



Utilization of forage by bison in the Gibbon, Madison, and Firehole areas of Yellowstone National Park

by Steven Ray Dawes

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management

Montana State University

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Abstract:

Bison in Yellowstone National Park have increased nearly 15-fold since 1968, from 300 to 4,300 by 1994, decreasing to 3,500 in 1996. This population expansion has led to increased numbers of bison migrating out of the Park, especially during severe winters. Egress from the Park led to controversial population control measures to combat the threat of brucellosis transmission to livestock outside the Park. During the winter of 1996/1997, the population was reduced (-38%) due to harsh winter conditions and brucellosis control procedures. It has been suggested that winter migration from the Park is the result of reduced winter forage availability due to excessive summer grazing on winter ranges in the Park. This study was designed to determine how bison used winter ranges during the summer months in the northwest portion of Yellowstone Park. The objectives were to: (1) determine summer use impacts on forage availability on the Gibbon, Madison, and Firehole winter ranges; (2) estimate plant productivity, removal, and fall standing crop at 6 study sites; (3) track bison distribution within the study area; (4) determine if seasonal use patterns are related to plant community, snow depth, or utilization intensities at specific sites; and (5) evaluate the efficiency of portable multispectral radiometer technology (MSR) in assessing range utilization. Exclosure cages were moved, and plots were clipped 3 times each summer to determine forage use and estimate productivity and removal. Fall standing crop was estimated with clipped plots adjacent to the cages. Road and site counts were conducted weekly to track bison distribution in the study area. Spearman correlations were used to test for associations between seasonal use patterns and utilization intensities, plant communities, and snow depth. MSR technology was evaluated with calibration clipping and regression analysis. ANOVA revealed moderate and highly variable differences between biomass in protected (caged) and unprotected (uncaged) plots. The extensive variability among paired plots makes a weak case for ungulate impacts. Only eleven of 92 paired t-tests (12%) indicated differences in standing biomass between caged and uncaged plots ($p < 0.05$). The Terrace Springs study site had significant tests in nearly all clipping periods probably, due to bison use. Estimates of forage production and removal were generally higher when calculated with cages moved at 5-6 week intervals than with cages fixed for the whole growing season. The MSR normalized difference vegetation index (NDVI) readings were not well correlated ($r^2 < 0.80$) with clipped biomass. Overall correlation coefficients were 0.71 in 1996 and 0.42 in 1997. Unless refinements in sampling techniques improve correlations, MSR technology should be used only to supplement conventional clipping treatments. Road and site counts in summer were not significantly correlated with estimated forage utilization. Winter counts of bison indicated that Terrace Springs, Fountain Flats Drive, and the Interchange site received almost constant use from November 1996-May 1997. Average snow depth over 6 sites was 27.3 cm. Use by bison at specific sites was not well correlated with snow depth. While increasing populations numbers have probably caused bison to feed on winter ranges during summer, I found little evidence such use is causing a broad detrimental effect on winter forage availability on the Gibbon, Madison, Firehole winter ranges.

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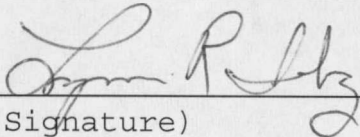
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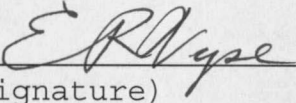
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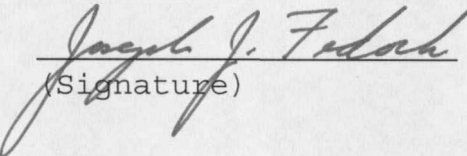
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ABSTRACT

Bison in Yellowstone National Park have increased nearly 15-fold since 1968, from 300 to 4,300 by 1994, decreasing to 3,500 in 1996. This population expansion has led to increased numbers of bison migrating out of the Park, especially during severe winters. Egress from the Park led to controversial population control measures to combat the threat of brucellosis transmission to livestock outside the Park. During the winter of 1996/1997, the population was reduced (~38%) due to harsh winter conditions and brucellosis control procedures. It has been suggested that winter migration from the Park is the result of reduced winter forage availability due to excessive summer grazing on winter ranges in the Park. This study was designed to determine how bison used winter ranges during the summer months in the northwest portion of Yellowstone Park. The objectives were to: (1) determine summer use impacts on forage availability on the Gibbon, Madison, and Firehole winter ranges; (2) estimate plant productivity, removal, and fall standing crop at 6 study sites; (3) track bison distribution within the study area; (4) determine if seasonal use patterns are related to plant community, snow depth, or utilization intensities at specific sites; and (5) evaluate the efficiency of portable multispectral radiometer technology (MSR) in assessing range utilization. Exclosure cages were moved, and plots were clipped 3 times each summer to determine forage use and estimate productivity and removal. Fall standing crop was estimated with clipped plots adjacent to the cages. Road and site counts were conducted weekly to track bison distribution in the study area. Spearman correlations were used to test for associations between seasonal use patterns and utilization intensities, plant communities, and snow depth. MSR technology was evaluated with calibration clipping and regression analysis. ANOVA revealed moderate and highly variable differences between biomass in protected (caged) and unprotected (uncaged) plots. The extensive variability among paired plots makes a weak case for ungulate impacts. Only eleven of 92 paired t-tests (12%) indicated differences in standing biomass between caged and uncaged plots ($p < 0.05$). The Terrace Springs study site had significant tests in nearly all clipping periods probably, due to bison use. Estimates of

forage production and removal were generally higher when calculated with cages moved at 5-6 week intervals than with cages fixed for the whole growing season. The MSR normalized difference vegetation index (NDVI) readings were not well correlated ($r^2 \leq 0.80$) with clipped biomass. Overall correlation coefficients were 0.71 in 1996 and 0.42 in 1997. Unless refinements in sampling techniques improve correlations, MSR technology should be used only to supplement conventional clipping treatments. Road and site counts in summer were not significantly correlated with estimated forage utilization. Winter counts of bison indicated that Terrace Springs, Fountain Flats Drive, and the Interchange site received almost constant use from November 1996-May 1997. Average snow depth over 6 sites was 27.3 cm. Use by bison at specific sites was not well correlated with snow depth. While increasing populations numbers have probably caused bison to feed on winter ranges during summer, I found little evidence such use is causing a broad detrimental effect on winter forage availability on the Gibbon, Madison, Firehole winter ranges.

INTRODUCTION

History

The role of the American Bison (*Bison bison*) in the history of Indian and European people in North America is significant (Dary 1974). The plains Indian tribes were intimately tied to the bison, and their civilization declined as the bison herds were extirpated. The bison slaughter began in earnest in the early 1870's and lasted approximately 12 years. At its peak, the economic importance of the bison industry to the United States exceeded that of the beaver and whaling industries combined (Dary 1974).

Bison population estimates from settlement to the late 1800's are problematic, spotty, and mostly anecdotal. All contain serious flaws, and none were the result of methods remotely approaching today's scientific standards (Shaw 1995). While estimates range from 30 to 65 million animals (Reynolds et al. 1982), any accuracy finer than tens of millions is questionable (Shaw 1995).

Modern Management

The historical population of mountain bison (*B. bison athabascae*) in Yellowstone National Park (YNP) was thought to be about 1,000 in 1880. Numbers declined to 40-50 by 1902 due to sport, subsistence, and market hunting, the capture of calves for private herds, and poaching (Meagher 1973). By 1902, intensive management was initiated to ensure the survival of the species, and plains bison (*B. bison bison*) were introduced to YNP to augment the native population, producing the hybrid inhabiting the park today. Three wintering herds (Lamar Valley, Pelican Valley, and Mary Mountain herds) eventually formed and remained distinct from one another until the early 1980's (Dobson and Meagher 1996). None are now geographically isolated year round, but the names have been retained to designate the winter populations (Meagher 1973).

Until 1966, bison were managed under a variety of programs, with population control only on the northern range (Dobson and Meagher 1996). Actions included: feeding hay in fenced pastures, capture and live removals, regulated public

hunts, and shooting by Park personnel within Park boundaries (YNP Interagency Fact Sheet 1994). Beginning in 1966, a "limited interference" approach was adopted, whereby fencing was removed and no supplemental feeding was undertaken (Meagher 1973). Bison were free to roam the Park and subjected to minimal interference from man.

Following the adoption of this policy, the population of bison increased from 300 in 1968 to 4,300 animals in 1994 (YNP Interagency Fact Sheet 1994) declining to 3,500 animals by 1996. However, with the harsh winter of 1996/1997 and the killing of more than 1,000 bison in an attempt to prevent the spread of brucellosis to cattle, the July 1997 population was estimated at 2,200 animals (Meagher, unpubl. data). Brucellosis was first diagnosed in park bison in 1917 (YNP Interagency Fact Sheet, 1994).

As population levels increased over the last 30 years, bison have been reported, with increasing regularity, foraging on their traditional wintering grounds during the summer months (Irby pers. commun., Meagher unpubl. data). The impacts of summer foraging on winter forage availability are unknown. It has been suggested, however, that summer use of winter sites has led to winter forage shortfalls

which in turn cause bison to migrate from the Park, particularly during harsh winters (Irby pers. commun., Meagher unpubl. data). This study was designed to assess summer foraging impacts on winter ranges in the northwest portion of the Park.

The 6 winter forage areas selected for study consist mainly of grass/forb communities. Bison feed mostly on grasses. Seasonal diets in North Dakota consist of 75-90% grasses, with browse species in late winter to early spring contributing 16% (Norland et al. 1985). Reynolds et al. (1982) found the diets in 3 of 4 free-roaming bison herds dominated by grasses and sedges. Bison select flat landscapes dominated by grass. Breaks, timber stands, and sagebrush bottoms are used much less frequently (Norland et al. 1985). In YNP, forage availability within preferred sedge and upland feeding sites appears to regulate bison feeding patterns (Meagher 1973). Observations by Vinton and Hartnett (1992) showed bison do not discriminate among plant species in grazed patches. However, Reynolds et al. (1982) stated that where available, sedges and grasses are selectively grazed with dietary shifts between the 2 associated with plant phenology.

Defoliation of grasses can have positive or negative short or long-term effects depending on timing, intensity, and species (Vinton and Hartnett 1992). Overuse of grasses often reduces nutrient allocation to roots or may stop growth completely (Coughenour 1991). In overgrazed grass communities, reductions in litter and leaf shade reduce water available for growth because of increased runoff and evaporation due to higher soil temperatures (Coughenour 1991). Winter grazing increases shoot nitrogen in grasses in spring (Coughenour 1991, Merrill et al. 1994), but 2 abundant grasses on winter ranges in YNP, *Agropyron spicatum* and *Festuca idahoensis*, are sensitive in a number of biological parameters to grazing during the growing season (Evanko and Peterson 1955).

Although no studies have been done to quantify bison forage utilization of seasonal ranges in and around the Park, information collected by Dr. Mary Meagher (1973 and unpubl. data) indicates changes in distribution and habitat use have occurred as bison numbers have increased and man's activities in and around the Park have intensified over the last 4 decades. The consequences of these changes on winter

forage plants and affiliated habitats are unknown, and this lack of knowledge is 1 factor behind the current controversy surrounding bison management in Yellowstone National Park.

Hypotheses

Ho: Summer grazing by bison on winter ranges will produce no significant differences in dry forage weight between grazed (unprotected) and ungrazed (protected) plots.

H₁: Summer grazing by bison on winter ranges will produce significant differences in dry forage weight between grazed and ungrazed plots.

The specific study objectives were to:

1. Examine how bison utilized forage on winter ranges during the summer and early fall, May-October 1996 and May-August 1997, in the Gibbon, Madison, and Firehole drainages.
2. Estimate productivity, removal, and fall standing crop at 6 study sites.
3. Evaluate the portable multi-spectral radiometer (MSR) technology as another method of estimating forage availability in YNP.

4. Track bison seasonal distribution and habitat use within the Gibbon, Madison, and Firehole drainages.

5. Determine if seasonal use patterns are related to plant community composition, snow depth, or utilization intensities at specific sites.

STUDY AREA

YNP occupies 9,000 km² in the northwest corner of Wyoming and adjacent areas in eastern Idaho and southwestern Montana. A generic description of the Park was given by Meagher (1973) and of the study area by Craighead et al. (1973). Park geology is dominated by glaciated tertiary and quarternary volcanic deposits (Keefer 1976). Soils are mainly volcanic rhyolite in origin (Aune 1981).

The study area was located within the Gibbon, Madison, and Firehole River drainages (Figure 1). Elevations ranged from 2,079-2,252 m. Portions of the area were dominated by lodgepole pine (*Pinus contorta*) stands of varying densities, open meadows or parks, and geothermal areas.

Based on preliminary observations, 6 winter pastures with varying vegetation features were chosen to evaluate summer forage utilization on winter ranges. The Gibbon Meadows site was a grass/forb/shrub community bounded on 3 sides by lodgepole pine stands. Snow melt flooded the site each spring. The site dried out slowly over summer, but

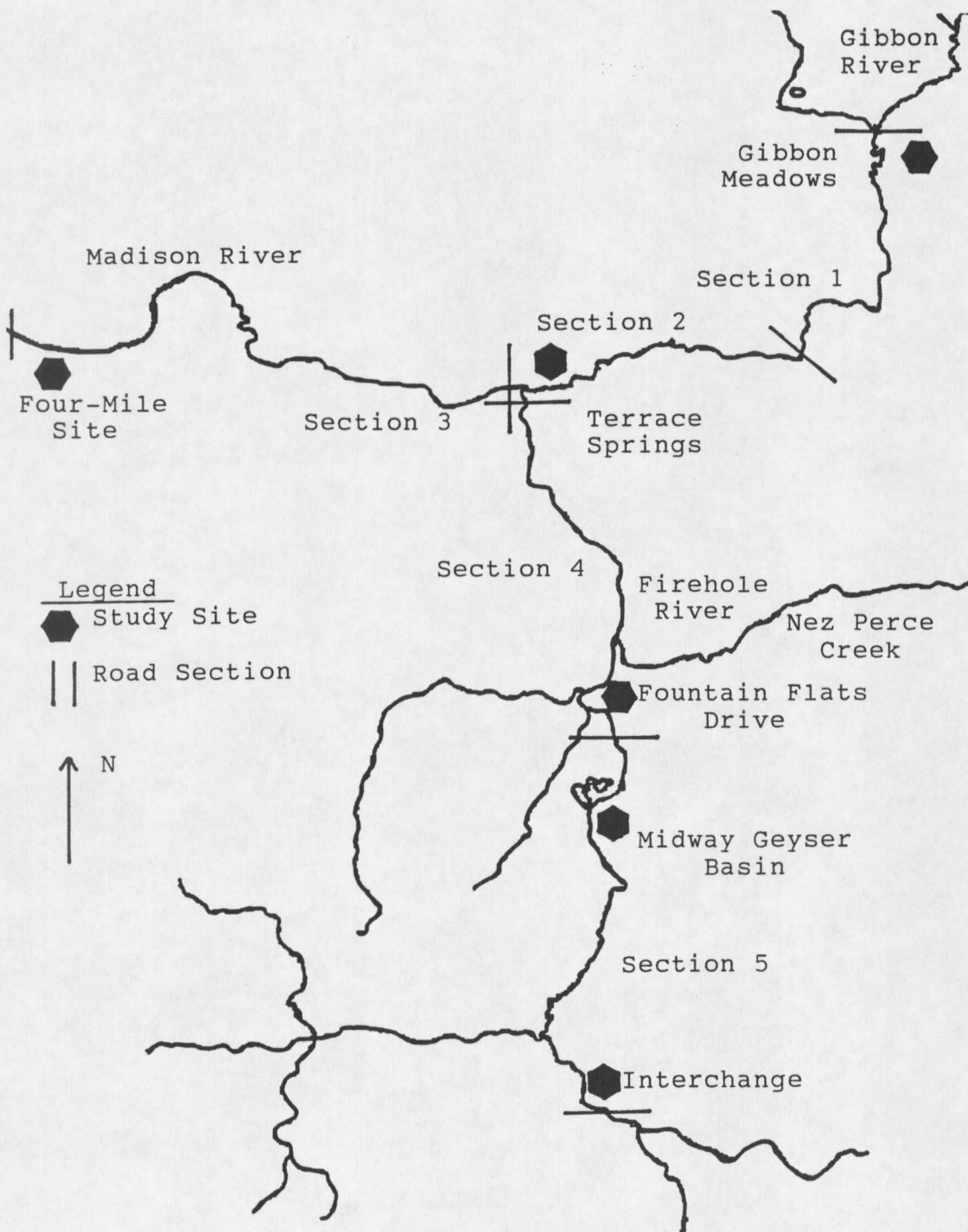


Figure 1. Study site and road section locations.

pools of water were found throughout the summer, and the west end of the site was under water year-round.

The Terrace Springs site was a grass/forb community displaying both riparian and thermal influences. The riparian areas supported dense vegetation, while the thermal areas were characterized by sparse foliage and sand. The site was located in the flood plain of the Gibbon River with drainage from hot springs upslope traversing the site.

The Four-Mile Site was a grass/forb/sagebrush (*Artemisia tridentata*) meadow which was burned in 1988. The site was well drained, had friable sandy loam soil, and was influenced by pocket gophers (*Thomomys* spp.).

The Fountain Flats Drive site was heavily influenced by thermal springs making the site wet throughout the year. Vegetation was predominately *Eleocharis rostellata* with a mixture of grasses and forbs in the drier areas.

The Midway Geyser Basin site was dominated by grass and forbs and had riparian and thermal influence. It was bounded to the west by the Firehole River and to the east by coniferous forest. Vegetation ranged from lush dense

graminoids along the Firehole to sparse forbs and grasses in the thermal area.

The Interchange site was characterized by year-round standing water supporting a dense cover of *Eleocharis rostellata* with sparse grass and forbs intermixed. *Pedicularis groenlandica* covered the southwest corner of the site.

The climate in the study area was cool continental with long cold winters and heavy snowfalls (Meagher 1973). Snowfall can start in late October and last through May in some years. Summers are short and generally cool (Aune 1981). Thermal influences within the study area keep the Gibbon, Madison, and Firehole Rivers mostly ice-free during the winter. Minimum and maximum temperatures, monthly mean temperatures, monthly precipitation, snow depth, and snow water equivalents for September 1994 through August 1997 are given in Appendix Table 15.

Large mammals potentially using forage within the study area in approximate order of biomass included, elk (*Cervus elaphus*), bison, grizzly bear (*Ursus arctos*), moose (*Alces alces*), and mule deer (*Odocoileus hemionus*).

Herbivorous small mammals included: snowshoe hare (*Lepus americanus*), mountain cottontail (*Sylvilagus nuttalli*), yellow-bellied marmot (*Marmota flaviventris*) (Streubel 1989), Uinta ground squirrel (*Spermophilus armatus*), red squirrel (*Tamiasciurus hudsonicus*), and northern pocket gopher (*Thomomys talpoides*). Biomass of these species and potential contribution to forage effects were unknown.

METHODSForage Utilization

The 6 winter range sites [Gibbon Meadows (GM), Terrace Springs (TS), Four-Mile Site (4MS) Fountain Flats Drive (FFD), Midway Geyser Basin (MGB), and Old Faithful Interchange (IC)] selected for this study were centered around Madison Junction for logistic convenience and were marked and gridded in May 1996 (Figure 1). The sites have been registered using GPS technology (Appendix Table 16). The sites are designated as low (GM/4MS), medium (MGB/TS), or high (FFD/IC) use sites based on historical bison use as identified by Park personnel.

Exclosure cages were used to assess summer forage use on the 6 study sites. Cage construction and clipping treatments were modified after Brown (1954) and Frank and McNaughton (1992). One hundred exclosure cages, measuring 1.2 x 1.2 x 1.5 m², were constructed using cattle panels and steel fence posts. Twenty more cages, measuring 1.8 x 1.8 x 1.8 m², were available from a previous study. In June 1996, 20 cages per study site were randomly placed using an

XY coordinate system, then monitored from June-October 1996 and May-August 1997. At each site, 10 of 20 cages were randomly selected as season-long sample units (fixed cages) and 10 other cages as partial season sample units (movable cages). Circular 0.33-m² plots were clipped with garden shears to \approx 13 mm near all cages in June 1996 to estimate available forage at the beginning of the study. Clipped material was separated into live (photosynthetic) and dead (non-photosynthetic) biomass.

In July 1996, all movable cages were moved in a randomly chosen direction (west). A limiting distance of 2 m was chosen to avoid previously clipped plots during subsequent moves. Vegetation in a 0.33-m² plot was then removed both in and outside the cage at its former location and separated into live and dead classes. The direction of the outside clip (north) was randomly chosen. The distance (1 m) of the outside clip was arbitrarily chosen. This sample was taken to estimate forage removal for a 6-week period in June and July. Live biomass was separated by forage class (grass, forb, and shrub) to provide an estimate of the relative abundance of each class during the growing season. In September, movable cages were moved again.

The same clipping routine used in July was repeated. This sample was used to estimate forage removal from July to September, a period of 6 weeks.

In October, all cages were moved and a final clip was conducted. This clip provided estimates of removal from September-October (6 weeks), of total production without ungulate foraging (fixed cages), removal over summer based on fixed cages, and forage availability for the coming fall and winter (plots outside all cages).

The clipping routine was repeated in May, July, and August 1997. In May 1997 all cages were moved. This clip was used to estimate winter removal and to establish a forage availability baseline for the field season. The July sample was used to estimate forage removal from May-July, a period of 6 weeks. In August, all cages were removed from the sites and a final clip was conducted. This clip provided estimates of removal from July-August (6 weeks), of total production in fixed cages, removal for the summer (difference between fixed cage weights and uncaged plots), and forage availability for the coming fall and winter (plots outside all cages).

Vegetation samples were stored in paper bags and transported to drying facilities in YNP or Bozeman. Clipped samples were oven-dried at 60° C for 48 hours, then weighed using an Ohaus electronic scale with an accuracy of +/- 0.1 g.

Two factor ANOVA tests were conducted using MSUSTAT (Lund 1988) to ascertain if the differences between forage clipped from caged and uncaged plots varied among study sites and clipping periods. Percent differences in dry forage weights from fixed cage clippings and movable cage clippings were tested separately. Differences in live and dead forage between caged and uncaged plots at individual sites by clipping session were tested using Student's t-tests in the MSUSTAT package (Lund 1988). Alpha error levels of <0.05 were considered significant. Because logistics precluded large sample sizes, I also noted differences with alpha levels of 0.05-0.10 as near significant under the assumption that larger sample sizes might have revealed more significant differences. This allowed me to identify ambiguous but potentially relevant evidence of utilization.

I estimated forage production and utilization at individual sites using both fixed and movable cages. Forage measurements using fixed cages do not account for compensatory responses of plants to herbivory and can thus over or under estimate production (McNaughton et al. 1996). Frank and McNaughton (1992) employed movable cages in YNP and determined that herbaceous communities in YNP could display compensatory regrowth following grazing in subjectively placed plots. I used my sites to determine if compensatory responses could be detected on randomly placed plots. Formulas for calculating production and removal are given in Appendix Table 17.

Multi-Spectral Radiometry uses differential reflectivity of light in near infrared (NIR) and red (R) bands and has been used as an index to green growing biomass (Nantt 1995). Use of a hand-held Multi-Spectral Radiometry (MSR) unit represents a potentially more efficient means of estimating biomass than clipping (Nantt 1995).

To test the utility of ground MSR technology as a tool in investigating forage use and availability in YNP, I employed a portable MSR unit for ground tests. Sunlight reflectance readings were taken on protected (caged) plots

prior to clipping. Readings in the 660 (red) and 830 (near infrared) nm ranges were used to develop the normalized difference vegetation index (NDVI), a measure of greenness or absorbed radiation. Regression analysis was then conducted comparing the NDVI to the weight of clipped dried green biomass from protected plots. I chose coefficients of determination (R^2) of ≥ 0.80 to indicate accurate predictions of forage weight per plot. A least squares regression line can then be employed to convert NDVI values into an estimate of forage weight for unclipped plots.

To determine plant species composition at each study site, vegetation transects were conducted using a modification of Daubenmire's method (Daubenmire 1959). There were 5 transects per site and 5 plots per transect. Transect lines were 50-m long and spaced 50-m apart, with plots spaced 10-m apart along the line. The starting point and direction for each transect set within the study site were randomly chosen. The direction and spacing of the lines and plots were determined by the compass and pace method. Spearman rank correlations were used to estimate the strength of the relationships between 3 indices of vegetation quality (canopy coverage of all vegetation, of

graminoids, and of desirable graminoids [Meagher 1973, Mueggler and Stewart [1980], Norland et al. 1985]) and forage removal.

Indices of Ungulate Use

I used a combination of fecal pile counts and visual observations to provide an index of site use by bison and elk during the summer. A 200x2-m transect was established at each site. The starting point and direction of the transect were randomly chosen. Counts of feces on transects were conducted in June and October 1996 and May and August 1997. Bison fecal piles were marked with fluorescent paint at the beginning of the field season. Unmarked droppings were counted and marked at the end of the season. Spearman rank correlations were used to indicate the strength of the association between estimated seasonal removal and seasonal fecal counts.

Counts of bison and elk at vegetation sampling sites and in strips along roads between sample sites were made weekly. Counts at vegetation sampling sites occurred throughout the study. Counts on road segments were made only during the summer and autumn. Count corridors were

divided into 5 sections based on habitat and terrain (Figure 1). Spearman rank correlations were used to estimate the strength of the associations between the 2 indices of use, site and road segment counts, and seasonal estimates of forage removal.

I used regression analysis and Spearman rank order correlations to investigate the relationship between indices of bison use (fecal and site counts) and differences between vegetation biomass in grazed and ungrazed plots, and summer removal.

Relationships Between Bison Use Indices and Timber Stands

Twenty-one fecal transects were run in timber stands adjacent to vegetation sampling sites in June 1996 to assess bison use of these habitats. The transects were 100x2-m long, spaced 100-m apart. Deadfall, which could hinder bison movement, was estimated using United States Forest Service methodology (Brown 1974).

Snow Depth

To determine how snow depth may affect bison use of the study sites, snow depth at each site was recorded weekly

during the winter of 1996/1997 using the cages for reference. This procedure entailed a simple visual inspection using the spacing (15.2 cm) between the bars of the cages to estimate snow depth. If snow depth differed around the cages, then the average depth was calculated. Concurrent bison counts were also done. Relationships between snow depth and bison counts (by month and over the winter) and between snow depth and estimated winter removal were calculated using Spearman rank correlations.

RESULTSForage Utilization

During the 3 periods of enclosure, June-October 1996, October 1996-May 1997, and May-August 1997, 2 factor ANOVA of percent differences between protected and unprotected paired plots on season-long fixed cages with site and enclosure periods as factors revealed significant site differences, ($df_{5,162}$, $F = 3.93$, $P < 0.01$), no significant period differences ($df_{2,162}$, $F = 0.45$, $P = 0.64$), and no significant site-period interaction ($df_{10,162}$, $F = 1.49$, $P = 0.15$) for live vegetation. With dead vegetation, there were no significant site differences ($df_{5,162}$, $F = 1.31$, $P = 0.26$), no significant period differences ($df_{2,162}$, $F = 0.82$, $P = 0.44$), but significant site-period interaction ($df_{10,162}$, $F = 2.38$, $P = 0.01$).

With cages moved during each clipping period (July, September, October 1996; May, July, and August 1997), ANOVA for live vegetation revealed no significant site differences ($df_{5,269}$, $F = 1.11$, $P = 0.36$), no significant period differences ($df_{5,269}$, $F = 1.23$, $P = 0.30$), and no significant

site-period interactions ($df_{20,269}$, $F = 0.95$, $P = 0.53$).

Tests for dead vegetation had no significant site differences ($df_{5,269}$, $F = 1.03$, $P = 0.40$), period differences ($df_{5,269}$, $F = 2.15$, $P = 0.07$), or site-period interactions ($df_{20,269}$, $F = 1.02$, $P = 0.44$).

Overall, ANOVA indicated that summer use of winter ranges by bison did not vary consistently among sites or periods for fixed or movable cages. Because ANOVA did not indicate whether differences between caged and uncaged plots were significant, or identify scattered but potentially important differences among sites in individual periods, I examined individual site and period differences using paired t-tests. Forty-nine paired t-tests using 1996 data resulted in 4 significant and 7 near significant ($0.05 < P \leq 0.10$) differences between caged and uncaged plots (Table 1). The majority of the near significant differences occurred during the October (final) clip. The significant tests occurred in July and October. In 5 of 6 sampling periods, Terrace Springs had differences in 1 or both categories. This site was heavily used during winter and spring and was the only site where I found consistent impacts due to bison use.

Gibbon Meadows had a near significant test for live grass in July and a significant test for dead biomass in October. In October, the Four-Mile Site and Midway Geyser Basin approached significance for live biomass and the Interchange site for dead standing biomass.

In 1997, 43 paired t-tests were conducted, and these produced 7 significant and 5 near significant ($0.05 \leq P \leq 0.10$) differences between caged and uncaged plots (Table 1). The majority of these differences occurred during the May clip, immediately following winter and spring use by bison. Three significant and 3 near significant tests occurred during the July and/or August clips. Of the 4 sites identified as moderately or heavily used historically by bison in winter, only 1 (Terrace Springs) consistently showed impacts attributable to bison use. The 2 low use sites exhibited no detectable use in summer 1997.

In July 1997, 5 of 6 sites had no significant differences. Terrace Springs was the exception. Dried weight of green biomass was lower in uncaged plots than caged plots ($P = 0.01$). In the August clip, live herbaceous biomass was significantly greater in fixed cage plots at the Four-Mile Site and approached significance in movable cages

at the Gibbon Meadows and Midway Geyser Basin sites. The difference between dead standing biomass in protected and unprotected plots for the Interchange site also approached significance in the August clip for the movable cages.

Table 1. Results of paired t-tests showing alpha levels at $<0.05(**)$ and $0.05 \leq P \leq 0.10(*)$, No entry indicates alpha >0.10 . All differences identified by asterisks involved higher values in protected plots than in unprotected plots. (GM=Gibbon Meadows, TS=Terrace Springs, 4MS=4-Mile Site, FFD=Fountain Flats Drive, MGB=Midway Geyser Basin, IC=Interchange).

Period Site	Fixed Cage Vegetation		Movable Cage Vegetation	
	Live	Dead	Live	Dead
Jul 1996				
GM			*	
TS			**	
4MS				
FFD				
MGB			*	
IC				
Sept 1996				
GM				
TS			*	
4MS				
Oct 1996				
GM		**		
TS	*	**	**	
4MS			*	
FFD				
MGB	*			
IC		*		
May 1997				
GM				
TS				
4MS	**		**	
FFD		*		
MGB	*			

Table 1. Continued

Period	Fixed Cage	Vegetation	Movable Cage	Vegetation
Site	Live	Dead	Live	Dead
May 1997				
IC		**		**
Jul 1997				
GM				
TS			**	
4MS				
FFD				
MGB				
IC				
Aug 1997				
GM			*	
TS	**			
4MS	**			
FFD				
MGB			*	
IC				*

Available forage was estimated at the start and finish of both summers based on clipping of unprotected plots. Forage availability differed widely between sites, both in early and late season estimates. In June and October 1996, 195-783 and 240-1,509 kg/ha, respectively, were available. Available forage in 1997, was 174-1,011 kg/ha in May and 582-2,340 in August (Table 2).

For the 2 years combined, standing crop inside and outside the cages based on movable cages was 21.5% and 45.5% higher, respectively, than those of fixed cages (Tables 3 and 4).

Table 2. Forage availability (kg/ha) for June and October 1996, May and August 1997.

Clip	Site	Forage	Clip	Site	Forage
June 1996	GM	513	May 1997	GM	585
	4MS	321		4MS	231
	TS	195		TS	222
	MGB	306		MGB	174
	FFD	315		FFD	435
	IC	783		IC	1011
October 1996			August 1997		
	GM	708		GM	1041
	4MS	240		4MS	582
	TS	288		TS	1191
	MGB	492		MGB	987
	FFD	948		FFD	1794
	IC	1509	IC	2340	

Table 3. Standing crop (kg/ha) inside and outside (SD) and estimated percent removal, calculated from means, based on fixed cage data.

Site	Inside		Outside		% Removal	
	1996	1997	1996	1997	1996	1997
GM	1140 (1005)	1359 (66)	480 (483)	69 (642)	42.1	5.1
4MS	537 (546)	879 (594)	201 (360)	270 (375)	37.4	30.7
TS	837 (645)	1704 (1290)	555 (420)	696 (774)	66.3	40.8
MGB	807 (927)	924 (714)	276 (348)	a	34.2	a
FFD	366 (396)	930 (561)	a	189 (690)	a	20.3
IC	1647 (552)	2514 (1617)	207 (567)	a	12.6	a

^aRepresents no detectable standing crop or removal.

Table 4. Standing crop (kg/ha) inside and outside (SD) and estimated percent removal, calculated from means, based on movable cage data.

Site	Inside		Outside		% Removal	
	1996	1997	1996	1997	1996	1997
GM	1554 (2676)	1233 (903)	564 (2049)	213 (576)	36.3	17.3
4MS	717 (1326)	903 (1350)	315 (1236)	228 (393)	43.9	25.2
TS	1323 (945)	2196 (990)	1101 (789)	753 (180)	83.2	34.3
MGB	1821 (1701)	1947 (1767)	306 (111)	555 (192)	16.8	28.5
FFD	483 (717)	957 (717)	183 (195)	171 (60)	37.9	17.9
IC	1893 (678)	1770 (678)	282 (153)	a	14.9	a

^aRepresents no detectable standing crop or removal.

Percent differences between production and removal also reflect higher production and usage with the movable cage technique (Table 5).

Table 5. Percent difference^a in production and removal comparing movable to fixed cage techniques.

Site	Production		Removal	
	1996	1997	1996	1997
GM	36.3	-9.3	17.5	208.0
4MS	33.5	2.7	57.0	-15.6
TS	58.1	28.9	98.0	8.2
MGB	125.7	110.7	11.0	-1421.0
FFD	32.0	2.9	-188.0	-9.5
IC	14.9	-21.3	36.0	-20.7

^aMovable-Fixed/Fixedx100 = Percent difference between movable and fixed cage techniques.

One hundred sixteen MSR reflectance readings were taken. Regression analysis was conducted comparing NDVI to dry biomass weight of clipped plots. Six regressions resulted in 2 r^2 's between 0.70-0.79 and 4 < 0.70 (Table 6). r^2 's of ≥ 0.80 were desired, which would allow for accurate prediction of live biomass in unclipped plots.

Grasses and grasslike plants (*Carex* and *Juncus* spp.) were the dominant ground cover on all sites except Terrace Springs, where forbs had greater canopy coverage than graminoids. Litter was abundant during summer only at

Table 6. Regression analysis for MSR reflectance readings, by year and month of clip.

Year Month	n	r ²
1996	46	0.71
July	33	0.75
Sept	13	0.41
1997	70	0.42
May	23	0.01
July	47	0.56

the Interchange site, Gibbon Meadows, and the Four-Mile Site. Bare ground was highest at Midway Geyser Basin and Fountain Flats Drive. Shrubs were common at Gibbon Meadows (*Potentilla* spp.) and patchy at the Four-Mile Site (*Artemisia* spp.). Mean canopy coverage for 6 sites are shown in Figure 2. Species at each site are identified in Appendix Table 19.

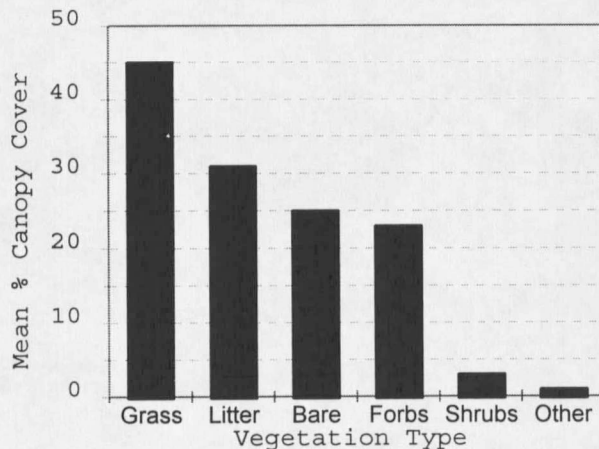


Figure 2. Mean percentage canopy coverage at the 6 study sites combined.

Spearman correlations indicated no associations between the percent canopy coverage in the categories tested and removal (Table 7). Preferred graminoids included species recognized as desirable forage by Mueggler and Stewart (1980). (*Agropyron spicatum*, *A. smithii*, *A. dasysachyum*, *Deschampsia caespitosa*, *Festuca idahoensis*, *Poa pratensis*, *Juncus balticus*, *Eleocharis rostellata*, *Carex lanquinosa*, and *C. microptera*) My casual observations of feeding bison also indicated they did not seem to differentiate between forage classes dominating the canopy while feeding.

Table 7. Spearman correlations (r_s) between canopy coverage of total vegetation, total graminoids, and preferred graminoids and removal.

Year	Vegetation Variable	r_s	P-Value
1996	Total Vegetation	0.54	0.27
	Total Graminoids	0.20	0.70
	Preferred Graminoids	0.54	0.27
1997	Total Vegetation	0.26	0.62
	Total Graminoids	0.86	0.87
	Preferred Graminoids	-0.42	0.40

Fifty-eight plant species, 2 shrubs, 24 graminoids, and 32 forbs were identified in Daubenmire plots. Dominant species at Gibbon Meadows were *Poa pratensis* (Kentucky bluegrass), an unknown grass species, *Fragaria vesca*

(woodland strawberry), and *Potentilla fruticosa* (shrubby cinquefoil). At the Four-Mile Site the dominant species was *Agropyron spicatum* (bluebunch wheatgrass). At Terrace Springs *Poa pratensis* (Kentucky bluegrass) and *Trifolium pratense* (red clover) were dominant. At Midway Geyser Basin *Chrysopsis villosa* (hairy golden aster) and *Carex microptera* (small-winged sedge) dominated. At Fountain Flats Drive *Eleocharis rotellata* (beaked sedge), *Aster ascendens* (everywhere aster), and *Triglochin maritium* (seaside arrow grass) had the highest canopy cover. At the Interchange site, *Eleocharis rostellata* (beaked sedge) dominated.

Indices of Ungulate Use

All sites had fresh fecal deposits in October 1996, but only Terrace Springs, Midway Geyser Basin, and Fountain Flats Drive had new material deposited in August 1997 (Table 8).

Road count totals in 1997 were much lower than in 1996 (189 vs. 994 for bison, 71 vs. 240 for elk) (Figure 3). From June to November 1996, Section 3 (Madison Junction to Four-Mile Site) had the highest count for bison and elk,

while Section 2 (Madison Junction to Gibbon Falls) had the lowest bison total. No elk were seen in Section 4 (Madison Junction to Fountain Flats Drive). Section 4 had the highest total bison count for May-August 1997; Section 5 (Fountain Flats Drive to Old Faithful) had the lowest.

Table 8. Counts of fecal piles at 6 sampling sites from 200x2-m transects for June and October 1996, May and August 1997. October and August counts reflect only differences between June & October 1996 and May & August 1997.

Site	1996		1997	
	June	October	May	August
GM	3	2	2	0
4MS	75	26	41	0
TS	157	91	47	30
MGB	77	21	67	15
FFD	20	18	56	31
IC	56	3	67	0

Counts of animals at sites with cages were lower in 1997 than in 1996 (Figure 3). Site totals of bison declined from 295 to 162. Elk numbers were virtually unchanged. Terrace Springs and Fountain Flats Drive had the highest observed bison use in 1996. Terrace Springs was the only site used extensively by bison in summer 1997. Monthly totals and means by study site for November 1996-August 1997 are given in Appendix Table 18.

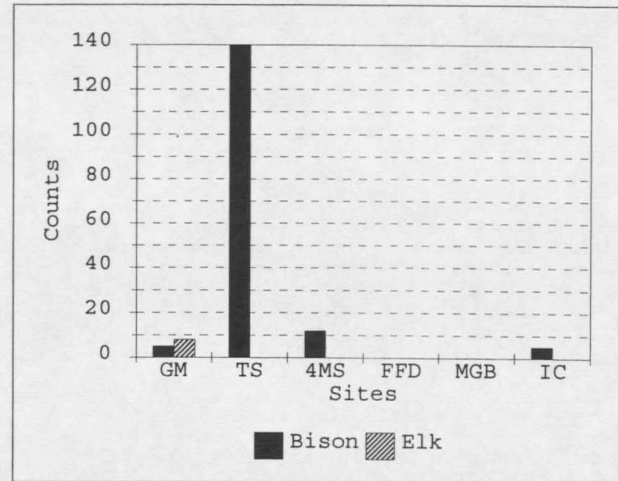
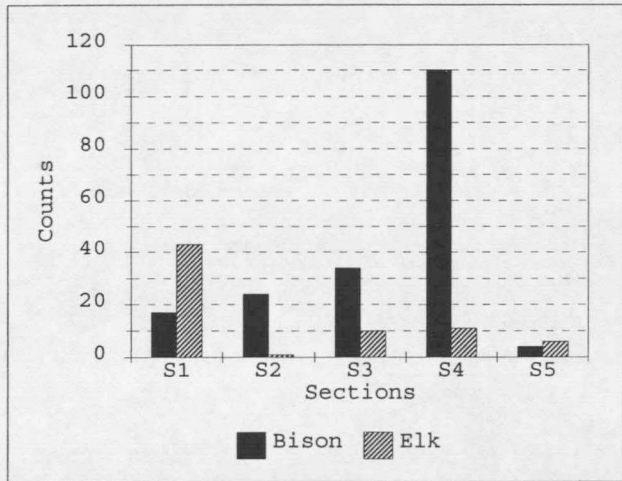
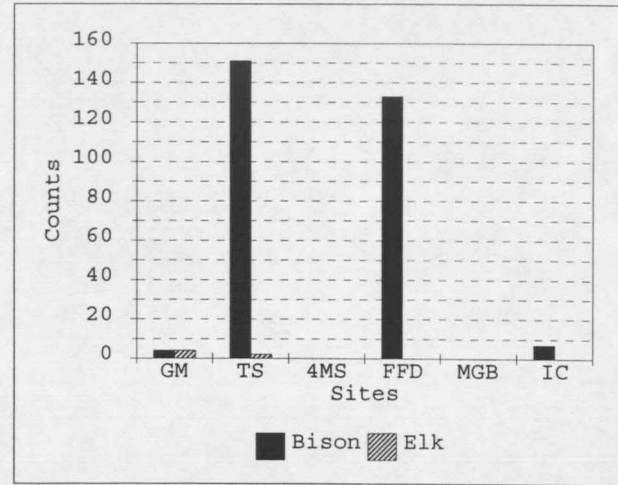
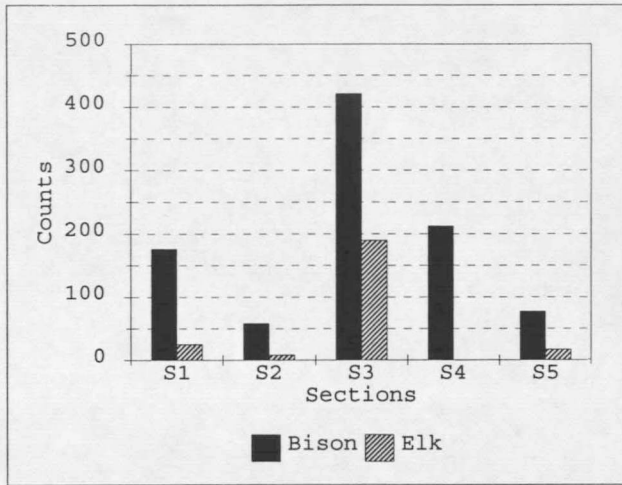


Figure 3. Road section and site counts of bison and elk for 1996 (top) and 1997 (bottom). Sections and sites are identified in Figure 1.

Regression analysis was conducted with bison or fecal counts as the independent variable and the percent difference between inside and outside the cages of both live and dead biomass as the dependent variable (Table 9). Of the 19 regressions I calculated, only 1 significant associations were found. $R^2 = 0.61$, denoting a moderate fit.

Table 9. Regression analysis (n = 6 sites) for bison and fecal counts vs. percent difference between protected and unprotected plots, and fecal counts vs. bison counts on winter sites.

<u>Independent Variable</u>	<u>Dependent Variable</u>	<u>R²</u>	<u>Slope</u>
1996			
Jun-Oct Bison Count	Oct Live Vegetation ^a	0.00	-
Jun-Oct Bison Count	Oct Dead Vegetation ^a	0.01	+
Jun-Oct Bison Count	Oct Live Vegetation ^b	0.00	-
Jun-Oct Bison Count	Oct Dead Vegetation ^b	0.00	+
Oct Fecal Count	Oct Live Vegetation ^a	0.08	+
Oct Fecal Count	Oct Dead Vegetation ^a	0.06	+
Oct Fecal Count	Oct Live Vegetation ^b	0.13	+
Oct Fecal Count	Oct Dead Vegetation ^b	0.16	+
Oct Fecal Count	Oct Bison Count	0.08	-
1997			
Nov-May Bison Count	May Dead Vegetation ^a	0.04	+
Nov-May Bison Count	May Live Vegetation ^a	0.28	-
Jun-Aug Bison Count	Aug Live Vegetation ^a	0.11	+
Jun-Aug Bison Count	Aug Live Vegetation ^b	0.16	+
May Fecal Count	May Dead Vegetation ^a	0.61	+
May Fecal Count	May Live Vegetation ^a	0.00	+
Aug Fecal Count	Aug Live Vegetation ^a	0.24	-
Aug Fecal Count	Aug Live Vegetation ^b	0.24	-
May Fecal Count	May Bison Count	0.34	+
<u>Aug Fecal Count</u>	<u>Aug Bison Count</u>	<u>0.26</u>	<u>+</u>

^aFrom all cages.

^bFrom fixed cages.

Spearman correlations found no association between forage removed in summer and 3 indices of animal use, fecal, site, and road counts (Table 10).

Table 10. Spearman correlations (r_s) between animal indices and summer removal, 1996/1997.

Year	Count Type	r_s	n	P-Value
1996	Fecal	0.14	12	0.78
1996	Site	-0.23	6	0.66
1996	Road	0.60	5	0.28
1997	Fecal	0.39	12	0.43
1997	Site	0.62	6	0.19
1997	Road	0.40	5	0.50

Relationships Between Bison Use Indices and Timber Stands

Distribution of feces in June 1996 indicated bison use of timbered habitats decreased rapidly with distance from edge. Counts apparently decreased more rapidly in stands where heavy deadfall was encountered than in stands with light or moderate deadfall. (Table 11).

Snow Depth

Mean monthly snow depth was calculated based on weekly snow depths measured from November 1996 through May 1997 (Table 12). Average snow depth at Gibbon Meadows was 2 times greater than the other 5 sites. Fountain Flats Drive

and Terrace Springs had the lowest averages. There was no association between mean monthly snow depth and bison use of the study sites during winter (Table 13). I also found no association between mean snow depth overwinter and my estimates of winter forage removal at individual sites, ($r_s = -0.63$, P-value = 0.17).

Table 11. Timber stand fecal counts based on 100x2-m transects.

Site	Meters into Stand	Fecal Count	Deadfall
TS	Edge	22	Heavy
	100	11	
	200	5	
4MS	Edge	5	Heavy
	100	0	
	200	3	
MGB	Edge	30	Moderate
	100	22	
	200	27	
FFD	Edge	28	Light to Heavy
	100	10	
	200	6	
	300	5	
	400	11	
Madison Junction	Edge	16	Light to Heavy
	Edge	14	
	100	5	
	200	2	
	300	7	
	400	10	
	Edge	30	

Table 12. Snow depth (cm) at 6 study sites
November 1996-May 1997. (^^^=no reading)

Month	GM	4MS	TS	MGB	FFD	IC
November	15.2	5.0	5.0	5.0	^^^	7.6
December	55.8	25.4	50.8	29.4	15.2	20.3
January	82.8	46.9	43.9	24.1	7.0	65.5
February	96.5	33.0	27.9	22.8	20.3	31.7
March	96.5	60.9	31.7	14.2	0.0	32.0
April	77.4	7.6	5.5	0.0	0.0	7.6
May	22.8	0.0	0.0	0.0	0.0	0.0
Average	63.5	25.5	16.5	18.2	16.5	23.6
Max	101.6	94.0	55.8	35.5	76.2	78.1

Table 13. Spearman correlations (r_s) between snow depth and bison numbers on 6 study sites by month, and over 7 months, November 1996-May 1997.

Month	r_s	P-Value
November	0.22	0.66
December	-0.23	0.66
January	-0.55	0.26
February	-0.60	0.23
March	-0.14	0.80
April	-0.38	0.46
May	-0.31	0.55
November-May	-0.64	0.17

DISCUSSION

Forage Utilization

Frank (1990) and Frank and McNaughton (1992,1993) outline potential positive and negative impacts of herbivores on herbaceous vegetation on the Park's northern range. Medium intensity grazing on early season growth should increase forage production [where water, soil, temperature, and plant species composition permit (see Hobbs, 1996)] through grazing-induced stimulation of plant growth, nutrient addition via feces/urine, and by causing soil surface changes that increase soil temperatures and water infiltration. Heavy grazing through the growing season could inhibit production through repeated regrazing of individual plants and soil compaction. Heavy grazing under drought conditions would exacerbate these effects. If the negative impacts Frank and McNaughton identified in subjectively selected sites are widespread in YNP, major changes in herbivore management would be needed to stabilize plant community dynamics.

My results, based on ≈ 1.4 - 2.8 times greater numbers of

paired plots than were sampled by Frank (1990), in a stratified random design produced ambiguous results. ANOVA indicated moderate and highly variable differences between biomass in caged and uncaged plots. Although protected plots tended to have means 39% higher in 1996 and 24% higher in 1997 than unprotected plots at individual sites, the extreme variability among paired plots at individual sites did not allow me to conclude that ungulates were responsible for these differences. The site effect identified for the growing season in fixed cages probably did reflect differences in herbivore use among sites. Terrace Springs had high differences in biomass between protected and unprotected plots throughout the 1996 growing season. Gibbon Meadows and the Interchange sites had near significant differences only in live grass and only in July 1996. There was little differences between caged and uncaged plots at the other sites. Three of the 4 sites which had the greatest differences during the growing season were sites I selected as moderate or high use wintering areas by bison.

The significant site-period interaction for dead vegetation in fixed cages was apparently the result of

herbivore use patterns over winter. Those sites heavily used by bison during winter 1996-1997 had lower biomass of residual forage in unprotected than in protected plots by May 1997. Two sites not used by bison had no difference. At the Midway Geyser Basin, a moderately used site, no standing vegetation was left in either protected or unprotected plots.

The lack of site-period interaction in tests based on dead vegetation in movable cages comparable to those tests of fixed cages, was influenced by unexpected overwinter differences among sites. Only 1 of the 3 heavily used sites showed an overwinter decline in standing forage. Standing forage inside and outside of cages was comparable in 1, and no standing dead forage was detected in caged or uncaged plots in the other. The disappearance of vegetation enclosed by cages at Midway Geyser Basin and Terrace Springs over winter was unexpected. This may represent loss of vegetation due to snow compaction and vegetative decay or rodent activity under the snow.

The failure of ANOVA and Student's t-tests to identify more differences in forage removal among sites and periods that were consistent with intensities of use by ungulates

could be an artifact of the study design. A stratified random sampling design such as I used was unlikely to identify small growing season effects due to ungulate herbivory for 2 reasons:

- 1) Bison do not graze vegetation uniformly. They graze dominant patches in May, then tend to regraze the same patches again throughout the season (Vinton and Hartnett 1992) rather than graze new areas which may contain more biomass but are less palatable and nutritious. Random placement of cages resulted in sampling unused and repeatedly used patches. In most sites, the proportion of the site used was low, but in moderately used sites, the 2 types of patches inflated variance. The large variances I calculated required large differences between means at protected and unprotected plots to produce statistically significant tests.

- 2) With the exception of the Interchange site, vegetation at all our sites was patchy in distribution, with canopy cover ranging from heavy to nonexistent at small spatial scales within each site. My random placement of cages captured this distribution pattern, and it was reflected in large standard deviations around means at

individual sites.

Despite the limitations of the sampling design, the sites where I conducted clipping experiments covered the range of use intensities exhibited by bison and the range of herbaceous vegetative cover in the study area. I was able to use this variability to detect site specific patterns of use that illustrate the complexity of the bison vegetation interaction in the study area.

Gibbon Meadows was initially selected as an example of a low use winter site. I observed only 9 bison at this site during the study. Fecal transects confirm that bison rarely used the site and only 15 elk were counted during the study. Twenty-one Student's t-tests showed only 2 significant and 1 near significant differences between protected and unprotected plots. These differences were probably due to the patchy nature of vegetation distribution on the site, as there was no evidence, ie. grazed plants, of bison feeding.

Terrace Springs, historically considered a medium use winter site by Park staff, was heavily impacted by ungulate use. During the 15-month period of the study, bison were seen on the site in 53% of my counts. The heaviest use occurred during the winter and spring. From November 1996-

June 1997, bison were on the site in every month except March. Twenty-three elk were counted during this same time frame, but elk use during the winter was mainly confined to the thermal areas upslope from the cages (Garrott pers. commun. 1997). Bison also concentrated on this site in June of both years with a high count of 101 animals in 1996 and 131 in 1997. As a result, the fall standing crop at Terrace Springs was not as great as it potentially could have been without summer use by bison in both 1996 (high bison population) and 1997 (\approx 38% lower bison population).

Defoliation through repeated grazing causes plant tillers to have lower growth rates, accumulate less biomass, and suffer higher mortality rates (Vinton and Hartnett 1992). Continuous winter use coupled with the added effect of grazing during the May-June greenup period may prevent forage plants at Terrace Springs from recovering from the effects of grazing in many years. There are no earlier plant species lists or vegetation surveys that could confirm the potential for community changes related to grazing, but the frequent occurrence of Kentucky bluegrass, an exotic, suggests that over use by ungulates may have altered the vegetation species composition.

Four-Mile Site, designated as a low use area by Park staff, had only 12 bison counted during the study. There were no significant differences between caged and uncaged plots but 1 near significant test ($P = 0.08$) for 1996. In 1997, my tests showed significantly less standing live vegetation in unprotected plots than in protected plots during the May and August samples. One possible reason for the lack of concurrence between clipping results and counts could have been missed bison groups. Counts were conducted on a weekly basis throughout the study, thus not every animal moving through the site would be seen. If a group of bison fed in and around a cluster of cages, this would account for the significant results of the t-tests and is the most plausible explanation. However, in addition to bison, pocket gophers (Thomomys spp.) are prevalent throughout the site.

Studies have shown that pocket gophers affect range and soil condition, and most important for this study, forage availability. Whether the effects are beneficial, (Elison and Aldous 1952, Ingles 1952) or deleterious (Julander et. al 1959, Moore and Reid 1951) is a matter of debate. Given that a large portion of the winter diet of

pocket gophers is comprised of green stems of grasses and sedges, and summer food is mostly roots growing in tunnels (Ingles 1952), these animals could be partially responsible for the significant or near significant statistical differences in live biomass noted in May and August 1997. No differences for dead material were noted in 1996 or May 1997, and dead biomass was not evident after the May clip.

Fountain Flats Drive was selected as a high use winter site. During the course of the study 336 bison were counted on the site. Over 50% of this total was counted during 1996, with the majority occupying the site during the August-September rut. Despite this, no detectable use was found during the October clip session. The remaining bison were observed from November 1996-May 1997. No bison were observed during the 1997 summer field season. The use of this site throughout the winter and spring was consistent with the near significantly lower biomass in unprotected plots in the May sample. By July, green biomass had recovered, and no statistical differences were found in the July or August samples. No dead biomass was evident after the May sample.

Midway Geyser Basin has historically been considered a

medium use site even though we observed only 25 bison in 14 months. Despite low bison counts during summer 1996, the difference in live biomass between caged and uncaged plots approached significance ($P = 0.07$) in the October 1996 sample. No differences or near differences were detected earlier in the 1996 summer. The difference in live biomass between protected and unprotected plots was significant in May 1997 ($P = 0.03$) and approached significance ($P = 0.08$) in August 1997. Short-term use by a large group of bison or elk could have been missed in counts but still could have impacted the site.

The Interchange site is regarded as a high use area by YNP staff and other researchers. During winter, November 1996 through April 1997, 232 bison were counted. During the course of the study, only 12 bison were counted outside the winter months. There were no detectable differences between caged and uncaged plots in 1996 although 2 tests, live grass in July and dead biomass in October, approached significance. As with other sites, these differences could be the result of unobserved use by bison or variability in plant distribution. Bison were seen in every month from

November 1996 through May 1997. The significantly lower ($P < 0.01$) biomass for dead uncaged vegetation in the May 1997 sample was consistent with continuous use of biomass on this site during the winter. During the 1997 summer, no bison were counted on the site, and statistical tests for July and August 1997 samples showed no difference between caged and uncaged vegetation for live or dead vegetation, although the test for dead vegetation in August indicated a difference might have been detectable with a larger sample size.

McNaughton et al. (1996) suggested the use of movable cages as a means of incorporating plant responses to herbivory into conventional assessments of herbivore impacts on communities. Forage estimates based on movable cages at 6 sites in YNP were generally higher than estimates based on fixed cages. However, at some sites, production and removal estimates were higher for the fixed cages. When movable enclosure cages are placed selectively on areas known to be regrazed several times during a season, then increased production and removal estimates probably do reflect a herbivore impact (Frank and McNaughton 1993). My cages, however, were placed randomly on selected winter use sites

with highly variable vegetative cover and distribution. With the exception of Terrace Springs, site counts and Student's t-test results, do not indicate substantial use of my exclosure sites during the summer by bison, elk, or other large herbivores. Thus, it is not possible to conclude that herbivory is solely responsible for the discrepancies noted between the two methods of forage estimation. Seasonal climatic changes and vegetation variability, may contribute as well. I can not state unequivocally that my movable cages detected any grazing effects that would not have been identified with seasonally fixed cages. McNaughton (1996) acknowledged limitations of the movable cage approach.

Adequacy of Sample Size for Caged Plots

Small sample size was a problem due to constraints placed upon the investigators. I was limited in the number of cages (120) and sites (6) because of concerns over aesthetic impacts to Park visitors. Additionally, I was limited in the manpower and money required to buy, build, and transport large numbers of cages on and off the sites and to move cages and clip vegetation during the field season.

In an attempt to see what effect larger sample sizes would have had on my paired t-tests, sites were grouped by the month of each clip (Table 14). Fifty percent of these tests showed significance compared to 12% of the individual site tests. These results suggest that more exclosure cages randomly distributed through the study area would have identified more significant winter, early growing season, and late growing season effects on fall/winter forage availability in 1996 but not in 1997.

Table 14. Means (SD) of dry biomass (g/0.33 m²) for paired t-tests of clipped sites grouped by month of clip.

Month	Inside Cage	Outside Cage	P-Value
1996			
July, n=60 prs			
Live	41.5 (30.9)	30.8 (24.8)	0.00
Dead	4.9 (5.8)	6.3 (9.1)	0.09
Sept, n=30 prs			
Live	16.3 (14.5)	13.5 (11.2)	0.17
Dead	5.8 (7.6)	6.1 (8.7)	0.65
October, n=120 prs			
Live	10.5 (24.5)	7.1 (21.0)	0.00
Dead	18.4 (22.0)	16.0 (20.9)	0.03
1997			
May, n=120 prs			
Live	8.3 (11.4)	5.1 (4.7)	0.00
Dead	18.8 (31.2)	9.7 (15.7)	0.00
July, n=60 prs			
Live	35.3 (29.5)	28.9 (28.5)	0.02
Dead	2.4 (7.9)	1.8 (7.8)	0.39
August, n=120 prs			
Live	42.6 (30.8)	44.1 (72.0)	0.81
Dead	3.7 (17.0)	1.7 (7.3)	0.17

Relationships Between Bison Use Indices and Timber Stands

Bison mostly foraged in open meadows but were observed feeding at the peripheries of timber stands. Bison were also seen moving through stands but not feeding. Reynolds (1978) reported that bison use forest habitat for loafing and ruminating during the winter months. My counts of feces in June 1996 indicated that bison in YNP do use forested types, but the rapid decline in fecal density as I moved into stands suggests that open vegetation is the primary feeding habitat in the Park.

Assessment of the Utility of the Multi-Spectral Radiometer

Part of the failure to achieve consistent high correlations between forage biomass measured in clipping and MSR readings was due to the size of the clipped plots vs. the size of the area read by the MSR sensors. The MSR works best when sensor height is >1.8 m from the ground (Norland, pers. commun. 1997). This height samples an area of 0.75 m^2 . Due to the size of my cages, I could only clip an area equal to 0.33 m^2 . Thus, only $1/3$ of the area on which the MSR estimate was based was included in the clipped

sample. In uniform vegetation this would not be a problem. In vegetation with high variability, at the spatial scale I sampled, it could be.

Other factors that evidently reduced correlations were standing water, low (<30% canopy coverage) green biomass values, patches of bare ground, and senescent vegetation (Aase et al. 1987, Norland pers. commun. 1998). Of these factors, the latter three probably contributed most to the lackluster performance of the MSR.

CONCLUSIONS

At the end of the growing season, I could detect 1 or more differences ($P < 0.10$) between standing crops in protected and unprotected plots at 5 of 6 sites in 1996 and 4 of 6 in 1997. Although means for protected plots were higher than those for unprotected plots in all significant or near significant tests, the poor correlations with fecal and sighting indices suggests that those differences were, at most, only partially due to elk and bison foraging. Terrace Springs was the exception. Forage removed was likely due to continuous winter use by bison in 1996-1997 and heavy use in June 1996 and 1997. Samples I used only had adequate power to detect forage removals of $\approx 50\%$, but many herbaceous plant communities can tolerate foliar removal of $< 50\%$ without detrimental long-term effects (Payne and Young, 1948). If this generalization is valid for herbaceous communities in YNP, there is little evidence to support the contention that summer utilization of winter ranges is deleterious to plant communities in the Gibbon, Madison, Firehole areas. It appears that the Gibbon, Madison, and Firehole winter ranges can sustain the level of

growing season utilization associated with the pre-1997 bison population.

Multi-spectral radiometer technology can be useful but was limited by several factors. Until (and if) sampling refinements are made, it may be used as a supplement to standard clipping treatments but not as a substitute.

Fecal counts were useful in determining past presence of animals, but failure to find feces did not unequivocally demonstrate the absence of animal use. The amount of forage removed while feeding was not correlated with fecal density.

Weekly counts along road transects and at specific sites can give a coarse picture of bison and elk distribution and movements. However, there appeared to be no direct link between weekly animal counts and intensity of forage utilization at specific sites in the Madison, Gibbon, and Firehole drainages. More frequent diurnal and nocturnal counts could improve the association.

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APPENDIX

Table 15. Mean monthly, minimum and maximum monthly temperatures (C), total monthly precipitation, snow depth, and snow water equivalent (cm) from September 1994 to August 1997.

MONTH/YEAR	AVERAGE	MAXIMUM	MINIMUM	PRECIPITATION	SNOW DEPTH	SWE*
SEPTEMBER 1994	13.2	23.3	3	1.3	0	0
OCTOBER	4.4	10.2	-1.4	6.3	0	2
NOVEMBER	-7.6	-2.8	-12.4	9.3	48.3	12.2
DECEMBER	-8.4	-4.2	-12.7	10.7	73.7	37.3
JANUARY 1995	-10.3	-5.6	-15	11	101.6	52.1
FEBRUARY	-6.4	-0.1	-12.8	3.3	109.2	63
MARCH	-3.8	2.1	-9.7	13	116.8	78.7
APRIL	1	6.4	-4.4	6.1	86.4	85.1
MAY	8.9	16.4	1.3	8.7	12.7	79.5
JUNE	-0.7	17.8	3.1	12.5	0	21.6
JULY	15.2	23.8	6.4	5.8	0	0
AUGUST	15.9	25.8	6	3.5	0	0.3
SEPTEMBER	11.1	19.3	2.8	2.6	0	0.3
OCTOBER	3.2	9.4	-2.9	4.7	0	3
NOVEMBER	-1.2	2.8	-5.1	8.4	33	10.7
DECEMBER	-8.6	-3.9	-13.2	7.9	48.3	27.7
JANUARY 1996	-11.6	-5.6	-17.6	9.6	86.4	39.1
FEBRUARY	-9.6	-2.6	-16.5	6	94	52.1
MARCH	-4.4	2.6	-11.4	7.1	114.3	66.8
APRIL	1.8	8	-4.4	4.7	83.8	74.9
MAY	5.4	11.2	-0.3	14.1	17.8	67.8
JUNE	13.7	22.7	4.6	2.5	0	12.4
JULY	17.8	26.8	8.8	3.2	0	0
AUGUST	16.8	26.2	7.4	1.7	0	0
SEPTEMBER	10.8	18.8	2.7	3.2	0	0.3
OCTOBER	4.9	11.4	-1.7	5.4	0	2
NOVEMBER	-2.2	0.6	-5.1	7.1	5	11.4
DECEMBER	-9.1	-3.7	-14.6	10.1	25.4	32.8
JANUARY 1997	-11.2	-2.9	-19.4	7.5	46.9	72.6
FEBRUARY	-11	-0.7	-21.3	3.7	33	85.9
MARCH	-4.4	2.7	-11.7	3.1	60.9	101.6
APRIL	-2.8	4.4	-10.5	9.1	7.6	110
MAY	4.5	12	-1.7	3.1	0	77.2
JUNE	10.2	18.1	2.3	8	0	6.6
JULY	12.6	20.4	4.7	5.7	0	0
AUGUST	13.3	21.4	5.1	3.5	0	0
AVERAGE	2	9.2	-4.7	6.5	33.5	35.8

*SNOW WATER EQUIVALENT

Table 16. Size (ha) and location (UTM) of study sites.

Site	Size	Location
Gibbon Meadows	2	520625 m E/4949779 m N
Four-Mile Site	9	499172 m E/4943489 m N
Terrace Springs	9	512400 m E/4943220 m N
Midway Geyser Basin	2	512905 m E/4930838 m N
Fountain Flats Dr.	9	513821 m E/4934887 m N
Interchange	4	512379 m E/4922574 m N

Table 17. Formulas used in forage calculations

<u>Calculations</u>	
<u>Fixed Cages</u>	
Total Production:	Final Cut Inside Standing Crop $\times 3 \times 10$. ex. $38 \text{ g}/.33\text{m}^2 \times 3 \times 10 = 1140 \text{ kg/ha}$
Total Offtake:	Final Cut Inside Standing Crop-Final Cut Outside Standing Crop $\times 3 \times 10$. ex. $37.9 - 21.9 = 16 \text{ g}/.33\text{m}^2 \times 3 \times 10 = 480 \text{ kg/ha}$
Percent Offtake:	Total Offtake/Total Production $\times 100$. ex. $480/1140 = 42.1\%$
<u>Movable Cages</u>	
Total Production:	Sum of Differences (In-Out)+ Final Cut In Over All Clips $\times 3 \times 10$. ex. $(37.3 - 26.6) + (19.5 - 19.6) + (33 - 24.8) + 33 =$ $51.8 \text{ g}/.33\text{m}^2 \times 3 \times 10 = 1544 \text{ kg/ha}$
Total Offtake:	Sum of Differences (In-Out) Over All Clips $\times 3 \times 10$. ex. $(37.3 - 26.6) + (19.5 - 19.6) + (33 - 24.8) =$ $18.8 \text{ g}/.33\text{m}^2 \times 3 \times 10 = 564 \text{ kg/ha}$
Percent Offtake:	Total Offtake/Total Production $\times 100$. ex. $564/1544 = 36.3\%$
<u>Percent Difference Between Movable and Fixed Cages</u>	
Movable vs. Fixed Production:	Movable-Fixed/Fixed $\times 100$. ex. $1544 - 1140/1140 = 36.3\%$
Movable vs. Fixed Offtake:	Movable-Fixed/Fixed $\times 100$. ex. $564 - 480/480 = 17.5\%$
<u>Forage Removed Between Clips</u>	
Amount Removed:	Inside-Outsidex 3×10 . ex. $23.4 - 17.3 = 6.1 \text{ g}/.33\text{m}^2 \times 3 \times 10 = 183 \text{ kg/ha}$
<u>Forage Availability</u>	
Sum of outside clips at the beginning and end of each field season.	

Table 18. Bison and Elk counts for November 1996-August 1997

Bison

Site	November	December	January	February	March	April	May	June	July	August	Total	Avg	Stds
GM	0	0	0	0	0	0	0	0	5	0	5	0.5	1.6
4MS	0	0	0	0	0	0	12	0	0	0	12	1.2	3.8
TS	3	15	64	7	0	13	0	140	0	0	242	24.2	45.1
MGB	2	3	12	4	4	0	0	0	0	0	25	2.5	3.7
FFD	0	7	144	30	0	22	0	0	0	0	203	20.3	44.8
IC	5	8	112	39	55	15	5	0	0	0	239	23.9	36.1
Total	10	33	332	80	59	50	17	140	5	0	726	72.6	100.6
Avg	1.7	5.5	55.3	13.3	9.8	8.3	2.8	23.3	0.8	0			
Stds	2.1	5.8	61.9	16.8	22.2	9.6	4.9	57.2	2	0			

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Elk

Site	November	December	January	February	March	April	May	June	July	August	Total	Avg	Stds
GM	0	0	3	0	0	0	0	0	8	0	11	1.1	2.6
4MS	0	0	0	0	0	0	0	0	0	0	0	0	0
TS	3	0	10	4	2	4	0	0	0	0	23	2.3	3.2
MGB	2	17	10	7	7	0	0	0	0	0	43	4.3	5.8
FFD	0	0	0	0	0	0	0	0	0	0	0	0	0
IC	0	11	0	1	0	0	2	0	0	0	14	1.4	3.4
Total	5	28	23	12	9	4	2	0	8	0	91	9.1	9.5
Avg	0.8	4.7	3.8	2	1.5	0.7	0.3	0	1.3	0			
Stds	1.3	7.5	4.9	2.9	2.8	1.6	0.8	0	3.3	0			

Table 19. Vegetation types, mean canopy coverage (frequencies in parentheses)
for 25 Daubenmire plots per study site.^a

	GM	4MS	TS	MGB	FFD	IC
<u>Grass & Grasslike Plants</u>						
<i>Agropyron smithii</i>				9.8(12.0)	tr(8.0)	
<i>Agropyron dasystachyum</i>				tr(4.0)		
<i>Agropyron spicatum</i>		14.6(72.0)		1.4(16.0)		
<i>Agropyron trachycaulum</i>			tr(12.0)			
<i>Agrostis stoloneferia</i>			tr(4.0)	6.2(8.0)		
<i>Carex lanuginosa</i>	2.0(4.0)					
<i>Carex microptera</i>	4.0(4.0)			8.0(12.0)		
<i>Carex</i> spp.		4.6(44.0)				
<i>Carex stenophylla</i>		tr(20.0)				
<i>Danthonia intermedia</i>	1.2(8.0)	tr(12.0)				
<i>Deschampsia caespitosa</i>	5.2(20.0)		2.0(4.0)	3.0(16.0)		
<i>Eleocharis rostellata</i>				tr(4.0)	16.2(20.0)	85(96.0)
<i>Festuca idahoensis</i>		tr(4.0)		tr(24.0)		
<i>Juncus balticus</i>	1.8(28.0)		tr(12.0)	5.0(24.0)		5.8(8.0)
<i>Juncus bufonis</i>						
<i>Oryzopsis hymenoides</i>		tr(4.0)				
<i>Phleum pratense</i>	2.6(24.0)		1.8(4.0)	1.2(28.0)		
<i>Poa pratensis</i>	12.4(44.0)		39.0(96.0)	1.3(12.0)	6.6(16.0)	1.6(16.0)
<i>Spartina gracilis</i>				1.0(16.0)	8.0(12.0)	
<i>Poa secunda</i>		tr(12.0)		1.0(36.0)		
<i>Stipa columbiana</i>						
<i>Stipa comata</i>		1.4(28.0)		tr(24.0)		
<i>Triglochin maritimum</i>				tr(4.0)	9.6(20.0)	
Unknown grass	11.6(32.0)					
<u>Forbs & Shrubs</u>						
<i>Achillea millefolium</i>	2.4(12.0)	T(12.0)	2.0(24.0)	tr(12.0)	1.2(8.0)	
<i>Agoseris glauca</i>	1.4(12.0)	8.0(36.0)	tr(12.0)		tr(4.0)	
<i>Allium</i> sp.						4.0(8.0)

Table 19. Continued

	GM	4MS	TS	MGB	FFD	IC
<u>Forbs & Shrubs</u>						
<i>Antennaria microphylla</i>	3.2(12.0)	2.1(24.0)	6.2(20.0)	tr(12.0)		
<i>Arabis</i> sp.		1.7(40.0)		tr(40.0)		
<i>Arenaria</i> sp.		tr(20.0)		tr(32.0)		
<i>Artemisia tridentata</i>		1.0(4.0)				
<i>Aster ascendens</i>		2.0(36.0)		tr(4.0)	11.0(20.0)	1.0(4.0)
<i>Aster chilensis</i>		tr(12.0)				
<i>Campanula rotundifolia</i>		tr(4.0)	tr(12.0)			
<i>Castilleja pallescens</i>			tr(4.0)			
<i>Chrysopsis villosa</i>				6.0(60.0)		
<i>Cirsium arvense</i>						
<i>Cirsium scariosum</i>			tr(4.0)		5.4(8.0)	
<i>Crepis modocensis</i>				tr(8.0)		
<i>Dodecatheon conjugens</i>						
<i>Epilobium paniculatum</i>				tr(4.0)		
<i>Eriogonum umbellatum</i>		3.5(20.0)	tr(12.0)	tr(4.0)		
<i>Fragaria vesca</i>	11.6(24.0)					
<i>Lupinus argenteus</i>		4.0(76.0)				
<i>Medicago lupulina</i>			tr(4.0)			
Moss spp.		tr(4.0)				
<i>Orthocarpus luteus</i>			tr(4.0)			
<i>Pedicularis groenlandica</i>					20(20.0)	
<i>Phacelia hastata</i>				tr(4.0)		
<i>Phlox hoodii</i>		tr(16.0)		tr(32.0)		
<i>Polygonum douglasii</i>		4.6(40.0)				
<i>Potentilla diversifolia</i>	8.4(40.0)					
<i>Potentilla fruticosa</i>	13.4(40.0)		2.2(8.0)			
<i>Senecio crassulus</i>					5.6(12.0)	4.0(8.0)
<i>Sisyrinchium idahoensis</i>			tr(16.0)			
<i>Solidago missouriensis</i>	2.0(4.0)				2.0(4.0)	

Table 19. continued

	GM	4MS	TS	MGB	FFD	IC
<u>Forbs & Shrubs</u>						
<i>Trifolium pratense</i>	0.6 (8.0)		34.8 (64.0)	tr (12.0)		
Unknown forb		tr (20.0)	2.6 (12.0)	tr (8.0)		1.0 (4.0)

^atr = <1.0%

Table 20. Road transect sections length (km) and mean width (m).

Section	Length	Mean Width
1	8.2	129
2	7.9	225
3	16.0	149
4	8.9	113
5	16.9	348

Table 21. Means (SD in parenthesis) of dry biomass (g/0.33 m² clipped plot inside & outside of cages) for paired t-tests of individual clipped sites. (GM=Gibbon Meadows, TS=Terrace Springs, 4MS=4-Mile Site, FFD=Fountain Flats Drive, MGB=Midway Geyser Basin, IC=Interchange).
 * = 0.05 ≤ P ≤ 0.10
 ** = P < 0.05

Site	Inside Cage	Outside Cage	P-Value
July 1996			
GM, n=10 prs			
Live Grass	27.9 (18.3)	20.0 (9.3)	0.10*
Live Forbs	9.3 (8.2)	6.6 (6.2)	0.21
Live Shrubs	0.61 (1.8)	1.5 (4.2)	0.23
Dead Grass	5.8 (5.6)	6.8 (3.4)	0.41
Dead Shrubs	0.01 (0.03)	0.91 (2.0)	0.20
TS, n=10 prs			
Live Grass	32.5 (25.5)	11.8 (9.6)	0.03**
Live Forbs	14.9 (11.8)	9.3 (6.1)	0.11
Dead Grass	0.51 (0.98)	0.32 (0.67)	0.65
Dead Forbs	0.03 (0.09)	0.0	0.34
4MS, n=10 prs			
Live Grass	13.5 (12.3)	9.8 (5.5)	0.23
Live Forbs	9.9 (8.9)	7.5 (5.8)	0.38
Dead Grass	2.8 (2.0)	3.9 (2.2)	0.21
Dead Forbs	2.5 (1.7)	2.5 (3.0)	0.97
FFD, n=10 prs			
Live Grass	26.0 (25.0)	21.0 (19.0)	0.15
Live Forbs	7.7 (12.0)	3.5 (3.9)	0.30
Dead Grass	4.3 (4.5)	7.0 (15.7)	0.52
MGB, n=10 prs			
Live Grass	30.5 (39.0)	31.6 (43.8)	0.83
Live Forbs	15.0 (20.3)	10.5 (7.2)	0.54
Dead Grass	0.1 (0.21)	0.46 (0.77)	0.14
Dead Forbs	0.77 (1.2)	0.63 (0.95)	0.51
IC, n=10 prs			
Live Grass	60.7 (17.2)	52.6 (16.5)	0.10*
Live Forbs	1.3 (1.2)	0.92 (1.1)	0.49
Dead Grass	12.5 (7.6)	16.0 (9.0)	0.16

Table 21. Continued

Site	Inside Cage	Outside Cage	P-Value
September 1996 ^a			
GM, n=10 prs			
Live	19.5 (12.3)	19.1 (11.0)	0.90
Dead	9.8 (11.2)	10.5 (13.3)	0.64
TS, n=10 prs			
Live	25.2 (16.0)	16.5 (11.0)	0.09*
Dead	1.2 (1.7)	1.0 (1.1)	0.75
4MS, n=10 prs			
Live	4.1 (2.8)	5.0 (7.1)	0.58
Dead	6.3 (4.0)	6.7 (4.0)	0.75
October 1996, Fixed Cages(Final Cut) ^b			
GM, n=10 prs			
Live	7.4 (22.0)	2.1 (5.7)	0.50
Dead	30.5 (11.5)	19.8 (11.7)	0.01**
TS, n=10 prs			
Live	21.2 (16.4)	7.0 (4.2)	0.07*
Dead	6.7 (5.1)	2.4 (3.2)	0.02**
4MS, n=10 prs			
Live	2.0 (4.2)	0.56 (0.96)	0.33
Dead	15.9 (14.0)	10.6 (5.3)	0.29
FFD, n=10 prs			
Live	4.7 (4.5)	6.1 (6.7)	0.45
Dead	7.5 (8.7)	13.0 (17.6)	0.11
MGB, n=10 prs			
Live	26.1 (29.7)	17.5 (18.5)	0.07*
Dead	0.75 (1.2)	0.36 (0.76)	0.42
IC, n=10 prs			
Live	0.0	0.0	
Dead	54.9 (18.4)	47.9 (18.9)	0.09*
October 1996, Movable Cages(Final Cut) ^b			
GM, n=10 prs			
Live	0.0	0.0	
Dead	32.9 (20.9)	24.8 (13.0)	0.27
TS, n=10 prs			
Live	5.2 (5.2)	2.6 (3.0)	0.04**
Dead	3.7 (2.2)	3.0 (4.7)	0.63
4MS, n=10 prs			
Live	2.5 (3.0)	0.71 (1.1)	0.08*
Dead	11.0 (11.0)	7.3 (6.3)	0.39

Table 21. Continued

Site	Inside Cage	Outside Cage	P-Value
October 1996, Movable Cages (Final Cut) ^b			
FFD, n=10 prs			
Live	4.8 (8.3)	4.3 (6.0)	0.85
Dead	5.2 (4.6)	9.3 (14.5)	0.32
MGB, n=10 prs			
Live	50.5 (53.0)	43.8 (57.6)	0.36
Dead	0.0	0.0	
IC, n=10 prs			
Live	0.0	0.0	
Dead	53.6 (19.7)	52.7 (25.6)	0.89
May 1997, Fixed Cages ^b			
GM, n=10 prs			
Live	2.4 (1.9)	4.3 (7.3)	0.34
Dead	15.5 (13.2)	20.7 (4.5)	0.40
TS, n=10 prs			
Live	8.0 (5.4)	5.5 (3.8)	0.17
Dead	2.7 (4.6)	0.82 (2.1)	0.12
4MS, n=10 prs			
Live	13.0 (7.9)	5.5 (3.0)	0.01**
Dead	2.4 (3.3)	2.9 (4.6)	0.74
FFD, n=10 prs			
Live	7.0 (8.6)	5.0 (4.1)	0.27
Dead	18.5 (26.4)	6.8 (10.0)	0.08*
MGB, n=10 pairs			
Live	12.5 (12.6)	6.2 (4.0)	0.08*
Dead	0.0	0.0	
IC, n=10 pairs			
Live	4.1 (4.9)	7.2 (7.5)	0.17
Dead	61.5 (29.9)	24.9 (15.7)	<0.01**
May 1997, Movable Cages ^b			
GM, n=10 prs			
Live	5.2 (5.5)	3.1 (4.0)	0.11
Dead	17.3 (16.8)	11.3 (9.2)	0.31
TS, n=10 prs			
Live	8.4 (6.2)	6.1 (5.2)	0.22
Dead	0.0	0.0	

Table 21. Continued

Site	Inside Cage	Outside Cage	P-Value
4MS, n=10 prs			
Live	10.9 (7.2)	5.2 (2.4)	0.01**
Dead	2.9 (3.6)	1.7 (1.3)	0.38
FFD, n=10 prs			
Live	8.4 (11.3)	3.5 (3.9)	0.13
Dead	13.5 (27.5)	13.6 (21.0)	0.99
MGB, n=10 pairs			
Live	18.9 (29.7)	5.9 (6.1)	0.14
Dead	0.0	0.0	
IC, n=10 pairs			
Live	2.3 (7.2)	3.5 (3.5)	0.61
Dead	74.7 (48.0)	32.0 (26.0)	0.01**
July 1997 ^b			
GM, n=10 pairs			
Live	24.9 (15.5)	25.3 (13.5)	0.95
Dead	1.2 (2.2)	1.3 (2.3)	0.92
TS, n=10 pairs			
Live	37.1 (25.6)	14.4 (9.9)	0.01**
Dead	0.0	0.0	
4MS, n=10 pairs			
Live	28.3 (20.0)	24.7 (14.2)	0.39
Dead	0.0	0.0	
FFD, n=10 pairs			
Live	23.9 (25.6)	16.5 (19.1)	0.24
Dead	0.0	0.0	
MGB, n=10 pairs			
Live	41.0 (30.8)	35.5 (37.1)	0.53
Dead	0.0	0.0	
IC, n=10 pairs			
Live	56.5 (44.2)	57.1 (41.5)	0.93
Dead	11.4 (15.9)	9.2 (17.9)	0.64
August 1997, Fixed Cages (Final Cut) ^b			
GM, n=10 pairs			
Live	45.3 (2.2)	43.0 (21.4)	0.54
Dead	0.0	0.0	

Table 21. Continued

Site	Inside Cage	Outside Cage	P-Value
TS, n=10 pairs			
Live	57.0 (43.0)	33.7 (25.8)	<0.01**
Dead	0.0	0.0	
4MS, n=10 pairs			
Live	29.3 (19.8)	20.3 (12.5)	0.01**
Dead	0.0	0.0	
FFD, n=10 pairs			
Live	31.1 (18.7)	91.8 (230.0)	0.41
Dead	0.0	0.0	
MGB, n=10 pairs			
Live	30.8 (23.8)	32.3 (38.8)	0.81
Dead	0.0	0.0	
IC, n=10 pairs			
Live	75.0 (39.3)	83.8 (34.6)	0.40
Dead	8.8 (14.6)	8.9 (19.2)	0.98
August 1997, Movable Cages (Final Cut) ^b			
GM, n=10 pairs			
Live	34.0 (10.9)	26.5 (11.4)	0.07*
Dead	0.0	0.0	
TS, n=10 pairs			
Live	48.1 (27.1)	45.7 (36.8)	0.80
Dead	0.0	0.0	
4MS, n=10 pairs			
Live	22.5 (14.8)	18.5 (7.1)	0.25
Dead	0.0	0.0	
FFD, n=10 pairs			
Live	26.2 (21.9)	27.9 (28.6)	0.74
Dead	0.0	0.0	
MGB, n=10 pairs			
Live	46.4 (44.5)	33.4 (31.8)	0.08*
Dead	0.0	0.0	
IC, n=10 pair			
Live	66.0 (21.6)	72.2 (24.2)	0.17
Dead	33.6 (49.0)	6.1 (13.8)	0.10*

^aFFD, MGB, and IC not clipped in September 1996 due to bison and weather conflicts.

^bNo entry equals no test.

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