

BISON FORAGE UTILIZATION IN THE UPPER MADISON DRAINAGE, YELLOWSTONE NATIONAL PARK

ABSTRACT

We monitored bison (*Bison bison*) use of forage on winter ranges in the Madison, Gibbon, and Firehole drainages of Yellowstone National Park (YNP) to determine how bison used wintering areas in these drainages and to determine if use patterns had detectable impacts on standing biomass. Bison were observed in wintering areas in the three drainages during all seasons of the year. Probability of bison occupying individual sites on a given day within the area during summer, autumn, winter, and spring, 1996-1997 ranged from 0-40 percent, 0-29 percent, 0-91 percent, and 0-67 percent, respectively. Sites identified as historic high use areas had high frequency of use (78 and 91%) during the 1996-1997 winter. Two sites identified as historic medium winter use had lower frequency of use (56%), and sites identified as historic low use areas had no observed use during the 1996-1997 winter. Exclosure cages placed at the six sites allowed us to estimate forage removal during summer 1996 through summer 1997. Over all sites and sampling periods, plots exposed to grazing had 23 percent less biomass (dry weight) than plots protected from grazing. Bison use at individual sites was weakly correlated ($r=0.28$, $P=0.05$) with estimated forage utilization and more strongly correlated with estimated grams of forage removed ($r = 0.55$, $P < 0.01$). Despite high variability in vegetation biomass within sites, we did identify one site, Terrace Springs, as heavily impacted by bison foraging during summer. A reduction of >50 percent in bison numbers in the Madison, Gibbon, and Firehole drainages between summer 1996 and summer 1997 did not reduce foraging pressure on the Terrace Springs site.

Key words: bison, *Bison bison*, forage utilization, Yellowstone National Park.

INTRODUCTION

Management of ungulates in YNP has been contentious since the Park was founded (Tyers 1981). Current controversies involve arguments over the impacts of ungulates on vegetation (Houston 1982, Kay 1990 1998, Kay and Wagner 1994, Coughenour 1991, Coughenour et al. 1994, Singer et al. 1994, 1998, Wagner et al. 1995, Boyce 1998, Wambolt 1998) and the potential for bison, and to a lesser extent, elk

(*Cervus elaphus nelsoni*), to transmit brucellosis to domestic livestock when they leave the Park (Cheville et al. 1998). Arguments over cause and effect have polarized natural resource groups that generally agree on the need for conservation. Some range and wildlife managers advocate allowing ungulate populations in YNP to change with minimal human interference (Houston 1982, Dobson and Meagher 1996, Boyce 1998). Other biologists view ungulates in YNP as prime candidates for human-sponsored population regulation (Kay and Wagner 1994, Wagner et al. 1995, Kay 1998). If ungulates are controlled by human actions, careful consideration

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should be given to determining what densities are appropriate. Wright (1998) noted that visitors to national parks expect to see large numbers of animals. In parks such as YNP, visitor satisfaction is closely linked to seeing numerous large mammals such as bison. If moderate reduction in large herbivores fails to remedy impacts on plant communities and/or problems associated with egress of animals from YNP, management efforts would be wasted. If large mammals were reduced to very low densities or if fencing were introduced to protect plant species or inconspicuous vertebrates, vocal criticism by visitors who value seeing large free-roaming animals can be expected, and management costs would markedly increase.

We describe how bison used one area of the Park, and we attempted to determine if bison herbivory had detectable impacts on forage biomass at specific sites within this area. Our study sites were located in the Madison, Gibbon, and Firehole drainages, an area in which large scale movement outside YNP is a recent phenomenon (Meagher 1998). Our study encompassed one growing season in which bison numbers were close to record highs, a severe winter in which bison numbers were reduced by starvation and control actions outside YNP by nearly 40 percent, and one relatively wet growing season post-population reduction.

Studies of ungulate foraging on seasonal ranges associated with YNP's northern winter range suggested that herbaceous plants are heavily grazed in winter, but subsequent regrowth is not affected by this utilization except under drought conditions (Frank and McNaughton 1992, Singer and Harter 1996). Woody species on the northern winter range are evidently much more heavily impacted by ungulate herbivory (Kay 1990, Singer et al. 1994, Singer and Cates 1995, Wagner et al. 1995, Wambolt 1998). Impacts of ungulates on summer

ranges associated with the northern winter range are difficult to detect (Frank 1990, Norland, pers. commun.). No data in these studies specifically addressed the impacts of bison forage utilization (including feeding and trampling). No data on impacts of forage utilization by any ungulates were available for the smaller winter ranges associated with the Madison, Gibbon, and Firehole Rivers, but Meagher (1998) noted increasing use of these areas over the past decade in non-winter months.

STUDY AREA

Study sites were located in the Madison, Gibbon, and Firehole drainages in the northwest corner of YNP (Fig. 1). Elevations in riparian corridors varied from 2,079-2,252 m. The corridors were characterized by gentle to moderate slopes supporting lodgepole pine (*Pinus contorta*) forests with a mixture of open meadows, shrub communities, forests, and geothermal features along the floodplains (Craighead et al. 1973). The climate is cold, continental with cool summers, cold winters, and high snow accumulation.

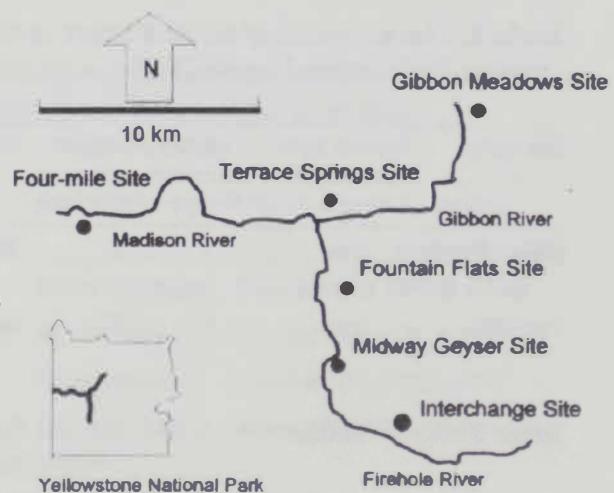


Figure 1. Map of the Madison, Gibbon, and Firehole study area in Yellowstone National Park showing locations of six sites where grazing exclosure cages were placed.

All sites where we placed enclosures were in open meadows or shrub lands, the physiographic types favored by bison in YNP (Meagher 1973, Reynolds et al. 1982, Norland et al. 1985, Ferrari 1998). Sampling was conducted at six sites (Fig. 1) selected to reflect low, medium, and high bison use during winters prior to the study (Bob Siebert, pers commun., Bob Garrott, pers commun.). Characteristics of each site are given in Table 1. The Gibbon Meadows site was located in a high snowfall area and was identified as a low winter-use area. The Four Mile site, also a low winter-use area, was primarily a movement corridor used lightly during early winter and spring. Both moderate winter-use sites, Terrace Springs and Midway Geyser, were thermally influenced. In both sites, riparian areas supported much more dense vegetation than the active (Terrace Springs) or fossil (Midway Geyser) thermal areas. The two sites with historic heavy winter-use, Fountain Flats and Interchange, were in meadows along the Firehole River but not closely associated with the river. Both had areas of standing water throughout the year.

METHODS

We used visual observations to provide an index of ungulate presence at sites and enclosure cages to measure ungulate effects on standing biomass. Ground counts of bison and elk within 100 m of the enclosure cages in each site were made weekly from May 1996 through August 1997. Results were expressed as proportions of counts with bison or elk near sites and as bison or elk-days per sampling period (mean animals per count during each period multiplied by the number of days between cage placement and clipping). We calculated an index of total ungulate use, animal unit-days, by adding mean bison sightings to mean elk sightings divided by 1.4. This conversion approximated the ratio of daily dry weight forage consumption by an average individual in a bison herd (6.7 kg) to an average individual in an elk herd (4.9 kg) (Westfall et al. 1993).

Enclosure cages were clustered in 2-9 ha areas in each site to facilitate relocation and to minimize visibility to Park visitors. Cage construction and clipping treatments were modified from procedures described by Brown (1954)

Table 1. Characteristics of six sites where enclosure cages were placed in the Upper Madison drainage, Yellowstone National Park.

Site name	Historic winter use level	Hectares sampled		Community type	Dominant plant species
		Forage	Animal use		
Gibbon Meadows	Low	2	9	Wet meadow	Bluegrasses (<i>Poa</i> spp.) Sedges (<i>Carex</i> spp.)
Four Mile	Low	9	25	Shrub grassland	Big sagebrush (<i>Artemisia tridentata</i>) bluebunch wheatgrass (<i>Agropyron spicatum</i>)
Terrace Springs	Medium	9	25	Dry to mesic riparian meadow	Kentucky bluegrass (<i>Poa pratense</i>) Mixed forbs
Midway Geyser	Medium	2	9	Dry to mesic riparian meadow	Western wheatgrass (<i>A. smithii</i>) /sedge/ rush (<i>Juncus</i> spp.)
Fountain Flats	High	9	25	Thermal springs/ wet meadow	Beaked spike-rush (<i>Eleocharis rostellata</i>)
Interchange	High	4	16	Wet meadow	Beaked spike-rush

and Frank and McNaughton (1992). One hundred exclosure cages, measuring $1.2 \times 1.2 \times 1.5 \text{ m}^2$, were constructed using cattle panels and steel fence posts. Twenty more cages, measuring $1.8 \times 1.8 \times 1.8 \text{ m}^2$, were available from a previous study. We estimated the number of cages needed per study site and the size of plots clipped within cages based on variances in biomass estimates given by Frank (1990). He identified grazing effects in subjectively chosen sites using 5-7 caged plots per site and a double-sampling method that employed plant intercepts by pins as a surrogate for actual measurement of plant biomass. We increased the number of plots per site to 10 or 20 for individual seasonal samples and based our biomass estimates on vegetation clipped in 0.33-m^2 circular plots. The mesh size on the fencing ($15 \times 15 \text{ cm}$) precluded bison muzzle entry into the exclosures. The 0.33-m^2 plot clipped within each cage left a minimum space of 27 cm from the edge of the clipped plot to the exclosure fencing. This distance minimized potential cage effects and prevented deer and elk from grazing in areas we clipped. Cage effects were not

measured but were expected to be small for the relatively short time intervals of exclosure and for the habitat types that we were sampling (Frank 1990, Irby, unpublished data).

In June 1996 20 cages per study site were randomly placed using an XY coordinate system to form a grid that allowed us to move cages within a grid cell at least six times (Table 2) without intercepting areas covered by cages in previous time periods. At each site, 10 cages were randomly selected as season-long sample units and 10 other cages as partial-season sample units. Partial-season cages were moved at 6-12 week intervals during the growing season (May-October). Fixed cages were left in place through the growing season. This allowed us to identify when grazing occurred during the growing season (partial-season samples), provided a crude indication of the ability of regrowth to compensate for early grazing (late-summer samples), and provided an estimate of the net effects of restricting access to forage for the whole growing season (season-long samples). All cages were left in place from November 1996 to May 1997. When cages were moved, the

Table 2. Sampling scheme used to estimate utilization of herbaceous vegetation during eight time intervals for six sites in the Madison, Gibbon, and Firehole River drainages, Yellowstone National Park, 1996-1997.

Period when vegetation was clipped	Exclosure period	Sample type	Utilization period measured
5-10 July 1996	1 Jun - 10 Jul 1996	Green vegetation	Early summer 1996 (6-7 wks)
15 Sep - 20 Oct 1996	15 Jul - 15 Sep or 15 Oct 1996	All vegetation	Late summer 1996 (8-12 wks)
15-20 Oct 1996	20 May - 20 Oct 1996	All vegetation	Summer 1996 (20-21 wks)
10-15 May 1997	20 Oct 1996 - 10 May 1997	Residual (dead) vegetation	Winter 1996-1997 (29-30 wks)
10-15 May 1997	April - May 1997	Green vegetation	Spring 1997 (6-7 wks)
5-10 Jul 1997	15 May - 10 July 1997	Green vegetation	Early summer 1997 (6-7 wks)
25-30 Aug 1997	10 Jul - 30 Aug 1997	All vegetation	Late summer 1997 (6-7 wks)
25-30 Aug 1997	15 May - 30 Aug 1997	All vegetation	Summer 1997 (13-14 wks)

new location was 2-4 m north (a random direction chosen at the beginning of the study) of the old location.

Vegetation samples collected inside and outside cages consisted of all standing plant material within circular, 0.33-m² plots. Samples were clipped with garden shears to approximately 13 mm above ground level. Plots outside of cages were always clipped 1 m from the eastern exclosure wall. Clipped material was separated into live (photosynthetic) and dead (non-photosynthetic) biomass. Vegetation samples were stored in paper bags and transported to drying facilities in YNP or at Montana State University. Clipped samples were oven-dried at 60° C for 48 hrs and weighed using an Ohaus electronic scale with an accuracy of \pm 0.1 g.

We used Wilcoxon's ranked sum tests to compare standing biomass inside and outside individual exclosure cages using the S-PLUS statistical package (MathSoft 1999). Corrections for continuity were used when ties occurred in comparisons. Comparisons were made for each site in each of eight designated seasons (Table 2). To better illustrate forage utilization, we converted dry weights to percent differences between protected and unprotected plots in graphic displays of data. This difference was expressed as "percent utilization" (inside biomass-outside biomass / inside biomass X 100). Because we paired plots on a spatial basis rather than subjectively pairing plots with similar vegetation, as Frank (1990) did, negative values (i.e., more biomass in unprotected plots than in paired protected plots) were possible. We truncated mean percent differences to a range of 0 to 100 percent in graphs to eliminate negative means. We assessed the association between bison and/or elk presence and estimated forage utilization by calculating the correlation between bison-days, elk-

days, and animal-use days (bison + elk) per hectare and two response variables (mean difference between vegetation protected by cages and vegetation exposed to ungulate grazing [expressed as grams per 0.33 m²] and estimated percent forage removal at individual sites) (Steel and Torrie 1960).

RESULTS

Bison numbers in the study area during 1996 and 1997 were highly variable due to movement of animals through the area. The Madison, Firehole, and Gibbon drainages served as a corridor connecting bison habitat in the Hayden Valley with habitat outside the west boundary of YNP. During winter and spring 1997, ground censuses yielded counts of 504 (May 1997) to 1,102 (January 1997) bison in the Madison, Gibbon, and Firehole drainages (Ferrari 1998). Approximately 400 bison were removed by control actions along the west boundary during winter 1996-1997 (Gogan, unpubl. data), and up to 100 died of starvation within the study area (M. Ferrari and R. Garrott, pers commun.). Fewer bison were in the area during summer. We were unable to make total counts during the 1996 and 1997 summers, but our weekly counts along roads paralleling the 3 drainages averaged 42 bison/count ($n = 22$) during June - October 1996 and 12 bison/count ($n = 16$) during May-August 1997 (Dawes 1998).

We observed bison and elk in open areas within the riparian corridor along the Madison, Firehole, and Gibbon Rivers in all seasons of the study. Bison were observed at one or more of the six sites where we placed exclosure cages on 32 of 59 counts (54%). Total numbers of bison sighted ranged from 0 to 168 individuals per count. We recorded the highest frequency of counts with one or more bison sighted in winter and spring 1997 (Fig. 2) and the lowest frequencies in late summer 1996 (17% of counts)

All Sites

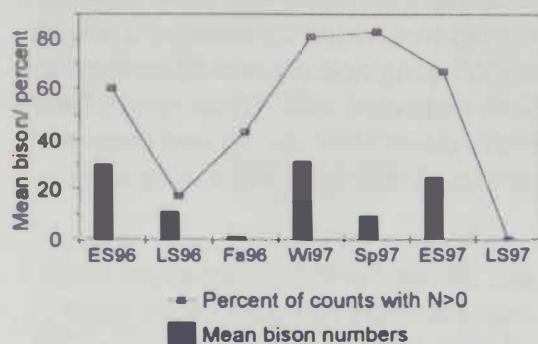


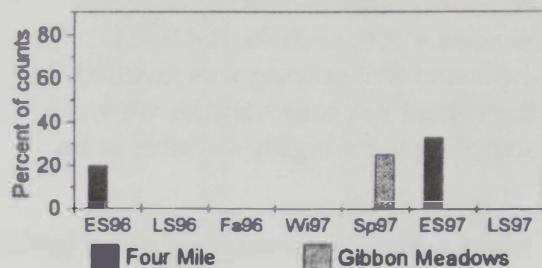
Figure 2. Frequency of bison sightings at one or more of six sites and number of bison sighted per count in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Period designations (number of counts per period) are: ES96 (5) = 16 June - 19 July 1996; LS96 (12) = 20 July - 12 October 1996; Fa96 (7) = 13 October - 30 November 1996; Wi97 (16) = 1 December 1996 - 31 March 1997; Sp97 (6) = 1 April - 15 May 1997; ES97 (6) = 16 May - 5 July; LS97 (7) = 6 July - 31 August 1997.

and 1997 (no bison observed). Mean numbers of bison per count were highest in early summer (1996 and 1997) and winter (Fig. 2). We observed elk at two of our sampling sites (7 elk total) during the summer and early autumn of 1996, four of the six sites during winter (a total of 77 elk counted), two sites during spring (6 elk total), and at one site during summer 1997 (8 elk total).

We only observed bison at the two sites with historic low levels of winter use by bison (Four Mile and Gibbon Meadows) during spring and early summer. Bison were observed <35 percent of counts at the two sites during these periods (Fig. 3). Bison were observed on both sites with historic moderate winter-use (Terrace Springs and Midway Geyser) in 56 percent of winter counts in 1997 (Fig. 3). Frequency of use of the Midway Geyser site was only high in winter. Bison

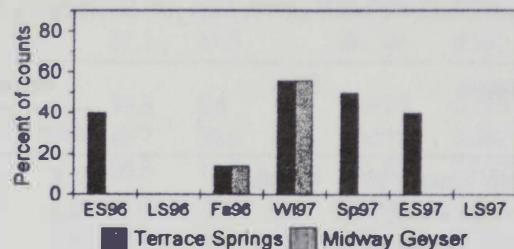
Winter Low-use Sites

(Four Mile and Gibbon Meadows)



Winter Medium-use Sites

(Terrace Springs and Midway Geyser)



Winter High-use Sites

(Fountain Flats and Interchange)

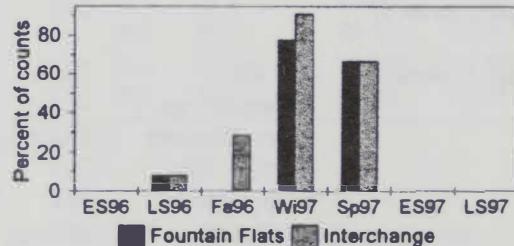


Figure 3. Frequency of sightings of bison at individual sites in the Madison, Gibbon and Firehole drainages, Yellowstone National Park, 1996-1997. Seasonal designations are given in Figure 2.

frequently used Terrace Springs in spring and early summer as well as winter. Bison were recorded at historic high winter-use sites in 78 percent and 91 percent of winter counts for the Fountain Flats and Interchange sites, respectively. Frequency of use of these sites also was high in spring (Fig. 3).

Over all sites, graminoids made up 77 percent, forbs 23 percent, and shrub leaves <1 percent of vegetation biomass.

The correlation between vegetation biomass inside and outside cages in vegetation classes used in analyses (n pairs = 600, $r = 0.76$, $P < 0.01$) indicated that pairing was justified, but the vegetation communities we were sampling were highly variable at the

0.33-m² scale (Table 3). The mean coefficient of variability (standard deviation divided by mean) for site by season comparisons was 83 percent for both protected and unprotected plots. Mean dried biomass clipped from plots protected from grazing varied from

Table 3. *Mean dried weight of forage (g/0.33m²) and standard deviations on means inside and outside exclosures for all sites by season and individual sites by season for the upper Madison study area, 1996-1997. Numbers of paired values used to calculate means are 10/site for summer samples and 20/site for winter/spring samples. Test statistics for a 1-tailed Wilcoxon=s rank-sum test (H_0 : In > Out) are W (rank-sum statistic, no ties) and Z (rank-sum statistic with correction for continuity for tests including ties).*

Season	Sites	Inside		Outside		Test statistic	1-tailed P
		Mean	SD	Mean	SD		
Early summer 96	(All sites)	41.6	30.9	31.1	24.7	Z=1.99	0.024*
Late summer 96		30.2	29.5	28.1	30.5	Z=0.39	0.350
Total summer 96		29.1	22.7	21.2	18.5	Z=2.19	0.014*
Winter 97		18.7	31.1	9.7	15.6	Z=1.19	0.116
Spring 97		8.2	11.3	5.0	4.6	Z=1.71	0.044*
Early summer 97		35.2	29.5	28.8	28.4	Z=1.45	0.074*
Late summer 97		46.1	41.6	38.7	32.0	Z=0.79	0.215
Total summer 97		46.6	33.4	41.6	35.0	Z=1.13	0.130
Early summer 96	Four Mile	23.4	17.8	17.4	9.9	W=114	0.264
	Terrace Springs	47.4	30.2	21.2	12.0	W=130	0.032*
	Gibbon Meadows	37.9	18.6	28.4	10.0	W=117	0.196
	Fountain Flats	33.7	24.1	24.0	19.4	W=115	0.240
	Midway Geyser	45.5	53.4	42.1	44.2	Z=-0.45	0.675
	Interchange	61.9	16.9	53.6	16.7	Z=1.10	0.136
Late summer 96	Four Mile	10.3	4.3	11.6	9.7	Z=0.19	0.425
	Terrace Springs	26.5	16.5	17.5	11.3	W=120	0.140
	Gib bon Meadows	29.4	13.6	29.6	10.4	W=103	0.456
	Fountain Flats	10.1	11.2	13.5	13.6	W=95	0.241
	Midway Geyser	50.5	53.1	43.9	57.6	Z=0.76	0.225
	Interchange	53.7	18.4	52.7	25.8	W=107	0.456
Total summer 96	Four Mile	17.9	12.6	11.2	4.9	W=119	0.158
	Terrace Springs	24.7	17.8	9.5	4.7	W=135	0.012*
	Gib bonMeadows	37.9	17.4	21.9	14.9	Z=2.16	0.016*
	Fountain Flats	12.2	6.8	19.1	14.7	W=94	0.218
	Midway Geyser	26.9	30.1	17.8	18.3	Z=1.10	0.136
	Interchange	54.9	18.4	47.9	19	Z=0.38	0.352
Winter 97	Four Mile	2.7	3.4	2.3	3.3	Z=-0.18	0.571
	Terrace Springs	1.9	3.5	1.5	3.6	Z=0.72	0.236
	Gib bon Meadows	16.2	14.2	15.8	12.5	Z=-0.23	0.580
	Fountain Flats	16.0	26.4	10.2	16.3	Z=0.30	0.380
	Midway Geyser	7.6	18.2	<0.1	0.2	Z=1.48	0.069*
	Interchange	68.1	39.5	28.4	21.5	Z=3.63	<0.001*

Table 3. (Cont.)

Season	Sites	Inside		Outside		Test statistic	1-tailed	P
		Mean	SD	Mean	SD			
Spring 97	Four Mile	12.0	7.4	5.4	2.7	Z=3.67	< 0.001*	
	Terrace Springs	8.0	5.5	5.9	4.3	Z=1.15	0.125	
	Gibbon Meadows	3.6	4.1	3.7	5.7	Z=0.77	0.220	
	Fountain Flats	7.7	9.8	4.3	3.9	Z=0.26	0.398	
	Midway Geyser	15.1	21.5	5.8	4.9	Z=1.85	0.032*	
	Interchange	3.2	6.1	5.3	6.0	Z=-2.16	0.980	
Early summer 97	Four Mile	28.3	20	24.7	14.2	Z=0.15	0.440	
	Terrace Springs	37.1	25.6	14.4	9.9	Z=1.97	0.025*	
	Gibbon Meadows	24.9	15.5	25.3	13.5	Z=0.01	0.500	
	Fountain Flats	23.9	25.6	16.5	19.1	Z= 0.07	0.248	
	Midway Geyser	41.0	30.8	35.5	37.1	W=116	0.218	
	Interchange	56.5	44.2	57.1	41.5	W=105	0.500	
Late summer 97	Four Mile	22.5	14.8	19.5	6.8	W=106	0.485	
	Terrace Springs	48.1	27.1	45.7	36.8	W=111	0.342	
	Gibbon Meadows	34.0	10.9	26.5	11.4	Z=1.63	0.052*	
	Fountain Flats	26.2	21.9	27.9	28.6	W=102	0.426	
	Midway Geyser	46.4	44.5	34.5	32.5	Z=0.57	0.285	
	Interchange	99.5	58.6	78.4	28.2	W=114	0.264	
Total summer 97	Four Mile	30.1	20.0	22.0	13.1	Z=0.83	0.202	
	Terrace Springs	56.8	42.9	33.7	25.8	W=119	0.158	
	Gibbon Meadows	45.3	22.1	42.9	21.4	W=110	0.370	
	Fountain Flats	32.9	19.1	26.6	23.7	W=118	0.176	
	Midway Geyser	30.8	23.8	32.3	38.8	W=116	0.218	
	Interchange	83.7	35.2	92.6	31.1	W=92	0.176	

* Biomass inside cages greater than biomass outside cages ($P < 0.10$).

zero, i.e., no vegetation >13 mm in height, to 228 g/0.33 m². Over all paired comparisons ($n = 600$), the mean difference between dried weights of herbaceous vegetation in plots protected from grazing (mean = 28.3 g, SD = 31.7) versus paired plots exposed to grazing (mean = 21.9 g, SD = 26.7) was 6.4 g, a 23 percent difference (Wilcoxon=s rank-sum continuity-corrected $Z = 3.39$, $P < 0.001$).

When all sites were combined, biomass in protected plots was greater ($P < 0.10$) than biomass in plots exposed to grazing (Table 3) in early summer 1996, total summer 1996, spring 1997, and early summer 1997. Combining sites, however, is inappropriate because enclosure cages were clustered at sites with very different vegetation

production and utilization patterns. When individual sites were tested by season, we found significantly greater biomass in plots protected from grazing at the Four Mile (spring 1997), Terrace Springs (early summer 1996, total summer 1996, and early summer 1997), Gibbon Meadows (total summer 1996 and late summer 1997), Midway Geyser (winter and spring 1997), and Interchange (winter 1997) sites (Table 3).

Correlations between estimated ungulate days of use and the difference in biomass between protected plots and plots exposed to grazing (g/ 0.33m²) over all sites and seasons were significant for bison-days (n pairs = 48, $r = 0.55$, $P < 0.001$) and animal-use days (n pairs = 48, $r = 0.53$, $P < 0.001$) but not for elk-days (n pairs = 48, $r = 0.09$, $P =$

0.56). When we correlated animal days of use per hectare with estimates of mean percent utilization for individual sites by sampling period, we identified weak, positive relationships for bison ($r = 0.28, P = 0.05$) and animal-use ($r = 0.28, P = 0.05$) days but no significant relationship for elk-days ($r = 0.08, P = 0.61$).

When we compared estimated percent utilization of forage with bison and elk days for individual sites in specific seasons (Fig. 4, 5, and 6), high estimated bison-days per hectare were only associated with high utilization at the Interchange site (Fig. 6) during winter. Moderate values for bison-days were associated with significant

utilization at the Terrace Springs (Fig. 5) site during early and total summer 1996 and early summer 1997 and at the Midway Geyser site in winter 1997. At other sites, significant utilization was associated with low bison counts, or high bison counts were associated with non-significant utilization values. Estimates of elk-days were low at all sites in all seasons.

DISCUSSION

Because of controversy surrounding investigations of ungulate impacts in Yellowstone (Cheville et al. 1998), we elected to minimize potential bias in sampling by strict spatial randomization within sites. Our goal

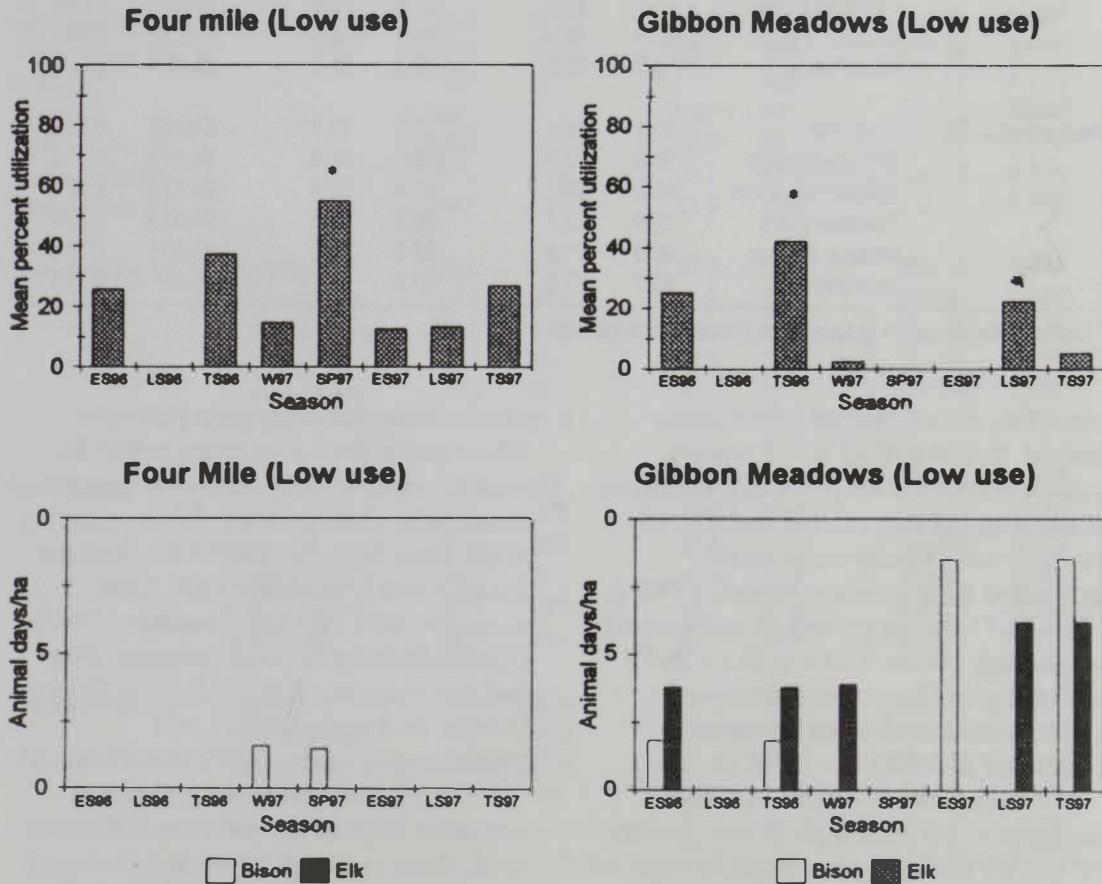
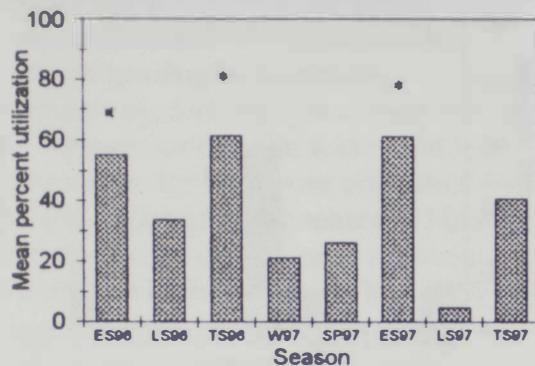
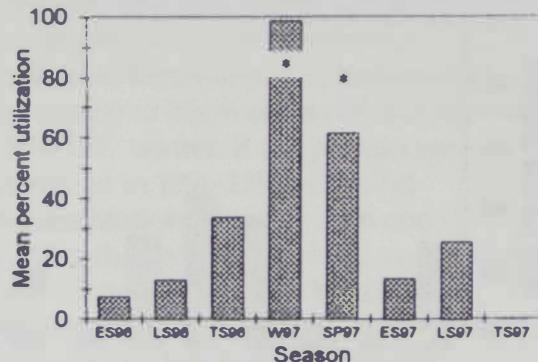


Figure 4. Mean estimated forage utilization (%) at two historic low winter-use sites (Four-Mile and Terrace Springs) and estimated bison-days and elk-days per hectare in each site by season in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Asterisks in utilization graphs indicate significantly greater biomass in exclosure cages than in plots outside cages (1-tailed Wilcoxon's paired tests, $P < 0.10$).

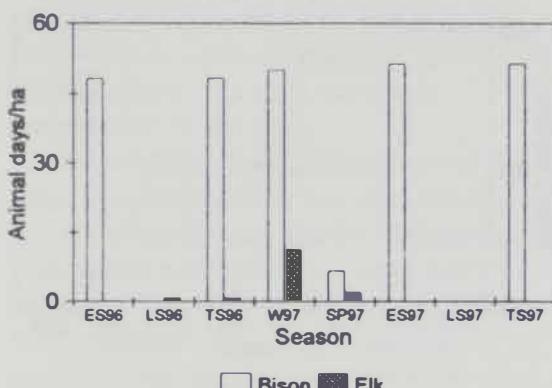
Terrace Springs (Medium use)



Midway Geyser (Medium use)

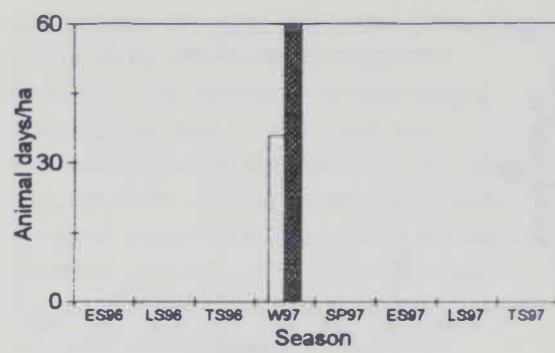


Terrace Springs (Medium use)



□ Bison ■ Elk

Midway Geyser (Medium use)



□ Bison ■ Elk

Figure 5. Mean estimated forage utilization (%) at two historic medium winter-use sites (Terrace Springs and Midway Geyser) and estimated bison-days and elk-days per hectare in each site by season in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Asterisks in utilization graphs indicate significantly greater biomass in exclosure cages than in plots outside cages (1-tailed Wilcoxon=s paired tests, $P < 0.10$).

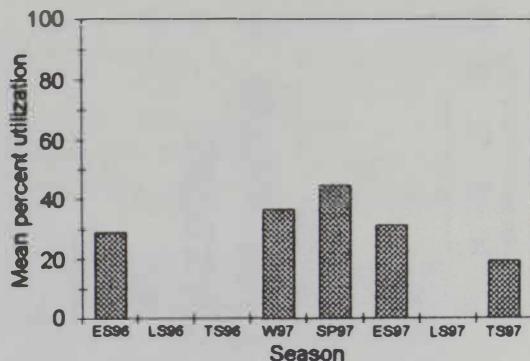
was not to demonstrate the possibility of ungulate impacts on herbivorous vegetation, as was that of Frank and McNaughton (1992, 1993), but to determine if measurable impacts occurred on wintering areas in the Madison, Firehole, and Gibbon drainages. We discovered that use of sites by ungulates and forage availability varied tremendously at the scale we were measuring, and thus, under-sampled study sites. We were only able to detect utilization >40 percent in most sites. We estimated that 327 pairs of 0.33-m^2 plots per site would be needed to detect a 20 percent difference and 1,355 pairs to detect a 10 percent difference in means (based on power analysis modules in Borenstein

and Cohen 1988) for the average site in the upper Madison study area using a completely randomized pairing system and parametric statistics (1-tailed t -test with $P < 0.05$ and power = 0.80). This sampling intensity was well beyond the capabilities we had.

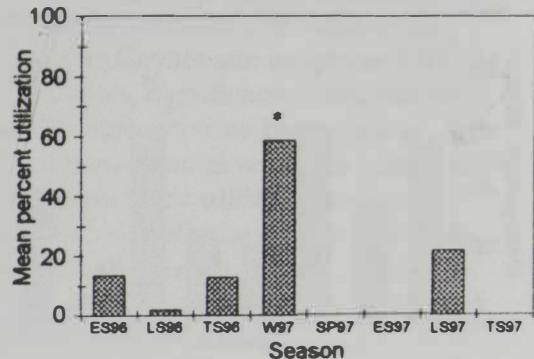
Despite their limitations, our data did shed light on foraging patterns in the study area.

Suitable bison habitat in the Madison, Firehole, and Gibbon drainages is limited to patches and linear swaths of open meadows in riparian corridors (Ferrari 1998). Bison used all sites where we placed exclosure cages during periods when vegetation was growing so the area cannot be considered only as a winter range. The

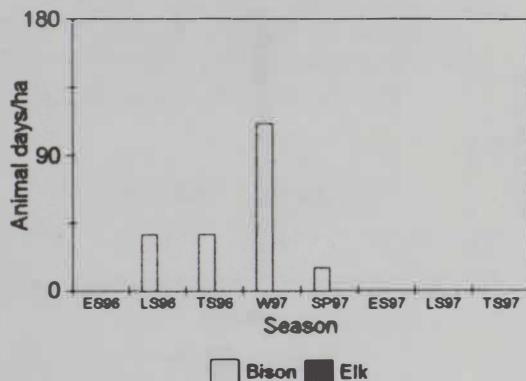
Fountain Flats (High use)



Interchange (High use)



Fountain Flats (High use)



Interchange (High use)

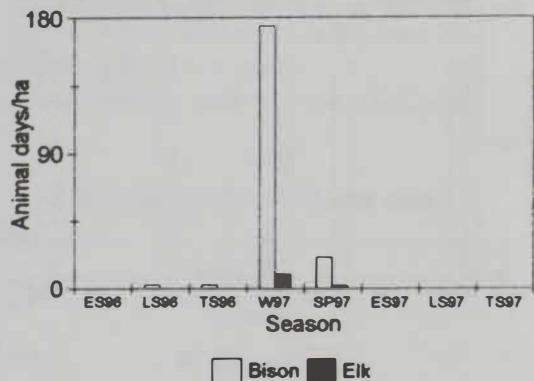


Figure 6. Mean estimated forage utilization (%) at two historic high winter-use sites (Fountain Flats and Interchange) and estimated bison-days and elk-days per hectare in each site by season in the Madison, Gibbon, and Firehole drainages, Yellowstone National Park, 1996-1997. Asterisks in utilization graphs indicate significantly greater biomass in exclosure cages than in plots outside cages (1-tailed Wilcoxon s paired tests, $P < 0.10$).

extent and seasonality of use varied widely among sites.

Estimated utilization of forage at the Four Mile site, a low winter-use site located in a migration corridor connecting wintering areas outside YNP with areas inside YNP, was highest in spring 1997 (55%). This was a period when bison that survived the harsh 1997 winter were moving back into the Park through this site and could easily have been missed in our weekly counts. We did not record any other significant seasonal utilization at this site and rarely saw buffalo or elk on the site.

Utilization in the other low winter-use site, Gibbon Meadows, was only statistically different from zero for the total summer 1996 and late summer

1997 sampling periods. Bison rarely were observed in this site, but it had the most consistent use by elk of any site we measured. It is likely, however, that the estimated percent utilization in summer 1996 (42%) and late summer 1997 (22%) were artifacts of vegetation variability rather than a response to 4 to 6 elk-days of use.

Estimated utilization at Terrace Springs, a medium winter-use site, was not significant during winter but was during early summer 1996 (55%), total summer 1996 (62%), and early summer 1997 (61%). Bison numbers observed at this site were 5-10 times greater than at low winter-use sites, and use during early summer was as high as use during winter. Although Frank and

McNaughton (1993) demonstrated that herbaceous forage in some plant communities in YNP responded to summer grazing by increasing productivity, forb and grass regrowth at the Terrace Springs site was not able to compensate for herbivore utilization by the end of the growing season. This site attracted bison during early summer under both high (1996) and low (1997) bison populations, and it had the highest canopy coverage of exotic grasses of the six sites (Dawes 1998). The high relative abundance of exotic species is consistent with, but does not prove, bison-induced changes in the species composition of the plant community at this site.

Bison and elk were observed at the other medium winter-use site, Midway Geyser, only during winter. Estimated utilization, however, was significant during winter (99%) and spring (62%) 1997. Significant spring utilization could be due to sampling error or consumption of regrowth protected by snow during late winter.

Estimated utilization at the Interchange site, a historic high winter-use area, was significant (58%) only in winter 1997. Estimated use per hectare by bison in winter 1997 was 3 times greater than at Midway Geyser. Higher use by bison and lower utilization of forage at the Interchange site compared to the Midway Geyser site in winter were consistent with differences in site productivity. The Interchange site had 10 times more forage available in winter than the Midway Geyser site. Bison numbers on the Interchange site declined in spring, and bison were seldom seen on the site during summer.

The other historic high winter-use site, Fountain Flats, did not have significant utilization in any season. Based on the number of bison we observed on this site, our failure to detect significant winter utilization was probably due to the extreme variability in forage productivity within the site.

The sites identified as historic high, medium, and low winter-use areas were ranked in that order in terms of estimated bison-days per hectare and frequency of bison observed during the 1996-1997 winter. If the pattern we observed in 1996-1997 is a valid representation for more than one winter, the probability that a site in high winter-use range in the Madison-Firehole-Gibbon complex will be occupied by bison on a given day during winter is >80 percent.

Our index of winter forage utilization, the previous year's standing vegetation, produced ambiguous evidence supporting a relationship between animal-days of use and estimated forage utilization in winter. The extreme variability in vegetation cover at some sites, especially Fountain Flats, is probably the best explanation for our failure to demonstrate unequivocal differences in plots protected from grazing versus those exposed to grazing. However, when ungulates remove snow from a site to reach forage, they promote melting and refreezing which protects the site from further foraging (Turner et al. 1994). Moving snow from one site to access forage may also create a crust at the site where it is moved thereby making foraging at the stacking site very difficult (P. Farnes, pers. commun.). Moving snow to reach forage, a common practice by bison in YNP (Meagher 1973), would thereby increase variability in utilization at the microsite level at sites used heavily by bison.

Mean standing dead biomass inside exclosure cages in May 1997 was <50 percent of mean standing biomass at the same sites recorded in exclosures in October 1996 at four of the six sites, indicating a major loss in biomass not related to grazing. The decline in forage protected by exclosures was probably due to some combination of herbivory by small mammals, mechanical removal of standing plant material due to snow

weight, and fungal/bacterial action on standing dead vegetation in thermally warmed soil covered by an insulating snow cover.

The mean percent difference between caged and uncaged plots for winter forage utilization we calculated for the four sites used most heavily by bison in winter (Terrace Springs, Midway Geyser, Fountain Flats, and Interchange), 54 percent, was similar to the average winter forage removal by ungulates, ~55 percent, reported for the northern range of YNP during 1986-1990 by Singer and Harter (1996). Given the extent of bison egress from Yellowstone and the high mortality within Yellowstone during the 1996-1997 winter, we expected higher utilization if forage were limiting in the Gibbon, Firehole, and Madison drainages. Snow depth at two of the three most heavily used sites (Fountain Flats and Terrace Springs) never reached chest height (~60 cm) on female bison, a depth that is believed to preclude most bison use (Telfer and Kelsall 1984), during the 1996-1997 winter and was >60 cm only during January 1997 at the Interchange site so snow depth should not have been a major factor limiting bison access to forage. Assuming snow crusting did not limit availability and small mammal herbivory, microbial activity, or mechanical processes did not mask utilization, bison that exited Yellowstone via the Madison River were not responding to absolute shortages of forage in the study area.

Reducing the number of bison in YNP did reduce the number of bison sighted at our sample sites during summer 1997. The reduction did not reduce apparent utilization during the early growing season in 1997 at the only site where we could unambiguously detect significant impacts on standing biomass due to bison during the 1996 growing season, Terrace Springs. This

suggests that moderate reductions in bison numbers are unlikely to limit overgrazing at specific sites favored by bison in YNP.

ACKNOWLEDGMENTS

This study was funded by the National Park Service. Assistance provided by Yellowstone National Park staff (R. Abegglen, J. Mack, L. Inafuku, Bob Seibert, W. Wimberley, and D. Young), the Montana State University herbarium (J. Rumely), field technicians (T. Andresen, C. Scott, and A. Gray), graduate students on other projects (M. Ferrari), and the U.S. Forest Service (D. Tyers and his summer field crew) was greatly appreciated.

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