PHYSIOLOGICAL RESPONSES OF YELLOWSTONE BISON TO WINTER NUTRITIONAL DEPRIVATION

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Abstract: Because nutrition is critically related to other aspects of bison (*Bison bison*) ecology, and the winter ranges inhabited by bison in Yellowstone National Park (YNP) are ecologically diverse, it was important to determine if nutritional deprivation differences occurred among winter ranges. We used chemistry profiles of urine suspended in snow to compare nutritional deprivation of bison from January to April 1988 on 4 sampling areas of 3 winter ranges in YNP. Declining ($P < 0.001$) trends of urinary potassium : creatinine ratios in bison on all 4 sampling areas indicated progressive nutritional deprivation through late March. Concurrent increases ($P \leq 0.001$) in mean urea nitrogen : creatinine ratios from late February through late March in 3 of 4 areas suggested that increased net catabolism was occurring. Diminished creatinine ratios of sodium and phosphorus reflected low dietary intake of these minerals throughout winter. Mean values and trends of urinary characteristics indicated nutritional deprivation varied among 3 winter ranges in YNP. Continued physiological monitoring of nutritional deprivation, along with detailed examination of other aspects of the bison's ecology, will provide greater insight into the role of ungulate nutrition in the dynamics of such a complex system and improve management.

J. WILDL. MANAGE. 58(1):24–34

Key words: bison, *Bison bison*, electrolytes, nutrition, physiology, potassium : creatinine, sodium : creatinine, urea nitrogen : creatinine, urine, Wyoming.

Approximately 2,700 bison winter on several ecologically diverse ranges throughout YNP (Meagher 1973, 1989*a*). Bison are exposed to winter weather conditions that vary in severity both spatially and temporally, and use of many habitats has been reported (Meagher 1973, Houston 1982, Despain 1987). Morphological, behavioral, and physiological adaptations have made bison uniquely well suited among ungulates for survival in the harsh winter environments of YNP (Meagher 1973, Peden et al. 1974, Christopherson et al. 1978, Hawley et al. 1981). However, indirect evidence has suggested that nutritional deprivation associated with severe winter weather on some ranges may have a regulating effect on the population (Meagher 1971, 1973; Singer and Norland 1993). However, little research has focused specifically on assessing nutritional deprivation in these animals.

Increased understanding of winter nutritional deprivation in bison, in part, requires a sensitive measure. As it has for other ungulates (Mould and Robbins 1981; DelGiudice et al. 1987, 1990, 1991*b*; Saltz and White 1991*a*,*b*), urinalysis has shown potential for monitoring nutritional deprivation in bison (Keith et al. 1981) as it progresses toward accelerated endogenous protein catabolism. Importantly, acquisition of large sample sizes necessary for studies of free-ranging animals in natural environments is facilitated by collection and chemical analysis of urine suspended in snow (DelGiudice et al. 1988, 1991*b*).

The wide and changing winter distribution of Yellowstone bison and marked environmental variation offered a unique opportunity to evaluate them for potential differences in nutritional deprivation. We hypothesized that there were differences in nutritional deprivation in Yellowstone bison from ecologically distinct areas (e.g., Northern Range, Madison-Firehole, and Pelican Valley) that would be reflected by differences in urine chemistry profiles.

The U.S. National Park Service, Natural Resource Preservation Fund, YNP, and the Research Service, U.S. Veterans Affairs Medical Center, Minneapolis, Minnesota, provided funds and logistical support. We thank M. L. Tufts,

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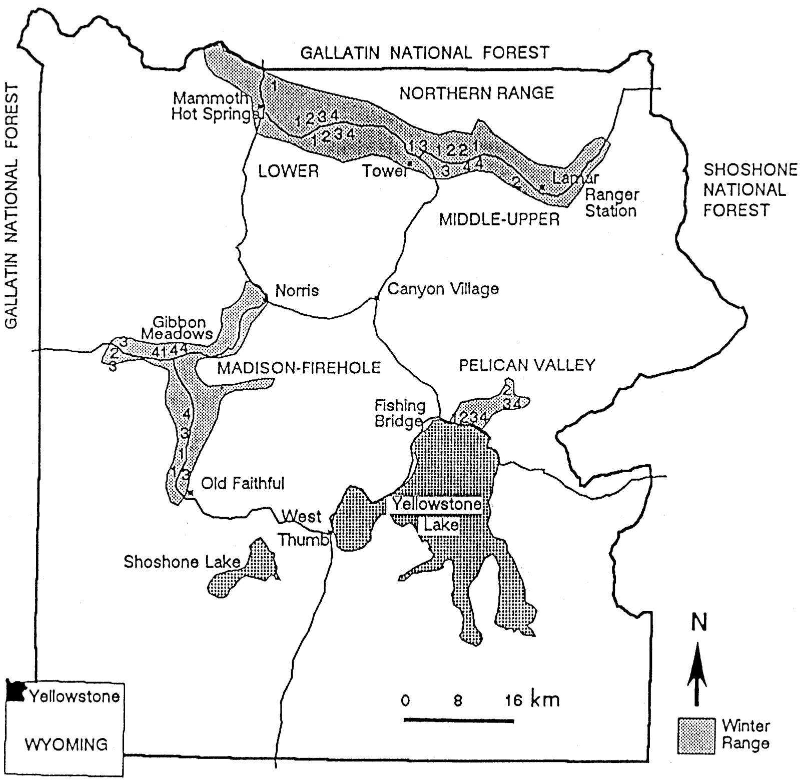

Fig. 1. Locations of 4 collections of urine voided in snow by bison on the lower and middle-upper Northern Range, Madison-Firehole Range, and at Pelican Valley, Yellowstone National Park, Wyoming, 13 January–4 April 1988. (Nos. 1–4 represent locations of urine collections.)

R. P. Fashingbauer, M. E. Massaros, and many YNP Resource Management personnel for field assistance. We thank M. M. Meagher for insights into bison ecology. M. R. Riggs provided statistical advice. E. O. Keith, M. M. Meagher, K. Noyce, S. C. Torbit, and 2 anonymous reviewers reviewed an early draft of the manuscript and provided useful comments. We acknowledge J. D. Varley and R. D. Barbee for support in initiating the study.

STUDY AREA

Northern Winter Range

We confined our sampling to bison residing within YNP (Fig. 1). Eighty-three percent (83,000 ha) of the Northern Range occurs within YNP boundaries (Houston 1982). Elevations range from 1,500 to 2,400 m and generally increase from west to east. Mean monthly minimum ambient temperatures at Mammoth and Tower Falls (Fig. 1) ranged from −14.2 to −1.8 C and from −21.2 to −7.6 C, respectively, and mean maximum temperatures ranged from −3.4 to 10.9 C and from −3.3 to 12.6 C, respectively (Natl. Oceanic and Atmos. Adm. 1987, 1988). During January–April, maximum snow depths ranged from 5 to 20 cm and from 13 to 36 cm at Mammoth and Tower Falls, respectively.

Houston (1982) characterized the vegetation as shrub steppe interspersed primarily with Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*). Grasslands covered half the range and included Idaho fescue (*Festuca idahoensis*), bearded wheatgrass (*Agropyron subsecundum*), and western sagebrush (*Artemisia tridentata*). About 850 bison coexisted with 17,500 elk (*Cervus elaphus*), as well as mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) (Houston 1982, Singer and Norland 1993).

Madison-Firehole Winter Range

The Madison-Firehole drainage lies in the west-central portion of YNP and is part of the larger Mary Mountain winter range (Fig. 1). Elevations of sampled areas range from approximately 2,200 to 2,450 m. Maximum snow depths during January–April ranged from 84 to 94 cm. Mean monthly minimum and maximum temperatures ranged from −21.2 to −6.4 C and from −1.1 to 9.2 C, respectively (Natl. Oceanic and Atmos. Adm. 1987, 1988).

Forests of lodgepole pine, Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) covered much of this range (Craighead et al. 1973). Mesic meadows along waterways and geothermal areas included bearded wheatgrass, sedges (*Carex* spp.), and reedgrasses (*Calamagrostis* spp.). Idaho fescue and meadow grass (*Poa* spp.) predominated in drier sites.

About 186–434 bison wintered in this area; movements occurred between this range and Hayden Valley (Meagher 1973; M. M. Meagher, U.S. Natl. Park Serv., YNP, unpubl. data). Nonmigratory elk (500–1,000) also wintered on parts of this range (Singer 1991).

Pelican Valley Winter Range

This area is located northeast of Yellowstone Lake at approximately 2,378 m elevation (Fig. 1). Mean monthly minimum and maximum temperatures ranged from −22.7 to −9.4 C and from −6.4 to 8.0 C, respectively (Natl. Oceanic and Atmos. Adm. 1987, 1988). During the study, maximum monthly snow depths ranged from 84 to 102 cm.

Pelican Valley was open grassland with a few geothermal spots distributed throughout (Graham 1978). Conifer stands of lodgepole pine, Engelmann spruce, and subalpine fir (*Abies lasiocarpa*) bordered the valley, and sedge bottoms existed along creeks and adjacent flatlands within the valley (Meagher 1973, Graham 1978). Dominant vegetation included sagebrushes (*Artemisia* spp.), Idaho fescue, tufted hairgrass (*Deschampsia caespitosa*), various sedge species, wheatgrasses (*Agropyron* spp.), purple onion grass (*Melica spectabilis*), and common milfoil (*Achillea millefolium*).

Generally, bison were the only ungulates that wintered there. Information indicated bison numbers varied between 100 and 500 animals since 1935 (Meagher 1971, 1976) and were estimated at 465 bison during this study (M. M. Meagher, U.S. Natl. Park Serv., YNP, unpubl. data).

METHODS

Snow-Urine Collections

We made 4 snow-urine collections during 13 January–8 February, 15–20 February, 6–19 March, and 28 March–4 April 1988, respectively (Fig. 1). We allowed approximately 2 weeks between consecutive sample collections within a given sampling area and confined our sampling to "mixed groups" of cows, calves, and subadults with mature bulls only occasionally present. Group composition and location (Universal Transverse Mercator) were recorded. Our objective was to collect 30 samples per collection within each area. To minimize the probability of duplicate sampling of an individual within a group, we limited the number of samples collected from a given group to ≤33% of the number of individuals present. We collected and handled samples following DelGiudice et al. (1991*b*).

Forty-seven captive >2-year-old bison cows at Livingston, Montana (68 km from YNP), served as nutritional controls for the final snow-urine collection. Mean mass of captive bison was 472 kg ($n = 38$). We collected 14 samples from these animals on 22 March 1988. Bison grazed on pastures, but their diet was supplemented with 14.1 kg/animal/day of alfalfa and brome hay (10% crude protein). Salt was available ad libitum. Previously reported urinary urea nitrogen : creatinine ratios of captive bison also served as reference values (Keith et al. 1981).

Chemical Analyses

Thawed samples were chemically analyzed for urea nitrogen (U), creatinine (C), and phosphorus (P) on an ABA-100 Bichromatic autoanalyzer. Sodium (Na) and potassium (K) concentrations were determined by flame photometry (DelGiudice et al. 1987).

Concentrations of U, Na, K, and P were compared as units excreted per mg creatinine (DelGiudice et al. 1991*b*). Large sample sizes, average urinary pH values >6 (DelGiudice, unpubl. data), and frozen storage of samples minimized potential creatinine variation due to physical factors (e.g., trauma, warm temperatures) (Fuller and Elia 1988). We multiplied Na:C, K:C, and P:C by 1,000 for ease of data comparison within this study and with other studies (DelGiudice et al. 1989, 1990, 1991*b*; see corrigendum, *J. Wildl. Manage.* 56:822).

Table 1. Mean size and calf : cow ratios of bison groups sampled for urine in snow, Yellowstone National Park, Wyoming, 13 January–4 April 1988.

	Northern Range						Madison–Firehole			Pelican Valley		
	Lower			Middle–upper								
	$\bar{x}$	SE	n[a]	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Group size	42	6	11	71	13	10	46	13	10	93[b]	7	6
(range)		(20–82)			(18–162)			(6–127)			(47–100+)	
Calves : 100 cows	34	3	11	25	7	10	33	7	10	18	1	8
(range)		(14–73)			(12–45)			(0–100)			(2–39)	

[a] Sample size is the number of bison groups sampled.
[b] Represents mean minimum group size. A minimum count of 100 animals was made for 2 large groups; therefore, these groups were excluded from this calculation.

Statistical Analyses

Throughout winter, only 6 of 468 snow-urine samples from the 4 areas exhibited U:C ratios indicative of severe dietary energy deprivation (DelGiudice et al. 1987, 1991*a,b*). Because these few values were not reflective of the physiological status of the general bison population, their data were deleted from the dataset prior to statistical analyses and were presented separately. Variances of creatinine ratios of urinary metabolites were $\log_e$ transformed; Levene's test detected no differences among variances at $\alpha = 0.05$ (Conover et al. 1981). We analyzed these data by 2- and 1-way analysis of variance (ANOVAs); sampling area and collection served as independent variables. Multiple group comparisons were made with least squares means if the ANOVA demonstrated significance at $P \leq 0.05$. Data from Collections 1 and 2 were pooled for early-winter comparisons among sampling areas, and late-winter comparisons included data from Collections 3 and 4. We used Spearman correlation analysis to investigate potential influences calf : cow ratios of sampled groups may have had on urine chemistry data. To accomplish this, a weighted mean number of calves per 100 cows (calves : 100 $cows_{wt}$) of sampled groups was derived for each area and collection. Calves : 100 $cows_{wt}$ for each sampled group were calculated by multiplying the observed calves per 100 cows within each group by the number of samples collected from that group, then dividing by the total number of samples per collection and sampling area.

RESULTS

Bison Group Composition

Size of sampled groups ranged from 6 to ≥ 100 bison (Table 1). We detected no spatial or temporal differences in unweighted calf : cow ratios of sampled bison groups among the 4 areas. Analysis of pooled data from all collections parkwide yielded a weak, direct correlation ($r_s = 0.50$, $P = 0.05$) between calves : 100 $cows_{wt}$ and mean urinary U:C ratios.

Physiological Responses

Free-Ranging Bison.—Interactions between collection and sampling area were significant ($P \leq 0.009$) for all urinary characteristics. On the lower Northern Range, mean urinary U:C ratios were diminished but stable through winter. However, U:C ratios varied in bison inhabiting the middle-upper portion of the Northern Range, the Madison-Firehole Range, and Pelican Valley (Fig. 2). On the middle-upper Northern Range, mean U:C decreased ($P < 0.01$) 70% from Collections 1 to 2, then increased ($P < 0.001$) 4-fold by Collection 3. Urinary U:C of Madison-Firehole bison increased ($P < 0.001$) 250% from Collections 1 to 3, and at Pelican Valley U:C values increased ($P < 0.001$) >5-fold by Collection 4.

Urinary U:C differed among the 4 areas throughout winter (Fig. 3). Madison-Firehole bison exhibited greater U:C ratios than bison in other areas during early ($P \leq 0.001$), and late ($P < 0.001$) winter. Mean U:C ratios were higher ($P \leq 0.01$) in lower Northern Range bison than in bison on the middle-upper Northern Range and at Pelican Valley during early winter; however, values were higher ($P \leq 0.005$) in Pelican Valley bison than in Northern Range bison by late winter. One urine sample from the lower Northern Range and 5 samples from Madison-Firehole bison yielded elevated U:C ratios indicative of severe energy deprivation and accelerated catabolism (Table 2).

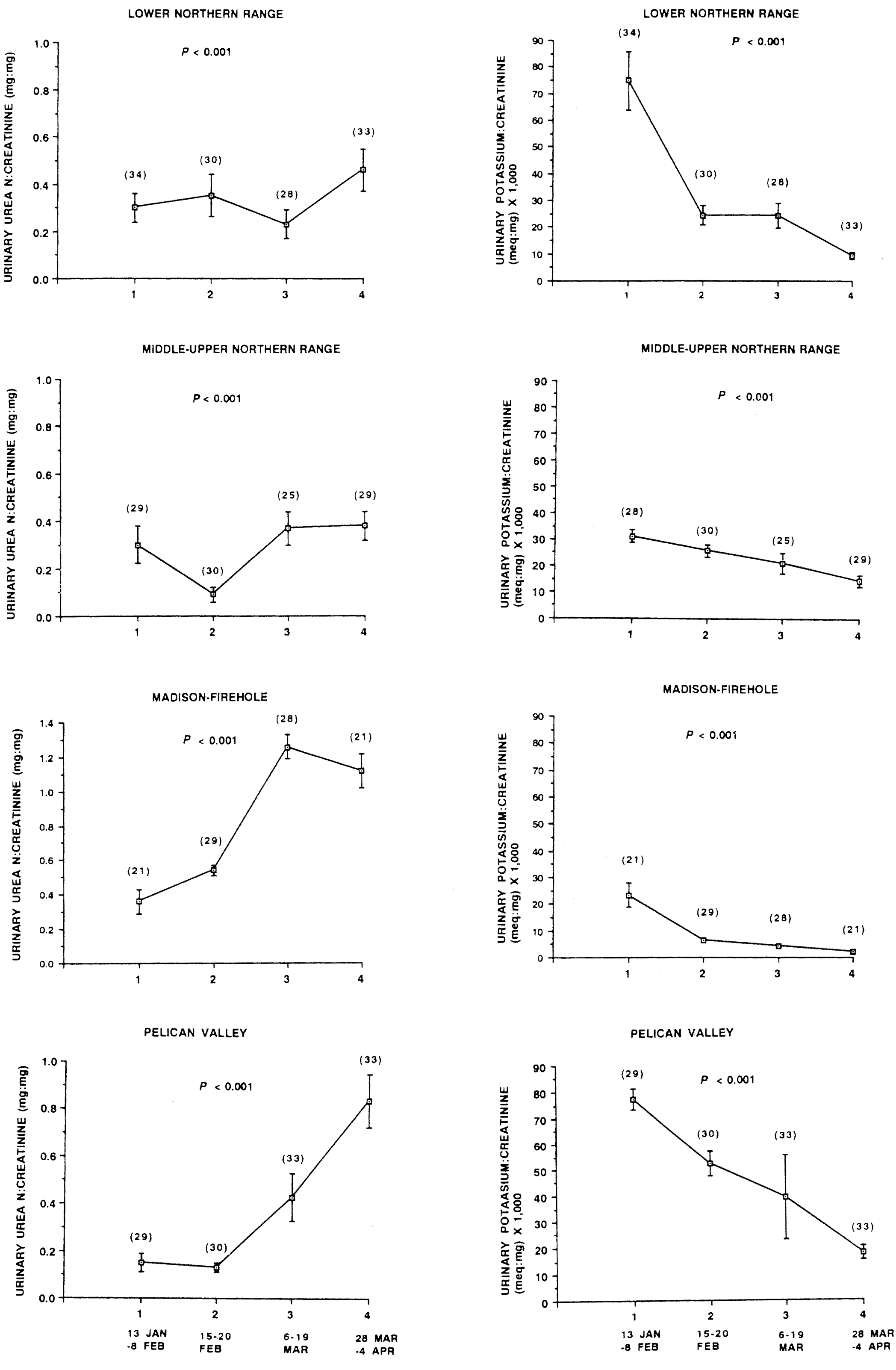

Fig. 2. Mean (±SE) urea nitrogen (N) : creatinine and potassium : creatinine ratios (sample sizes in parentheses) in bison urine collected from snow on the lower and middle-upper Northern Range, Madison-Firehole Range, and at Pelican Valley, Yellowstone National Park, Wyoming, 13 January–4 April 1988.

Mean urinary K:C ratios decreased 87.0, 53.9, 83.7, and 76.8% in bison on the lower and middle-upper Northern Range, Madison-Firehole Range, and at Pelican Valley, respectively (Fig. 2). On the lower Northern Range, K:C was lowest ($P < 0.001$) during the final collection. Mean K:C was lower ($P \leq 0.01$) during Collections 3 and 4 than during Collections 1 and 2 in middle-upper Northern Range, Madison-Firehole, and Pelican Valley bison.

Urinary K:C also differed among sampling areas throughout winter (Fig. 3). During early winter, K:C ratios were greater ($P < 0.001$) in Pelican Valley bison than in bison in other areas, and values were lowest ($P < 0.001$) at Madison-Firehole. During late winter, mean K:C remained lower ($P < 0.001$) in Madison-Firehole bison than in Northern Range and Pelican Valley bison; values were similar among the latter.

Mean urinary Na:C ratios were diminished throughout winter in all 4 areas (Table 3). These ratios remained stable in lower Northern Range and Madison-Firehole bison, but varied over time in middle-upper Northern Range and Pelican Valley bison. In the 2 latter sampling areas, mean Na:C was highest ($P < 0.01$) during Collection 4.

During early winter, Madison-Firehole bison exhibited higher ($P \leq 0.001$) Na:C ratios than bison inhabiting the other 3 sampling areas; mean values were similar among the latter (Fig. 3). During late winter, urinary Na:C remained higher ($P < 0.001$) in Madison-Firehole bison than in lower Northern Range and Pelican Valley bison.

Urinary P:C varied in lower Northern Range bison as winter progressed, but remained stable in bison in the other 3 areas (Table 3). Highest ($P \leq 0.01$) values in lower Northern Range bison occurred during Collection 1. Mean P:C values differed among the 4 areas throughout winter (Fig. 3). During early winter, P:C was greatest ($P \leq 0.003$) in lower Northern Range bison and lowest ($P < 0.001$) at Madison-Firehole. During late winter, P:C ratios were lower in bison at Madison-Firehole and Pelican Valley compared with Northern Range bison.

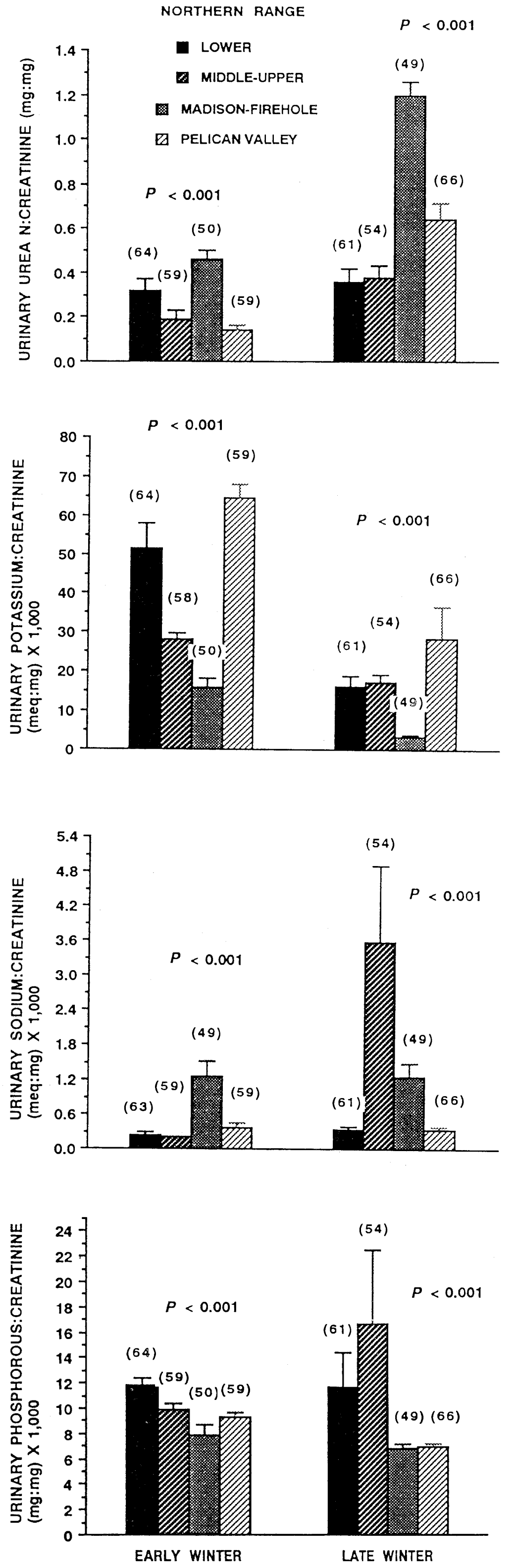

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Fig. 3. Comparison of early and late winter means (+ or ±SE) urea nitrogen (N) : creatinine and potassium : creatinine ratios (sample sizes in parentheses) in bison urine collected from snow on the lower and middle-upper Northern Range, Madison-Firehole, and at Pelican Valley, Yellowstone National Park, Wyoming, 13 January–4 April 1988.

Table 2. Urinary chemistry profiles indicative of severe energy deprivation in bison in Yellowstone National Park, Wyoming, 13 January–4 April 1988.

Sampling area Interval	n	U:C (mg:mg) $\bar{x}$	U:C SE	Na:C (meq:mg) × 1,000 $\bar{x}$	Na:C SE	K:C (meq:mg) × 1,000 $\bar{x}$	K:C SE	P:C (mg:mg) × 1,000 $\bar{x}$	P:C SE
Lower Northern Range									
13 Jan–8 Feb	1	4.6		0.3		3.9		23.1	
Madison–Firehole									
13 Jan–8 Feb	3	35.3	10.8	9.2	3.2	46.5	12.7	600	9.7
15–20 Feb	1	56.8		26.7		833		983	
6–9 Mar	1	5.4		0.0		59.4		148	

[a] U:C = urea nitrogen : creatinine, Na:C = sodium : creatinine, K:C = potassium : creatinine, and P:C = phosphorous : creatinine.

Reference Values.—Although not tested during late March, supplementally fed, captive bison exhibited mean U:C (1.6 ± 0.2 [SE] mg:mg, n = 14), Na:C (5.6 ± 3.2 meq:mg [× 1,000]), and K:C (243.3 ± 14.4 meq:mg [× 1,000]) values that were higher (2.4, 3.0, and 20.8 times, respectively) than these ratios in YNP bison (0.67 ± 0.1 mg:mg, 1.9 ± 0.6 meq:mg [× 1,000], and 11.7 ± 1.1 meq:mg [× 1,000], respectively) at that time. Urinary P:C was similar in captive (9.4 ± 0.6 mg:mg [× 1,000]) and free-ranging (9.5 ± 1.6 mg:mg [× 1,000], n = 116) bison.

DISCUSSION

Reference Values

During late March, presumably better nutrition of supplementally fed, captive bison compared with YNP bison was reflected collectively by greater urinary U:C and K:C ratios, as well as by relatively high Na:C ratios. Higher mean urinary U:C ratios have been noted in captive bison that gained mass while supplementally fed a 15% crude protein diet during January–March compared with bison fed a 6% crude protein diet that lost 9.9 ± 1.0% of their mass (Fig. 4) (Keith et al. 1981; E. O. Keith, Colorado State Univ., unpubl. data). Nevertheless, both groups of bison had U:C ratios higher than free-ranging Yellowstone bison during the January–early April period (Fig. 4). This suggests that although the crude protein content of food consumed by low protein-fed captive bison and Yellowstone bison was similar, easier access to food for captive bison likely allowed greater food intake. Elevated U:C and K:C ratios also have been reported for supplementally fed white-tailed deer (*Odocoileus virginianus*) and elk compared with animals without access to supplemental food (DelGiudice et al. 1989, 1991*b*).

Progressive Winter Nutritional Deprivation

Comparison of Winter Ranges.—Subtle differences in the magnitude and course of winter nutritional deprivation or restriction associated with varied environmental influences were indicated by temporal patterns of urinary U:C and K:C from bison on the different ranges and by comparison of their mean values during early and late winter. We speculate that deeper snow cover on the middle-upper Northern Range, as early as December, had a more compromising effect on the nutritional status of bison wintering there than of bison wintering on the lower portion of this range. Peak winter snow depth occurred on the middle and upper elevations of the Northern Range as early as December (43 cm) and was >5 times greater than at the lower elevations (8 cm) (Natl. Oceanic and Atmos. Adm. 1987). Lower mean U:C and K:C ratios of bison on the middle-upper portion of the range compared with bison at the lower elevations during early winter together indicated more extreme nutritional restriction in the former (Robbins et al. 1974, Keith et al. 1981, DelGiudice et al. 1987). Although progressive nutritional deprivation was reflected by decreasing trends in urinary K:C in both lower and middle-upper Northern Range bison, the concurrent increasing trend in mean U:C occurred earlier in the latter. Mean U:C ratios still were considered low, but it appeared that bison at the higher elevations were experiencing increased endogenous protein loss over a more prolonged period. Northern Range bison only recently (1975–76), during a severe winter, expanded their traditional core winter range east of Tower Falls to include the lower elevations sampled during this study (Meagher 1989*b*).

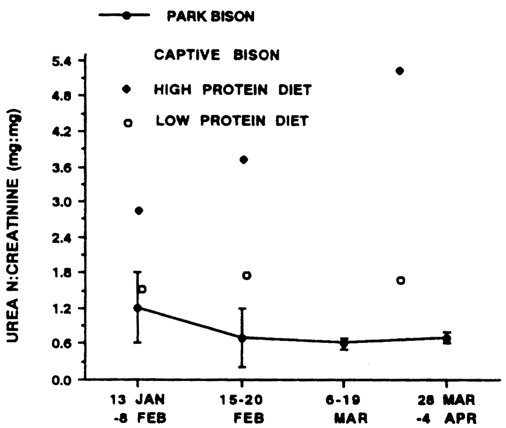

Fig. 4. Comparison of mean (±SE) urinary urea nitrogen (N) : creatinine ratios of Yellowstone National Park bison and mean reference urea N : creatinine values reported for captive bison fed low N (6% crude protein) and high N (15% crude protein) diets during winter (Keith et al. 1981:263).

By late March–early April, an acceleration of net catabolism of protein in Pelican Valley bison was suggested by the >5-fold increase in urinary U:C ratios, coincident with minimum K:C values and persistent maximum snow depths. The increase in U:C ratios and apparent net catabolism in bison by late winter may have been partially attributable to an increase in calf : cow ratios of Pelican Valley groups sampled during late winter (33 and 29 calves : 100 cows during Collections 3 and 4, respectively) compared with early winter (4 and 8 calves : 100 cows during Collections 1 and 2, respectively). Thus, there was greater potential for sampling calves during late winter when nutritional stress is expected to be most severe. During late winter, however, mean calf : cow ratios were comparable with sampled groups on the other ranges; similar K:C ratios and greater U:C values compared with Northern Range bison indicated greater deprivation (i.e., net catabolism) in Pelican Valley bison.

The greater nutritional deprivation we observed in Pelican Valley bison compared with Northern Range bison may be a combined effect of the large number of bison relative to carrying capacity, more severe winter conditions, and a higher proportion of sedges in their diet. The Pelican Valley population has experienced substantial winter-kill losses during March–April of severe winters when bison numbered ≥200; Meagher (1971, 1976) contended that 100 animals may be the maximum that can be sustained here regardless of winter severity. During win-

Table 3. Chemistries of bison urine collected from snow on winter ranges in Yellowstone National Park, Wyoming, 13 January–4 April 1988.

Snow-urine characteristic[a]	Sampling area	Collection: 13 Jan–8 Feb $\bar{x}$[b]	SE	n	15–20 Feb $\bar{x}$	SE	n	6–9 Mar $\bar{x}$	SE	n	28 Mar–4 Apr $\bar{x}$	SE	n	Collection effect $P \leq$
Na:C (meq:mg) × 1,000	Northern Range													
	Lower	0.3	0.08	33	0.1	0.02	30	0.4	0.13	28	0.3	0.08	33	0.065
	Middle–Upper	0.3	0.04	29	0.1	0.02	30	1.2	0.58	25	5.6	2.37	29	0.001
	Madison–Firehole[c,d]	1.8	0.50	20	0.9	0.22	29	1.1	0.27	28	1.5	0.39	21	0.110
	Pelican Valley	0.3	0.06	29	0.4	0.14	30	0.2	0.03	33	0.4	0.10	33	0.001
P:C (mg:mg) × 1,000	Northern Range													
	Lower	13.4	0.8	34	10.0	0.6	30	13.7	5.8	28	10.0	0.6	33	0.001
	Middle–Upper	11.9	0.9	29	7.9	0.3	30	19.3	10.4	25	14.5	6.3	29	0.080
	Madison–Firehole[d]	8.5	1.6	21	7.4	0.7	29	7.4	0.6	28	5.9	0.5	21	0.197
	Pelican Valley	8.8	0.3	29	9.8	0.5	30	6.7	0.4	33	7.0	0.4	33	0.085

[a] Na:C = sodium : creatinine, and P:C = phosphorous : creatinine.
[b] Data were analyzed by 1-way ANOVA after data were $\log_e$-transformed; however, original means and standard errors are presented.
[c] The part of the Mary Mountain winter range where bison were sampled.
[d] Data from 1 and 4 snow-urine samples collected from lower Northern Range and Madison–Firehole bison, respectively, are presented separately in Table 2.

ter of our study, considered relatively mild, a mid-February aerial survey counted 465 bison (M. M. Meagher, U.S. Natl. Park Serv., YNP, unpubl. data). We did not relate physiological data to mortality, but increased U:C ratios, higher than those reported here, have been associated with winter-killed ungulates (DelGiudice et al. 1991*b*).

Among bison ranges in YNP, Pelican Valley experiences the most severe winter weather. Deep snow and heavy crusting by early March is common due to the area's exposure to prevailing westerly and southwesterly winds (Meagher 1971, 1976). Such conditions increase energetic costs of locomotion and foraging (Parker et al. 1984, Wickstrom et al. 1984). They also contribute to dietary energy deficiencies that may lead to increased depletion of body protein (Torbit et al. 1985) indicated by increased U:C ratios of Pelican Valley bison. Furthermore, according to fecal analyses, the diet of Pelican Valley bison was composed primarily of sedges (77%), whereas grasses appeared to be dominant (64%) in the diet of Northern Range bison (F. J. Singer, U.S. Natl. Park Serv., Colorado State Univ., unpubl. data). Sedges are less digestible than grasses (Peden et al. 1974, Hawley et al. 1981). Greater access by Northern Range bison to upland grasses, and consequently to a diversity of forages, would further indicate that those animals should be in better condition.

Evidence suggested that winter nutritional deprivation was greatest in Madison-Firehole bison. Chemistry profiles indicated that 12.5% of sampled bison were experiencing severe dietary energy deficiency during the first snow-urine collection. Urinary U:C ratios approaching 4 mg:mg or higher are exhibited either in response to an unnaturally high protein–high energy diet or when severe dietary energy restriction induces a notable acceleration of protein catabolism (Keith et al. 1981; DelGiudice et al. 1987, 1991*a*). Because Yellowstone bison were not supplementally fed, and crude protein content of forages in bison diets is only 4–7% dry mass (Peden et al. 1974), U:C ratios ≥ 3.8 mg:mg indicated the latter. Similar to findings for other ungulates, an elevated urinary U:C (23.8 mg:mg) was reported for a winter-killed bison with $<10\%$ femur marrow fat (DelGiudice et al. 1991*a*, Saltz and White 1991*a*). A greater degree of undernutrition and catabolism was indicated in the remainder of the sampled Madison-Firehole bison by lower K:C values and higher U:C ratios throughout winter compared with bison on the other ranges. Lowest P:C ratios in Madison-Firehole bison throughout winter additionally indicated more advanced nutritional deprivation in these animals (Hays and Swenson 1984).

Warm sedge bottomlands are more extensive and widely dispersed at Madison-Firehole than at Pelican Valley (Meagher 1971, Graham 1978), and bison may obtain some benefit from green sedge shoots in these thermal areas (Craighead et al. 1973). However, about 800 elk shared this range with bison and foraging competition likely occurred (Singer and Norland 1993). Snow-free, warm bottomlands are regularly depleted of available forage by elk and bison by the end of each winter.

Sodium Deprivation.—Diminished dietary Na throughout winter was reflected by low urinary Na:C values on all winter ranges (Harlow and Seal 1981, Gans and Mercer 1984, DelGiudice et al. 1987). The Na content of most plants tends to be low throughout the year, and it decreases further during winter in many species (Short et al. 1966). Low Na:C ratios also have been reported for Yellowstone elk and free-ranging white-tailed deer subsisting solely on natural vegetation during winter (DelGiudice et al. 1989, 1991*b*).

Sodium intake was greater among Madison-Firehole bison than lower Northern Range and Pelican Valley bison throughout winter and was greater compared with middle-upper Northern Range bison during early winter. This may be attributed to higher Na content of the bottomland vegetation associated with the extensive thermal-influenced areas at Madison-Firehole. Natural salt licks of northern ungulates often occur in bottomland soils and have been reported to have Na contents 16 times greater than other habitats (Weeks and Kirkpatrick 1976). Greater Na:C ratios were noted for Madison-Firehole elk compared with elk wintering elsewhere in YNP (DelGiudice et al. 1991*b*).

MANAGEMENT IMPLICATIONS

Unlike other ungulates at northern latitudes, evidence from studies of captive bison have shown they may not voluntarily reduce their intake during winter (Hawley et al. 1981). However, progressive nutritional deprivation was evident in bison on all sampled winter ranges, and subtle, but potentially important, differences in degrees of deprivation were indicated by serial urine chemistry profiles. The almost complete absence of high U:C ratios ($\geq$4 mg:mg), indicative of severe energy restriction, reflected relatively mild winter conditions and indicated that nutritional stress in bison was mild.

Meagher (1971, 1973) contended that winter kill was the primary cause of natural mortality of Yellowstone bison. Our sequential physiological assessments of nutritional deprivation in bison reflected the combined influence of varied weather conditions, habitat quality, and other environmental perturbations. We did not elucidate the specific effect of such nutritional deprivation differences on body mass or survival of bison. However, continued monitoring of nutritional deprivation in this way, along with more detailed examination of changes or differences in forage availability, food habits, weather severity, reproduction, and survival, will provide greater insight into the role of ungulate nutrition in the dynamics of such a complex system. Murphy and Noon stated (1991:778) such monitoring should be "viewed as a set of ongoing experiments" and "a hypothesis-testing exercise," which over time will help in differentiating among various management options and improve management. Greater consideration should be given to calf : cow ratios in designing sampling schemes in future research.

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Received 12 October 1992.
Accepted 25 March 1993.
Associate Editor: Woolf.