Bison grazing patterns on seasonally burned tallgrass prairie

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Abstract

Patterns of bison (*Bison bison* L.) grazing were examined in a 2-year study on a tallgrass prairie site in Oklahoma subjected to a seasonally and spatially variable burning regime. Mixed groups of bison, composed of cows, yearlings, calves, and young (< 5 years of age) bulls, comprised 90% of the study population and showed selectivity by using burned areas significantly more than expected 23% of the time. Mixed groups avoided unburned areas 63% of the time. In contrast, bull groups of mature bulls > 5 years of age selected unburned areas for grazing 29% of the time and burned areas only 4% of the time. Temporal patterns in bison grazing were evident; selective use of burns persisted for only a short period during the first post-fire growing season, after which burns were grazed in proportion to availability and then selectively avoided as bison shifted grazing efforts to newer burns. Regression analysis verified that bison grazing was negatively related to burn age. Regression also showed that grazing patterns were positively related to burn patch size. Although burn types varied significantly in biomass and overall vegetative composition, bison exhibited only limited preference for any burn type, choosing those with higher relative cover of annual *Bromus* spp. and sedges. It appears that bison select recently burned areas with relatively low graminoid biomass for grazing, presumably choosing these areas based on forage quality rather than quantity.

Key Words: bison-fire interactions, temporal trends, bison social groups, sedges

Most North American prairies developed under the influence of fire and bison (*Bison bison* L.) grazing (Axelrod 1985), and numerous studies have documented the interaction between these phenomenon. Bison are strongly attracted to recently burned areas (Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993, Pearson et al. 1995), presumably because of increases in forage quality (Coppock et al. 1983) and quantity (Wallace et al. 1995). In tallgrass prairie, fires were frequent and seasonally-variable (Bragg 1982). However, even slight differences in the seasonal timing of burning can have profound effects on vegetation response (Towne and Owensby 1984). In general, fires that occur during the dormant season favor those species that are not actively growing, such as the warm-season grasses that now dominate tallgrass prairie (Collins and Wallace 1990). However, fires during the growing season when these warm-season species are active reduces their competitive ability and favors cool-season species (Howe 1994). What is not well understood is how burning tallgrass prairie at different times of the year, during both active and dormant growing seasons, affects both the vegetative response and the subsequent grazing use by native herbivores.

This study reports on the grazing patterns of bison in a tallgrass prairie landscape subjected to seasonally-variable prescribed burns. Study objectives were to investigate spatial and temporal patterns of bison grazing in relation to the burning regime. Specifically, we were interested in testing hypotheses that 1) seasonal burns differ significantly in vegetative parameters and 2) bison grazing patterns are influenced by variations in burn patch parameters such as vegetative, spatial and temporal characteristics. Because bison on this site are almost exclusively gramnivorous (Coppedge 1996), we specifically hypothesized that grazing preferences would be closely tied to areas with high cover of graminoids. We also evaluated grazing patterns of bison social groups. Bison, like many ungulates, practice sexual segregation where adult males and females remain spatially and/or temporally separated for most of the year (McHugh 1958, Main and Coblentz 1990). Because differential habitat use in bison social groups has received little research attention, we compared grazing patterns of bison social groups in this study to test the hypothesis that segregation results in different overall grazing patterns.

Methods

The Study Area

The study was conducted from January 1994 to December 1995 on the Nature Conservancy's Tallgrass Prairie Preserve (TPP), a 15,342-ha tallgrass prairie site in the Osage Hills of northern Oklahoma (36°50'N, 96°25'W). The Osage Hills are a southward extension of the Flint Hills region that lies primarily in Kansas. The Flint Hills are an upland area characterized by hilly topography and rocky soils that prevented extensive cultivation and contain the largest remaining tracts of native tallgrass prairie in North America.

Vegetation is dominated by big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* [L.] Nash), switchgrass (*Panicum virgatum* L.), and little bluestem (*Schizachyrium scoparium* [Michx.] Nash). Subdominant graminoids include rough dropseed (*Sporobolus asper* (Michx.) Kunth) and sedges

(*Carex* spp.). Common forbs are western ragweed (*Ambrosia psilostachya* DC.) and annual broomweed (*Gutierrezia dracunculoides* (DC.) Nutt.). Average monthly temperatures range from a low of -5.0° C in January to a high of 34.4° C in July. Average total annual precipitation is 877 mm; 70% occurs between April and September (Bourlier et al. 1979). Before establishment in 1989 the Tallgrass Prairie Preserve was grazed by cattle and burned in early spring every 1 to 2 years. It was never plowed.

Three hundred bison were reintroduced into a 1,973-ha part (the study area) of the preserve in October 1993. Following natural herd recruitment and the release of additional animals, the area allocated to bison was expanded by 292-ha in August 1995 to maintain a stocking density of 6–7 ha AU^{-1} during the study. Herd management was limited to annual roundups for inoculations, weighing, and culling.

Burning Regime

Beginning in September 1993 (1-month before bison reintroduction), preserve management began a prescribed burning program. Burns were conducted during 3 seasonal periods: summer (September); fall (November and December); and spring (March and early April). During each burning cycle, numerous sites were randomly chosen and sampled by preserve personnel; those with suitable fuel loads and firebreaks were selected for burning. Burns were conducted as headfires under conditions of low relative humidity, heavy fuel loads, and relatively high air temperatures (Table 1). Burn patch juxtaposition and burning history through the duration of this study was documented (Fig. 1).

Table 1. Average burning conditions for the 3 types of seasonal burns conducted at the Tallgrass Prairie Preserve, Oklahoma.[1]

Burn type	Air Temp.	Rel hum.	Windspeed	Fuel load	Ave. size range
	(° C)	(%)	(km h^{-1})	(kg ha^{-1})	(ha)
Spring	19	24	16	8,200	86 (66 – 98)
Summer	28	39	8	7,990	26 (14 – 49)
Fall	16	43	11	8,920	91 (51–137)

[1]Data courtesy R.G. Hamilton and J.S. Crockett.

Bison Grazing Patterns

The study area was surveyed during daylight hours 4 to 12 times per month. To assure temporal independence of observations (Swihart and Slade 1985), surveys were conducted only once per day, alternating between morning (0600 to 1200 hours) and afternoon (1200 to dark). The location, size, and type of all bison herds were recorded. Bison generally form 2 types of social groups; bull groups of mature (> 5 years of age) bulls and mixed groups of cows, yearlings, calves, and young (5 years of age) bulls (McHugh 1958). The activity in which the majority of individuals in the herd were engaged was recorded, and locations mapped on 1:24,000 USGS topographic quadrangles. Because grouping behavior in animals may violate statistical assumptions of independence (Alldredge and Ratti 1986), it is recommended that observations on grouping animals be composed of group counts and not counts of individuals (Thomas and Taylor 1990, Alldredge and Ratti 1992). However, because bison herd sizes varied widely in our study, in some cases by several orders of magnitude, we were concerned with the appropriateness of giving equal weight to observations on very small and very large herds. For example, groups of 2 and 200 animals would each be counted
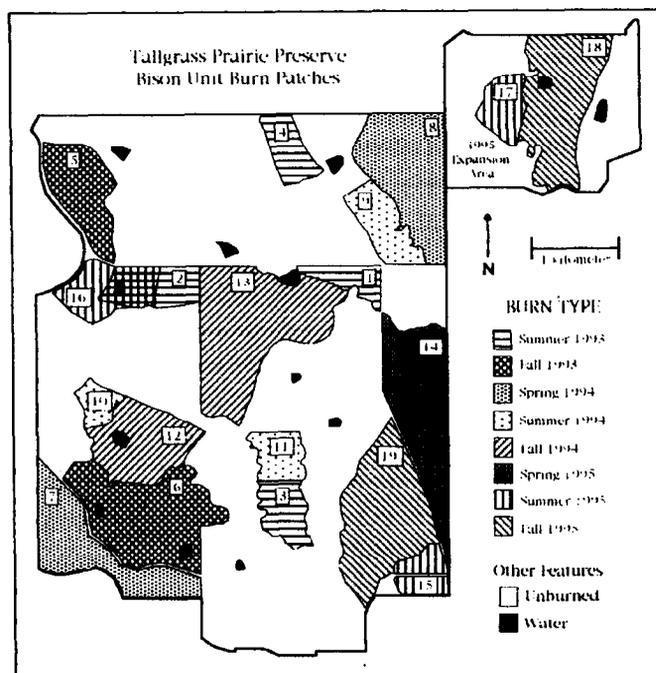
Fig. 1. Burning history of the bison unit of the Tallgrass Prairie Preserve, Oklahoma at the conclusion of the study in December 1995. Numbers refer to the order in which burns were conducted.

as a single observation, even though their members might not exhibit similar levels of selectivity nor the groups have equal ecological effects. We conducted preliminary analyses using both counts of individual animals and herd counts as observations to address this concern. Herd and individual counts gave similar selectivity results 66% of the time. Because we were interested in general population trends in habitat selectivity, and not that of individuals, herd count summarized by habitat patch were deemed acceptable for this study. In addition, because variation in herd sizes were mostly seasonal and we were not specifically addressing the effects of grazing in this study, we pooled group count data for each year into discrete seasonal study periods for analysis, defined as winter (Jan.–Mar.); spring (Apr.–Jun.); summer (Jul.–Sep.); and fall (Oct.–Dec.). Grazing use of burns and the remaining unburned portion of the study area was assessed in relation to overall availability with χ^2 analysis (Neu et al. 1974). To detect selection or avoidance of specific burn types and assess the significance of grazing patterns, 95% Bonferroni confidence intervals were constructed (Byers et al. 1984). To evaluate patch-specific grazing trends, observations were also summarized for individual burn patches (Fig. 1). These data were subjected to simple linear regression analysis to assess relationships between bison group observations and spatial-temporal burn patch characteristics. We followed the general protocol for regression analysis presented by Senft et al. (1983). Characteristics evaluated were burn patch age (in months), size (in ha), distance to permanent water (in km), and mean interpatch distance (in km). Because of small sample sizes from bull groups, we limited regression analysis to mixed group data (Neter et al. 1989). Similarly, because bulls join mixed groups for the summer mating season, there were too few observations on bull groups in the summer period to conduct tests on habitat use.

Vegetation

Vegetation was assessed by establishing 20 (1994) and 23 (1995) 1-ha plots in the study area each year. Plot locations were stratified to represent as many individual burn patches, burn types, and unburned areas as possible: thus, all but 2 burn patches present in the study area (Fig. 1) were sampled. Composition of the standing crop of current year's growth was estimated with the dry-weight-rank method (Gillen and Smith 1986), with herbage components grouped into 7 categories: tallgrasses (big bluestem, switchgrass, indiangrass), little bluestem, all other perennial grasses, annual grasses, sedges, legumes, and forbs (Table 2). Sampling dates represented the broad seasons of plant phenology–early growing season (June) and late growing season (August). To estimate biomass, all aboveground herbage in 20–25 20-x 50-cm quadrats was clipped in each plot each sampling date. Herbage was separated into current year's growth, litter, and mulch, and dried at 70° C to a constant weight. Total graminoid to forb ratios also were calculated by pooling composition data. The significance of variation in biomass and ratios was tested for each year (1994 and 1995) separately with a 2-way ANOVA, using burn type (spring, summer, fall, unburned) and sample date (June and August) as independent variables. Composition data were similarly tested using a MANOVA model with percent composition of the 7 forage groups as a multivariate dependent variable. Significance of terms in the MANOVA model was tested at $\alpha = 0.05$ with Wilk's λ (Johnson and Wichern 1992).

Table 2. Seasonal grazing patterns in 1994 by bison social groups in relation to available burn types and unburned areas on tallgrass prairie in Oklahoma. Grazing use is expressed as a percentage of total group observations.

Burn type	Group type	Winter (Jan.-Mar.)	Spring (Apr.-Jun.)	Summer (Jul.-Sep.)[1]	Fall (Oct.-Dec.)
		--- --- --- --- --- (%) --- --- --- --- ---			
Summer 1993	Bull	0.0–[2]	25.0		2.2
	Mixed	19.1+	15.0+	22.2+	7.9
Fall 1993	Bull	0.0–	20.0		8.8
	Mixed	2.9–	37.0+	29.6+	16.5
Spring 1994	Bull		25.0		24.4
	Mixed		23.3+	24.1+	4.7
Summer 1994	Bull				2.2
	Mixed				9.4
Fall 1994	Bull .				2.2–
	Mixed				5.5
Unburned	Bull	100.0+	30.0–		60.2
	Mixed	78.1–	24.7–	24.1–	56.0

[1]Due to small sample sizes, no analyses were conducted for bull groups during this season.
[2]Indicates significant selection (+) or avoidance (–) relative to availability as estimated from simultaneous 95% Bonferroni confidence intervals (Byers et al. 1984).

Results

Grazing Patterns

Specific grazing trends by bison social groups were evident (Tables 2–3). Bull groups selectively grazed burns only 4% of the time, while avoiding burns 46% of the time. In contrast, 23% of mixed group observations indicated burn selection, with only 13% showing avoidance of burns. Use of unburned areas also differed between social groups. Mixed groups avoided unburned areas 63% of the time, and never exhibited selection for unburned

Table 3. Seasonal grazing patterns in 1995 by bison social groups in relation to available burn types and unburned areas on tallgrass prairie in Oklahoma. Grazing use is expressed as a percentage of total group observations.

Burn type	Group type	Winter (Jan.-Mar.)	Spring (Apr.-Jun.)	Summer (Jul.-Sep.)[1]	Fall (Oct.-Dec.)
		--- --- --- --- --- (%) --- --- --- --- ---			
Summer 1993	Bull	15.2	6.7		0.0–[2]
	Mixed	9.5	0.0–	10.0	3.2
Fall 1993	Bull	15.2	20.0		0.0–
	Mixed	10.1	1.4–	0.0–	5.3
Spring 1994	Bull	18.2	0.0–		0.0–
	Mixed	9.0	5.8	3.3	1.1–
Summer 1994	Bull	3.0	0.0–		0.0–
	Mixed	9.0	18.8+	13.3	4.3
Fall 1994	Bull	3.0	40.0+		0.0–
	Mixed	7.4	42.0+	13.3	12.8
Spring 1995	Bull		0.0–		0.0–
	Mixed		16.0	10.0	6.4
Summer 1995	Bull				18.2
	Mixed			6.7	9.6
Fall 1995	Bull				0.0–
	Mixed				0.0–
Unburned	Bull	51.4	33.3		81.8+
	Mixed	55.0–	16.0–	43.4	57.3

[1]Due to small sample sizes, no analyses were conducted for bull groups during this season.
[2]Indicates significant selection (+) or avoidance (–) relative to availability as estimated from simultaneous 95% Bonferroni confidence intervals (Byers et al. 1984).

areas. Bull groups selected unburned areas 29% of the time, and avoided them in 14% of observations. Overall, pairwise seasonal comparisons for both study years (Table 2–3) showed only 46% agreement between grazing patterns of bull and mixed groups. Thus, the majority of observations (54%) indicate that grazing patterns differed between bison social groups.

Bison showed limited selectivity for fall burns, with 17% of observations showing selection for this burn type, 15% showing selectivity for summer burns, and 11% showing selectivity for spring burns. Patterns of avoidance, however, were more substantial. Thirty-five percent of bison observations indicated avoidance of fall burns, compared to 28% for spring burns and 15% for summer burns. Using the magnitude of differences between avoidance and selection observations to gauge bison preferences, bison most favored summer burns, followed by fall and spring burns.

Table 4. Results of regression analysis of spatial and temporal trends in bison grazing patterns. The percentage of total grazing observations from each burn patch was used as the dependent variable, with the burn patch age (in months), size (in ha), distance to permanent water (in km), and mean interpatch distance (in km) as independent variables. Only data from mixed groups were used in the analysis because these groups constituted the majority (90%) of the population. Observations on bull groups were too few in some seasons and from many burn patches to conduct regression analysis.

Variable	Equation	p	R^2
Burn size	$\hat{y} = 2.5 + 0.1x$	<0.002	0.12
Mean interpatch distance	$\hat{y} = 7.3 - 0.7x$	>0.715	0.00
Distance to permanent H_2O	$\hat{y} = 5.8 + 1.8x$	>0.579	0.00
Burn age	$\hat{y} = 12.6 - 0.6x$	<0.001	0.31

Table 5. Biomass (g/m²) and herbage composition (%) of tallgrass prairie in Oklahoma, 1994, by season (sample date) and burn type (Fig. 1).

| | Biomass | | Composition[1] | | | | | | | | | | | | |
| | | | TG | | LB | | OG | | AG | | SE | | FO | | LE | |
	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE
Season	(g/m²)									---- (%) ----						
June	328	(17)	26.6	(2.7)	29.6	(3.7)	16.2	(1.7)	1.6	(1.2)	3.1	(0.9)	20.0	(3.0)	2.9	(0.7)
August	436	(16)	31.9	(3.2)	29.1	(3.5)	10.5	(1.4)	0.2	(0.2)	0.5	(0.3)	25.2	(4.2)	2.5	(0.7)
Burn type																
Summer 1993	391	(41)	22.1	(3.4)	21.3	(5.2)	12.2	(1.4)	3.8	(2.9)	0.3	(0.1)	35.9	(5.7)	4.4	(1.3)
Fall 1993	321	(44)	23.8	(3.1)	22.8	(5.7)	15.2	(3.9)	0	(0)	3.1	(1.6)	33.2	(4.1)	1.8	(0.7)
Spring 1994	400	(40)	38.2	(5.8)	31.0	(2.4)	8.1	(2.6)	0	(0)	0.1	(0.1)	20.8	(5.1)	1.9	(0.8)
Unburned	399	(11)	31.9	(3.4)	35.3	(4.0)	14.7	(1.6)	0.3	(0.2)	2.5	(0.8)	12.6	(2.9)	2.6	(0.9)

[1] Component abbreviations are as follows: TG – tallgrasses; LB – little bluestem; OG – all other perennial grasses; AG – annual grasses; SE – sedges; FO – forbs; LE – legumes.

Temporal trends in grazing patterns were apparent. Older burns from 1993 and 1994 were generally used only in proportion to availability or avoided by bison during 1995 (Table 3). When newer and presumably more attractive burns appeared on the landscape (Fig. 1), bison shifted to these newer burns in 1995, regardless of burn season (Table 3). Regression analysis of grazing patterns on individual burn patches in relation to spatial-temporal characteristics verified this temporal trend. Although regression accounted for only 12–31% of the variation in bison grazing (Table 4), grazing observations were negatively related to burn age (p < 0.001) and positively related to burn size (p < 0.002). There was no significant relationship between bison grazing and mean interpatch distance (p > 0.7) or distance to water (p > 0.5).

Vegetative Characteristics

As would be expected, biomass was significantly higher (p < 0.001) during the latter August sampling than from the June sampling date during both study years (Tables 5–6). Biomass also varied significantly between burn types. In 1994, differences were negligible (p = 0.05), with fall 1993 burns having slightly less biomass than summer 1993 and spring 1994 burns and unburned areas (Table 5). Differences in biomass between burn types were more substantial during 1995 (p < 0.001). New burns, those conducted during summer 1994, fall 1994, and spring 1995, had significantly less biomass than older burns from the previous growing season and unburned areas (Table 6).

Surprisingly, all statistical tests for differences in grass to forb ratios between sampling dates and burn types were insignificant in both study years (all p > 0.09).

Vegetation composition varied significantly by sample date (p < 0.006) and burn type (p < 0.0004) in 1994 (Table 5). Perennial grasses, annual grasses, and sedges were most prevalent in June, while tallgrasses and forbs were most abundant in August. Annual grasses were much more abundant on summer 1993 burns than on other burn types. Sedges were most prevalent on fall 1993 and unburned areas. Forbs were most common on summer 1993 and fall 1993 burns. Levels of the 2 most prevalent vegetative components, tallgrasses and little bluestem, were highest on spring and unburned areas. Composition trends were similar for seasonal (p < 0.03) and burn type (p < 0.0004) differences in 1995 (Table 6). Annual grasses and sedges were most prevalent during the early growing season (June), while forbs and tallgrasses increased during the latter growing season (August). Tallgrasses and little bluestem levels during 1995 were highest on old burns from 1994 and on spring 1995 and unburned areas. Sedge levels remained highest on fall burns and unburned areas in 1995.

Table 6. Biomass (g/m²) and herbage composition (%) of tallgrass prairie in Oklahoma, 1995, by season (sample date) and burn type (Fig. 1).

| | Biomass | | Composition[1] | | | | | | | | | | | | |
| | | | TG | | LB | | OG | | AG | | SE | | FO | | LE | |
	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE
Season	(g/m²)									---- (%) ----						
June	300	(27)	23.3	(2.8)	21.4	(3.1)	13.0	(2.3)	2.2	(0.9)	9.3	(2.0)	29.2	(2.7)	1.7	(0.4)
August	521	(23)	28.1	(3.2)	18.5	(2.6)	15.9	(1.4)	0.1	(0.1)	3.6	(0.8)	32.3	(3.3	1.4	(0.4)
Burn type																
Summer 1993	509	(45)	21.7	(3.4)	18.4	(6.1)	15.9	(5.8)	3.9	(2.2)	2.4	(0.7)	34.3	(5.5)	3.4	(0.8)
Fall 1993	431	(61)	16.5	(1.9)	16.0	(3.3)	18.8	(2.6)	0.9	(0.6)	8.6	(3.5)	38.3	(2.5)	1.0	(0.4)
Spring 1994	488	(53)	32.5	(6.2)	32.2	(4.3)	12.1	(2.5)	0	(0)	2.4	(1.6)	19.8	(3.8)	1.1	(0.4)
Summer 1994	300	(96)	18.3	(5.8)	9.1	(3.3)	17.9	(4.0)	0.4	(0.1)	5.1	(1.3)	47.9	(7.2)	1.4	(1.1)
Fall 1994	300	(92)	27.8	(5.6)	12.9	(1.9)	15.4	(6.3)	0	(0)	10.3	(4.0)	31.1	(4.2)	2.5	(1.7)
Spring 1995	225	(62)	21.1	(4.3)	28.1	(6.0)	9.1	(2.4)	0	(0)	1.8	(0.9)	39.3	(2.5)	0.6	(0.6)
Unburned	429	(34)	34.6	(5.5)	20.9	(4.4)	12.0	(1.3)	1.1	(0.7)	10.5	(2.9)	20.2	(3.6)	0.8	(0.4)

[1] Component abbreviations are as follows: TG – tallgrasses; LB – little bluestem; OG – all other perennial grasses; AG – annual grasses; SE – sedges; FO – forbs; LE – legumes.

Discussion

Bison in this study generally showed preferences for grazing on burned areas, consistent with previous studies of bison habitat use (Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993, Pearson et al. 1995). However, what remained unknown until this study was how different seasonal burn patches that possess varying vegetative properties influence bison grazing patterns. The trend in grazing preference among burn types appears to proceed from summer burns to fall burns to spring burns to unburned areas. The only unique vegetative characters of summer burns were high forb levels and higher occurrences of the relatively minor annual grass component. This suggests an increase in grazing selection by bison with an increase in forbs. Bison, however, are primarily gramnivorous (Plumb and Dodd 1993) and usually avoid areas with abundant forbs (Trammel and Butler 1995). More importantly, our study of food habits for bison on this site have shown almost exclusive gramnivory, with graminoids comprising ≥ 99% of the diet (Coppedge 1996). This finding led to our hypothesis that grazing patterns would be related to high levels of graminoids on the landscape; however, without significant graminoid to forb ratio differences we cannot fully test this hypothesis. There is a possible explanation for this apparent conundrum. Selective grass herbivory by bison, by removing the competition between grasses and forbs, is known to favor forb growth and productivity (Fahnestock and Knapp 1993, 1994) and increase forb diversity and cover (Hartnett et al. 1996) in tallgrass prairie. Because our sampling was done at the midpoint of broad phenological periods and used a technique that provided a relative measure of composition, we believe that we were measuring the ungrazed forb response to the removal of graminoids by bison and that bison are not actually selecting summer-burned areas in response to an increase in forbs. We hypothesize that it is the seasonal timing of these burns in early September that is most attractive to bison. The tallgrasses that dominate the study area reach their nutritive peak much earlier in the growing season, generally in June (Waller et al. 1972). Thus, any late growing season regrowth on these summer burns is likely to be more palatable and digestible than the mature grasses available elsewhere. Combined with the fact that summer burns are the first post-growing season burns conducted during the burning cycle at the preserve, bison selection for these burns is probably a result of utilization of the best available habitats present at the time.

Bison also may be maintaining graminoids on burn patches at a relatively low biomass with frequent regrazing. Because of a general decrease in forage quality with increases in maturity level and biomass (Van Soest 1982), grazers in many situations face a trade-off between forage quality and forage quantity (Hobbs and Swift 1988). The "forage maturation hypothesis" (Fryxell 1991) suggests that frequent regrazing by large herbivores maintains areas of low to intermediate biomass as "grazing lawns" (McNaughton 1984, 1986), which contain forage of both acceptable quality and sufficient quantity to meet their foraging requirements (Stephens and Krebs 1986). The tallgrasses that dominate our study are quite variable in their nutritive content with changes in phenology (Waller et al. 1972, Adams and Wallace 1985), so bison may be selectively regrazing areas with low graminoid biomass based on nutritional cues and forage quality. Bison have been shown to significantly reduce graminoid standing crop on burned areas in Sandhills prairie (Pfeiffer and Steuter 1994).

Vinton et al. (1993) reported high grass to forb ratios on patches selected for grazing by bison on tallgrass prairie in Kansas. That site, however, possessed only spring burns. It appears that on our site, any burn with low graminoid biomass, regardless of burning season, is preferentially selected for grazing by bison.

Burn types varied significantly for most vegetative parameters, supporting our hypothesis that burn season results in different vegetative characteristics. Bison also showed some selectivity among burn types. Most preferred were summer burns, characterized by high forb cover, but also have a relatively high cover of annual grasses, namely *Bromus* spp. These are a common diet item for bison on this site (Coppedge 1996), and bison are known to choose burned sites in Kansas tallgrass prairie characterized by high levels of these exotic, cool-season grasses (Vinton et al. 1993). It appears that annual grasses are somewhat desired by bison, thus partially influencing their choice of grazing location. Fall burns also were selectively grazed by bison. The only unique vegetative characteristic of fall burns was a higher cover of sedges. These are a highly desired forage item for this bison population (Coppedge 1996). Together, these results support our hypothesis that bison do choose areas for grazing based at least partially on vegetative composition.

Two spatial factors shown to be important in similar studies of large grazers were not significant in this study. Foraging theory predicts that both large patches and patches more isolated or with longer travel times (in this study measured by mean interpatch distance) tend to have longer residence time by grazers (Stephens and Krebs 1986). Instead, we found that only burn size was important, supporting only part of the optimal foraging hypothesis. We suspect that a simple effect of scale may explain the lack of importance for mean interpatch distance. The animals can traverse the study area in only a few hours, thereby likely preempting the importance of travel time and its potential influence on grazing patterns. Similarly, distance to water, important in some studies of cattle grazing distribution (Senft et al. 1985, Pinchak et al. 1991), was unimportant to this study. Again, the size of the study area and the relatively uniform distribution of permanent water (Fig. 1) may have reduced the importance of this variable.

This study also found an interesting temporal trend in bison grazing patterns that had not been documented before—bison preference for newer burns while avoiding older patches. However, because the study area is an unusual situation with a prescribed burning program that is spatially and temporally variable, it is likely that similar trends could be observed for other herbivores in other locations under similar conditions. Our results demonstrating a temporal grazing trend for bison supports recent suggestions that herbivores have accurate spatial memory based on previous foraging experiences and can remember locations of and return to productive sites while avoiding unproductive areas where foraging experiences were poor (Bailey et al. 1996). Burn age, however, may be complicated by the issues of forage quality as previously discussed. Unfortunately because we did not make forage quality measurements in this study, this questions remains. The relationship between forage quality and burn age in tallgrass prairie and its effects on herbivore grazing patterns would be an interesting topic for future investigations.

Significantly different grazing patterns between mixed and bull groups of bison supports our hypothesis that sexual segregation results in differential habitat use. Main and Coblentz (1990) concluded that sexual segregation among ungulates arose as the result of different reproductive strategies, with females selecting areas

best suited for rearing offspring and males choosing habitats to maximize body condition. Differences in grazing patterns between bison social groups were most disparate in spring when calves are born and nutritional demands on females are highest. This is also the period immediately before the rut when males compete vigorously for breeding opportunities (McHugh 1958). Thus, spring grazing patterns of bison in this study certainly suggest that this pattern of social segregation may also apply to bison.

Our results do provide some insight into how standard range management practices may or may not apply to bison. For years it had been assumed that, for the most part, bison and cattle were ecologically similar. Recent increases in bison populations and availability have fostered bison ranching interests in the United States. Several studies have been conducted recently comparing the foraging behavior of cattle and bison. Because of differences in foraging and behavior, Plumb and Dodd (1993) concluded that significant differences do exist between the foraging ecology of bison and cattle, and that, depending on management objectives, either herbivore may be appropriate. Steuter et al. (1995) studied bison grazing distribution and interactions within a Sandhills landscape, and concluded that bison were well adapted to small prairie remnants. Hartnett et al. (1996) showed that carefully-managed bison within a small landscape are capable of positively affecting vegetational diversity. Our study has shown that bison grazing patterns are strongly influenced by a temporal and spatially-variable burning program within a single large area. A similar, well-executed burning program on any Great Plains rangeland might eliminate the need for multipasture, rotational grazing systems in bison ranching efforts, reducing the need for extensive cross-fencing and reducing overall maintenance requirements.

Conclusions

Bison grazing is influenced by temporal, spatial, and vegetative characteristics of the landscape. Temporal variation in the seasonal burning regime influenced the length of time bison were attracted to and grazed on burned patches. Burn patch size influenced bison utilization. Timing of seasonal burns influenced the vegetative community, which in turn affected bison grazing patterns as bison selected for newer, recovering patches with lower biomass. Bison social groups had different grazing patterns. Although bull groups were a small part of the population (<10%), they showed less attraction to burned areas than mixed groups of cows, calves, and yearlings. Conversely, bull groups showed more preference for unburned prairie while mixed groups avoided these areas.

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