWHR.

The following management actions will tend to decrease N_e , and thus increase the rate of loss of genetic variability, for a given wild horse population size:

1. Immunocontraceptive scenarios that remove females from the breeding pool for their entire lives. However, scenarios that take females out for brief periods, (e.g., 3 years only), seemingly have a very minor effect in reducing N_e . Thus, any such innovative contraceptive strategies deserve further investigation.

2. Any management removal scenario that returns the population to fewer, larger harems.

Additionally, any management scenario that includes a decrease in population size will decrease total N_e and thus increase the predicted rate of loss of genetic variability.

Work in Progress

Using a GIS, we intend to analyze the spatial distribution of harems in concert with information on the relative dominance of stallions. We will be using sampling of feces and urine to assess pregnancy rates of mares retained in stable harems and those mares that change harems. We will use remotely gathered data to assess condition and growth rates of core and peripheral harem horses. We plan to conduct more comprehensive analyses of the group and social dynamics, including 1998 data, and submit these results and interpretations to a peer-reviewed journal. We will evaluate management experiments with wild horses and bighorn sheep. The BRD Natural Resources Preservation Program will fund this latter effort in FY2000–2002.

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Literature Cited

- Allendorf, F. W. 1983. Isolation, gene flow and genetic differentiation among populations. Pages 51–65 in C. Schoenwald-Cox, editor. *Genetics and Conservation*, Benjamin/Cummings Publishing. Menlo Park, Calif.
- Berger, J. 1986. *Wild horses of the Great Basin*. University of Chicago Press, Illinois. 326 pp.
- Bureau of Land Management. 1984. *Herd management plan, Pryor Mountain Wild Horse Range, Wild Horse Removal Plan*. Miles City Office, Billings Resource Area, Mont.

- Bureau of Land Management. 1997. Pryor Mountain Wild Horse Range, Wild Horse Removal Plan. Miles City, Billings Resource Area, Mont.
- Caughley, G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Mass. 459 pp.
- Clutton-Brock, T. H., R. E. Guinness, and S. D. Albon. 1982. Red deer: Ecology and behavior of two sexes. University of Chicago Press, Chicago.
- Eberhardt, L. L., A. K. Majorowicz, and J. A. Wicok. 1982. Apparent rates of increase for two feral horse herds. *Journal of Wildlife Management* 46:367–374.
- Feist, J. D., and D. R. McCullough. 1975. Reproduction in feral horses. *Journal of Reproduction and Fertility, Supplement* 23:13–18.
- Frankel, O. H., and M. E. Soule. 1981. Conservation and Evolution. Cambridge University Press, Cambridge, United Kingdom. 327 pp.
- Garrott, R. A., and L. Taylor. 1990. Dynamics of a feral horses population in Montana. *Journal of Wildlife Management* 54:603–612.
- Garrott, R. A., T. C. Eagle, and E. D. Plotka. 1991. Age-specific reproduction in wild horses. *Canadian Journal of Zoology* 69:738–743.
- Harris, R. B., and F. W. Allendorf. 1989. Genetically effective population size in large mammals: An assessment of estimators. *Conservation Biology* 9:27–37.
- Hill, W. G. 1972. Effective population size with overlapping generations. *Genetics* 87:581–591.
- Houston, D. B. 1982. The northern Yellowstone elk: Ecology and management. Macmillan, New York. 474 pp.
- Jenkins, S. H., and M. C. Ashley. 1994. Population dynamics of feral horses: A meta-analysis of messy data. Poster presentation, American Society of Mammalogists, 75th Annual Meeting, Washington, D.C. 21 June 1994.
- Jimenez, J. A., K. A. Hughes, L. Graham, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 183:271–273.
- Keiper, R. R. 1976. Social structure of feral ponies. *Proceedings of the Pennsylvania Academy of Sciences* 50:89–90.
- Klingel, J. 1975. Social organization and reproduction in equids. *Journal of Reproduction and Fertility, Supplement* 23:7–11.
- LaCava, J., and J. Hughes. 1984. Determining minimum viable population levels. *Wildlife Society Bulletin* 12:370–376.
- Lacy, R. 1987. Loss of genetic diversity from managed populations: Interacting effect of drift, mutation, immigration, selection and population subdivision. *Conservation Biology* 1:143–158.
- Lacy, R. C., and T. W. Clark. 1989. Genetic variability in black-footed ferret populations: Past, present and future. Pages 83–103 in U. S. Seal, E. T. Thorne, M. A. Bogan, and S. H. Anderson, editors. *Conservation biology and the black-footed ferret*. Yale University Press, New Haven, Connecticut.
- Lemkuhl, J. F. 1984. Determining size and dispersion of minimum viable populations for land management planning and species conservation. *Environmental Management* 8:167–176.
- MarOom, M. D., and M. S. Reis. 1985. Ecology, social organization and behavior of the feral horses in the Peneda-Gerês National Park. *Arquivos de Museu Bocage Serie A* 1985, 3:169–196.
- McCort, W. 1979. The feral asses (*Equus asinus*) of Ossaban Island. Pages 71–83 in R. H. Denniston, editor. *Symposium on the ecology and behavior of wild and feral equids*. University of Wyoming, Laramie.
- Milton, J. B. 1993. Theory and data pertinent to the relationship between heterozygosity and fitness. Pages 17–41 in M. W. Thornhill, editor. *The natural history of inbreeding and outbreeding*. University of Chicago Press.
- Monard, A. M., P. Duncan, H. Fritz, and C. Feh. 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. *Behavioral Ecology and Sociobiology* 41:243–249.
- Nunney, L. 1993. The influence of mating system and overlapping generations on effective population size. *Evolution* 47:1329–1341.
- Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and G. A. Dover. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behavioral Ecology* 3:66–75.
- Perkins, A., E. Gevers, J. W. Turner, Jr., and J. F. Kirkpatrick. 1979. Age characteristics of feral horses in Montana. Pages 51–58 in *Symposium on the ecology and behavior of wild horses and feral equids*. University of Wyoming, Laramie.

- Ralls, K., K. Brugga, and J. Ballou. 1988. Inbreeding and juvenile mortality in small populations of ungulates. *Science* 206:1101–1103.
- Reed, J. M., P. D. Doerr, and J. R. Walters. 1986. Determining minimum population sizes for birds and mammals. *Wildlife Society Bulletin* 14:255–261.
- Ryman, N., R. Baccus, C. Reuterwall, and M. H. Smith. 1981. Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. *Oikos* 36:257–266.
- Sarre, S., and J. M. Georges. 1993. The application of fluctuating asymmetry in the monitoring of animal populations. *Pacific Conservation Biology* 1:118–122.
- Singer, F. J., E. G. Cothran, C. Papouchis, L. Coates-Markle, and Rev. F. Schwieger. 1997. Annual report. Effective population sizes, population dynamics, and group dynamics of the Pryor Mountain wild horses, 1994–1996. Biological Resources Division of U.S. Geological Survey, Fort Collins, Colo. 43 pp.
- Siniff, D. B., J. R. Tester, and G. L. McMahon. 1986. Foaling rate and survival of feral horses in western Nevada. *Journal of Range Management* 39:296–297.
- Sponenberg, P., and B. V. Beaver. 1983. Horse color. Breakthrough Publications, Inc. Columbia, South America. 124 pp.
- Thornhill, W. M., editor. 1993. The natural history of inbreeding and outbreeding. University of Chicago Press.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92.
- Tyler, S. J. 1972. The behavior and social organization of the New Forest ponies. *Animal Behavior Monograph* 5:85–196.
- Welsh, D. A. 1975. Population, behavioral and grazing ecology of the horses of Sable Island, Nova Scotia. Ph.D. thesis. Dalhousie University, Halifax, Nova Scotia. 403 pp.
- Wolfe, M. L., L. C. Ellis, and R. MacMullen. 1989. Reproductive rates of feral horses and burros. *Journal of Wildlife Management* 53:916–924.

Analysis of Genetic Variation in the Pryor Mountain Wild Horse Herd

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Introduction

Monitoring levels of genetic variation and understanding its significance within the Pryor Mountain Wild Horse Herd (PMWHH) is an important component of the management of this population. This is because the carrying capacity of the range requires that the number of horses maintained on some ranges be limited to a number very near the estimated minimum viable population size. At low population numbers, dramatic loss of genetic variation over a short time period is possible. Low genetic variability can result in decreased fecundity, increased mortality, decreased disease resistance, and an overall loss of vigor. Current levels of genetic variation in the PMWHH are relatively high but the risk of loss does exist. The purpose of this study is to analyze genetic variation in the population based upon samples collected from three separate times over a six year period (1991–1997). Future work will test for associations among genetic variability measures and traits associated with fitness with detailed analyses of parent/offspring relationships among individuals within the population.

Materials and Methods

The Pryor Mountain horses have been sampled and genetically tested in three separate years: 72

samples from individual wild horses were collected in 1991, 96 samples in 1994, and 122 in 1997. Blood samples were collected in all three years while hair samples were also collected for DNA analysis in 1997. In addition, feces samples were taken in 1997 for future DNA testing, although testing of DNA from fecal samples had not been perfected at the time of this report. Blood from each horse was separated into aliquots of whole red blood cells (rbc), rbc lysates, serum, and white blood cells (wbc). DNA was extracted from the wbcs and stored at -70° C for later analysis. Whole rbcs were analyzed for variation at blood group alloantigen loci using standard serological methods of agglutination and complement mediated hemolysis. Seven horse blood group loci (the *A*, *C*, *D*, *K*, *P*, *Q*, and *U* blood groups) were tested.

Serum and rbc lysates were tested for variation at 10 biochemical genetic loci using a variety of electrophoretic techniques. Serum was tested for the albumin (*Al*), esterase (*Es*), vitamin D binding protein (*Gc*), alpha-1-beta glycoprotein (*A1B*), protease inhibitor (*Pi*), and transferrin (*Tf*) loci while rbc lysates were tested for alpha hemoglobin (*Hb*), glucosephosphate isomerase (*GPI*), phosphogluconate dehydrogenase (*PGD*) and phosphoglucomutase (*PGM*). Blood group and biochemical loci were tested for all three years.

DNA analysis was based on 12 short tandem repeat (STR) or microsatellite (mSat) loci. The 12 loci

were horse mSats *HMS2*, *HMS3*, *HMS6*, *HMS7*, *HTG4*, *HTG6*, *HTG7*, *HTG10*. *ASB2*, *AHT4*, *AHT5*, and *VHL20*. The *HMS1* and *LEX7* mSat loci were also typed in 1994 but will not be considered here. DNA markers could not be tested for the 1991 samples but were tested for the other two years. Analyses were performed by amplification of genomic DNA by the Polymerase Chain Reaction (PCR) using fluorescent dye-labeled primers for each mSat locus. The PCR products were run through an ABI prism 377 automated DNA sequencer set up to analyze DNA fragments.

Genetic variability was measured by observed heterozygosity (H_o), Hardy-Weinberg expected heterozygosity (H_e), effective number of alleles (A_e), and the total number of observed alleles (TNV). Deviations in H_o relative to H_e was measured as $F_{is} = 1 - (H_o/H_e)$. H_o could not be calculated for blood group loci due to the presence of recessive alleles and ambiguous phenotypes. Variability measures were calculated separately for protein and mSat loci and for each sample year.

Results and Discussion

Frequencies of alleles at the biochemical and blood group loci for each of the three collection years are given in Table 1. No alleles that have not been observed in domestic horses were found in the Pryor horses. Allele frequencies for mSat loci from the 1994 and 1997 samples are given in Table 2. No unique mSat alleles were found in the Pryor horses tested.

Estimates of genetic variability for each year for the 10 biochemical and seven blood group loci are shown in Table 3. Also given are mean values of these measures for domestic horse breeds and feral horses from the United States. There are differences in most values among genes although none of the differences are statistically significant. However, several indicate important trends for changes over time and may be indicative of future changes within the population so they will be covered individually. Blood group and biochemical loci results will be discussed separately from mSat results.

The total number of allelic variants at blood group and biochemical loci decreased from 71 in 1991 and 1994 to 66 in 1997. Although the values were the same in 1991 and 1994, there was a difference in that the *Hb-All* allele was present at a very low frequency in 1991 but not seen in 1994 while the *Pi-X* allele was not

seen in 1991 but was seen in one individual in 1994. By 1997, neither of the above alleles were found and *Tf-E*, *D-bcm* and *K-a* alleles also were not observed. All of these alleles were quite rare (from one to five copies in the population sampled) so that the likelihood that these alleles would be lost is high. We do not know if the alleles have actually been lost or whether they simply were not sampled in 1997. However, the probability is high that these and other uncommon alleles will be lost through random genetic drift through time in the PMWHH.

There was no difference in TNV between 1994 and 1997 for the mSat loci (Tables 2 and 4). For each year, there were two alleles that were not seen in the other year. In each case, the alleles were present in only one or two copies. These could represent introduced variants or, possibly, new mutations as mSat systems have a relatively high mutation rate. In any event, the mSat loci were very similar to the blood group and biochemical loci in that there was a high proportion of the alleles that were at low frequency (less than 0.3) and almost no alleles had frequencies of 0.9 or greater. This pattern of distribution of allele frequencies (shown in Fig. 1a and 1b) is indicative of a population that has not experienced a recent bottleneck in population size. In the case of the PMWHH, this distribution pattern is probably due to the diversity of sources of introduced individuals.

It is obvious that a measure such as TNV is subject to the influence of sample size. However, in this case, all sample sizes were nearly the same, relatively large, and all samples were from the same population. For this reason, it is unlikely that sample size was an important consideration for this analysis, although for any year some rare alleles may have been missed by chance. The primary importance of a measure such as TNV in analysis of the Pryor herd is as an estimate of overall genetic diversity and as an indicator of the degree of outcrossing. It is highly likely that the large number of rare alleles within the Pryor herd is at least partially due to introductions. For example, the *Hb-All* and *D-bcm* alleles observed in 1991 were in horses from the Burns, Oregon, wild horse population that had been introduced into the Pryors. Other alleles, such as the *D-dghm*, *D-cegimn*, and *GPI-S* also may have been from other introductions such as horses from Rock Springs, Wyoming. However, some rare alleles may not have come from recent introductions but may have persisted in the population at low frequency for some time when the population size was larger.

Table 1. Allele frequencies for blood group and biochemical loci tested in the Pryor Mountain Wild Horse Herd for each sampling year.

	Tf D	E	F2	H2	0	R	Gc F	S			
1991	.083	.021	.270	.285	.153	.188	.736	.264			
1994	.085	.030	.230	.280	.205	.170	.775	.225			
1997	.074	.000	.255	.287	.181	.202	.713	.287			
	A1B F	K	S	A1 A	B	Es F	G	I	L	R	
1991	.111	.750	.139	.313	.687	.014	.125	.764	.021	.076	
1994	.090	.755	.155	.265	.735	.020	.115	.760	.025	.080	
1997	.149	.713	.138	.202	.798	.000	.170	.734	.021	.074	
	PGM F	S	GPI F	I	S	PGD F	S	Hb AII	BI	BIII	
1991	.056	.944	.014	.972	.014	.514	.486	.007	.680	.313	
1994	.050	.950	.025	.960	.015	.565	.435	.000	.685	.315	
1997	.000	1.000	.053	.947	.000	.654	.436	.000	.723	.277	
	Pi F	H	I	L	L2	N	O	P	R		
1991	.048	.021	.201	.297	.035	.028	.063	.021	.039		
1994	.030	.020	.175	.335	.020	.030	.035	.080	.030		
1997	.053	.032	.223	.263	.021	.011	.021	.053	.032		
	Pi (cont) S	T	U	W	X						
1991	.146	.014	.056	.021	.000						
1994	.145	.040	.045	.010	.005						
1997	.160	.032	.085	.014	.000						

Table 1. Concluded.

	A SYS											
	Adf	adg	b	c	bc	—						
1991	.441	.059	.129	.044	.000	.327						
1994	.440	.075	.073	.000	.045	.367						
1997	.357	.033	.181	.000	.055	.375						
	C SYS		K SYS		P SYS							
	A	—	a	—	a	ac	ad	b	d	—		
1991	.283	.717	.036	.964	.000	.248	.030	.052	.095	.575		
1994	.404	.596	.017	.983	.041	.235	.025	.052	.035	.612		
1997	.455	.545	.000	1.000	.000	.150	.150	.054	.323	.323		
	D SYS											
	Ad	d	dk	dgh	deo	dek	dfk	bc	cg	cegi	cfgk	
1991	.116	.203	.180	.052	.021	.000	.007	.007	.378	.036	.000	
1994	.074	.142	.199	.045	.017	.000	.006	.017	.460	.040	.000	
1997	.081	.179	.205	.011	.011	.012	.008	.000	.259	.054	.003	
	Q SYS				U SYS							
	Abc	ac	b	c	—	a	—					
1991	.162	.092	.091	.147	.508	.163	.837					
1994	.185	.085	.117	.125	.488	.211	.789					
1997	.179	.092	.077	.165	.487	.242	.758					

Table 2. Allele frequencies for microsatellite gen marker systems tested from Pryor Mountain Wild Horse Herd samplings in 1994 and 1997.

VHL20	I	J	K	L	M	N	O	P	Q	R
1994	.124	.271	.047	.012	.306	.065	.035	.071	.029	.041
1997	.131	.242	.037	.008	.398	.049	.037	.012	.020	.066
HTG4	K	L	M	N	O	P				
1994	.335	.026	.316	.045	.071	.206				
1997	.377	.020	.381	.012	.041	.168				
AHT4	H	J	K	L	M	N	O	P		
1994	.257	.243	.278	.007	.007	.014	.118	.076		
1997	.230	.201	.299	.025	.020	.012	.107	.107		
HMS7	L	M	N	O	P					
1994	.588	.162	.047	.196	.007					
1997	.615	.135	.020	.255	.004					
HTG6	G	I	J	K	O	P				
1994	.154	.111	.179	.031	.525	.000				
1997	.143	.111	.094	.016	.631	.004				
AHT5	J	K	L	M	N	O	Q			
1994	.146	.431	.160	.000	.236	.007	.021			
1997	.176	.398	.139	.004	.250	.016	.016			
HMS6	K	L	M	N	O	P				
1994	.007	.218	.176	.014	.225	.359				
1997	.025	.198	.144	.074	.193	.366				

Table 2. Concluded.

ASB2	B	K	M	N	O	P	Q	R		
1994	.022	.381	.052	.261	.037	.037	.201	.007		
1997	.120	.281	.033	.202	.099	.021	.240	.004		
HTG10	I	K	L	M	N	O	P	Q	R	
1994	.054	.018	.018	.149	.143	.321	.006	.131	.161	
1997	.098	.029	.004	.168	.131	.254	.000	.184	.131	
HTG7	K	M	N	O						
1994	.342	.196	.038	.424						
1997	.357	.242	.016	.385						
HMS3	I	M	N	O	P	R				
1994	.027	.020	.100	.153	.553	.147				
1997	.049	.016	.086	.169	.440	.239				
HMS2	J	K	L	M	N	O	T			
1994	.087	.051	.007	.428	.290	.116	.022			
1997	.105	.063	.000	.458	.239	.088	.046			

Table 3. Measures of genetic variation for all biochemical and blood group loci plus overall values for each of the three sampling years of the Pryor Mountain Wild Horse Herd.

Locus	TNV	H _o	H _e	A _e	F _{is}	X ²	df
Tf	6	.750	.781	4.530	.040	.113	15
A1B	3	.417	.406	1.683	-.026	.050	3
Es	5	.431	.394	1.651	-.093	.620	10
A1	2	.292	.431	1.750	.323	7.525	1
Gc	2	.417	.389	1.636	-.071	.364	1
PGD	2	.389	.500	1.998	.222	3.556	1
PGM	2	.111	.106	1.118	-.048	.167	1
GPI	3	.056	.055	1.058	-.010	.007	3
Hb	3	.486	.440	1.780	-.105	.791	3
Pi	13	.847	.839	6.004	-.010	.007	78
Mean or total values for biochemical loci							
	41	.419	.434	2.321	.034	13.200	116
Mean or total values for blood group loci							
	30		.495	2.837			
Mean or totals for all loci							
	71		.459	2.533			

Average number of alleles biochemical loci = 4.100

Average number of alleles group loci = 4.286

Average number of alleles all loci = 4.176

Table 3. Continued.

1994							
Locus	TNV	H _o	H _e	A _e	F _{is}	X ²	df
Tf	6	.750	.790	4.754	.051	.256	15
A1B	3	.360	.398	1.661	.095	.912	3
Es	5	.440	.402	1.672	-.095	.894	10
A1	2	.330	.390	1.638	.154	2.367	1
Gc	2	.430	.349	1.536	-.232	5.387	1
PGD	2	.550	.492	1.967	-.118	1.390	1
PGM	2	.100	.095	1.105	-.053	.277	1
GPI	3	.080	.078	1.084	-.026	.066	3
Hb	2	.390	.432	1.759	.097	.945	1
Pi	13	.780	.815	5.392	.043	.184	78
Mean or total values for biochemical loci							
	40	.421	.424	2.257	.007	12.667	114
A SYS	5		.666	2.990			
C SYS	2		.480	1.922			
D SYS	9		.752	4.139			
K SYS	2		.031	1.033			
P SYS	6		.632	2.730			
Q SYS	2		.329	1.491			
Mean or total values for blood group loci							
	31		.511	2.809			
Mean or total values for blood group loci							
	71		.460	2.484			
Average number of alleles biochemical loci = 4.000							
Average number of alleles blood group loci = 4.429							
Average number of alleles all loci = 4.176							

Table 3. Concluded.

1997							
LOCUS	TNV	H _o	H _e	A _e	F _{is}	X ²	df
Tf	5	.787	.772	4.416	-.020	.018	10
A1B	3	.447	.450	1.819	.007	.002	3
Es	4	.489	.424	1.743	-.154	1.117	6
A1	2	.277	.322	1.476	.141	.935	1
Gc	2	.234	.409	1.693	.428	8.600	1
PGD	2	.617	.492	1.968	-.254	3.035	1
PGM	1	.000	.000	1.000	.000	.000	0
GPI	2	.106	.100	1.112	-.064	.191	1
Hb	2	.383	.401	1.668	.045	.095	1
Pi	12	.894	.831	5.918	-.075	.267	66
Mean or total values for biochemical loci							
	35	.423	.420	2.281	-.008	14.261	90
Mean or total values for blood group loci							
	31		.544	3.266			
Mean or total values for all loci							
	66		.471	2.687			

Average number of alleles biochemical loci = 3.500

Average number of alleles blood group loci = 4.429

Average number of alleles all loci = 3.882

Table 4. Genetic variability measures for mSat loci for the Pryor Mountain Wild Horse Herd and mean values for 30 domestic horse breeds.

Variable		<u>Domestic horse breeds</u>	<u>Pryor Mountain wild horses</u>	
		(n = 30 breeds)	1994	1997
VHL20	H _o	0.769	.814	.820
HTG4	H _o	0.617	.663	.672
AHT4	H _o	0.707	.698	.844
HMS7	H _o	0.708	.523	.598
HTG6	H _o	0.571	.616	.500
AHT5	H _o	0.728	.640	.795
HMS6	H _o	0.696	.547	.762
ASB2	H _o	0.732	.477	.721
HGT10	H _o	0.685	.709	.779
HTG7	H _o	0.588	.663	.664
HMS3	H _o	0.748	.500	.721
HMS2	H _o	0.669	.581	.721
TTL	H _o	0.691	.702	.720
VHL20	H _e	0.760	.804	.756
HTG4	H _e	0.623	.736	.680
AHT4	H _e	0.705	.778	.795
HMS7	H _e	0.695	.587	.551
HTG6	H _e	0.593	.655	.558
AHT5	H _e	0.724	.713	.726
HMS6	H _e	0.705	.740	.763
ASB2	H _e	0.733	.736	.797
HTG10	H _e	0.741	.810	.827
HTG7	H _e	0.547	.663	.666
HMS3	H _e	0.724	.638	.709
HMS2	H _e	0.692	.711	.706
TTL	H _e	0.690	.714	.711
VHL20	F _{is}	-0.013	-.012	-.084
HTG4	F _{is}	0.001	.099	.012
AHT4	F _{is}	-0.007	.103	-.062
HMS7	F _{is}	-0.017	.109	-.086
HTG6	F _{is}	0.031	.059	.104

Table 4. Concluded.

Variable		<u>Domestic horse breeds</u>	<u>Pryor Mountain wild horses</u>	
		(n = 30 breeds)	1994	1997
AHT5	F_{is}	-0.004	.103	-.095
HMS6	F_{is}	0.014	.261	.001
AsB2	F_{is}	0.052	.352	.095
HTG120	F_{is}	0.072	.124	.058
HTG7	F_{is}	-0.022	.001	.003
HMS3	F_{is}	-0.029	.216	-.017
HMS2	F_{is}	0.034	.182	-.022
TTL	F_{is}	-0.001	.017	-.012
VHL20	A_e	4.524	5.055	4.094
HTG4	A_e	2.937	3.813	3.147
AHT4	A_e	A_e	4.497	4.836
HMS7	A_e	3.713	2.423	2.235
HTG6	A_e	2.641	2.901	2.273
AHT5	A_e	3.881	3.462	3.680
HMS6	A_e	3.534	3.872	4.215
ASB2	A_e	4.779	3.851	4.923
HTG10	A_e	4.424	5.198	5.835
HTG7	A_e	2.409	2.971	2.990
HMS3	A_e	4.020	2.763	3.456
HMS2	A_e	3.654	3.431	3.428
TTL	A_e	3.701	3.686	3.759
TNV	A_e	72.2	80	80

1994, and a deficit of H_o at the *Gc* locus in 1997 was seen. These two loci are tightly linked and deviations from expectations at the *Al* locus have been observed in domestic horses; however, we have no explanation for the observed deviations here. At mSat loci, there was a significant deficit of H_o at the *HTG4* locus, but as above, we have no explanation for the deviation at this time.

All data for genetic variation of the PMWHH show that genetic variability of the herd is high compared to domestic horse breeds and other feral horse populations. From the standpoint of genetic management, this is a good position to be in. Due to the relatively long generation length of horses (9–11 years) and long reproductive life span of individual horses, maintenance of genetic variability over the next 50 years should require no drastic actions. However, a note of caution must be raised here. The current level of genetic variation is based on high allelic diversity within the population. The concern is that nearly half of the alleles present (.485) in the herd exist at a frequency below 0.2 and nearly 30% (0.288) have a frequency below 0.1. These relatively rare alleles are thus at a relatively high risk of being lost, especially at low effective population sizes. At current variability levels, there are an average of 3.88 alleles per locus (for blood group and biochemical loci) but the heterozygosity level is that with an effective number of 2.69. Loss of alleles could have a greater impact on heterozygosity of the Pryor horses than would be anticipated based on current variability levels. The modeling work of John Gross provides better predictions of what might happen to genetic variation within the PMWHH.

The data to date show no trend towards loss of heterozygosity in the PMWHH but a period of only 6 years has been covered. There is a suggestion of a loss of a few rare alleles but since not all individuals were sampled in 1997 and the rarity of many of the alleles, not seeing some of them could be an artifact of sampling. However, several of the alleles not observed were ones probably derived from the Burns horses. As there was a conscious effort to decrease the influence of the introduced horses through removal, these alleles may actually have been lost. It will require a longer time frame and, hopefully, sampling of all individuals to determine what changes are actually taking place. The ability to test DNA from feces will make this type of study more feasible.

The significance of heterozygosity to the PMWHH remains an open question. Examination of H_o and H_e

of horse age cohorts over the entire study period does not suggest any significant changes in heterozygosity with age or through time (data not shown). Preliminary analysis of demographic and reproductive characteristics of individuals compared to individual genetic data suggest that there could be some association among these variables; however, far more demographic data is necessary. Much of this data has been collected but is not ready for analysis. Additionally, some important stallions have not been tested for genetic variation. Feces have been collected for some of these individuals but have not yet been analyzed.

Another important part of the genetic analysis is parentage testing used to determine if the presumed parent/offspring relationships determined by observation were correct. For the 1994 data, there were 37 horses that had genetic data and had one or more presumed parent with genetic data. For all 37 horses, a potential sire was identified. In 16 of these 37 cases, the presumed sire was not the correct sire based on the genetic comparison (43%). There were 22 horses where both sire and dam (mother) were tentatively identified. Of these, the sire was incorrectly identified while the dam was correct in two cases. The sire did qualify while the dam was excluded in four cases, and both sire and dam were excluded as parents in four cases. The sire and dam both qualified as the parents in the remaining cases. Parentages were more likely to be incorrect for horses born in 1992 or earlier (58%) than for those born after 1992 (36%). The high percentage of incorrectly identified parentage through 1994 likely is due to incorrect identification of horses at the time of blood sampling or other factors. In the case of sires, stallions are often identified as the father of a foal simply because its dam is in its harem. This data would indicate that the harem stallions have sired far less offspring of mares in their harem than expected. Harem structure in this population appears to be fairly fluid. This especially has been true since the 1994 gather.

Efforts are still underway to examine parentage for the horses collected in 1997. Part of the delay is that a number of important stallions were not gathered and sampled. Feces samples were collected from these individuals and if we can type DNA from feces, a fairly complete analysis can be done. Preliminary results show a much higher percentage of presumed parent assignments to be correct. Of 42 cases where there was genetic data for a mare and a presumed offspring, the assignment was correct 39 times. For 35 cases where a stallion could be checked as the sire of an offspring,

the assignment was correct 25 times and incorrect 9 times (one case was questionable). In 22 of 25 cases both sire and dam were correctly identified. This is probably due to improved identification. The data at this point do show that more than just harem stallions are breeding but not many more. Further work should give us a much more precise estimate of the number of breeding males, which is an important component of effective population size estimation.

The combination of multiple genetic sampling and demographic analyses makes the PMWHH the most intensively studied feral horse population in the world. From the standpoint of genetic variation, the PMWHH has high variation and genetic diversity. However, because of the restrictions on the number of horses that can be maintained on the available land, the effective population size of the Pryor herd will be very close to the absolute minimum number required to limit the loss of genetic variation to 1% per generation. Because a high proportion of the allelic diversity of the population is in alleles with a frequency of less than

0.2, the possibility of loss of alleles over relatively short time periods is high. The loss of these uncommon alleles is not necessarily detrimental, so this may not affect overall heterozygosity levels. However, the current data suggest that the variability of the PMWHH is potentially fragile and careful management will be required. Completion of analyses that are still underway will provide increased understanding of the population structure of the Pryor herd and the significance of genetic variability within the PMWHH. The development of the ability to test genetic variation from DNA obtained from fecal samples will greatly enhance the ability to monitor genetic variation of the PMWHH. The current status of the population appears to be quite healthy and recent management practices have not had any detrimental effect on genetic variability. However, because of the restrictions on population size, the PMWHH will remain vulnerable to potential perturbations, both natural and due to management decisions, so that continued monitoring is highly recommended.

Genetic and Demographic Consequences of Removals and Contraception on Wild Horses in the Pryor Mountain Wild Horse Range

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Abstract. Wild horse populations frequently exhibit growth rates in excess of 15% per year and can rapidly achieve population sizes that are capable of causing long-term habitat degradation. To prevent habitat damage, most wild horse populations are controlled by periodic gathers and removal. Because many horse populations are regulated to a small size (<100) there are concerns about the genetic consequences of alternative control measures.

I developed an individual-based model to simulate the dynamics of populations controlled by removal and/or contraception and applied the model to horses on the Pryor Mountain Wild Horse Range. The model simulated age-specific breeding by males and females and tracked the sex, age, genetic constitution, and mating success of all individuals. Changes in gene frequencies and heterozygosity resulted from simulated Mendelian inheritance of (initially) 41 alleles at 10 loci. Model parameters were estimated from data on the Pryor herd and other wild horse populations, and the model projected changes in gene frequencies of the Pryor population. The model simulated changes in gene frequencies, heterozygosity, and inbreeding through time under a range of management strategies. Simulated management strategies included combinations of population objectives of 90 to 180 horses (1 year and older) and removal and/or contraception of animals of random, young, or old ages.

Model results showed that over a period of 200 years, all simulated population sizes were likely to lose selectively neutral alleles with an initial frequency of less than about 3%. This included nearly 30% of all alleles. Removals or contraceptive treatments that focused on older animals hastened the loss of genetic variation, while delaying average age of reproduction either through removals or contraception of young animals had the opposite effect. Differences in rates of loss of genetic variation were greater between treatments of old and young animals than between populations that differed in size by a factor of two. Populations controlled by removals were characterized by large fluctuations in size and exceeded the population objective by an average of more than 20%. These populations contained a high proportion of young horses. In contrast, populations controlled by infertility treatments exhibited a low variance in size and average population size was within 3% of population objective. Age structure of these populations was uniform (i.e., nearly equal numbers of young and old horses). While contraceptives appear to be a highly attractive alternative, a combination of removal and contraception could reduce the frequency and magnitude of removals, while permitting managers to rapidly control overabundant herds and correct an undesirable sex or age structure. These results are broadly applicable to many long-lived species in harvested populations and they clearly demonstrate the potentially large and negative effects of harvests or removals of older individuals.

Keywords: Contraceptives, genetics, genetic diversity, heterozygosity, infertility, population model, wild horses.

Introduction

Wild horses in the United States are protected by the Wild Free-roaming Horse and Burro Act of 1971. Most wild horses populations in the United States inhabit rangelands and their management falls under jurisdiction of the Bureau of Land Management (BLM 1997). Wild horse populations in the western United States exhibit growth rates that frequently exceed 15% per year (Garrott et al. 1991a) and they can rapidly achieve population sizes that raise concerns about long-term habitat damage. A total of about 35,000 inhabit ranges in the western United States, but only 25% of the 186 wild horse herds under active management have a population objective of greater than 150 horses (BLM 1997). The small size of these herds raised concerns about long-term maintenance of genetic viability and questions on the best methods to manage population sizes to sustain genetic variation.

The situation at the Pryor Mountain Wild Horse Range (PMWHR) is illustrative of the predicament faced by agencies with a mandate to control an isolated population characterized by high reproductive potential, long life span, and limited area of available habitat. In these situations, management plans must balance measures to minimize the risk of long-term habitat degradation with long-term retention of genetic variability and population persistence. These goals result in conflicting needs to minimize herd size to control habitat degradation while maximizing herd size to conserve genetic variation. In 1998, about 150 horses inhabited the PMWHR, close to the estimated range carrying capacity (BLM 1997). The small size of this population concerns those mandated to sustain a viable and healthy population, because genetic variation rapidly disappears in small populations (Wright 1931). Studies of this herd show that it has the reproductive potential to double in size every 4–5 years and attain a size that poses risks to habitats and mountain sheep and deer that inhabit the PMWHR (Garrott and Taylor 1990).

Wild horse populations have been controlled primarily through periodic gathers and removals. Programs were developed to place horses in private ownership, but these efforts have proven to be exceedingly expensive (>\$16 million in 1995; BLM 1997) and it has become impossible to place all horses or maintain them in captivity for long periods. As a

result, there is great interest in the potential use of contraceptives to reduce fertility of horses and other overabundant species (Sturtevant 1970; Hoffman and Wright 1990; Garrott et al. 1991b; Holden 1992; Eagle et al. 1992; Fayrer-Hosken et al. 1997). Use of contraceptives could provide opportunities for a variety of new management scenarios, including permanent infertility, delayed reproduction, or permitting mares to reproduce once and then preventing further breeding. Simulations of horse population dynamics have shown that a relatively high level of infertility would likely be needed to maintain a low growth rate in horse populations (Garrott 1991), but no analyses have specifically considered the consequences of alternative management actions on long-term persistence of genetic resources in horses or similar mammals.

Management strategies to control growth rates of abundant populations by removal or contraception must focus on three decisions: How many animals should there be? What sex and age of animals are to be removed or made infertile? How often are animals removed or treated? I developed a simulation model designed to evaluate consequences of actions to manage horses. The model specifically simulates the use of removals only, contraceptives only, or a combination of removal and contraception that was identified by the BLM as a likely alternative to manage the PMWHR population (L. Coates-Markle, personal communication). The model was applied to the PMWHR herd to evaluate a set of realistic management alternatives, but the results lend insight to the consequences of management actions used or considered to control or harvest many other species of mammals, including mountain lions, bison, deer, elk, elephant, and some carnivores (Hoffman and Wright 1990; Bradley 1994; Fayrer-Hosken et al. 1997; Kirkpatrick et al. 1997). Despite widespread appreciation of the genetic consequences of small population size, virtually all common guidelines for managers stress the actions that modify overall population size or reproductive variance. I offer analyses that clearly demonstrate the importance of age-related management actions and show that in long-lived species, actions that increase (or decrease) generation time can have an effect equal to doubling the size of the population. These results are important because it is frequently difficult to increase population size, but relatively simple to modify the age of animals removed or harvested.

Methods

An individual-based population model was developed to simulate the dynamics of the PMWHR horse population. The model operated on a yearly time step and simulated the processes of breeding, recruitment, removal, contraception, natural mortality, and aging. Each individual in the population was explicitly represented and its sex, age, genetic constitution, number of mates, and reproductive status was followed from birth to death. Model outputs included the sex and age of individuals in the population, number of mates (by age) of males and females, genetic heterozygosity, and frequency of each allele.

Model Processes and Parameter Estimates

Vital Rates and Breeding

Wild horses on the PMWHR have exhibited high rates of survival and reproduction (Garrott and Taylor 1990; Singer et al. 1998), consistent with observations of wild horse populations throughout the western United States (Berger 1986; Garrott et al. 1991a). Estimates of fecundity and survival were derived from observations of the Pryor herd, emphasizing data subsequent to management changes that occurred about 1990 (Garrott and Taylor 1990; Singer et al. 1998). No density-dependent regulation of survival or reproduction was included in the model because the horse population is regulated at a level well below estimates of range carrying capacity and evidence for density dependence was equivocal. Singer et al. (1998) found a significant correlation between growth rate population size, but neither recruitment nor survival varied significantly with population ($P > 0.10$).

Breeding was simulated by looping through all females in the population and determining whether the female bred by comparing a uniform random deviate to the probability of recruitment, and then selecting a mate. Information on general patterns of age-specific breeding success of wild stallions was used to drive mate selection (Berger 1986:200). The likelihood of a stallion being selected to mate with a female was determined by the number of breeding-age males in the population and age-specific probability of breeding. To determine which stallion mated with a particular breeding mare, every male in the population was

assigned the appropriate age-specific probability of breeding (Table 1). The cumulative breeding probabilities were placed in a vector of length n where n was the total number of breeding-age stallions. For each female that recruited, a random deviate between 0 and the sum of breeding probabilities was generated and compared to values in the vector. The male that corresponded to the vector index of the first vector value that exceeded the deviate was then chosen as the mate for that female. All matings were independent. Factors that determined harem formation, size, and retention were too poorly known to include in the model.

After the parents of an offspring were determined, Mendelian inheritance was simulated by randomly selecting one allele from each parent at 10 independent loci. At the beginning of each set of simulations, individuals were assigned alleles in the frequency in which they occurred in the PMWHR population (G. Cothran, personal communication). Each simulation began with a total of 41 alleles distributed over 10 loci; each locus had 2 to 13 different alleles with initial frequencies from 0.0035 to 0.844.

Treatments: Population Objective, Removal, and Contraception

The current management plan for the PMWHR includes a population objective of 120 horses, excluding foals (BLM 1997). A population objective, or animal management level (AML), is defined as the minimum number of horses that remain after a removal event. Foals are usually excluded in determining the AML, and in this paper foals are always excluded from counts used to determine compliance with a population objective or to categorize a population size. Simulations included an AML of 120 horses, a 25% decrease in AML (to 90 horses), and increases of 25% and 50%, to 150 and 180 horses, respectively. These objectives might be realized through supplemental feeding, acquisition of additional habitat, or other strategies. No specific means to sustain this increased objective is implied.

Removals and/or contraceptive treatments of wild horses were simulated by applying rules based on current population size, post-treatment population objective, sex and age of animals to be treated, the minimum number of horses in each sex/age class that were to be unaffected by the treatment, and for removals, the length of time since a previous removal.

Table 1. Demographic parameters used in all simulations of wild horse dynamics.

Males			Females		
Age	Survival	Probability of mating	Age	Survival	Probability of recruiting
1-4	0.98	0.00	1-2	0.98	0.00
5-6	0.98	0.10	3-4	0.98	0.50
7-8	0.98	0.26	5-16	0.98	0.60
9-16	0.98	0.64	17-22	0.75	0.47
17-19	0.75	0.50	23-24	0.50	0.47
20-22	0.62	0.25	25	0.00	0.00
23-24	0.50	0.25			
25	0.00	0.00			

To determine the annual control treatment, the population was first compared to population thresholds used to categorize the population as small, normal, or large. If the population size was less than or equal to the lower threshold, it was categorized as small. If the population size was greater than the lower threshold and less than or equal to the higher threshold, it was categorized as normal. If greater than the upper threshold, it was considered large. Foals were not included in population counts to determine annual treatments.

Population size could alter both the timing and magnitude of treatment. It is expensive to gather and remove wild horses (Boyles 1986; BLM 1997) and managers seek to minimize the frequency of these events. The model therefore simulated a removal event only when the population had grown to a sufficient size. Removals or contraceptive treatments always occurred when the population was categorized as large, regardless of how long it had been since a previous treatment. Removals also occurred when the population was categorized as normal and a threshold number of years had passed since the previous removal. This time threshold was set at 3 years for removal-only treatments and 5 years for removal-and-contraceptive treatments. For removal-only treatments, the threshold between a small and normal population was set at 150% of the population objective and the threshold between a normal and large population was

set at 200% of the population objective. A removal never occurred when the population was categorized as small. Foals were never included in counts of horses for categorizing herd size and foals were never removed from the population.

Several variables determined which animals were removed from the population. The first variable was the population objective, which was the number of horses remaining after a removal was completed. Removal treatments were categorized as random, old, or young for the age of horses emphasized in the treatment. Random animal treatments selected horses without regard to sex or age until the population objective was reached. For old animal treatments, the oldest horses in the population were selected first, leaving a few males and females in each multi-year age class. Similarly, treatments categorized as young first removed the youngest animals, again leaving a few males and females in each multi-year age class. Males and females were removed to leave a slightly female-biased sex ratio, consistent with observations of other wild horse populations and prior BLM removals (Berger 1986:91).

The portion of mares treated with contraceptives varied with population size. For each treatment, the level of contraception was initially calibrated to achieve a stable population size. However, demographic stochasticity often resulted in a population that either grew or declined. In these situations, the rate of

application of contraceptives was increased or reduced until the population declined or increased to a size that fell within the normal range. For populations regulated by contraceptives, normal was defined as a size (excluding foals) of 85 to 110% of the population objective. Contraceptive treatments were administered every year and treated mares remained infertile for 1 year. As with removals, females were selected for contraceptive treatments based on age, using rules that selected breeding-age females randomly, or that resulted in treatment of the oldest or youngest mares first.

Genetic Analyses and Calculations

Observed heterozygosity¹ (H_o ; Equation 1), expected heterozygosity (H_e ; Equation 2), and the inbreeding coefficient (F_{is} ; Equation 3) were calculated following Hartl and Clark (1997; Equations 1–3), where N is the number of loci:

$$H_o = \frac{\sum_{n=1}^N \frac{\text{heterozygotes at locus}_n}{\text{number of individuals}}}{N} \quad (1)$$

$$H_e = \frac{\sum_{n=1}^N \left(1 - \sum_{k=1}^{\infty} (\text{freq of allele } k)^2 \right)}{N} \quad (2)$$

$$F_{is} = 1 - \frac{H_o}{H_e} \quad (3)$$

¹Heterozygosity is a way of quantifying genetic variation. A heterozygous individual contains two different copies of a particular gene. An individual is said to be homozygous if the genes are the same. At the population level, the observed heterozygosity is the average of all individuals. A higher value for observed heterozygosity indicates greater genetic variation.

In the absence of agency-mandated objectives for conserving genetic diversity, changes in genetic resources were evaluated relative to a goal of achieving a 90% probability of conserving 90% of selectively neutral genetic variation for 200 years. This is a slightly less ambitious objective than suggested by Soulé et al. (1986). Frequencies of all alleles at each loci were recorded and used to evaluate rates of loss of alleles.

Initial Conditions, Simulation Procedures, and Evaluation of Results

All simulations started with an initial population of 147 horses that matched the sex and age structure of the PMWHR herd in fall 1998. The initial population consisted of 65 males aged 1 to 22 years and 82 females aged 1 to 17 years. Treatments were evaluated from results of 500 simulations that lasted 200 years each.

A variety of output files were written to permit evaluation of the causes of differences between treatments. Each year the age structure of the population, age and sex of individuals removed, and the age of females treated with contraceptives were recorded. Summary files included data on age-specific fecundity and lifetime reproductive success of males and females. These outputs were used to construct life tables of simulated populations from which standard demographic statistics such as growth rate and generation time were calculated (Carey 1993). Annual growth rates for removal treatments accommodated removals such that:

$$\lambda_t = \frac{N_t}{N_{t-1} + R_{t-1}} \quad (4)$$

where λ_t is the apparent annual growth rate at year t , N is the total number of animals in the given year, and R is the number of animals removed from the population between year $t-1$ and t . The initial age structure led to instability for the first 10–25 years in simulations of populations regulated by contraceptives. Data from the first 30 years of each simulation were thus excluded from analyses of rates of contraception and population processes.

Results

Treatment Levels and Demographic Responses

Removals and contraception treatments resulted in population dynamics that were fundamentally different. Populations controlled by removals increased rapidly and declined precipitously when a removal occurred. In contrast, populations controlled by contraceptives remained relatively stable. As a result of these dynamics, average size of populations controlled by removals averaged 18–27% greater than the AML, whereas populations controlled by contraception remained within 3% of the AML (Fig. 1). Populations controlled by a combination of contraception and removal were on average 18–5% greater than the AML for population objectives of 90–180, respectively. The coefficient of variation of populations controlled by removal averaged 17%, compared to 8% for populations controlled by contraceptives alone and 11% for populations controlled by contraceptives and removals.

Average annual growth rates (λ) of populations controlled by removals were 1.15 when young horses were removed, 1.16 when old horses were removed, and 1.17 for random removals. Population objective

had no influence on average growth rate. The maximum difference in growth rate within a removal treatment (old, young, or random) was 0.004. For populations controlled by contraceptive and removals of younger horses, λ varied with population objective and ranged from 1.05 to 1.09 for simulated populations with objectives from 180 to 90, respectively. For these treatments, differences in λ were driven by differences in the application rate of contraceptives.

To achieve a stable population with contraceptive-only treatments, an average of 78%, 73%, or 74% of all females 2 years or older were rendered infertile for treatments of young, old, or a random selection of adult mares (Table 2). Depending on population objective, this resulted in treatment of an average of 34 to 69 mares per year. For treatments that combined both contraceptives and periodic removals, an average of 50%, 58%, 61%, or 64% of breeding-age mares were rendered infertile each year for population objectives of 90, 120, 150, and 180 horses, respectively. These levels of infertility required treating, on average, 25 to 57 mares each year. When simulated populations were controlled by a combination of removals and contraception, more than 90% of all removals took place at a 5- or 6-year interval regardless of population objective. About 60 horses (range of means = 50–64) were culled from the population each time a removal occurred (Table 2).

For removal-only treatments, more than 90% of removals occurred at 3-year intervals regardless of population objective or the age of horses removed. Each time a removal occurred, an average of about 35% of all horses were removed (range of means = 33% to 37%; Table 3). The number of animals removed was directly related to growth rates; the lowest rate of removal was for treatments of younger horses and the greatest was for random removals (Table 3). Removal of a random selection of horses required harvesting about 20% more horses than when younger horses were removed.

Removals and contraception treatments resulted in populations that had drastically different age structures, but differences in age structure were due to the removal or contraceptive treatment and not to population objective. Within a removal or contraceptive treatment, the portion of the population in a particular age class remained constant across all population objectives simulated. All simulated removal treatments resulted in age structures characteristic of growing populations, while contraception resulted in the flat

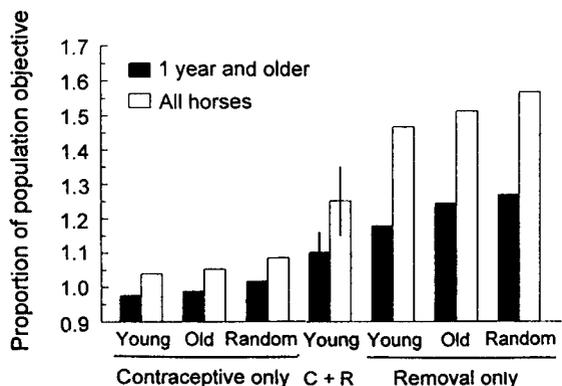


Fig. 1. Average size of populations with and without foals as a percentage of population objective, where C + R is control using both contraceptive and removals. Population size relative to the population objective varied only for C + R treatments; vertical bars show the largest values (for an objective of 90) and smallest value (for an objective of 180).

Table 2. Percent and number of horses 1 year or older affected by simulated contraception treatments of the Pryor wild horse herd, and the average number of foals in the herd.

Age treated	Population objective	Percent treated	Number treated (mean \pm 1 s.d.)	Average number of foals
Contraception-only Treatments				
Young	90	78	32 \pm 7.6	5.7
	120	74	43 \pm 8.8	7.9
	150	73	52 \pm 8.5	9.7
	180	74	64 \pm 10.9	12.0
Old	90	73	31 \pm 6.4	5.8
	120	73	41 \pm 7.4	7.7
	150	74	54 \pm 9.9	10.0
	180	74	62 \pm 9.4	11.6
Random	90	74	32 \pm 8.1	5.9
	120	78	44 \pm 8.9	7.7
	150	78	54 \pm 10.1	9.6
	180	78	65 \pm 11.2	11.5
Contraception and Removal Treatments				
Young	90	50	25 \pm 4.7	17.2
	120	58	37 \pm 5.2	16.4
	150	61	46 \pm 6.0	16.5
	180	64	57 \pm 6.6	16.5

age structure characteristic of a stable population (Fig. 2). The average number of foals in the population at the time of a removal varied from 20 to 67 depending on AML and treatment (Table 3). Since foals were not counted towards the AML, populations with a large number of foals in the year of a removal far exceeded the AML in the subsequent year. This occurred because survival rates were high for both foals and adults, and the number of foals far exceeded the number of animals dying from natural causes.

Contraception of older mares or removal of older horses resulted in much longer average generation

times than treatments that removed younger females or delayed reproduction. Average generation time of mares varied by more than a factor of three, from a minimum of 4.7 years (contraception of older mares) to a maximum of 16.8 years (contraception of younger mares; Fig. 3). Differences in generation time for males varied far less than that of females, from a minimum of 10.4 years to a maximum of 12.6 years (Fig. 3). Generation time for males was the same for all treatments except for removals of random or old horses; these treatments resulted in declines in generation time. For both sexes, differences related to

Table 3. Simulated removal treatments for the Pryor wild horse herd. Percent and number (± 1 standard deviation) of horses 1 year and older removed at each event, and the average number of foals at the time of harvest.

Age treated	Population objective	Number removed per event (mean \pm s.d.)	Number removed per year	Number removed per event	Harvest interval (years)	Foals at time of harvest
Contraception and Removal Treatments						
Young	90	58 \pm 10.7	12	0.35	5	20.1
	120	54 \pm 9.7	11	0.28	5	20.8
	150	54 \pm 10.0	11	0.24	5	22.5
	180	53 \pm 9.8	11	0.21	5	23.8
Removal-only Treatments						
Young	90	61 \pm 8.3	20	0.34	3	30.2
	120	81 \pm 9.7	27	0.33	3	40.2
	150	100 \pm 11.1	33	0.33	3	49.9
	180	119 \pm 13.1	40	0.33	3	59.8
Old	90	65 \pm 8.2	22	0.35	3	31.9
	120	87 \pm 9.9	29	0.35	3	42.6
	150	108 \pm 11.1	36	0.35	3	52.8
	180	129 \pm 12.4	43	0.35	3	63.3
Random	90	72 \pm 7.7	24	0.37	3	33.7
	120	96 \pm 9.0	32	0.37	3	44.9
	150	120 \pm 10.3	40	0.37	3	55.9
	180	144 \pm 11.4	48	0.37	3	67.1

population objectives were small compared to those between treatments that affected different-aged segments of the population.

Effects of Treatments on Heterozygosity

Initial mean H_o averaged 0.433 (range of means = 0.432–0.434; range of individual simulations = 0.388–0.479). After 200 years, mean H_o varied from a low of 0.301 (70% of initial H_o) for control by removal of old animals with a population objective of 90 to a high of 0.413 (95% of initial H_o) for populations controlled by contraception and removal of younger mares with a population objective of 180 (Fig. 4). The method of control and age of animal treated or removed had a

greater effect on retention or loss of H_o than did population size over the ranges simulated. Treatments that affected older individuals uniformly resulted in more rapid declines in H_o than treatments of young animals. For all simulated combinations of population objective and control strategy, more than 10% of all simulations failed to retain 90% of initial H_o . Using H_o as a measure of genetic diversity, these simulated control strategies failed to meet the objective to achieve a 90% probability of retaining 90% of neutrally selective diversity for 200 years.

Inbreeding coefficients (F_{is}) after 200 years of simulation averaged 0.092 (range of means = 0.086–0.096) across all treatments and population objectives. F_{is} tended to be lower for small population sizes,

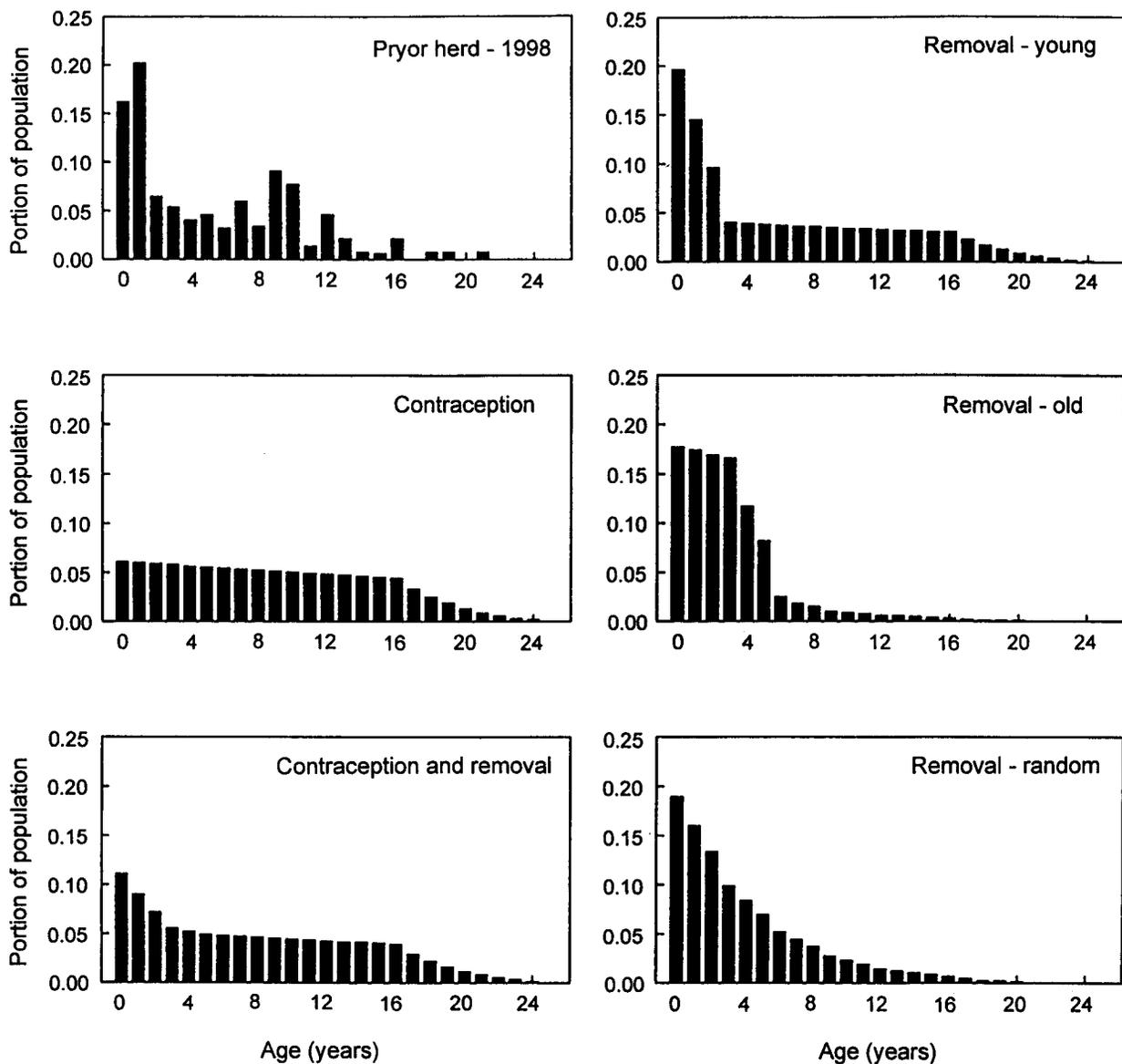


Fig. 2. Age structure of the initial population and simulated populations controlled by contraception, removal, or a combination of both.

especially for population objectives of 90 and 120. This counterintuitive trend probably resulted from the greater loss of rare alleles in smaller populations, which also reduced H_e in these scenarios.

The use of allele frequencies from the PMWHR herd resulted in simulation of populations in which 34% of all alleles had an initial frequency of 0.05 or less and in which 12% of all alleles occurred at a frequency of 0.02 or less. With an AML of 90 all simulated control strategies resulted in an average loss of more than 25% of alleles (Fig. 5). Almost half (48%) of all alleles failed to persist for 200 years when old animals were removed from herds with a population objective of 90. Among treatments simulated, contraception of young animals or a combination of contraception and removal of young animals resulted in the greatest persistence of alleles. Under these treatments, an average of 83% of alleles persisted for 200 years. These treatments had a 90% chance of retaining 76% of the initial alleles for 200 years. For other treatments, the lower 10th percentile of results included retention of as few as 47% of alleles initially present (Fig. 5).

Rates of loss of alleles were highly and non-linearly related to allele frequency. Alleles with an initial frequency of less than about 0.025 tended to be rapidly lost during the first 50 years of simulations. The absolute rate of loss of alleles with initial frequencies >0.025 tended to remain constant throughout the 200 year simulations (Fig. 6).

Discussion

Simulation results clearly identified contrasting effects of population control by contraception or removals. Compared to removals, infertility treatments reduced variance in population size and resulted in lower standing populations. Because the average size of populations managed by infertility was about 25% smaller than those managed by removals, population objectives could reflect these differences, further enhancing the retention of genetic variation. Short-duration contraceptives have been used to successfully control growth of horses on Cumberland Island, Georgia, and Assateague Island, Virginia (Goodloe 1991; Kirkpatrick et al. 1997) and may be suitable for other populations where individuals are easily approached, such as the Pryor herd. Existing chemical contraceptive treatments are effective for only a limited

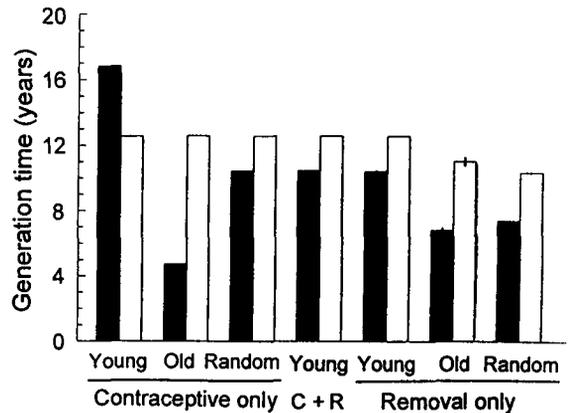


Fig. 3. Generation time of mares (darker bars) and stallions (lighter bars) in simulated populations controlled by contraceptives only, contraceptives and removal (C + R), or removals of young, old, or a selection of random-age individuals. Vertical bars are standard deviations of means of treatments that differ with population objectives of 90 to 180 hours.

period and require repeated applications to maintain infertility. These treatments are not likely to be successfully applied to widely dispersed populations, but a recognition of the advantages of contraceptives over removals has stimulated active and promising research (Muller et al. 1997). Infertility treatments remain a high priority because they can be far less expensive than removal and adoption programs (Garrott et al. 1992; BLM 1997) and they generally receive widespread public support.

Regardless of control method, it is apparent that intensive management will be necessary to restrict the size of populations with a high growth potential. Contraceptives can eliminate or reduce the need to remove and place wild horses, but complete reliance on contraceptives can lead to other problems. A reliance on contraceptives provides no mechanism for controlling the sex ratio of a population, which may become highly skewed, and it provides a rather weak means for controlling populations that escape management size. The most flexible and realistic program is therefore likely to combine the advantages of infertility and removals. Contraceptives can readily be used to slow

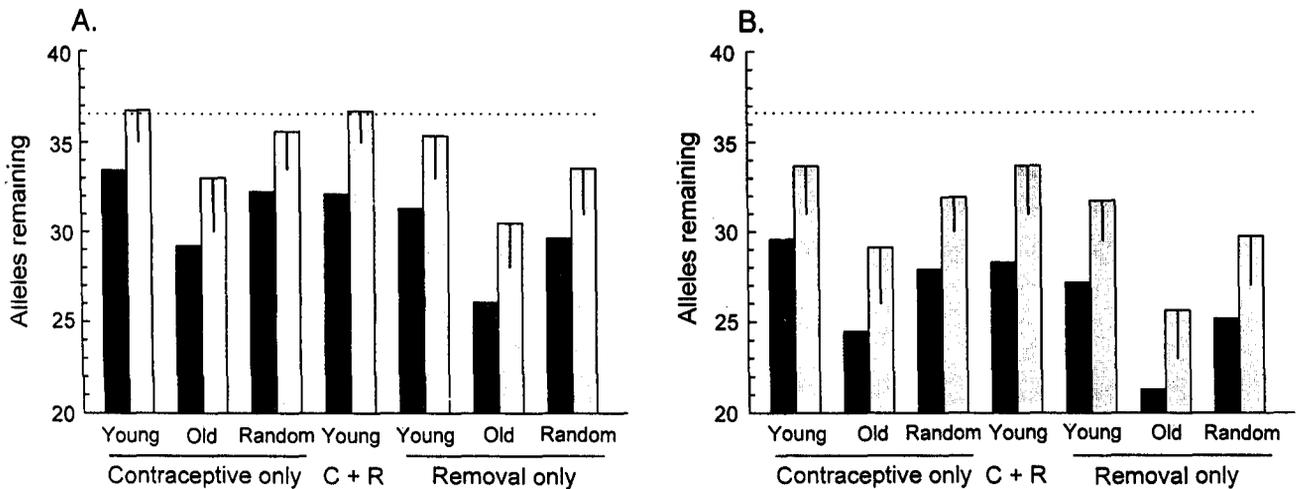


Fig. 4. (A) Observed heterozygosity after 100 years and (B) 200 years in simulated populations controlled by contraceptives only, contraceptives and removal (C + R), or removals of young, old, or a selection of random-age individuals, for population objectives of 90 (dark bars) or 180 (light bars). Vertical lines descend to the 10th percentile of observations; the horizontal line is at 90% of initial heterozygosity. Initial heterozygosity was 0.43.

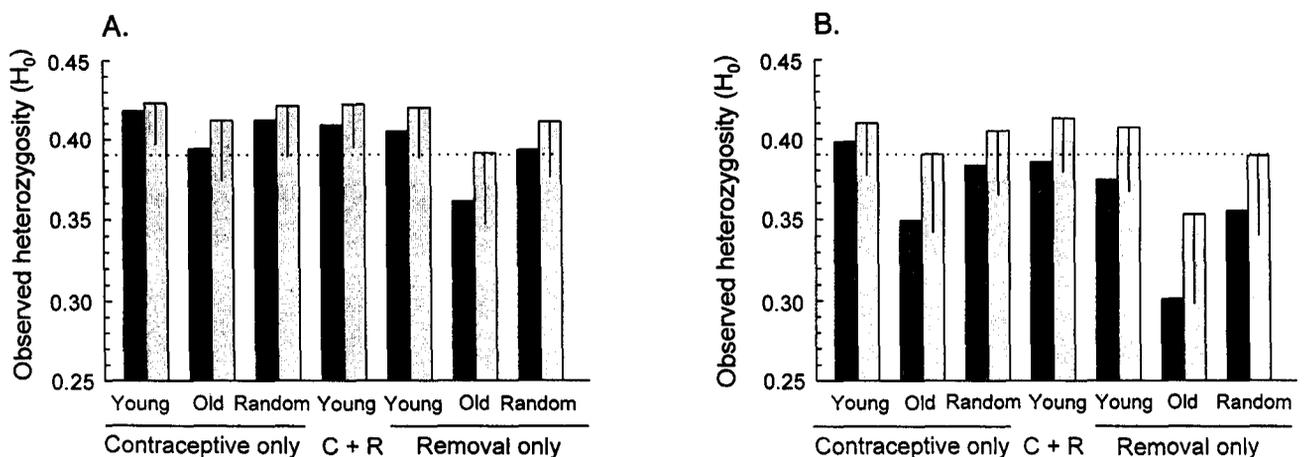


Fig. 5. Number of alleles persisting in simulated populations controlled by contraceptives only, contraceptives and removal (C + R), or removals of young, old, or a selection of random-age individuals, after 100 years (A, left chart) and 200 years (B, right chart), for population objectives of 90 (dark bars) or 180 (light bars). Vertical lines descend to the 10th percentile of observations; the horizontal line illustrates 90% of the number of alleles at the start of simulations.

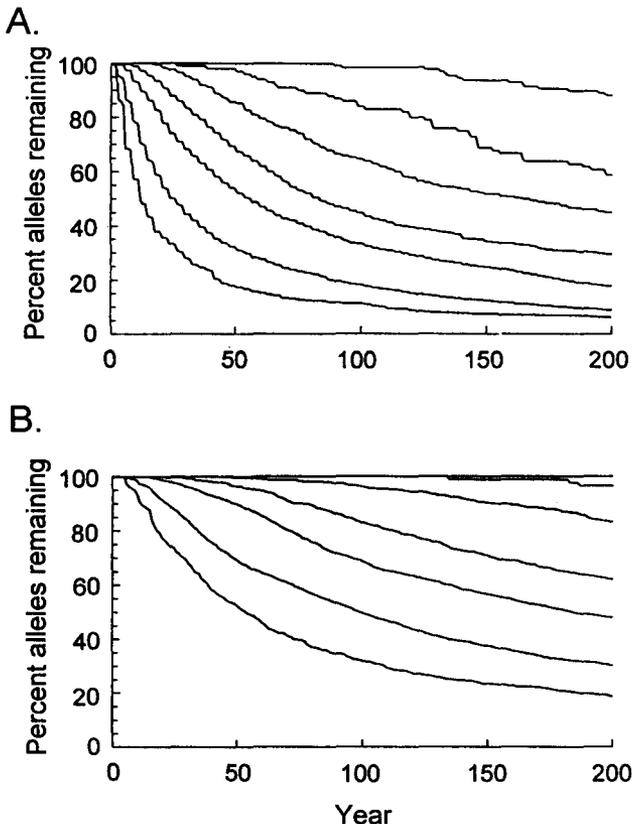


Fig. 6. Persistence of alleles with different initial frequencies over 200 years of simulation. (A) Population controlled by removal of random-aged horses with a population objective of 90. (B) Population controlled by contraceptives and removal with a population objective of 150. From the bottom of the plots, lines pertain to alleles that occurred with initial frequencies of 0.005, 0.01, 0.02, 0.05, 0.10, 0.15, and 0.20.

growth rates, while removals provide a mechanism for modifying sex ratios and rapidly bringing a population into compliance with size dictated by a management plan.

Genetic Considerations - Alternatives to Increasing Population Size?

Simulation results emphasized the importance of age structure and demography on processes that govern rate of loss of genetic variation. Recommendations for preserving genetic variation have focused on increasing population size, and few papers even consider

other strategies that can dramatically affect long-term persistence of genetic diversity. This oversight is not due to misunderstandings among geneticists [Ryman et al. (1981); Hedrick and Miller (1992) Fig. 5; Lande (1995) Fig. 4.4], but rather a lack of appreciation among wildlife managers and biologists of the importance of generation time and effective population size for maintaining genetic variation. Age-specific treatments may offer a viable alternative to increases in population size for long-lived species subject to management control. Dramatic differences in rate of loss of genetic variation between treatments that removed young or old animals are especially pertinent to evaluating management plans since many large mammals of conservation interest are still harvested, either for sport alone or, increasingly, as part of a community-based conservation plan. Both types of harvest usually emphasize removal of older animals from the populations. Consistent harvest of older individuals can have a large effect on genetic variation even when population sizes exceed those simulated here by an order of magnitude (Ryman et al. 1981).

Projected losses of genetic variation were strongly influenced by the frequency distribution of alleles used to initialize simulations. The Pryor herd exhibited an unusually high level of heterozygosity (Wooten and Smith 1985) and contained many rare alleles. If this herd had been isolated for an extended period, many of the rarer alleles would already have been lost and the effects of population size or age of treated animals would have been less. This leads to a rather surprising conclusion: as existing genetic variation declines, fewer individuals are needed to retain a high portion of the existing variation. This can occur because rare alleles will have already been lost from the population, and those alleles that occur at a relatively high frequency are slowly lost (Fig. 6). In natural populations, an equilibrium level of genetic variation will result from processes that increase and decrease natural variation. Mutations increase variation, but they occur at a slow rate and must be maintained to contribute to long-term heterozygosity. On the other hand, genetic drift results in loss of variation.

The use of multiple measures of genetic variation revealed that under these situations allelic diversity was a much more sensitive indicator of changes in genetic variation than was H_e . Nonetheless, both measures indicated a high probability (>10%) of losing more than 10% of initial variation, even when using the best management option simulated. It is impossible to achieve levels of contraception or removals as

precise as those simulated; under field conditions, rates of loss of genetic variation will differ from those simulated. For treatments of young animals, observed rates of loss of variation will be greater than simulated, while the opposite will likely result from treatments of older animals.

In this model, changes in genetic variation resulted only from genetic drift. While the inclusion of mutations would have resulted in lower rates of loss of variation, genetic drift is by far the dominant process leading to changes in gene frequencies in small populations (Nunney and Campbell 1993; Lynch 1996). This occurs for two main reasons. First, sampling errors are exacerbated in small populations, and second, the portion of genetic variation that is selectively neutral increases as population size declines. Selection tends to be far less important in small populations because, as population size declines, a much larger selection coefficient (selective advantage) is necessary for selection to act in a deterministic manner. For quantitative characters, this situation arises from the distribution of selective forces over a large number of loci, thus selection on any one locus is small enough to be overwhelmed by random genetic drift (Lynch 1996). A consequence of the dominance of random drift is that an allele with strongly negative effects can become fixed in the population. In large populations, a small selective disadvantage may be sufficient to reduce the frequency of a deleterious allele, whereas this is unlikely to occur in small populations.

Several factors not included in the simulation analysis could result in a more rapid loss of genetic variation than these results suggest. Periodic catastrophes could lead to temporary reductions in population size. The Pryor herd suffered a high winter loss in 1977–1978 (Garrott and Taylor 1990) and catastrophes are thought to be an important factor in other large mammal populations (Young 1994, 1999; Ebb and Boyce 1999). Other factors that may be important and require further investigation include density dependence, compensatory reproduction, and the role of environmental stochasticity. All of these factors could contribute to a more rapid loss of genetic variation. This stresses the conservative use of these results to guide management decisions.

These simulations identified several important genetic and demographic concepts. For managed populations, actions that delay the age of reproduction

will reduce the loss of genetic variation. Measures of allelic diversity are likely to be more sensitive than population-level measures of heterozygosity. Use of contraceptives will, in general, result in lower standing populations and a much less variable population size. Overall, these results support use of management strategies that rely less on removal and more on infertility treatments to reduce long-term loss of genetic variation.

Complicating Factors: Population Subdivision, Natural Selection, and Mutation

A variety of factors not incorporated in the model could affect rate of loss of heterozygosity. The most important are probably spatial structure, stochastic variation in demographic processes, and catastrophes. Under certain conditions, subdividing the population into smaller subpopulations can be an effective means to better retain *population-level* genetic variability (Nunney 1993; Lande 1995). When a population is divided into a number of subunits without gene flow, rates of genetic drift and fixation of mutations are enhanced relative to a single large population. As alleles become fixed in a subpopulation (i.e., variation is completely lost at that locus in a subpopulation), that component of genetic variability is permanently maintained as long as the subpopulation persists. Long-term maintenance of population-level genetic variation can thus be enhanced by population subdivision, even though genetic variability of each individual and subpopulation is lower than would be expected in a single, larger population. A strategy that exploits spatial structure may therefore be useful when the overall population size is large, there are many subpopulations, and the objective is to preserve population level heterozygosity. Such a strategy is likely to be inappropriate when there are few subpopulations, the overall population size is small, or the objective is to maintain genetic variation at the level of individuals rather than the level of the population as a whole. Since animal health is assumed to correlate with individual-level heterozygosity, it is clear that management strategies to preserve genetic vitality will usually always favor actions that enhance movement of animals and reduce spatial structure. The major exception to this strategy is when isolated populations have developed adaptations to local conditions. Under

these conditions, movement of animals between a locally adapted population can result in outbreeding depression. This situation is likely to be extremely unusual in large mammals that have the ability to disperse long distances.

Simulations reported here explicitly removed stochastic variation in demographic processes to the extent possible. This strategy was employed to make the model as simple as possible while retaining processes that permit the evaluation of realistic management alternatives. Once we understand the behavior of the simple models, we can attempt to evaluate more complicated variants. These simulations probably provide optimistic projections on the loss of genetic diversity, and future models that more completely incorporate observed annual variation in recruitment and the occasional catastrophe will likely suggest more rapid loss of both alleles and heterozygosity. Projections from these simulations are therefore a first approximation, and are best used to evaluate the relative merits of management strategies.

Several processes not represented in the model are likely to influence the exact implementation of a control plan. Recent analysis of growth rates of the Pryor herd provided evidence of a relation between overall growth rate and population size, but not between specific processes that result in population growth (i.e., recruitment or survivorship; Singer et al. [1998]). Density-dependent reductions in recruitment or survival were thus not included in the model. In addition, there are indications of adaptive changes in sex ratio with changing population density, but this effect was statistically insignificant and was therefore not simulated. Finally, there is a high likelihood mares subjected to contraception will exhibit compensatory reproduction in years subsequent to treatment. No compensatory adjustment in recruitment was included.

Current simulations do not include selection or mutations. Selection (natural or otherwise) results in a more rapid loss of genetic variation among selected and linked genes. Mutations, on the other hand, serve to increase genetic variation. In populations with an effective size less than several hundred individuals, the expected amount of variation is largely the result of the balance between loss from genetic drift and new variance from mutation (reviewed by Lynch [1996]). Lynch notes that this conclusion is general and varies little with nonadditive gene action or with linkage relationships. Simulating Mendelian inheritance of selectively neutral variation is therefore appropriate for evaluating the likely loss of genetic variation over time

in populations with a genetic effective size of less than several hundred individuals.

General Recommendations for Managers

Simulation results and principles of population genetics suggest that removal or contraceptive strategies that focus on young animals, rather than older ones, will best retain genetic variation. A common suggestion is to let mares breed once and then treat them with contraceptives. These simulations show that, from a genetic standpoint, this would be an especially poor policy. These analyses suggest that current population sizes are inadequate to ensure the long-term maintenance of existing genetic variation, in large part because the population has an unusually high level of existing heterozygosity and a large number of alleles that occur at low frequency. Some alleles in the PMWHR herd are also rare among horse populations in general (Gus Cothran, personal communication).

Overall, the best strategy for regulating the horse population appears to be one that employs contraceptives to reduce population growth rate and periodic removals to reduce population size and manage undesired changes in sex ratio or age structure. Such a strategy reduces the need to sustain an excessively high level of infertility that may be impossible to achieve with existing technologies, and it can greatly reduce the frequency of large-scale gathers and removal of horses.

An evaluation of the suitability of alternative management options was hampered by the absence of clear management objectives with respect to genetic variation. Currently, there are no criteria to indicate "success". There is a high level of interest in horses on the PMWHR because, to some people, they represent an important and genetically unique animal. This level of interest will cause debate of any proposed management plan. This debate is unlikely to subside in the absence of clear guidelines.

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Literature Cited

- Berger, J. 1986. Wild horses of the Great Basin. University of Chicago Press, Chicago.
- Boyles, J. S. 1986. Managing America's wild horses and burros. *Journal of Equine Veterinary Science* 6:261–265.
- Bradley, M. P. 1994. Experimental strategies for the development of an immunocontraceptive vaccine for the European red fox (*Vulpes vulpes*). *Reproductive Fertility and Development* 6:307–317.
- Bureau of Land Management. 1997. The 10th and 11th reports to Congress on the administration of the Wild Free-roaming Horses and Burros Act for fiscal years 1992-1995. U.S. Government Printing Office, Washington, D.C. United States Government Printing Office 1997-573-153/40527.
- Carey, J. R. 1993. Applied demography for biologists. Oxford University Press, New York.
- Eagle, T. C., E. D. Plotka, R. A. Garrott, D. B. Siniff, and J. R. Tester. 1992. Efficacy of chemical contraception in feral males. *Wildlife Society Bulletin* 20:211–216.
- Ebb, J. D., and M. S. Boyce. 1999. Distribution of population declines in large mammals. *Conservation Biology* 13:199–201.
- Fayrer-Hosken, R. A., P. Brooks, H. J. Bertschinger, J. F. Kirkpatrick, J. W. Turner, and I. K. M. Liu. 1997. Management of African elephant populations by immunocontraception. *Wildlife Society Bulletin* 25:18–21.
- Garrott, R. A. 1991. Feral horse fertility control: Potential and limitations. *Wildlife Society Bulletin* 19:52–58.
- Garrott, R. A., and L. Taylor. 1990. Dynamics of a feral horse population in Montana. *Journal of Wildlife Management* 54:603–612.
- Garrott, R. A., D. B. Siniff, and L. L. Eberhardt. 1991a. Growth rates of feral horse populations. *Journal of Wildlife Management* 55:641–648.
- Garrott, R. A., D. B. Siniff, J. R. Tester, and E. D. Plotka. 1991b. Contraception as a tool for managing feral horse populations in the western United States. Pages 294–303 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: Populations*. Elsevier Applied Science, New York, New York.
- Garrott, R. A., D. B. Siniff, J. R. Tester, T. C. Eagle, and E. D. Plotka. 1992. A comparison of contraceptive technologies for feral horse management. *Wildlife Society Bulletin* 20:318–326.
- Goodloe, R. 1991. Immunocontraception, genetic management, and demography of feral horses on four eastern U.S. Barrier Islands. University of Georgia, Athens.
- Hartl, D. L., and A. G. Clark. 1997. Principles of population genetics. Sinauer Associates, Sunderland, Mass.
- Hedrick, P. W., and P. S. Miller. 1992. Conservation genetics: Techniques and fundamentals. *Ecological Applications* 2:30–46.
- Hoffman, R. A., and R. G. Wright. 1990. Fertility control in a non-native population of mountain goats. *Northwest Science* 64:1–6.
- Holden, C. 1992. Birth control for animals. *Science* 256:1390.
- Kirkpatrick, J. F., J. W. Turner Jr., I. K. M. Liu, R. Fayrer-Hosken, and A. T. Rutberg. 1997. Case studies in wildlife immunocontraception: Wild and feral equids and white-tailed deer. *Reproduction Fertility and Development* 9:105–110.
- Lande, R. 1995. Breeding plans for small populations based on the dynamics of quantitative genetic variance. Pages 318–340 in J. D. Ballou, M. Gilpin, and T. J. Foose, editors. *Population management for survival and recovery*. Columbia University Press, NY.
- Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. Pages 471–501 in J. C. Avise and J. L. Hamrick, editors. *Conservation genetics: Case histories from nature*. Chapman and Hall, New York.
- Muller, L. I., R. J. Warren, and D. L. Evans. 1997. Theory and practice of immunocontraception in wild mammals. *Wildlife Society Bulletin* 25:504–514.
- Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable population size: Demography meets population genetics. *TREE* 8:234–239.
- Ryman, N., R. Vaccus, C. Reuterwall, and M. H. Smith. 1981. Effective population size, generation

- interval, and potential loss of genetic variability in game species under different hunting regimes. *Oikos* 36:257–266.
- Singer, F. J., L. Zeigenfuss, L. Coates-Markle, and F. Schweiger. 1998. Demographic analysis, group dynamics, and genetic effective number in the Pryor Mountain wild horse population, 1992–1997. Pages 3–40 *in* Second annual report to U.S. Bureau of Land Management, Billings Resource Area Office, Mont.
- Soulé, M. A., M. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: How long a voyage, how many staterooms, and how many passengers? *Zoo Biology* 5:101–114.
- Sturtevant, J. 1970. Pigeon control by chemosterilization: Population model for laboratory results. *Science* 170:322–324.
- Wooten, M. C., and M. H. Smith. 1985. Large mammals are less genetically variable? *Evolution* 39:210–212.
- Wright, S. J. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- Young, T. P. 1994. Natural die-offs of large mammals: Implications for conservation. *Conservation Biology* 8:410–418.
- Young, T. P. 1999. Catastrophes are still interesting. *Conservation Biology* 13:202.



SECTION III.

ECOSYSTEM MODELING

Ecosystem Modeling of the Pryor Mountain Wild Horse Range

Executive Summary

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Introduction

The U.S. Bureau of Land Management (BLM) is responsible for the maintenance of a “thriving ecological balance” on the Pryor Mountain Wild Horse Range (PMWHR) and has deemed it necessary to conduct periodic management removals of wild horses since 1970 to halt and prevent range degradation (BLM 1997). The PMWHR includes lands which are administered by the National Park Service (NPS); specifically, portions of the Bighorn Canyon National Recreation Area (BCNRA), as well as lands administered by the BLM and the U.S. Forest Service (Hall 1972; BLM 1984). It has been federally mandated that wild horses have access to the NPS lands, by inclusion of the BCNRA in the designated PMWHR. However, in setting the appropriate numbers of wild horses, other NPS management objectives must be weighed, including protection of native plant communities and wildlife. In the past, horse carrying capacities have been calculated using a widely accepted method that sums up total forage biomass and applies a proper use factor of 50% utilization. The appropriate number of horses on the PMWHR must be explained in terms of measurable and predictable changes brought about by different horse densities in the abundance and composition of soils, plants and wildlife, and in the condition and welfare of the horses. These responses depend on plant species, the levels and patterns of herbivory, climate, soil properties, and their distributions on the landscape. Forage varies annually and spatially over the landscape. Horse distributions vary seasonally, and parts of the landscape are used more heavily than others. Although it is unlikely that these wild horses will ever be allowed to self-regulate, there is a need to estimate the results if

that were to occur. A general approach is necessary, which can assess the effects of herbivory on soils, plants, and animals in a dynamic and spatially heterogeneous landscape. Here, a neutral, ecosystem modeling approach was used, which makes no specific assumptions about management objectives, levels of proper use, ideal range conditions, or equilibrium biotic communities.

The objectives of this study (Coughenour 1999) were to: (a) evaluate a general, ecosystem modeling approach to support more informed policies for managing large ungulates; and (b) assess the effects of different numbers of horses on ecosystem structure and function on the PMWHR. This is an alternative approach than traditional approaches to evaluating carrying capacity based solely on forage supply or animal population dynamics.

Methods

Ecosystem Model Description

An ecosystem simulation model called SAVANNA (Coughenour 1992, 1993) was used to represent ecosystem dynamics and interactions on the PMWHR landscape. SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems. The model simulates processes at landscape levels through regional spatial scales over annual to decadal time scales. The model is composed of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels. The time-step of the

model is one week. SAVANNA is a spatially explicit model (i.e., it is sensitive to spatial position). Typically, the landscape is divided into 5,000–10,000 grid-cells. The model simulates water and nutrient balance, plant growth, and herbivory on each grid-cell. Here, grid-cell size was 500 x 500 m.

SAVANNA is driven by monthly weather data. The model spatially interpolates precipitation data using inverse distance weighting, correcting for elevation differences between the weather station and grid-cell. The water balance submodel simulates soil moisture dynamics and use on each patch type on each grid cell. Soils map data are used, in conjunction with soil properties for each soil type, to determine soil water-holding capacities of each subarea on each grid cell. The water budget includes terms for precipitation, interception, runoff, runoff, infiltration, deep drainage, bare soil evaporation, and transpiration.

The net primary production (NPP) submodel simulates plant biomass production and dynamics. Plant biomass production is affected by light, water, temperature, nitrogen, and herbivory. This submodel is explicitly linked to the water budget submodel through transpiration and plant water use. Biomass is allocated to leaves, stems, and roots. Due to water or temperature stress or phenological stage, plant tissues die and turn over at a nominal rate that reflects their maximal longevities. The model represents plant nitrogen uptake and losses due to herbivory and tissue mortality.

A litter decomposition and nitrogen cycling submodel simulates the breakdown of dead plant materials and animal feces. Nitrogen is released during decomposition to mineral forms that can be taken up by the plants. Nitrogen enters the system through atmospheric wet and dry deposition and biotic fixation, and leaves the system through denitrification and urine volatilization.

Animal forage intake is determined by diet selection, forage abundance, forage quality, and snow cover. Forage intake rate is expressed as a function of forage biomass. As forage biomass increases from zero to a specified level, forage intake rate increases. Forage intake rate is also affected by snow depth. Animals choose among available plant types and tissues to achieve a preferred diet composition. Diet composition is affected by the relative availability of different forage types as well as preferences or avoidances.

The animal energy balance submodel simulates body weight of the average animal of each species, based on differences between energy intake and energy

expenditure. Energy intake depends on forage biomass intake and forage digestibility. Expenditures depend on body weight and travel patterns.

The ungulate population dynamics submodel represents changes in the number of animals in each age class for each sex. Birth and death rates are affected by animal condition indices. This is the way the model represents population responses to factors affecting forage availability, including plant growth rates, snow depth, and forage removal by other animals.

The ungulate spatial distribution submodel simulates animal distributions over the simulated landscape or region on a weekly basis. Habitat suitability is affected by slope, temperature, forage biomass, forage intake rate, snow depth, distance to water, and tree cover.

Model Parameterization

Six groups of plants were simulated: grasses, forbs, shrubs, mountain mahogany (*Cercocarpus*), juniper, and coniferous trees. These groups were chosen to meet the objectives of this modeling analysis, without making the model overly complex.

A vegetation map existed for BCNRA (Knight et al. 1987), but none existed for the remainder of the PMWHR. Consequently, I developed a PMWHR vegetation map by merging the BCNRA vegetation map with a modeled vegetation map for the remaining area. The modeled vegetation map was based on a map of forest cover, from USGS quad sheets, the soils map, and qualitative relationships between major vegetation types, elevation, and soils observed on the Knight et al. (1987) map.

There are three relatively distinct herds of horses in the PMWHR, occupying habitats that are separated by distinct topographic barriers (Hall 1972; BLM 1984, 1997; Singer et al. 2000). Each of the three herds was modeled separately and distributions were limited to their respective range areas. Seasonal movements were modeled as dynamic responses to changing forage and snow conditions, with a seasonal avoidance of areas below 1,500 m in summer. The locations of known horse watering points within the horse range were digitized from information provided by BLM personnel (L. Padden, BLM, personal communication). A map of distance to water was calculated using GIS. Bighorn sheep were kept within the seasonal ranges observed by Irby et al. (1994). Within these ranges, the model redistributed animals in relation to forage biomass and

forage energy intake rate. Mule deer winter on the PMWHR, but during summer, most migrate to ranges north of the PMWHR (Irby et al. 1996). The model was parameterized so that the entire deer herd was on the PMWHR during December–April, and 10% were on the PMWHR during June–October.

In simulations using observed population data, the summarized horse data from USDI/BLM (1997) were used, based on data from Taylor (1990 memo), and Garrott and Taylor (1990). Sheep population data were obtained from Coates and Schemnitz (1989) and Kissell et al. (1996). Mule deer population size was based on information from Kissell (1996). Horse culling data from the BLM (1997) were used in simulations using observed culling data. Deer were culled to maintain the population between 500 and 700. Bighorn sheep have never been culled and hunting is restricted to a few ram-only permits each year.

Data from Detling and Gerhardt (1996) were used to parameterize the plant growth model and test its predictions. The objective was to maximize the model's skill in providing realistic simulations, by making maximal use of information contained in the field data and literature. Root biomass was estimated by fitting model aboveground predictions to the aboveground data. Biomass dynamics on plots inside grazing exclosures were verified first, followed by the dynamics of grazed plots. Grazing intensities in the grazed simulations were estimated by varying horse density to best simulate observed differences between exclosed and grazed plant biomass dynamics.

Results

Model Tests

The model performed well in simulating herbaceous plant growth with and without grazing. The model successfully simulated herbaceous biomass dynamics across a wide range of sites and weather years. The proportions of grasses and forbs, rates of transfers from live to dead, and rates of transfers of dead tissues to soil were adequately simulated. The model simulated reasonable population dynamics and distributions of horses, bighorn sheep, and mule deer. The rates of forage offtake per animal, and the compositions of the herbivore's diets were realistic. Overall, the model provided estimates of plant production and animal behavior that were consistent with available data.

Dynamics

A simulation was run with horse numbers held at 270 animals (the number first counted by Feist and McCullough [1975]) during the period from 1950–1969. The model simulated markedly reduced herbaceous biomass compared to no horses. Forb biomass comprised a greater proportion of total peak standing crop, while grasses comprised a smaller proportion, compared to no horses. Root biomass was also diminished. Total aboveground plant growth, including transfers to dead and litter, decreased under grazing. In another simulation, horse populations were allowed to grow freely, to limits imposed by the environment. Plant responses were not markedly different from those observed with a fixed number (270) of horses. Horse numbers initially increased, leveled off at around 400, and then plunged dramatically in 1960–1961 in response to a drought in 1960. Thereafter, horse numbers gradually increased to 270.

In simulations of the period from 1970–1996 without horses, grass biomass generally increased over time. Forb biomass increased less, so the proportion of forbs in total herbaceous biomass decreased. With observed horse numbers over this period, grass biomass varied from year to year, but there was no long-term trend. The ratio of grass to forbs was similar throughout. When horses were not culled, biomass of grasses decreased over time.

With no grazing, root biomass of grasses fluctuated, but there was no trend. Grass roots eventually became more abundant than forb roots. With observed animal numbers, grass and forb roots varied within a range that was slightly less than with no animals, and there was no long-term trend. With no culling, root biomasses of both plant groups were lower and decreased over time. Herbaceous basal cover increased during the first 15 years of simulations with no animals. Grass and forb cover increased when grazed with observed animal numbers, but then leveled off at lower levels than with no animals.

Forage intake rate for horses varied seasonally and annually. Generally, most stressful years for forage intake were also years with deeper snow depths. Maximum intake rates for the Dryhead herd were consistently lower than for the other two herds, as a result of the lower forage biomass on the Dryhead summer range. Intake rates were markedly reduced when horse herds were not culled. Maxima and minima

were both reduced at higher horse densities, as a consequence of intraspecific competition for forage. Sheep intake rates were far less variable than horse intake rates, primarily because they could shift to browse species which continued to be abundant during the winter and were not used by horses.

Spatial Distributions

Maps of simulated total aboveground net primary production (ANPP; i.e., total aboveground plant growth) with and without horses were similar, but there were certain areas where production was diminished with horse grazing. These included the area just south of the Sorenson Extension boundary, and areas in the south-central portions of the Sykes and Burnt Timber Ridge horse ranges. With observed horse numbers, grass ANPP was 60–80% lower in some areas than without horses. With no horse culling, there were areas where grass ANPP was reduced by 80–90% and forb ANPP was reduced by 50–70%. With observed numbers of horses, roots decreased by 25–75% in some areas, but these areas constituted a small fraction of the landscape. With no horse culling, areas of decreases rose to 50–90%, and a larger fraction of the landscape showed decreases in the 25–50% range.

Horse grazing shifted species composition towards a greater preponderance of forbs in most places, but the shifts were differentially distributed across the landscape. There was a greater species shift at the higher elevations, with forb proportions increasing to 40–70% at some high elevation areas. Litter and shoot biomass reductions cause an increase in bareground, with potential secondary effects on soil temperature, runoff, and soil erosion.

With the observed numbers of horses, grass herbivory levels reached 70–80% over significant portions of the landscape. However, much of the landscape was lightly (<20%) or moderately (20–60%) grazed. Grasses on the southern parts of the Sykes Ridge and Burnt Timber Ridge, and northern part of the Dryhead Range were heavily (>60%) or very heavily (>80%) grazed. Grazing intensity on the high elevation summer range was mostly moderate. High rates of grass offtake were far more prevalent when there was no horse culling. Grasses on 30% of the landscape were grazed in excess of 50%. Grasses on 8% of the landscape were utilized >90%.

Horse densities were heterogeneously distributed on the landscape. With observed horse numbers, highest use areas at low elevations were 2–5 head per

km² year-long. Heavy use areas at the top of the mountain were higher, reaching 6–8 head per km² year-long. When horses were not culled, densities reached higher levels everywhere, with low elevation high-use areas reaching 5–8 head per km² and high elevation high-use areas reaching 7–10 head per km² year-long.

The fraction of the landscape receiving >80% herbivory varied markedly from year to year. During 1970–1996, 37–67% of the landscape received light (0–10%) herbivory with observed horse numbers and 13–38% received 10–50% herbivory. However, 3–14% experienced herbivory in the 50–80% range and 2–31% received >80% herbivory.

With no horse culling, the fraction of the landscape where grasses were grazed >80% rose to 21–44%. The fraction of the landscape grazed 50–80% was 3–13% with 100–150 head, 4–13% with 150–200 head, 4–14% with 200–250 head, and 3–15% with no culling. The fraction of the landscape where grasses were grazed >80% was 8–31% with 100–150 head, 12–34% with 150–200 head, 16–34% with 200–250 head, and 21–45% with no culling.

As horse numbers were increased, herbaceous ANPP on the primary horse range decreased by 10–13% for each additional 50 horses. There was approximately 75% the herbaceous production with 200 horses as with 50 horses. With 350 horses, ANPP was about 60% of that with 50 horses. There was 60% as much herbaceous biomass with 200 horses as there was with 50 horses. With 350 horses there was <50% the biomass as with 50 horses.

The effects of disallowing trespass use of U.S. Forest Service (USFS) lands northeast of the PMWHR was examined by running the model for the period 1970–1996 at seven different horse densities. There was a slight reduction in plant growth with no access to USFS lands compared to full access. The proportion of forbs was similar with or without USFS access, but there was a slight increase in forbs without USFS access. A similar response was simulated for root biomass. Horse condition was also slightly lower when USFS access was disallowed. Differences between runs with and without USFS access were negligible with less than 150 horses, but increased at higher numbers of horses.

Interactions with Bighorn Sheep

Neither sheep condition index nor sheep forage intake rate were affected by increasing horse numbers. One reason for this appeared to be a high degree of

spatial segregation, where sheep ranges overlapped onto a small fraction of the total horse range. A second reason was dietary separation. A significant fraction of sheep diets were from evergreen shrubs, which were an insignificant component of horse diets (Kissell 1996). Finally, sheep appeared to be strongly influenced by their own density within their own range.

Increasing numbers of sheep had very little impact on horse condition or horse forage intake, but did have a substantial effect on sheep condition and sheep forage intake rate. This suggests that there was a considerable degree of intraspecific competition for food within the prescribed sheep range. As sheep depleted forage within their prescribed range, horses had substantial options for foraging elsewhere.

In simulations using stochastic weather, horse numbers fluctuated within the ranges specified by culling targets at the 100–150 and 150–200 levels. When culling to 200–250, however, there was a drop in population sizes below the 200 level, as a result of horse interactions with vegetation and climate. When horses were not culled at all, there was marked variation among horse population trajectories. Horses reached at most 350 in the stochastic runs without culling. When horses were culled, or not present, the final median number of sheep was about 175, irrespective of horse numbers. When horses were not culled, the final median number of sheep was about 160.

Comparisons to Previous Analyses

Model predictions of forage biomass agreed with the actual forage productivity estimates used in the BLM's 1984 carrying capacity assessment, but not with the 1984 potential productivity estimates. The model agreed reasonably well with the potential productivity estimates of the BLM's 1992 carrying capacity assessment, but not with the 1992 actual productivity estimates.

It was difficult to make an exact comparison between the traditional range site-based carrying capacity estimates and the estimates of appropriate horse numbers using the ecosystem modeling approach, since the two methods measure carrying capacity differently. The ecosystem approach demonstrated that the proper use factor of 50% used in the range site approach is exceeded on portions of the landscape, even with 100 horses. Averaged over the entire

landscape, offtake is actually much less than 50%, even with as many as 200 horses. The simple proper use factor is of limited utility when grazing is so heterogeneously distributed.

Conclusions

1. The model responded realistically to climate, soil properties, grazing, and their interactions. Model predictions were consistent with current knowledge about the underlying processes of ecosystem water and nutrient budgets, plant and animal ecophysiology, and animal population dynamics.

2. Horses increased to over 300 in many weather scenarios, and even to >450, if they were not culled. This could be regarded as the ecological carrying capacity of the population. The rate of increase of the simulated population was as observed, under the observed levels of forage availability per animal. It can be inferred from model results and other data that the horses have a capacity to increase to high densities relative to forage resource, and persist in environments with relatively low forage biomass. In other words, at ecological carrying capacity, horse numbers would be relatively high and plant biomass would be relatively low. The result is consistent with other studies which indicate that in natural grazing ecosystems, native equids tend to be predator rather than food limited.

3. As horse numbers increased, total forage production on the primary horse range decreased by 10–13% for each additional 50 horses. On average, there was approximately 75% as much forage production with 200 horses as with 50 horses.

4. Grazers decreased aboveground biomass, as expected. Model simulations and data indicated that most of the reduction was in standing dead rather than in live biomass. In the absence of grazing, dead biomass was more likely to accumulate.

5. The model simulated an increase in the relative abundance of forbs compared to grasses as herbivory pressure increased. There is only weak support for such a species shift in the data. However, changes in forb composition would be expected based on the lower relative abundances of forbs than grass in animal diets.

6. Basal cover and root biomass decreased under increased herbivory due to decreases in above and belowground primary production relative to root

turnover. This was consistent with the generally accepted theory that forage productive potential varies with range condition.

7. The model agreed reasonably well with the actual forage productivity estimates used in the BLM's 1984 carrying capacity assessment and with the potential productivity estimates of the BLM's 1992 assessment. However, there were discrepancies between the model and the 1984 potential productivity estimates (if ranges were in excellent condition), and between the model and the 1992 actual productivity estimates. These discrepancies suggested that there is uncertainty associated with previous estimates of maximum forage production and range condition.

8. The proper use factor of 50% that is used in the range site approach is exceeded on portions of the landscape, even with 100 horses. Averaged over the entire landscape, however, offtake is actually much less than 50%.

9. Grazing was heterogeneously distributed. With observed horse numbers, highest use areas at low elevations were 2–5 head per km² year-long. Heavy use areas at the top of the mountain were higher, reaching 6–8 head per km² year-long. During 1970–1996 with observed horse numbers, 40–70% of the landscape experienced light herbivory of grasses. However, 5–20% received >80% herbivory and 5–15% experienced herbivory in the 50–80% range. The fraction of the landscape receiving >80% herbivory varied markedly from year to year.

10. The percent of the landscape where grasses were grazed in excess of 80% increased from 16% at 125 horses to 25% at 225 horses, however in a given year the maximum percentage varied from 31% with 125 horses to 36% at 225 horses. The mean proportion of herbaceous plant growth consumed on the entire landscape varied from a mean of 15% at 125 horses to a mean of 23% at 225 horses.

11. A simple proper use factor is of limited utility when grazing is heterogeneously distributed. Instead, a proper use factor must be two-tiered, specifying both the spatial stratification of grazing intensities, and the acceptable grazing pressure within strata. For example, proper use could be specified as a maximum acceptable fraction of the landscape that is grazed in excess of 80%. Alternatively, a proper level of use should be applied to key areas of the landscape which are typically most heavily grazed. It would be useful to reach a consensus about the level of acceptable use in these terms, which are more realistic than a simple proper use factor.

12. Horses had little effect on bighorn sheep populations due to a high degree of spatial segregation, dietary separation, and the fact that sheep are strongly influenced by their own density within their own range. Sheep ranges overlapped with a small fraction of the total horse range. This result should be interpreted with caution since potential sheep habitat that is still unoccupied may be affected differently by horses. There is a need to assess potential horse-sheep interactions throughout the potential sheep range.

13. A GIS model of sheep habitat appeared to be too restrictive in the PMWHR, probably because it did not consider the effects of low forage availability, and the need for sheep to forage further from escape terrain. Although the GIS-based approach could be modified to incorporate effects of forage production and snow, an alternative, and probably better approach is to implement a less restrictive GIS habitat model in a spatial simulation model of forage production and snow cover, as was done here.

14. Continuous rather than threshold responses to increasing horse made the task of deciding upon an appropriate number of horses difficult. The analysis showed no optimal number of horses, as in a peak level of performance of ecosystem processes. With as few as 50 horses, there was some decrement of plant growth. Given this, the optimum number of horses may be the minimum number needed to safely ensure the population and genetic viabilities of the horses. This number would minimize decrements to vegetation productivity, while ensuring continued viability of the horse herd.

15. It would be desirable to spread out horse grazing impact so that the fraction of the landscape receiving heavy use is reduced. To achieve a more uniform distribution of percent offtake, it would be necessary to distribute horses in proportion to plant production, which varies markedly across the landscape.

16. At ecological carrying capacity, plant cover would be considerably lower than it is now. The range would appear to be extremely heavily utilized as grass offtake would climb to over 90% in many more areas. Some areas would be nearly barren. Herbaceous biomass above and belowground would be reduced to less than 20% of potential in many areas. There would probably be secondary effects on wildlife. With greater exposure due to reduced plant and litter cover, soil erosion rates would likely be higher than at present. Horses would be in generally lower body condition. Total annual horse mortality would be high, due to a larger total number of horses, and the fact that annual

births would have to be balanced by higher deaths. Thus, to meet range management and animal welfare objectives, the population must be managed below its ecological carrying capacity.

17. The effects of curtailing recent horse trespass onto USFS lands northwest of the PMWHR boundary on forage production and horse energy balance would be negligible.

18. As part of an adaptive management process, the model should be revisited periodically, to check the consistency of its predictions with actual results. Ecosystem monitoring should be designed to test some of the key model predictions. The model should then be revised and a new assessment should be carried out.

19. Better data are needed for estimating plant production in the long-term absence of grazing. It would be best to monitor biomass at the 4 long-term exclosure sites and the 12 additional exclosure sites that were established in 1992 and 1994.

20. The combination of field research and ecosystem modeling that has been carried out in the PMWHR serves as an example for improving the scientific management and conservation of wild equids on rangelands in the western United States and other regions of the world.

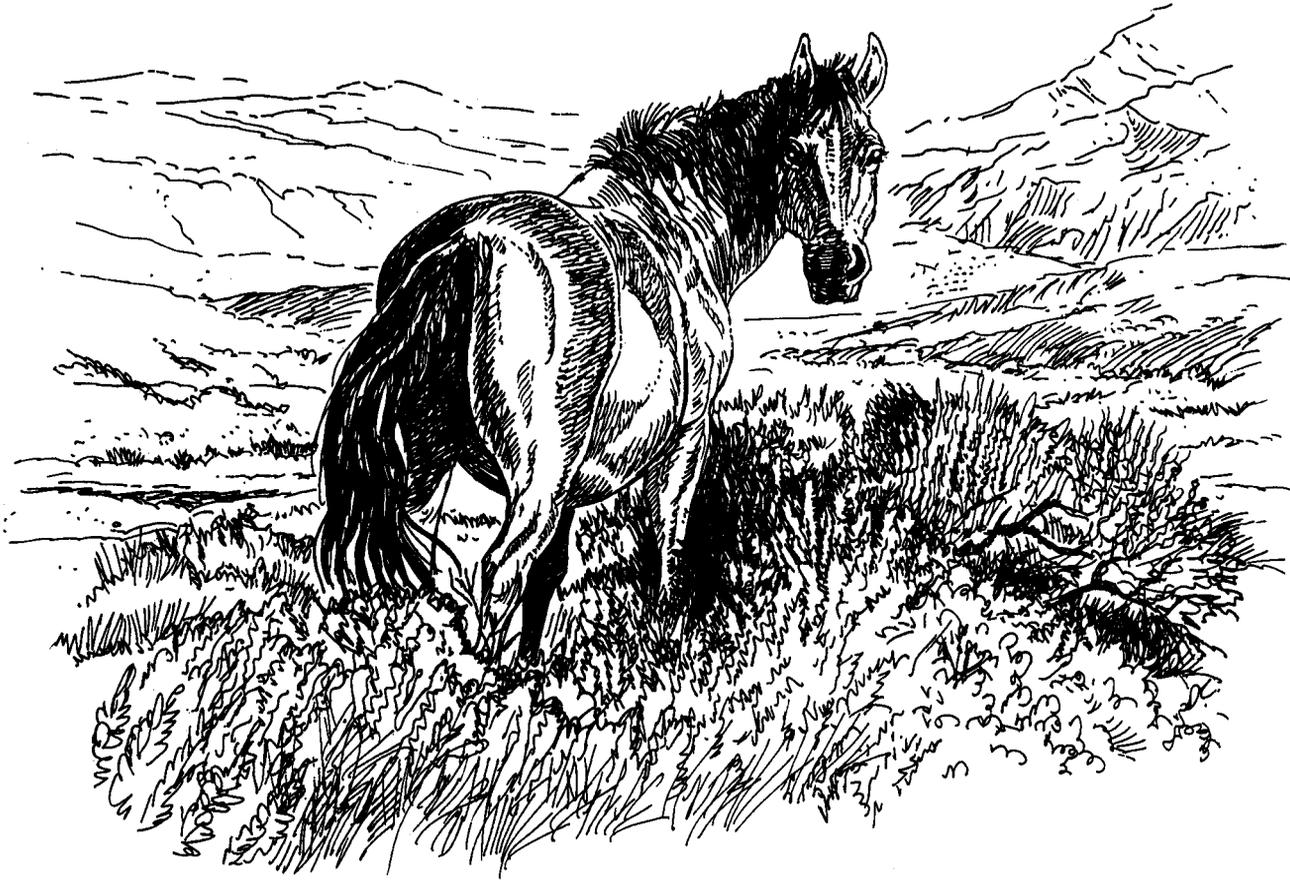
Literature Cited

- Bureau of Land Management. 1984. Herd management area plan, Pryor Mountain Wild Horse Range. U.S. Department of the Interior, Bureau of Land Management, Miles City District Office, Billings Resource Area, Mont.
- Bureau of Land Management. 1997. Pryor Mountain Wild Horse Range, Wild Horse Removal Plan. U.S. Department of the Interior, Bureau of Land Management, Miles City District Office, Billings Resource Area, Mont.
- Coates, K. P., and S. D. Shemnitz 1989. The bighorn sheep of Bighorn Canyon National Recreation Area and Pryor Mountain Wild Horse Range: Ecological relationships and management recommendations. Completion report to National Park Service and Bureau of Land Management. New Mexico State University, Las Cruces.
- Coughenour, M. B. 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: A prototype model and its potential use for monitoring drought. Pages 787–810 *in* D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. Ecological Indicators, Volume I. Elsevier Applied Science, London and New York.
- Coughenour, M. B. 1993. The SAVANNA landscape model - documentation and user's guide. Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins.
- Detling, J. K., and T. Gerhardt. 1996. Monitoring vegetation in the Pryor Mountain Wild Horse Range. Second annual report. Colorado State University, Fort Collins.
- Feist, J. D., and D. McCullough. 1975. Reproduction in feral horses. *Journal of Reproduction and Fertility Supplement* 23:13–18.
- Garrott, R. A., and L. Taylor. 1990. Dynamics of a feral horse population in Montana. *Journal of Wildlife Management* 54:603–612.
- Hall, R. 1972. Wild horse biology and alternatives for management. Pryor Mountain Wild Horse Range. U.S. Bureau of Land Management, Billings District Office.
- Irby, L. R., R. J. Mackie, and R. E. Kissell, Jr. 1994. Competitive interactions between bighorn sheep, wild horses, and mule deer in Bighorn Canyon National Recreation Area and Pryor Mountain Wild Horse Range. Second annual report to the U.S. National Park Service. Montana State University, Bozeman.
- Kissell, R. J., Jr. 1996. Competitive interactions among bighorn sheep, feral horses, and a mule deer in Bighorn Canyon National Recreation Area and the Pryor Mountain Wild Horse Range. Ph.D. dissertation. Montana State University, Bozeman. 148 pp.
- Kissell, R. Jr., L. R. Irby, and R. J. Mackie. 1996. Competitive interactions among bighorn sheep, feral horses, and mule deer in Bighorn Canyon National Recreation Area and Pryor Mountain Wild Horse Range. Completion report to the U.S. National Park Service. Montana State University, Bozeman.
- Knight, D. H., G. P. Jone, Y. Akashi, and R. W. Myers. 1987. Vegetation ecology in the Bighorn Canyon National Recreation Area. Final report. University of Wyoming, National Park Service Research Center, Laramie.
- Singer, F. J., L. Zeigenfuss, L. Coates-Markle, and Reverend F. Schwieger. 2000. A demographic analysis, group dynamics, and genetic effective number in the Pryor Mountain wild horse population 1992–1997. *In* Managers' summary - Ecological studies of the Pryor Mountain wild horses. U.S. Bureau of Land Management and National Park Service report. U.S. Geological Survey, Biological Resources Division, Fort Collins, Colo.

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**U.S. Department of the Interior
U.S. Geological Survey**

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