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POTENTIAL ECOLOGICAL IMPACT OF DIET SELECTIVITY AND BISON HERD COMPOSITION

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ABSTRACT—Behavioral segregation between the sexes of bison (*Bos bison*), coupled with artificially manipulated sex ratios of bison herds, might profoundly influence prairie ecosystems. Therefore, we measured carbon isotopes in hair collected from bison from the Tallgrass Prairie Preserve in northeast Oklahoma to determine if adult male, adult female, and juvenile bison segregate on the basis of botanical composition of their diet. Sex ratio of bison herds in the Great Plains and behavioral differences between sexes were used to assess potential effects of sex ratio on tallgrass prairie. Botanical composition of diet differed among the three bison groups, in that C₄ grasses contributed most to adult bull diets and least to juvenile diets. Bison sex ratio in half of the herds surveyed was highly skewed toward females. Because of behavioral differences between adult male and female bison, different sex ratios in bison herds might result in different vegetation structure, composition, and patchiness.

Key Words: bison, carbon isotope, grasslands, prairie conservation, sex ratio, tallgrass prairie

Introduction

Bison (*Bos bison*) were major forces shaping Great Plains prairie ecosystems (Larson 1940; Stebbins 1981; Knapp et al. 1999), in combination with fire and drought (Axelrod 1985). Bison therefore have been reintroduced to prairies in the Great Plains to restore biodiversity (Hamilton 1996; Hartnett et al. 1996; Truett et al. 2001). However, when considering bison-grazing as an ecological tool, some behavioral differences within this species might not have been fully considered when constructing bison herd composition for reintroduction programs.

Bison have exhibited sexual segregation for at least 35,000 years (Berger and Cunningham 1994). Adult males might differ from females in habitat selection (Berger and Cunningham 1994; Coppedge and Shaw 1998a), group size (Berger and Cunningham 1994; Schuler 2002), diet composition (Coppedge and Shaw 1998b; Post et al. 2001), and mobility (Berger and Cunningham 1994; Schuler 2002). Because of sexual segregation, different sex ratios in bison herds potentially generate different levels of disturbances across the landscape. Bison population numbers in the Great Plains are managed artificially instead of controlled by natural processes, and because of behavior differences associated with sexual segregation, adult male and female bison could differ in their impact on vegetation structure and composition and spatial patchiness.

The objectives of our study were (1) to determine if adult male bison differ from females and juveniles in their diet composition in the tallgrass prairie, and (2) to compile data on sex ratios of bison herds in parks, preserves, and refuges as a basis for discussing implications of sex ratios for restoration and conservation of grasslands in the Great Plains.

Methods

We collected data in November 2001 from free-ranging adult and juvenile bison of both sexes from the Nature Conservancy's Tallgrass Prairie Preserve (TGPP) in the Osage Hills of northern Oklahoma (36°50'N, 96°25'W). The bison herd of TGPP consisted of 78 bulls (≥ 3.5 yrs old), 492 cows (≥ 3.5 yrs old), 419 juveniles (>1 and ≤ 2.5 yrs old), and 370 calves (<1 yr old). Animals had free access to the entire bison area on the preserve,

which had been expanded progressively concomitant with the expansion of the bison herd to maintain a stocking density of 6-7 ha AU⁻¹ (Coppedge and Shaw 1998a). Bison had free access to salt with trace minerals, but they did not receive supplemental feed at any time (Hamilton 1996). About one-third of the bison area was burned every year in patches in early spring, summer, and fall randomly selected from areas not burned in the previous year (Hamilton 1996).

During the fall roundup of bison, we used an electric clipper to collect hair samples from the heads of bison, rather than posterior body hair, to reduce the influence of seasonality of hair growth (i.e., bison body hair is grown in fall and shed in spring). The origin and age of animals were identified by transponders carried by each animal. We used hair samples only from animals born on the TGPP. We cut small pieces from the base of the hair, loaded them into tin cups (≈ 100 mg), and sent them to the Department of Biology, University of Utah, for analysis of stable isotopes of carbon. The ratio of stable isotopes is expressed in δ notation in parts per thousand, where

$$\delta^{13}\text{C} (\text{‰}) = \left(\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} \right) - 1 \times 1,000.$$

The ratio of stable carbon isotopes has been used successfully to quantify diets of herbivores relative to the difference in ¹³C content between plants with C₃ and C₄ photosynthetic pathways. This difference is also reflected in consumer tissues including hair (Kelly 2000). Average $\delta^{13}\text{C}$ values for C₃ and C₄ plants are -26.5‰ and -12.5‰ , respectively (Chisholm et al. 1986). For statistical analysis we divided the animals into three groups: bulls (≥ 3 yr old), cows (≥ 3 yrs old), and juveniles (animals of both sexes ≥ 1 and ≤ 2.5 yrs old). All statistical procedures were performed using Statistical Analysis Software (SAS Institute, Inc. 1999). We tested the data for homogeneity of variance by using Levene's test ($F = 1.38$, $p = 0.2664$) and for normality by using the Shapiro-Wilk test ($\text{Pr} < W = 0.1519$). We subjected data to analysis of variance (PROC GLM), and we used least-significant-difference (LSMEANS/PDIFF) to test differences in diet content among groups at $\alpha = 0.05$.

To obtain information about sex ratios in bison herds accessible to the public, we contacted parks, preserves, and refuges in the Great Plains where bison are known to be present (National Bison Association 2002). From herd records provided by these contacts, we determined if herds were increasing or stable in size and sex ratio.

TABLE 1

MEAN AND STANDARD ERROR OF THE MEAN (SEM) OF $\delta^{13}\text{C}$ IN HAIR COLLECTED FROM BISON BULLS, COWS, AND JUVENILES AT THE TALLGRASS PRAIRIE PRESERVE

Group	N	$\delta^{13}\text{C}$ (‰)	
		Mean*	SEM
Bulls	7	-12.6 ^a	0.32
Cows	15	-13.4 ^b	0.21
Juveniles	14	-14.1 ^c	0.22

* Mean values with different superscripts are different at $\alpha = 0.05$.

Results

Bison groups differed with respect to stable carbon isotope ratio ($\delta^{13}\text{C}$) in hair ($F = 7.16$, $p = 0.0019$). Carbon isotope ratio differed between bulls and cows ($p = 0.0470$), between bulls and juveniles ($p = 0.0005$), and between cows and juveniles ($p = 0.0315$) (Table 1). Diet of all groups clearly was dominated by C_4 plants, and C_4 contribution to the diet was greatest for bulls. Diet of juveniles was composed of the least amount of C_4 plants.

Sex ratio was highly skewed (>1:2 M:F) toward females in 6 of 12 establishments contacted in the Great Plains where bison were known to be present (Table 2). Sex ratio of herds of six establishments was close to 1:1. Herds of most establishments (10 of 12) were stable in terms of herd size, yet in four of these, sex ratio was skewed to females.

Discussion

Given mean ^{13}C isotope enrichment of 3.1‰ between keratin (horn, hoof, and hair) and diet in large ruminants (Cerling and Harris 1999), we estimated $\delta^{13}\text{C}$ for diets of bulls, cows, and juveniles in the Tallgrass Prairie Preserve of about -15.7‰, -16.5‰, and -17.2‰, respectively. These values are similar to those found in bison dung at the TGPP ($\delta^{13}\text{C} = -16.8$) (Tieszen et al. 1998). Therefore, $\delta^{13}\text{C}$ values obtained from bison hair confirm that

TABLE 2

**BISON HERD SIZE, SEX RATIO, AND STATUS IN GREAT PLAINS
PARKS, PRESERVES, AND REFUGES**

Location	Number of adults (Total herd size)	Sex ratio (M:F)	Area ^a (ha)	Herd status
Badlands National Park, SD	452 (755)	1.4:1	25,920	Stable
Cross Ranch Preserve, ND	42 (86)	1:9.5	1,251	Stable
Custer State Park, SD	(950)	1:6.9	7,144	Stable
Fort Niobrara National Wildlife Refuge, NE	242 (350)	1:1.3	5,670	Stable
Konza Prairie Biological Station, KS	175 (280)	1:5.26	3,489	Increasing
National Bison Range, MT	203 (404)	1:1.14	7,594	Stable
Niobrara Valley Preserve, NE ^b	171 (383)	1:13.3	3,038	Stable
	132 (281)	1:10	4,860	
Ordway Memorial Prairie, SD	189 (267)	1:9.5	1,215	Stable
Tallgrass Prairie Preserve, OK	570 (1359)	1:6.3	4,247	Increasing
Theodore Roosevelt National Park, ND ^b	15 (230)	1:0.98	9,748	stable
	129 (263)	1:1.05	18,682	
Wichita Mountains Wildlife Refuge, OK	400 (600)	1:1	24,300	Stable
Wind Cave National Park, SD	255 (475)	1:1.68	11,441	Stable

^a Area accessible to bison; area and herd size are increasing at Tallgrass Prairie Preserve.

^b Two herds in separate areas.

bison in tallgrass prairie consume diets composed primarily of C₄ grasses (i.e., warm-season tallgrasses), as has been reported previously (Coppedge and Shaw 1998b), but these data also show that the proportion of C₄ plants in the diet is greatest in bulls, intermediate in cows, and least in juveniles. The C₃ contribution to bison diets at TGPP is mostly the grassland-like sedges (dominated by *Carex* spp.) (Coppedge and Shaw 1998b), which are higher in dry matter digestibility than C₄ grasses (Caswell et al. 1973). We therefore conclude, as did Post et al. (2001) for the Konza Prairie Biological Station (KPBS), that diet quality is highest for juveniles and lowest for bulls in this tallgrass prairie. This assumes no difference in digestive ability among bulls, cows, and juveniles.

Our results are similar to those reported by Post et al. (2001) in that bulls selected lower-quality diets than cows, juveniles, and calves at KPBS. However, because C₄ plants contributed more to cow diets than to juvenile diets in our study, cows apparently chose lower-quality forages than juveniles. In

contrast, diets of cows and juveniles were similar throughout the year at KPBS except during April when juvenile diets contained greater amounts of C_3 plants than did cow diets (Post et al. 2001). One would expect the opposite, that is, greater contribution of C_3 plants to juvenile diets at KPBS, given greater abundance of C_3 plants in tallgrass prairies located at more northern latitudes (Paruelo and Lauenroth 1996; Tieszen et al. 1997). In addition to the possibility that at TGPP juveniles might select sedges on recently burned patches to a greater extent than cows during the winter and spring (Coppedge and Shaw 1998b), other explanations include differences in sample material (hair vs. dung), fire and grazing management, and sample size (Post et al. 2001).

Juveniles from both sexes remain in female groups, so differences in diet composition between juveniles and cows could be explained by greater botanical selectivity exerted by juveniles. If so, juvenile grazing time might be longer than that of cows. However, a study at the TGPP comparing time budgets between adult and juvenile bison found no difference across seasons in time spent grazing (Maichak 2002). However, Maichak (2002) classified adults as those animals ≥ 1 yr old, whereas we classified adults as those animals ≥ 3 yrs old. Conversely, cows might selectively avoid C_3 plants, although this seems unlikely given the higher-quality forage provided by C_3 plants.

Our results demonstrated that adult male and female bison at TGPP, a southern tallgrass prairie, selected different proportions of C_3 and C_4 plants, a particularly notable result given the primary contribution to the C_3 plant group at TGPP is forbs rather than C_3 grasses (Coppedge et al. 1998), and bison preferentially select diets of grasses and sedges (Coppedge and Shaw 1998b). Therefore, differences in botanical composition of diet, combined with other forms of sexual segregation between adult male and female bison, could result in different vegetation structure and/or composition in the tallgrass prairie ecosystem. Previous studies at TGPP (Coppedge and Shaw 1998a; Coppedge et al. 1998) demonstrated the interaction between bison grazing and fire in shaping vegetation structure and composition. Research across the Great Plains has shown that, at least during the growing season, bison preferentially graze recently burned patches (Coppock and Detling 1986; Shaw and Carter 1990; Coppedge and Shaw 1998a; Biondini et al. 1999; Schuler 2002). This particular behavior results in heterogeneous use of the landscape, with some areas under heavy grazing pressure and others under light grazing pressure or no grazing.

Not only do adult male and female bison segregate outside the rut, but group size also differs (Komers et al. 1993; Berger and Cunningham 1994;

Schuler 2002). At TGPP, adult male bison formed groups of a few individuals, whereas females and their young formed groups that varied from 23 individuals in autumn and winter to 206 individuals in summer (Schuler 2002). Large groups were generally mixed and had formed during summer, when adult males joined female groups. Female groups are comprised of adult females, their young, and juvenile male and female bison (Berger and Cunningham 1994; Schuler 2002). Considering that male groups are smaller in number than female groups, inductive reasoning leads us to expect that at a 1:1 (M:F) sex ratio, males would be more evenly distributed across the landscape than females. If indeed male and female bison differ in impact on vegetation across the landscape, then one could expect the spatial pattern of vegetation structure and composition to vary with sex ratio of adult male and female bison at a specific stocking rate.

However, the influence of sex ratio might be limited if the major impact of bison on the structure and composition of tallgrass prairie is due mainly to grazing recently burned patches during spring and summer (Coppedge and Shaw 1998a). If sex ratio negligibly influences vegetation structure and composition, herd composition would have little relevance to management and conservation of tallgrass prairie. Sex ratio would exert a minor role if the majority of adult males join cow-calf groups during the growing season. Although at TGPP most bulls join cow-calf groups until 2-3 months before rut (Schuler 2002), bull groups exist throughout the year (Coppedge and Shaw 1998a; Schuler 2002). Conclusions about this issue are tenuous because sex-group studies at TGPP observed a population in which males represented less than 20% of the adults, so behavior of adult male bison in response to sex ratio is uncertain.

Sex ratio in extant ungulates generally favors females (Berger and Gompper 1999), but male:female ratio in natural populations of bison in the Great Plains ranged from 0.81 to 0.98, only a slight departure from 1. Sex ratios of contemporary herds were highly skewed toward females (Table 2) in six of the preserves where bison were reintroduced as a disturbance process to restore biodiversity. Skewed sex ratios are advantageous in expanding herds because having more females than males allows more rapid building of herd numbers, preserves the option of selling excess animals, and avoids managing large numbers of potentially dangerous mature bulls. However, the majority of herds with skewed sex ratios already had reached herd stability. These bison herds generally are gathered once annually, when artificial culling is performed. As a result, sex ratio greatly favors females at TGPP, and males ≥ 6 yrs old are culled to reduce handling problems (R.G. Hamilton, pers. comm.). It should be recognized that this approach to managing

herd composition represents a reproductive perspective rather than an ecological approach to managing male bison in the population. Our knowledge is limited on the contrasting ecological roles of adult male and female bison on Great Plains grasslands, but maintaining sex ratios close to those found in natural populations would be ideal given the uncertainty of the effects of sex ratio.

Conclusions

Bison have been the large ungulate of choice for restoring natural patterns of herbivory, but sex ratio is skewed in favor of females in many bison herds. For varied reasons, these herds probably disturb prairies of Great Plains differently from those of presettlement times. It might be argued that differences we found in diet selection between male and female bison are insufficient to be ecologically meaningful. Even so, male and female bison also select different portions of the landscape. Therefore, in those herds in which females greatly outnumber males, structure, composition, and patchiness of the vegetation might differ considerably from the landscape in which males and females are about equal in proportion. For example, females might have a greater impact on creating and maintaining grazing lawns dominated by C_4 grasses within recently burned sites (Coppedge et al. 1998) than would be expected under equal sex ratios, and males might have less influence on sites selected preferentially by them (e.g., less recently burned sites containing accumulated litter and C_3 plants, especially forbs). The lower grazing pressure exerted by bulls on C_4 grasses within less recently burned sites might be reflected in vegetation composed of lesser amounts of forbs than what might otherwise be expected. Because sexual segregation is a common feature of bison populations irrespective of habitat type, sex ratio might influence vegetation in similar ways in other prairies in the Great Plains, for example, in prairies not managed with fire. Our study indicates that additional research is warranted to examine the magnitude of the ecological effect of herd composition given differences in diet selection between adult male and female bison.

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References

- Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:163-201.
- Biondini, M.E., A.A. Steuter, and R.G. Hamilton. 1999. Bison use of fire-managed remnant prairies. *Journal of Range Management* 52:454-61.
- Berger, J., and C. Cunningham. 1994. Social spacing and land use systems. In *Bison: Mating and Conservation in Small Populations*, ed. M.C. Pearl, 74-97. New York: Columbia University Press.
- Berger, J., and M.E. Gompper. 1999. Sex ratio in extant ungulates: products of contemporary predation or past life histories? *Journal of Mammalogy* 80:1084-1113.
- Caswell, H., F. Reed, S.N. Stephenson, and P.A. Werner. 1973. Photosynthetic pathways and selective herbivory: A hypothesis. *American Naturalist* 107:465-80.
- Cerling, T.E., and J.M. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:347-63.
- Chisholm, B., J. Driver, S. Dube, and H.P. Schwarcz. 1986. Assessment of prehistoric bison foraging and movement patterns via stable-carbon isotopic analysis. *Plains Anthropologist* 31:193-205.
- Coppedge, B.R., D.M. Engle, C.S. Toepfer, and J.H. Shaw. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology* 139:235-46.
- Coppedge, B.R., and J.H. Shaw. 1998a. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* 51:258-64.
- Coppedge, B.R., and J.H. Shaw. 1998b. Diets of bison groups on tallgrass prairie in Oklahoma. *Prairie Naturalist* 30:29-36.

- Coppock, D.L., and J.K. Detling. 1986. Alteration of bison and black-tailed prairie dog grazing interactions by prescribed burning. *Journal of Wildlife Management* 50:452-55.
- Hamilton, R.G. 1996. Using fire and bison to restore a functional tallgrass prairie landscape. *Transactions of the North American Wildlife and Natural Resources Conference* 61:208-14.
- Hartnett, D.C., K.R. Hickman, and L.E.F. Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49:413-20.
- Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78:1-27.
- Knapp, A.K., J.M. Blair, J.M. Briggs, S.L. Collins, D.C. Hartnett, L.C. Johnson, and E.G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49:39-50.
- Komers, P.E., F. Messier, and C.C. Gates. 1993. Group structure in wood bison: nutritional and reproductive determinants. *Canadian Journal of Zoology* 71:1367-71.
- Larson, F. 1940. The role of the bison in maintaining the short grass plains. *Ecology* 21:113-21.
- Maichak, E.J. 2002. Behavioral variation in bison (*Bos bison bison*) on a tallgrass prairie. Master's thesis, Oklahoma State University, Stillwater.
- National Bison Association. 2002. www.bisoncentral.com/nba/mission.asp (accessed November 25, 2002).
- Paruelo, J.M., and W.K. Lauenroth. 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications* 6:1212-24.
- Post, D.M., T.S. Armbrust, E.A. Horne, and J.R. Goheen. 2001. Sexual segregation results in differences in content and quality of bison (*Bos bison*) diets. *Journal of Mammalogy* 82:407-13.
- SAS Institute, Inc. 1999. *SAS User's Guide*, vers. 8. SAS Institute. Cary, NC.
- Schuler, K.L. 2002. Seasonal variation in bison distribution and group behavior on Oklahoma tallgrass prairie. Master's thesis, Oklahoma State University, Stillwater.
- Shaw, J.H., and T.S. Carter. 1990. Bison movements in relation to fire and seasonality. *Wildlife Society Bulletin* 18:426-30.
- Stebbins, G.L. 1981. Coevolution of grasses and herbivores. *Annals of Missouri Botanic Garden* 68:75-86.
- Tieszen, L.L., B.C. Reed, N.B. Bliss, B.K. Wylie, and D.D. DeJong. 1997. NDVI, C₃ and C₄ production, and distributions in Great Plains grassland land cover classes. *Ecological Applications* 7:59-78.

- Tieszen, L.L., L. Stretch, and J.V. Kooi. 1998. Stable isotopic determination of seasonal dietary patterns in bison at four preserves across the Great Plains. In *International Symposium on Bison Ecology and Management in North America*, ed. L. Irby and J. Knight, 130-40. Bozeman: Montana State University.
- Truett, J.C., M. Phillips, K. Kunkel, and R. Miller. 2001. Managing bison to restore biodiversity. *Great Plains Research* 11:123-44.

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