

The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle

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Abstract. The Great Plains of North America evolved with significant influence from bison (*Bison bison*), but is presently dominated by cattle (*Bos taurus*). While there are a variety of opinions concerning differences between these two species, there is a lack of scientific comparisons, including those that incorporate important ecological variation. We developed a framework to study and compare the grazing behavior and effects of bison and cattle within grassland ecosystems. Environmental (e.g., resource distribution, disturbance) and animal (e.g., number, social organization) factors play a critical role in determining grazing effects and should be incorporated into discussions that compare the effects of bison and cattle. Using this framework we specifically compare the grazing behavior of both species in tallgrass prairie and discuss the implications of these differences in the context of conservation. We collared bison and cattle with global positioning systems and used resource selection functions to estimate the importance of various environmental factors on site selection. Both species preferred recently burned areas and avoided steeper slopes. Cattle selected areas that were closer to water, while bison were not limited by distance to water; cattle also preferred areas with woody vegetation, while bison avoided them. Incorporating broad scale environmental complexity allows for an effective comparison of ecological differences between bison and cattle. While there are similarities and differences in these species, a comprehensive analysis of all conditions and scenarios is not possible. It is clear, however, that the greatest differences between these species will likely be evident from broad scale studies across complex landscapes. In addition to species, conservation and land managers need to consider other environmental factors that are critical to grazing effects and overall conservation.

Key words: fire; grassland; grazing; herbivory; restoration; species comparisons; tallgrass prairie.

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INTRODUCTION

The role of herbivores in grassland ecosystems has been an important topic debated by ecologists and ecosystem managers for more than a century. The Great Plains of North America are central to this discussion as most flora and fauna evolved with significant impact from large herbivores and other disturbances (Axelrod 1985, Anderson 2006). Until their near extirpa-

tion in the late 1800s, American Bison (*Bison bison*) were keystone herbivores within the Great Plains, sharing complex landscapes with other herbivores and predators for nearly 10,000 years (Knapp et al. 1999, Anderson 2006). Since their near extinction, the vast and complex landscapes that contained the roaming herds have been replaced by fragmented agricultural lands where domestic cattle are the dominant grazers. Restoration and conservation of bison has been

pursued by private citizens, conservation organizations, and government agencies with a primary goal of conserving the species and restoring critical ecosystem processes and functions.

Grazing by large herbivores can affect a system in many different ways (Milchunas et al. 1988, Augustine and McNaughton 1998, Anderson et al. 2006). The effects of grazing are often viewed in isolation of each other, removing all complexity and variation besides that of grazing. Such work has enhanced the understanding and management of grasslands. The evolutionary effects of grazing, however, are much more complex than traditional, small scale experimental designs can replicate (Levin 1992, Fuhlendorf et al. 2009). Grazing is a dynamic process that interacts with complex landscapes to form disturbance patterns that are critical to many ecosystem functions, including biodiversity (Collins et al. 1998, Tews et al. 2004). Because of this, the effects of grazing are influenced by many factors, including those associated with animals and the environment.

The species of animal alone is not the only determinant of grazing effects. Age, sex, number, and social organization of animals contribute to altering behavior and ecological influences. In addition to the structure of the grazer community, environmental factors (e.g., disturbances, climate, predation, resources) will also contribute to grazing effects. When discussing grazing or grazing behavior, a traditional reductionist approach is to focus on one factor without considering the complexity of other factors. In the Great Plains of North America, ecologists, conservation biologists, and land managers have studied and debated the effects of grazing by bison and domestic cattle (*Bos taurus*), often without including other interacting factors (Hartnett et al. 1997, Steuter and Hiding 1999). Common managerial differences associated with bison and cattle also confound differences in effects between the two species (Towne et al. 2005). Cattle herds are often associated with ranches that are based on commodity production, where animals are commonly separated for most of the year based on sex or age (e.g., cows and calves, bulls). In the Great Plains of North America, cattle are rarely, if ever, managed as wildlife or with a conservation focus. Bison, on

the other hand, may be managed as either production or conservation herds.

While similarities and differences between cattle and bison are widely discussed and debated, the peer reviewed literature comparing the two is largely inconclusive. For example, in popular press, government reports, and scientific literature, it is often stated that bison spend less time near water or riparian areas than cattle (Manning 1995, Hartnett et al. 1997, Fritz et al. 1999, Reynolds et al. 2003, National Park Service 2009). Indeed, van Vuren (1982) found a greater percentage of observations of cattle closer to water than bison. Unfortunately, it is apparent that the confounding management strategies of the two species were not taken into account, specifically with regard to stocking rate or animal density: “a herd of about 300 wild bison . . . shares its summer range with several hundred range cattle” (van Vuren 1982). With no clear definition of how many animals were present or specific management plans for each species, a reliable conclusion cannot be made. Direct comparisons of foraging ecology or behavior between bison and cattle have also been minimal. Plumb and Dodd (1993) found that in general, bison spent less time feeding with shorter grazing bouts than cattle, but had greater number of bouts per day.

We argue that recognizing ecological differences between bison and cattle would be best studied on large, complex landscapes that do not limit behavior to finer scales (Holland et al. 2004, Boyce 2006, Bowyer and Kie 2006). Incorporating landscape variability will allow for a more effective comparison of grazing behavior and effects between bison and cattle, as animals can interact with environmental factors that contribute to grazing effects. We describe the design, results, and limitations of a current study comparing bison and cattle behavior on complex landscapes that include other disturbances (e.g., fire). We then develop a conceptual model to facilitate the discussion of the conservation value of reintroducing bison within human dominated landscapes of the Great Plains.

METHODS

The Tallgrass Prairie Preserve: a model for experimental design

The Nature Conservancy Tallgrass Prairie Preserve, located in northeast Oklahoma, USA, is a 16,000 ha natural area that is managed for biodiversity and heterogeneity (Hamilton 2007). The preserve lies at the southern end of the Flint Hills of the Great Plains. Vegetation is classified as tallgrass prairie, with small patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Precipitation and various climate measurements are measured on site by an Oklahoma Mesonet station (Brock et al. 1995). Total precipitation for April through September for 2009 and 2010 (time period of study) was 64.7 and 72.5 cm, respectively. Long term mean total for April through September is 62.2 cm (14.94 standard deviation).

Within the site, there is one large bison unit (9532 ha) and seven smaller cattle units (430–980 ha) (Fig. 1). Only perimeter fences are present and animals are free to roam within their respective units. There is minimal handling of both bison and cattle with no supplemental feeding. Bison are maintained in their respective unit all year; herd size is approximately 2,300 animals. Sex ratio of the bison herd is approximately seven females per male; ages of females range from 0–10 years, while males are 0–6 years. Cattle units are stocked with stocker steers approximately one year old (mixed European breeds); cattle are only present April through September. Cattle herds vary with each unit, ranging from 169 to 463 animals. Bison and cattle units are stocked with similar moderate stocking rates (bison: 2.1 AUM/ha; cattle: 2.4 AUM/ha). The entire preserve is managed extensively with fire and in such way that fire and grazing are allowed to interact (Hamilton 2007, Fuhlendorf et al. 2009). Bison and cattle units are shifting mosaics with fire occurring in discrete portions of the landscape (Fig. 1). Fire-grazing interactions become present as animals select between recently burned areas and those with greater time since fire (Archibald et al. 2005, Fuhlendorf et al. 2009).

To specifically examine herbivore site selection, we deployed global positioning system (GPS) collars on seven female bison (four to six years in age) from November 2008 through November 2010 and seven cattle (steers, one year in age; one per unit) from April through September of 2009 and 2010. For bison, GPS batteries were replaced and new animals chosen in November 2009; for cattle, new animals were chosen and new batteries used in April 2010. We recorded location information of animals at two different frequencies, alternately weekly from 12 minutes to one hour. Schedule of GPS fixes was equal for bison and cattle. We imported all GPS location data into a spatially enabled database (PostgreSQL/PostGIS) and reduced bison data to match that of cattle (April–September). We mapped treatment unit perimeters, fire histories, and water sources (ponds and streams) with handheld GPS units, aerial photographs, and United States Geological Survey 7.5 minute topographic maps. Slope and aspect were calculated from digital elevation models for the area (United States Geological Survey; 10 m resolution). We transformed aspect data by simple trigonometric functions; two variables were created, northing = cosine(aspect) and easting = sin(aspect). Herbaceous and woody vegetation was determined for the site using a GeoEye-1 satellite image acquired September 20, 2009.

We compared similarity of units by randomly placing 1,000 sampling points within each unit. At each sampling point, distance to water, distance to patch edge, distance to woody vegetation, slope, northing, and easting were calculated. Measured characteristics among animal units were compared individually using analysis of variance and did not differ between units ($P > 0.05$). We used Ivlev electivity indices (Ivlev 1961, Jacobs 1974) to evaluate the use of riparian areas by bison and cattle. Riparian areas were defined by putting a 20 and 40 m buffer around all mapped water sources. We calculated electivity indices using the formula $E_i = (r_i - p_i) / (r_i + p_i)$ where r_i is the fraction of GPS locations recorded in a riparian area by animal i and p_i is the fraction of area enclosed by the sum of buffers available to animal i . A value of +1 indicates complete preference to riparian areas, while a value of -1 indicates complete avoidance. Indices were calculated for each collared bison

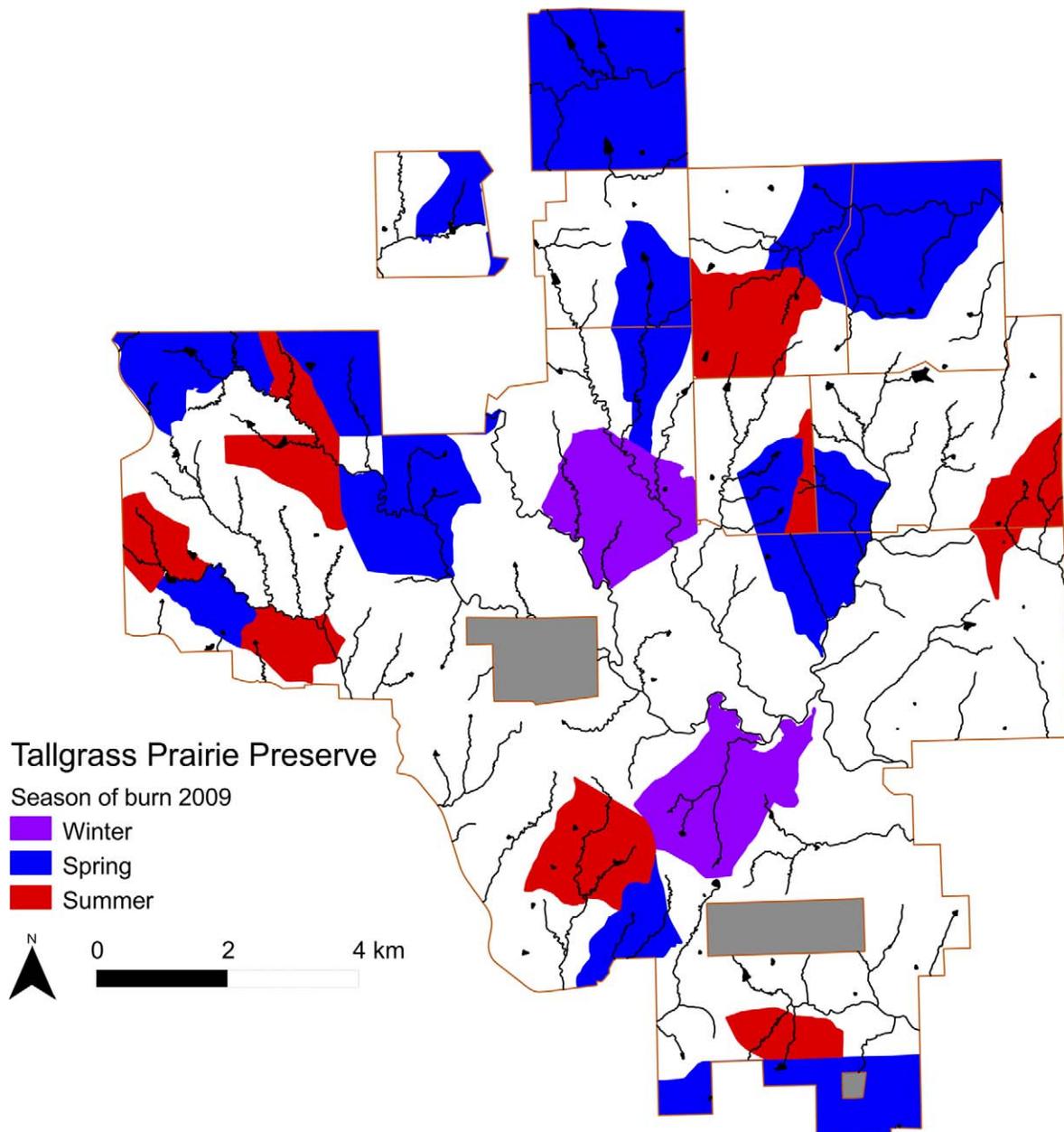


Fig. 1. Map of prescribed fire and water distribution within bison and cattle units at The Nature Conservancy Tallgrass Prairie Preserve, OK, USA, September 2009. Solid orange lines represent perimeter fences and delineate units. Black interior lines and areas represent water sources. Gray areas inside bison unit represent inholdings which bison cannot access. The large southern unit is 9532 ha in size and contains bison year round. The northern units are 430–980 ha in size and contains mixed European breeds of cattle April–September. Differing colors represent season of burn for 2009 and illustrate the patchiness of fire. Patches from previous years are not shown, but vary from one to five years since fire. Grazing animals have free access to all burns within their respective units (no internal fences present).

and cattle individual, separating water sources into ponds, streams, and pond/stream combination. Indices between bison and cattle were compared for each size riparian area (i.e., 20 and 40 m) using a *t*-test. We also used Ivlev electivity indices to compare bison and cattle preferences for recently burned areas (six months or less since fire). We calculated indices for each collared animal based upon recently burned area available; we compared indices using a *t*-test.

To examine the influence of environmental factors on the grazing behavior of bison and cattle, we estimated resource selection functions using mixed-effect logistic regression models (used/available design; Boyce et al. 2002, Manly et al. 2002). To depict available habitat, we created five random locations for each observed location. We calculated the amount of time since fire, distance to water, distance to fire patch edge, slope, northing, and easting for all locations. We also classified each location as herbaceous or woody vegetation. To determine if the presence of woody vegetation is confounded with water sources (i.e., the presence of woody vegetation is primarily near water sources), we quantified the distribution of woody vegetation around water sources. The percentage of woody vegetation within 20 and 40 m of water sources across the site was 3% and 7%, respectively. Furthermore, we examined variables for collinearity and found none ($r^2 < 0.27$ for all variable combinations), indicating that variables are not confounding with one another (i.e., woody vegetation is not limited near water sources). To account for variation among individual animals within resource selection functions, individuals were included as a random intercept within logistic regressions. To account for fire availability among units and potential response variation to fire, time since fire and its interaction with other variables (e.g., time since fire \times distance to water; see below) were included as random slopes within logistic regressions (Gillies et al. 2006).

We created models using various combinations of environmental factors; as the influence of time since fire is likely to be highly influential (Vinton et al. 1993, Fuhlendorf and Engle 2004, Archibald et al. 2005), we included interaction terms for this variable with all others individually (i.e., time since fire \times distance to water, time since fire \times slope, etc.). In all models with interaction terms,

main effects of both variables were included. To allow for comparison of environmental factors and to more easily interpret interaction terms, we standardized variables by subtracting the mean and dividing by the standard deviation (Gelman and Hill 2007). We compared and ranked models using Akaike information criterion (AIC; Burnham and Anderson 2002). We used bootstrapping procedures to further estimate the precision of resource selection coefficients of the top ranked model. We calculated 95% confidence intervals of coefficients after 1,000 iterations of randomly sampled datasets. To further examine variation among individual animal behavior, we calculated resource selection functions for each animal per year (28 animals total) using top ranked models. We performed all analyses in R (R Development Core Team 2009) with additional use of the *lme4* (Bates and Maechler 2010), *doMPI* (Weston 2009), *foreach* (Revolution Computing 2009) and *Rmpi* (Yu 2010) packages.

RESULTS

Of bison locations, 9 and 15% fell within riparian areas of size 20 and 40 m, respectively (ponds and streams combined). Of cattle locations, 13 and 20% fell within riparian areas of size 20 and 40 m, respectively. Mean Ivlev electivity indices of riparian areas varied significantly between bison and cattle with all water sources and riparian area sizes ($P < 0.01$; Fig. 2). Cattle had a greater preference for ponds (Fig. 2A), while bison avoided streams (Fig. 2B). When ponds and streams were combined, bison had a small avoidance of water, while cattle had a greater preference for it (Fig. 2C). These data show the difference between bison and cattle in their use of water and riparian areas, in similar fire-managed landscapes with abundant water.

Bison and cattle strongly preferred recently burned patches (Table 1). Mean percentages of GPS locations in areas with six months or less since fire did not vary between bison and cattle ($P = 0.11$). With bison, 68% of locations were found in recently burned areas (less than six months), while cattle were 58%. The amount of area burned within six months was approximately 25% of the landscape in both bison and cattle units. Bison and cattle were nearly three times likely to be in a burned area than by random

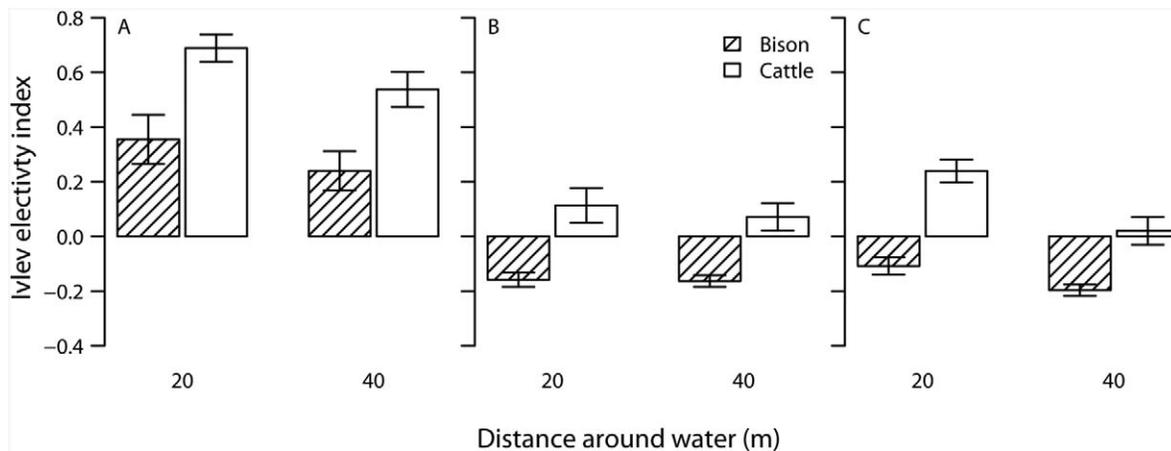


Fig. 2. Ivlev electivity indices for riparian areas, separated by bison and cattle at the Tallgrass Prairie Preserve, OK, USA. Bars are means ($n = 14$; animals), error bars are one standard deviation. Potential values range from -1 (complete avoidance) to $+1$ (complete preference). Distance around water indicates the size of buffer placed around water sources. A) Ivlev electivity indices for ponds only, separated by bison and cattle. Cattle preferred riparian pond areas more than bison. B) Ivlev electivity indices for streams only, separated by bison and cattle. Cattle preferred riparian stream areas more than bison; bison demonstrated a small avoidance to riparian stream areas. C) Ivlev electivity indices for ponds and streams combined, separated by bison and cattle. Cattle preferred all riparian areas more than bison; bison demonstrated a small avoidance to all riparian areas. Mean electivity indices of riparian areas varied significantly between bison and cattle for all water sources and buffer sizes ($P < 0.01$).

Table 1. Percentage of individual bison and cattle locations and annual means and confidence intervals (95%; bottom row) in recently burned areas (six months or less) at the Tallgrass Prairie Preserve, OK, USA, April through September 2009 and 2010.

Bison 2009	Bison 2010	Cattle 2009	Cattle 2010
68.3	64.1	78.6	42.4
71.5	59.1	55.7	88.7
69.1	66.9	77.5	100.0 [†]
68.8	67.8	60.8	73.2
75.3	69.0	25.0	55.0
66.2	65.2	100.0 [†]	37.4
75.1	75.1	67.6	40.6
70.6 (2.6)	66.7 (3.6)	60.9 (15.8)	56.2 (16.5)

[†]Due to fire patch design; not included in mean or confidence interval calculation.

chance alone. Mean Ivlev electivity indices of recently burned areas were 0.57 (0.01) and 0.43 (0.15) for bison and cattle, respectively (standard deviations in parentheses); indices did not differ between species ($P = 0.12$).

Estimation of resource selection functions permitted a detailed examination of environmental factors that influence selection behavior. Of models examined, the combination of interaction terms of time since fire with all variables (less northing and easting) appeared to have the best

fit for both bison and cattle (Table 2). Resource selection functions for bison revealed that time since fire had the strongest influence in determining site selection. Furthermore, bison tended to avoid steeper slopes and wooded areas. Distance to water did not influence selection (Table 3). Interactions of time since fire with other environmental factors indicates the connectedness of fire with grazing behavior. The influence of time since fire increased as slope and distance to patch edge increased; conversely, the influence

Table 2. The difference in Akaike information criterion (Δ AIC) and the number of parameters (K) for varying models of resource selection for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (*water*; m), distance to patch edge (*edge*; m), slope (*slope*; degrees), northing (*north*; degrees), easting (*east*; degrees), wooded area (*wood*), and time since fire (*tsf*; days).

Model	K	Δ AIC
Bison		
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i> + <i>tsf</i> \times <i>north</i> + <i>tsf</i> \times <i>east</i>	15	1.8
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i> + <i>north</i> + <i>east</i>	13	0.00
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	2.7
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>wood</i>	11	3.8
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	4006.4
<i>tsf</i> \times <i>water</i> + <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	882.4
<i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	505.7
<i>tsf</i> + <i>water</i> + <i>slope</i> + <i>edge</i> + <i>wood</i>	7	6328.7
Cattle		
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i> + <i>tsf</i> \times <i>north</i> + <i>tsf</i> \times <i>east</i>	15	3.26
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i> + <i>north</i> + <i>east</i>	13	0.00
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	2.71
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>wood</i>	11	15.89
<i>tsf</i> \times <i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	126.34
<i>tsf</i> \times <i>water</i> + <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	42.78
<i>water</i> + <i>tsf</i> \times <i>slope</i> + <i>tsf</i> \times <i>edge</i> + <i>tsf</i> \times <i>wood</i>	10	329.18
<i>tsf</i> + <i>water</i> + <i>slope</i> + <i>edge</i> + <i>wood</i>	7	451.37

Notes: We included main effects in all models with interaction terms. Interaction terms represented with \times .

Table 3. Estimated resource selection function coefficients of the top ranked model for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (*water*; m), distance to patch edge (*edge*; m), slope (*slope*; degrees), northing (*north*; degrees), easting (*east*; degrees), wooded area (*wood*), and time since fire (*tsf*; days).

Parameter	Estimate [†]	SE	Z value	P	CI [‡]
Bison					
intercept	-1.8460	0.120	-15.34	<0.01	(-1.8513, -1.8384)
time since fire	-1.5521	0.353	-4.40	<0.01	(-1.5538, -1.5509)
distance to water	0.0324	0.007	4.51	<0.01	(0.0316, 0.0328)
slope	-0.5785	0.011	-49.59	<0.01	(-0.5793, -0.5778)
distance to patch edge	-0.3351	0.009	-35.87	<0.01	(-0.3360, -0.3344)
woody vegetation	-1.9116	0.077	-24.53	<0.01	(-1.9164, -1.9092)
northing	-0.0117	0.005	-2.33	0.02	(-0.0120, -0.0115)
easting	0.0246	0.005	4.87	<0.01	(0.0242, 0.0251)
time since fire \times distance to water	0.1548	0.007	19.48	<0.01	(0.1543, 0.1550)
time since fire \times slope	-0.3814	0.013	-28.23	<0.01	(-0.3818, -0.3809)
time since fire \times distance to patch edge	-0.5412	0.011	-48.86	<0.01	(-0.5420, -0.5408)
time since fire \times woody vegetation	0.0509	0.041	1.24	0.21	(0.0478, 0.0549)
Cattle					
intercept	-0.8892	0.644	-1.38	0.16	(-0.8963, -0.8824)
time since fire	-1.2611	0.313	-4.03	<0.01	(-1.2621, -1.2602)
distance to water	-0.0768	0.006	-11.11	<0.01	(-0.0785, -0.0755)
slope	-0.1696	0.007	-21.50	<0.01	(-0.1699, -0.1691)
distance to patch edge	-0.5019	0.011	-42.44	<0.01	(-0.5025, -0.5015)
woody vegetation	1.4398	0.053	27.16	<0.01	(1.4390, 1.4404)
northing	-0.0044	0.005	-0.84	0.40	(-0.0048, -0.0040)
easting	-0.0109	0.005	-2.08	0.03	(-0.0112, -0.0107)
time since fire \times distance to water	-0.0514	0.059	-2.08	0.03	(-0.0520, -0.0511)
time since fire \times slope	0.0199	0.049	0.40	0.68	(-0.0210, -0.0190)
time since fire \times distance to patch edge	-0.2667	0.219	1.22	0.22	(-0.2692, -0.2648)
time since fire \times woody vegetation	0.4213	0.382	1.10	0.27	(0.4201, 0.4219)

[†]Standardized variables are shown for coefficient comparison and interaction term interpretation.

[‡]Confidence interval (95%) calculated from bootstrapping procedures (1,000 iterations).

of time since fire decreased as woody vegetation and distance to water increased. This decrease is minimal due to the initial strong influence of fire. The probability of selection for bison, based upon time since fire, distance to water, and the interaction of those two factors, is displayed in Fig. 3. In recently burned areas, bison avoid water slightly; in areas with greater time since fire, bison are not influenced by water.

Similar to bison, cattle also selected recently burned areas and avoided steeper slopes. Unlike bison, however, the most influential environmental factor was the preference of woody vegetation. Moreover, cattle appeared to minimize distance to water, opposite that of bison (Table 3). Interactions of time since fire with other variables further shows the importance of fire to understanding grazing within these ecosystems. As distance to water and patch edge increase, so does the influence of time since fire; the presence of woody vegetation, however, decreases the influence of time since fire. The probability of selection for cattle, based upon time since fire, distance to water, and the interaction of the two, is displayed in Fig. 4. Cattle minimize their distance to water in both recently burned areas and areas with greater time since fire.

Resource selection functions for individual animals revealed variation in site selection (Table 4). Though individual animals generally followed trends indicated by the population model, cattle tended to be more variable in their response to environmental factors. Individual bison and cattle still strongly preferred recently burned areas (minimizing the amount of time since fire), but the response of cattle varied considerably among individuals. All individual cattle minimized their distance to water, while only three bison did so. Other factors, including interactions with time since fire, varied among animals. Because different animals were chosen each year, we cannot separate the variation among animals and the variation between years.

DISCUSSION

The design of this study more effectively permits comparisons between bison and cattle, both in examining grazing behavior differences between the species (results presented here) and their ecological effects (e.g., plant response, water

quality, etc.; data not collected). Our design incorporates more of the variability found in complex landscapes than previous studies, allowing animals to interact and respond to variation and complexity across the landscape. Bison and cattle had similarities in some aspects of their behavior. Both species had a strong preference for recently burned areas, similar to separate studies of the individual species (Coppedge et al. 1998, Fuhlendorf and Engle 2004). Along with similarities we also identified two key differences. Cattle preferred areas with woody vegetation, while bison avoided them. This likely plays a critical role in thermal regulation, with woody canopy cover providing shade from solar radiation. Detailed mapping of the thermal environment is required to determine the influence of heat on the grazing behavior of bison and cattle. Additionally, because location information obtained by the GPS does not differentiate between grazing or resting, it is unclear if the preference for woody vegetation is a result of grazing or resting behavior. It does show, however, behavioral preferences and differences that are likely to influence both selection and grazing decisions, especially when studying behavior at broad spatial scales.

Selection for sites closer to water was also greater in cattle than bison; bison appeared to maximize their distance to water while cattle minimized it. These differences occurred in a well watered landscape and may be even more important in lands with greater distance between water sources. Though water included ponds and streams, ephemeral water sources were not included due to difficulty in measuring them at this spatial scale. Differences in use of ephemeral water between bison and cattle may explain measured differences. Additionally, both bison and cattle distribution and behavior may be influenced by precipitation patterns (Lott 2002, McAllister et al. 2006). At broader scales such as the Tallgrass Prairie Preserve, variability in spatial precipitation patterns may exist (Augustine 2010). Though not quantified, spatial variability in precipitation would likely influence animal distribution indirectly through vegetation responses and ephemeral water sources.

Although we did not collect data on ecological implications of grazing, it is likely that distribution differences between bison and cattle would

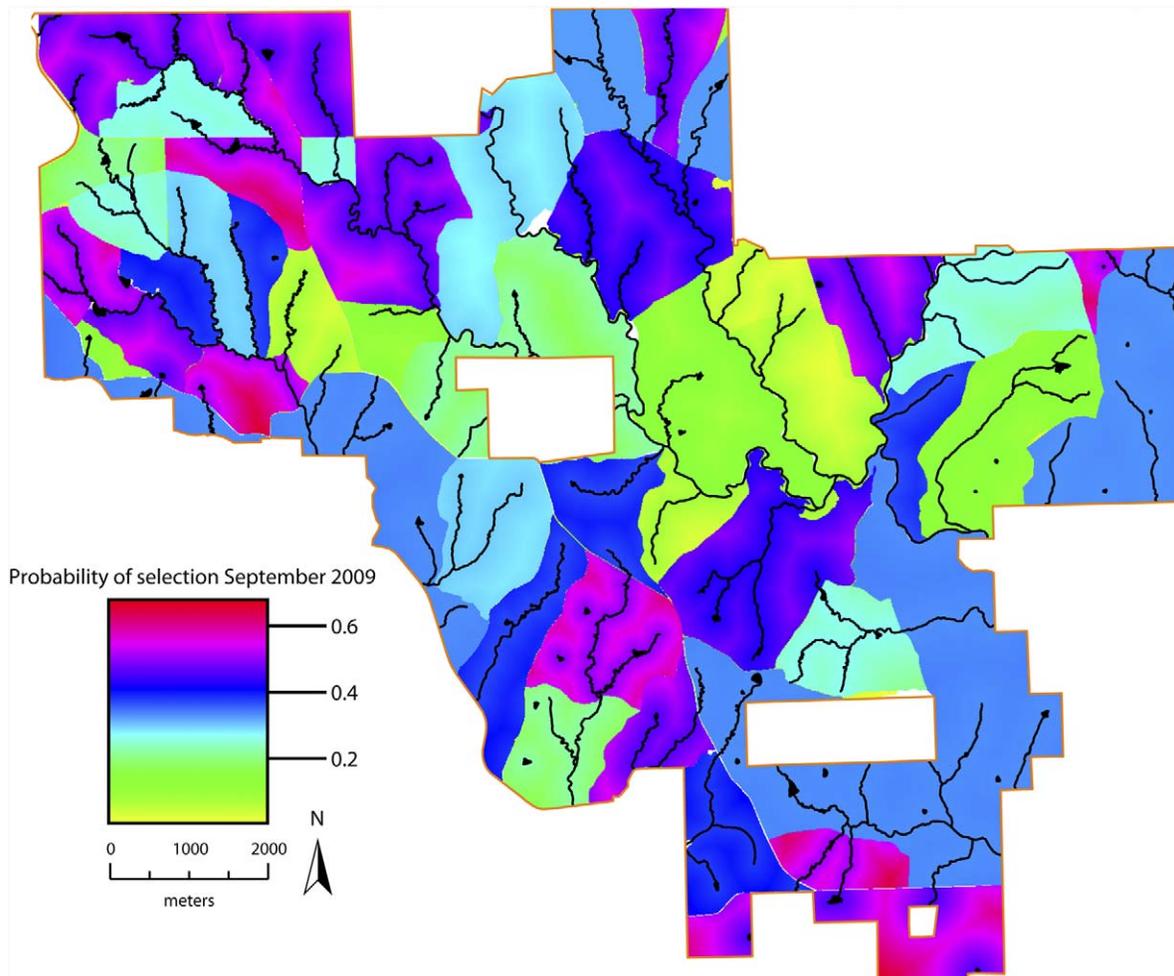


Fig. 3. Probability of selection for bison at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Fig. 1 for recently burned areas. Bison prefer recently burned areas and do not minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

result in contrasting effects. The preference or focusing of grazing in a particular area (large or small) will influence vegetation community and characteristics. The continued attraction of both bison and cattle to recently burned areas alters vegetation structure which affects biodiversity (Fuhlendorf et al. 2006), fire behavior (Leonard et al. 2010), invasive species populations (Cummings et al. 2007), invertebrate populations and communities (Engle et al. 2008), and nutrient cycling and distribution (Anderson et al. 2006). The preference of riparian and woody vegetation areas by cattle will also likely result in vegetation

and system changes. Reduced herbaceous cover, biomass, and productivity generally result from cattle grazing within riparian areas (Kauffman et al. 1983, Clary 1995, Belsky et al. 1999). Preference for water sources may also affect stream bank morphology, hydrology, and water quality (Kauffman and Krueger 1984, Trimble and Mendel 1995, Belsky and Blumenthal 1997). Concentration of livestock around ponds and streams may also likely increase nutrient concentrations (Schepers and Francis 1982, Belsky et al. 1999). We note, however, that direct comparisons of bison and cattle grazing effects on riparian

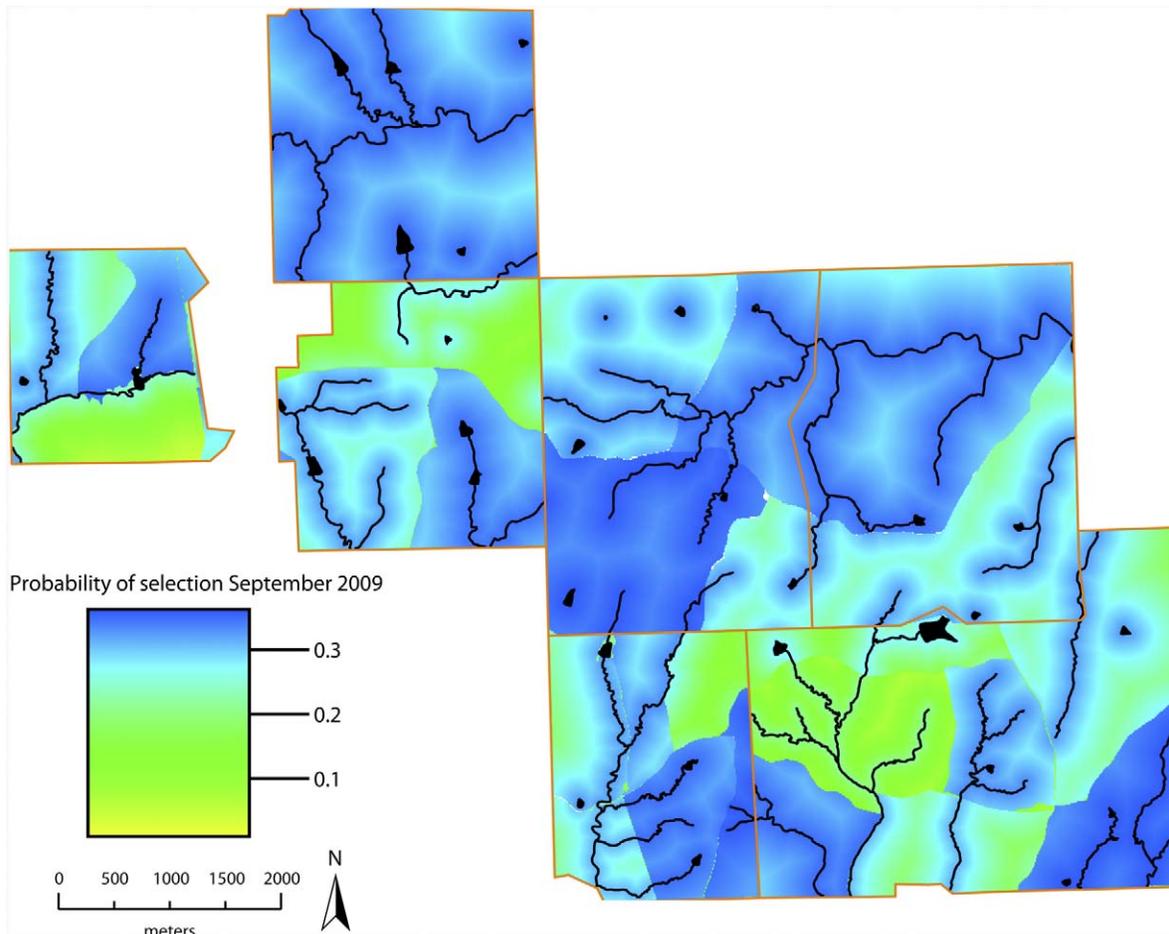


Fig. 4. Probability of selection for cattle at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Fig. 1 for recently burned areas. Cattle prefer recently burned areas and minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

processes are largely lacking.

It is difficult to account for the many factors that may create differences or similarities between bison and cattle, and like all studies of processes on complex landscapes, this study is not without limitations. Though stocking rates were similar between bison and cattle units, cattle were only present during the growing season (April–September), while bison remained throughout the year. Differences in the social and temporal organizations of cattle and bison herds may also confound differences. The bison herd was a mixture of males and females of various ages grazing together, while cattle herds were

yearling stocker steers. A yearlong, cow-calf cattle operation would permit even better comparisons between the two species, particularly with regard to ecological effects. Though treatment units were large and incorporated landscape complexity, they were not of equal size. We could expect that animal behavior would be sensitive to and vary with available area. Smaller units would limit animal movement and behavior, restricting selection and interaction with other environmental factors. Available area would be important particularly regarding cattle preference for water, as smaller units would constrain animals closer to water. While cattle

Table 4. Estimated resource selection function coefficients[†] of the top ranked model for individual bison and cattle at the Tallgrass Prairie Preserve, OK, USA each year of study (2009 and 2010); model parameters include distance to water (water; m), distance to patch edge (edge; m), slope (slope; degrees), northing (north; degrees), easting (east; degrees), wooded area (woody), and time since fire (tsf; days).

Year	tsf	water	slope	edge	woody	north	east	tsf × wtr	tsf × slp	tsf × edge	tsf × wdy
Bison											
2009	-1.69	-0.01	-0.72	-0.55	-2.44	0.01	0.06	0.12	-0.48	-0.78	-1.85
2009	-1.29	0.20	-0.48	-0.12	-2.45	0.00	0.03	0.31	-0.22	-0.34	-1.64
2009	-1.74	0.19	-0.61	-0.50	-1.22	0.01	-0.01	-0.05	-0.35	-0.78	-0.47
2009	-1.16	0.00	-0.63	-0.43	-1.55	-0.03	0.06	0.15	-0.58	-0.59	-0.93
2009	-1.91	0.23	-0.45	-0.40	-2.45	-0.03	0.02	0.30	-0.31	-0.64	-2.38
2009	-1.35	-0.02	-0.62	-0.14	-2.59	-0.02	0.02	0.11	-0.37	-0.39	-2.23
2009	-1.57	0.10	-0.56	-0.36	-1.46	-0.03	0.00	0.00	-0.37	-0.43	-1.19
2010	-1.38	0.13	-0.51	-0.07	-1.38	0.03	0.00	0.20	-0.08	-0.26	0.30
2010	-1.16	0.13	-0.49	-0.14	-1.35	0.00	-0.03	0.10	-0.16	-0.22	0.27
2010	-1.37	0.06	-0.54	-0.25	-0.82	0.01	0.01	0.14	-0.17	-0.37	0.40
2010	-1.52	0.11	-0.51	-0.06	-0.71	0.01	-0.02	0.19	-0.16	-0.20	0.32
2010	-1.46	0.06	-0.57	-0.14	-0.40	0.04	-0.02	0.07	-0.07	-0.38	1.16
2010	-1.38	0.00	-0.79	-0.13	-1.59	0.02	0.00	-0.02	-0.30	-0.33	-0.11
2010	-1.79	-0.15	-0.43	-0.17	-1.21	-0.02	0.03	-0.08	-0.08	-0.32	0.11
Variation [‡]	0.23	0.10	0.10	0.17	0.70	0.02	0.03	0.12	0.16	0.19	1.12
Cattle											
2009	-1.70	-0.05	-0.46	-0.81	-1.66	0.04	-0.01	-0.19	-0.32	-1.20	-1.68
2009	-1.44	-0.33	-0.11	-0.87	2.74	-0.06	-0.02	0.26	0.05	-1.78	-0.23
2009	-1.16	-0.30	-0.02	-0.28	2.37	0.00	-0.01	-0.19	0.18	-0.94	0.18
2009	-0.37	-0.03	-0.15	-0.69	1.61	-0.01	0.01	-0.23	0.00	0.53	-0.47
2009	-0.36	-0.11	-0.25	-0.18	1.42	0.02	0.01	-0.09	-0.12	0.08	0.10
2009	-0.79	-0.22	-0.28	-0.12	1.24	0.00	0.00	-0.25	-0.08	0.03	0.40
2009	-3.35	-0.62	-0.15	-0.61	1.49	0.00	-0.04	-0.95	-0.04	-0.97	0.43
2010	-0.37	-0.09	-0.27	-0.07	1.60	0.01	0.00	-0.81	-0.01	0.00	0.04
2010	-2.72	-0.45	-0.42	-0.82	3.66	0.04	-0.02	-0.55	-0.47	-0.99	1.44
2010	-1.24	-0.38	-0.12	-0.37	1.86	0.05	-0.04	-0.56	0.14	-0.41	-0.72
2010	-1.59	-0.17	-0.02	-0.43	1.24	0.00	0.01	-0.39	-0.10	-0.38	-0.41
2010	-0.48	-0.29	-0.24	-0.32	2.79	-0.05	0.04	-0.44	-0.33	0.18	-0.50
2010	-2.09	-0.21	0.04	-1.18	1.31	-0.03	-0.01	-0.79	-0.03	-0.55	0.44
2010	-1.16	-0.13	-0.40	-0.41	0.82	0.00	-0.01	-0.21	-0.42	-0.39	-0.24
Variation [‡]	0.91	0.17	0.16	0.33	1.22	0.03	0.02	0.33	0.2	0.63	0.71

[†]Standardized variables are shown for coefficient comparison and interaction term interpretation.

[‡]Variation measured by calculating the standard deviation of coefficients within species.

units within the Tallgrass Prairie Preserve are smaller than the bison unit, they are larger than the majority of land holdings within the Great Plains; size likely did not limit the distance to water. This study also compared bison to European cattle breeds that are typical for livestock production objectives on tallgrass prairies. Other breeds of cattle are likely to respond differently (Rook et al. 2004, VanWagoner et al. 2006). Brahman or Texas longhorn breeds, for example, are likely to be adapted to more arid environments where water is limiting and may behave more similarly to bison.

In the Great Plains of North America, bison are reintroduced for primarily two objectives: species conservation and restoration of ecosystem processes. Reintroduction to conservation areas, development of private herds, and recent efforts in identifying pure herds to conserve genetics

have been successful in restoring wild bison populations to many areas. Conservation of this species is a unique success story that deserves acknowledgement. Bison are also reintroduced to restore keystone effects (Knapp et al. 1999). Conservation groups as well as government agencies reintroduce bison to both small prairie remnants and large landscapes to restore historical disturbance patterns. In most cases, this is done without considering the many other factors that influence grazing behavior or effects. While the first objective for reintroduction can be accomplished by building up bison herds throughout the Great Plains, the second objective is not possible without the consideration or reintroduction of other environmental or animal factors. For example, we show that both of these herbivores have a strong preference for recently burned areas. This may suggest that the reintro-

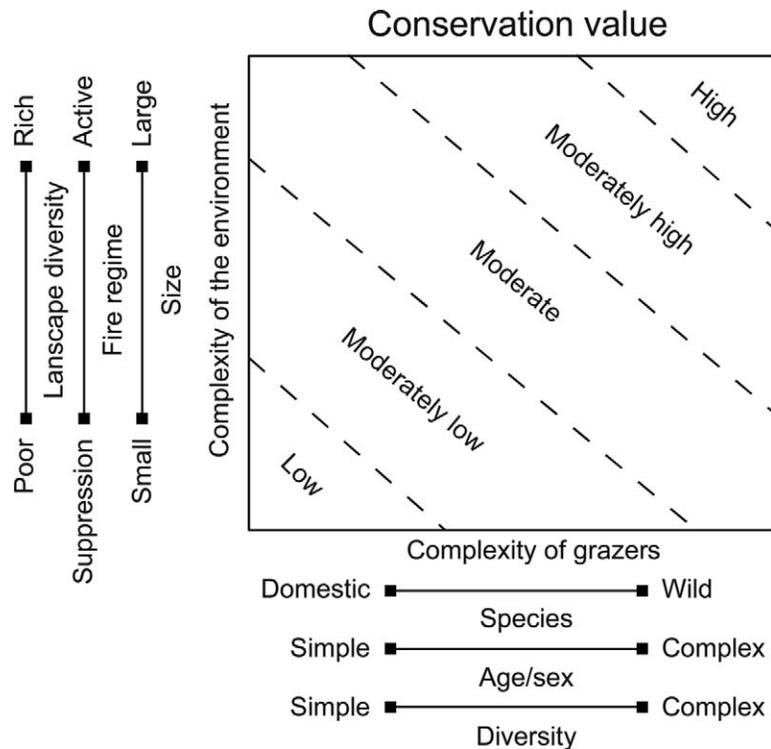


Fig. 5. Conceptual model to evaluate conservation value with respect to animal and environmental factors. Conservation value is defined as the contribution to regional conservation efforts, which includes the promotion of native plants, animals, and ecosystem processes. Species of animal alone does not automatically increase the value in regard to conservation; other factors play an important role in overall conservation value.

duction of bison, or the evaluation of differences between these species, may be largely irrelevant unless fire and other complexities are incorporated (Fuhlendorf et al. 2009). It is likely true that other factors, such as predators, would also greatly alter animal behavior and grazing effects (Ripple and Beschta 2003).

Conservation efforts regarding bison reintroduction should be evaluated to not only see if specific objectives are met, but how efforts contribute to overall conservation. We developed a conceptual model to evaluate the conservation value of different options regarding bison reintroduction (Fig. 5). We define conservation value as the contribution to regional conservation efforts, including promotion of native plants, animals, and ecosystem processes. The model is based on two primary factors that influence grazing behavior and effects, primarily complexity of grazers and the environment. Complexity of grazers refers to factors such as species,

diversity, and social organization that contribute to the overall conservation value. Although this study examined only differences between two species, increasing species diversity with multiple species will add additional complexity to the system and alter the effects of grazing (du Toit and Cumming 1999, Hooper et al. 2005, Burns et al. 2009). Other native species in North American grasslands, such as prairie dogs (*Cynomys* spp.) are also important components of the system; as an example, incorporating prairie dogs will increase conservation value (Coppock et al. 1983).

The social organization of ungulates, particularly age and sex ratios, also contribute to ecosystem functioning, complexity, and conservation (Sheldon and West 2004, Gordon et al. 2004, Milner et al. 2007). Variation in animal factors will also contribute to interactions with the environment. For example, the body size of animals (also related to age and sex) influences

preferences for burned areas, playing an important role in spatiotemporal heterogeneity (Wilsey 1996, Sensenig et al. 2010). Simple social organization, such as the yearling stocker steers within cattle units of this study, limit variability and decrease conservation value. With particular regard to livestock production, complexity of grazers may be improved by increasing individual variation or combing differing breeds or species (VanWagoner et al. 2006, Searle et al. 2010). Historically, bison were a keystone species, but their impacts were dependent upon how they interacted with the environment, disturbances, and other herbivores. Increasing the complexity of grazers (more species diversity, more wild herbivores, etc.) increases the conservation value, but this value is also dependent upon environmental factors. The simple replacement of domestic cattle with bison may contribute to bison conservation, but may have minimal impact on the broader conservation value of ecosystems. In an extreme example, replacing cattle with bison in a small, intensively managed, and simplified livestock production operation (e.g., a feedlot or small pasture) has little conservation value. Restoring other important processes such as fire, predation, etc. are just as important as the large herbivore upon the landscape (Ripple and Beschta 2003, Fuhlendorf et al. 2009).

Conservation value is also dependent upon the environmental complexity of the area. The majority of these factors are independent of the species of herbivore. In mesic grasslands of the Great Plains (tallgrass and mixed grass prairies), fire-grazing interactions have been shown to be a dominant driver of animal distribution and integral ecosystem process (Fuhlendorf and Engle 2004, Vermeire et al. 2004, Anderson et al. 2006). Similar to the example given above, the simple replacement of cattle with bison without a restoration of fire regimes will not result in disturbance patterns that are critical for conservation and biodiversity. In our study, time since fire was a primary driver in bison and cattle grazing behavior. The suppression of fire or the simplification of fire-grazing interactions within fire prone systems will limit conservation value, regardless of the herbivore species. Environmental factors that are critical to grazing effects and other ecosystem processes need to be accounted for in study designs that evaluate the role of

grazing in conservation efforts. In North American grasslands, key environmental factors include fire regimes (Wright and Bailey 1982, Knapp et al. 1998, Brockway et al. 2002), landscape complexity and size (Herkert 1994, With et al. 2008), water distribution (Bailey et al. 1996, Augustine 2010), and woody vegetation (Archer et al. 1995, Briggs et al. 2002). These do not only influence grazing and the resulting effects, but play a broader role in ecosystem functioning. On lands with minimal environmental complexity, any differences between bison and cattle will likely contribute little to conservation value.

Grasslands are endangered worldwide (Hoekstra et al. 2005). While propositions to restore or conserve grasslands regularly focus on native herbivores (e.g., Sanderson et al. 2008), it is often overlooked that the majority of grasslands are privately owned and used for domestic livestock production (particularly true in the Great Plains of North America; Samson and Knopf 1994). Low and high conservation values can be achieved with bison or cattle. Though bison are the iconic symbol of the Great Plains of North America, and it is critical that we conserve the species, there are not enough data to confidently state that landscapes with bison are inherently better than landscapes with cattle for overall conservation or biodiversity. Both species can be mismanaged and cause degradation of habitat as well as ecological processes. Using domestic cattle to achieve some conservation objectives may be more practical or relevant, as cattle currently make up the vast majority of herbivores in many grasslands. Conservation value of productions cattle herds can be improved by increasing the size and complexity of landscape available. Allowing cattle to move at broader spatial scales and to interact with biotic and abiotic factors, may increase conservation value substantially, perhaps more so than replacing cattle with bison at finer scales. Popular management strategies that constrain animal movement and behavior (through use of fencing and rotation) may prevent many important interactions between the animal and environment, potentially reducing conservation value. As more studies effectively and appropriately compare grazing behavior and effects at broad and fine spatial scales, additional reliable conclusions will

be made that may change conservation efforts or directions.

We argue that for future studies and comparisons between bison and cattle (as well as other species) it is critical that we limit our extrapolation with discussions of the abiotic and biotic environment in which these studies occur. Though it is unlikely that we will be able to conduct studies that encompass all possibilities in environmental and herbivore complexity, we must begin to contextualize our discussions and limit our inferences. From a conservation perspective it is important to understand the ecological effects of cattle grazing for livestock production, and explore approaches to alter these patterns to more effectively achieve conservation objectives. It is not productive to look for differences or similarities between bison and cattle to justify certain management objectives or agenda. In the face of the vast variability and complexity in which these species are nested within, generalizations are limited and over inferences likely.

Conservation of bison is important as an iconic species and a keystone herbivore (Knapp et al. 1999). From a broad context, however, conservation efforts need to recognize that cattle will continue to be a dominant feature on the Great Plains and grasslands worldwide, and that some conservation objectives may be met using cattle. It is critical to understand grazing behavior and ecological effects of both species in simple and complex landscapes relevant to conservation. There is an important place for species comparisons, but this is just one aspect of grassland conservation and may not be the most important for future conservation of biodiversity.

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