

Conservation implications of native and introduced ungulates in a changing climate

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Abstract

In many grasslands, grazing by large native or introduced ungulates drives ecosystem structure and function. The behavior of these animals is important as it directs the spatial effects of grazing. To the degree that temperature drives spatial components of foraging, understanding how changes in climate alter grazing behavior will provide guidance for the conservation of ecosystem goods and services. We determined the behavioral response of native bison (*Bison bison*) and introduced cattle (*Bos taurus*) to temperature in tallgrass prairie within the Great Plains, USA. We described the thermal environment by measuring operative temperature (the temperature perceived by animals) through space and time. Site selection preferences of ungulates were quantified using resource selection functions. Woody vegetation in tallgrass prairie provided a cooler thermal environment for large ungulates, decreasing operative temperature up to 16 °C in the heat of the summer. Cattle began to seek thermal refugia at lower air temperatures (24 °C) by selecting areas closer to woody vegetation and water sources. Bison, however, sought refugia within wooded areas at higher air temperatures (36 °C), which occurred much less frequently. Both species became more attracted to riparian areas as air temperature increased, with preferences increasing tenfold during the hottest periods. As predicted warming occurs across the Great Plains and other grasslands, grazing behavior and subsequent grazing effects will be altered. Riparian areas, particularly those with both water and woody vegetation, will receive greater utilization and selection by large ungulates. The use of native grazers for conservation or livestock production may mitigate negative effects caused by increased temperatures.

Keywords: Bison, cattle, climate change, grazing behavior, livestock, operative temperature, tallgrass prairie, warming

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Introduction

The Great Plains region of North America developed with significant impact from disturbances such as herbivory and fire. After the megafaunal collapse near the end of the Pleistocene, American bison (*Bison bison*), Manitoban elk (*Cervus canadensis*), and American pronghorn (*Antilocapra americana*) became the primary large grazers of these grasslands until pre-European settlement (Axelrod, 1985; Potter *et al.*, 2010). Due to their abundance, bison (as well as ancestors, *B. antiquus* and *B. occidentalis*) influenced many processes across the landscape, influencing ecosystem structure and function (Knapp *et al.*, 1999; Anderson, 2006). Much of the flora and fauna coevolved with and adapted to grazing by these and other herbivores (Axelrod, 1985). Following European settlement, however, bison populations declined rapidly due to hunting and competition from domestic livestock and were estimated at less than 1 000 individuals by the late 1800s (Hornaday,

1889; Seton, 1927). During the 20th century, the large and complex landscapes once occupied by native ungulates were largely converted to fragmented agricultural lands. Domestic livestock, primarily introduced European cattle (*Bos taurus*), replaced herds of bison, and livestock populations grew as ranching became a successful economic enterprise. The 2011 estimate of cattle for meat production and their gross income within the United States was 92 million individuals and \$63 billion, respectively, with nearly half or more of both estimates from within the Great Plains (National Agricultural Statistics Service, 2012).

During the same period of cattle and agricultural growth, bison restoration was pursued (and currently continues) by private citizens, government agencies, and conservation organizations for the purposes of species conservation, the restoration of ecosystem processes, and agricultural production (Knapp *et al.*, 1999; Sanderson *et al.*, 2008). Bison numbers have increased from nearly extinct to approximately 20 000 + in conservation herds and 400 000 + in commercial livestock operations (Gates *et al.*, 2010). Efforts to restore bison populations are considered a success, even though the

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number of animals is miniscule compared with that of introduced cattle. Indeed, bison restoration throughout the Great Plains cannot be fully separated from the cattle industry as there is increasing demand and use of bison for agricultural purposes by livestock producers (i.e. meat; Joseph *et al.*, 2010), bison are often treated legally as livestock (Montana Legislature, 2011), and more than 90% of rangeland within the region is privately owned and used for livestock production (Samson & Knopf, 1994).

The similarities and differences between bison and cattle are often discussed and debated between advocates, conservation biologists, and land managers, and are commonly used to promote a specific agenda or ideology. For example, popular press, government agency reports, and scientific literature often maintain that bison spend less time near water than cattle and are, therefore, better suited for grazing when protection of riparian systems is a concern (Manning, 1995; Hartnett *et al.*, 1997; Fritz *et al.*, 1999; Reynolds *et al.*, 2003; National Park Service, 2009). Similar claims comparing bison and cattle abound, though direct and appropriate comparisons (i.e. similar management, animal density, etc. of the two species) are few. Furthermore, statements often focus on the species of animal as the sole determinant of grazing effects, ignoring other important factors such as animal and landscape diversity or management practices. Recognizing the ecological differences and effects between native animals and introduced livestock is important to better understand and improve ecosystem restoration and livestock management.

Grazing effects are not only solely determined by the species of herbivore but also shaped by many biotic and abiotic factors. Climate is an important part of the structure and function of grazed ecosystems, and influences large herbivore behavior and grazing effects accordingly. Increased anthropogenic activity has resulted in changes in temperature and rainfall patterns at broad scales and current climate models predict a continued warming trend in the Great Plains (IPCC, 2007). Although studies have examined the potential effects of climate change on large ungulates and the ecosystems in which they graze, many are focused on the response of forage quantity and quality (Shaw *et al.*, 2002; Craine *et al.*, 2010), sustainability of livestock grazing (Hanson *et al.*, 1993; Shaw *et al.*, 2011; Lohmann *et al.*, 2012), or the interactive effects of grazing and climate change (most often with simulated grazing; Wan *et al.*, 2002). The response of grazing behavior to climate change is equally important, as it will drive the spatial distribution and intensity of grazing, altering the overall grazing effects. The thermal environment is particularly significant as the thermo-

regulatory needs of grazing animals can take precedence over foraging (Smith, 1988; Stuth, 1991; Loza *et al.*, 1992). Examining behavioral differences between native and introduced ungulates will aid in understanding present-day ecosystem structure and function and improve land management and restoration in a changing climate.

Understanding the effect of climate change on ecosystem processes is important for the conservation of ecosystem goods and services, including biodiversity, heterogeneity, agricultural production, etc. Grasslands worldwide are endangered and threatened (Hoekstra *et al.*, 2005), increasing the need to better understand climatic change within these ecosystems in order to inform management and restoration. To better understand the implications of increasing temperature on ungulate behavior, we evaluated the effects of ambient air temperature and the operative thermal environment (defined below) on native bison and introduced cattle in tallgrass prairie. In particular, we address two questions: 1. How does the thermal environment vary across the landscape? 2. How do bison and cattle alter site selection with increasing temperature? We show that air temperature interacts with landscape features to influence the behavior of both species and that bison seek thermal refugia at higher temperatures than cattle. Native ungulates may be better suited for both conservation purposes and livestock production in a warming climate.

Materials and methods

We examined ungulate behavior at The Nature Conservancy Tallgrass Prairie Preserve, located in northeast Oklahoma, USA. The preserve is a 16 000 ha natural area managed primarily for biodiversity. Livestock production is a secondary product as land is leased to producers for grazing. The plant community is 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. Cross timbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Air temperature, precipitation, and various climate measurements are measured on site every 5 min by an Oklahoma Mesonet weather station (Brock *et al.*, 1995; McPherson *et al.*, 2007). The time period for this study was the growing seasons of years 2009–2011. Mean monthly air temperature and precipitation varied during the study, with values below and above long-term averages for the site (Table 1).

There is one large bison unit (9 532 ha) and seven smaller cattle units (430–980 ha) within the preserve. Only perimeter fences are present and animals are free to move 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; the 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 to

Table 1 Monthly temperature and precipitation at the Tallgrass Prairie Preserve, USA, April through September. Values represent long-term averages (\pm SE; 1994–2011) or monthly averages or totals for specific years (2009–2011)

Month	Temperature (°C; \pm SE)	2009 (°C)	2010 (°C)	2011 (°C)	Precipitation (cm; \pm SE)	2009 (cm)	2010 (cm)	2011 (cm)
Apr	14.7 (0.4)	13.6	16.53	16.1	108.5 (11.5)	173.4	55.3	145.2
May	19.4 (0.2)	18.1	19.1	18.4	113.9 (13.1)	65.7	139.7	68.5
Jun	23.9 (0.3)	24.9	25.5	16.7	138.6 (22.9)	139.4	138.6	58.1
Jul	26.4 (0.3)	24.5	26.4	30.3	91.5 (13.8)	95.4	130.5	68.0
Aug	26.2 (0.4)	23.7	26.6	28.7	76.3 (11.2)	120.4	149.0	86.3
Sep	21.5 (0.3)	19.4	21.6	20.1	77.8 (13.2)	52.0	107.9	34.2

10 years, whereas males are 0–6 years. Cattle units are stocked with stocker steers (males) approximately 1 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). Fire-grazing interactions result as animals select between recently burned areas and those with greater time since fire (Archibald *et al.*, 2005; Allred *et al.*, 2011a).

We measured operative temperature to characterize the thermal landscape of tallgrass prairie. Operative temperature integrates air temperature and solar radiation to determine the environmental temperature as perceived by animals (aka black bulb temperature; Bakken, 1976; Dzialowski, 2005; Signer *et al.*, 2011). We recorded operative temperature by measuring air temperature inside the center of a black steel sphere (15 cm diameter) placed at ground level. To capture temporal variation, operative temperature was recorded every 5 min during eight separate sampling periods. Sampling periods were 1 week and stratified across seasons (spring, summer, fall, winter) from 2010 to 2012. To capture spatial variation, we used four 50 m randomly placed transects that varied in landscape features (time since fire, ranging from 0 to 50 months; woody vegetation, herbaceous or woody; topography, slope ranging from 0 to 10%). Within each transect, two by two meter plots were established at 0, 25, and 50 m; operative temperature was recorded at every corner of each plot resulting in 12 sampling points per transect. Transects were moved daily (2 to 5 km) during each sampling period to capture spatial variation and to improve thermal landscape characterization. We used linear regression to model operative temperature relative to air temperature recorded from the onsite weather station (also collected at a 5 min frequency) for locations that varied in time since fire and woody vegetation (primary drivers of bison and cattle grazing behavior; Allred *et al.*, 2011b). To correspond with animal data (see below), we omitted temperature data collected in winter.

To examine the influence of temperature on herbivore behavior and site selection, we deployed global positioning system (GPS) receiver collars on seven female bison and seven cattle (steers, one per unit) from April through September of 2009, 2010, and 2011. GPS collars were of the same design and

color, and placed on different animals each year. We recorded location information of animals at two different time frequencies, alternating weekly from 12 min to 1 h, which was identical for bison and cattle. We imported all GPS location data into a spatially enabled database (PostgreSQL/PostGIS). We mapped fire histories and water sources (ponds and streams) with handheld GPS units, aerial photographs, and United States Geological Survey 7.5 min topographic maps. Herbaceous and woody vegetation was mapped for the site using a GeoEye-1 satellite image (1.5 m resolution) acquired September 20, 2009. The presence of woody vegetation within the area is not correlated with surface water sources (Allred *et al.*, 2011b).

In addition to location information, GPS collars deployed on animals recorded temperature every 5 min. Temperature sensors are located within the plastic encasement that houses electronics and batteries, and resides underneath the neck of the animal. Although this is not an appropriate or accurate measure of animal body temperature, it can be used to determine if bison and cattle respond differently to air temperature. A one-to-one relationship on a regression (i.e. slope equals one) of collar and air temperature (recorded by the reference weather station) indicates that collar temperature is simply tracking air temperature and is not influenced by the animal's location. Deviation from a one-to-one relationship indicates that animals are altering collar temperature by changing physical location or shifting site selection preferences. We thus examined the relationship of collar temperature with air temperature for bison and cattle using linear regression. Relationships for bison and cattle were regarded as different if 95% confidence intervals of slope coefficients did not overlap.

To determine if bison or cattle altered selection behavior with temperature, we estimated resource selection functions using logistic regression models (Boyce *et al.*, 2002). Rather than including all potential environmental factors as predictors (e.g., slope, aspect, elevation, etc.) we focused only on time since fire, distance to water, and distance to woody vegetation as these are primary drivers of bison and cattle site selection in tallgrass prairie (Allred *et al.*, 2011b). To represent available resources, we created three random locations (within the area available to each animal) for each observed location. We calculated time since fire, distance to water, and distance to woody vegetation for all locations; we also associated ambient air temperature to all locations. Our principal resource selection function included interactions of air temperature

with time since fire, distance to water, and distance to woody vegetation to first determine if temperature altered behavior. Because interactions with air temperature were significant, we estimated resource selection functions at different air temperature classes. Air temperature was subdivided into degree classes of four degree intervals (e.g., 4–7 °C, 7–10 °C, and so on). Resource selection functions were then estimated using location data within each air temperature class. To compare coefficients of environmental predictors, we standardized variables by subtracting the mean and dividing by the standard deviation (Gelman & Hill, 2007). We used bootstrapping procedures to estimate the precision of coefficients from resource selection functions for each air temperature class. We calculated 95% confidence intervals of coefficients after 1,000 iterations of randomly sampled datasets. All analyses were performed in (R Development Core Team, 2012).

Results

Large temperature differences between open and shaded areas suggest the significance of thermal refugia for large herbivores and other organisms in tallgrass prairie. Though operative temperatures of both herbaceous and woody vegetation increased linearly with air temperature, temperatures within wooded environments increased much less than those in herbaceous

environments (Fig. 1a). This resulted in a cooler thermal environment at higher air temperatures, as well as a warmer environment at lesser temperatures (20–23 °C). The greatest differences were particularly noticeable during the warmest parts of the day, when differences in approximately 16 °C could be present (Fig. 1b). Though recently burned areas have less vegetation due to combustion of vegetation and grazing preferences of postfire regrowth, the amount of time since fire did not significantly influence operative temperature within herbaceous or woody vegetation ($P > 0.05$).

Interactions of air temperature with environmental factors indicated that bison and cattle site selection preferences varied according to air temperature (Table 2). Of the environmental influences examined, time since fire had the greatest influence on site selection. Estimation of resource selection functions at varying temperature classes showed patterns of selection and probability of use with increasing temperature (Figs. 2 and 3). Native bison sought thermal refugia (shade) at higher temperatures than introduced cattle. Cattle preference for woody vegetation appeared at approximately 26 °C and continued to strengthen as temperature increased. Bison, however, did not prefer

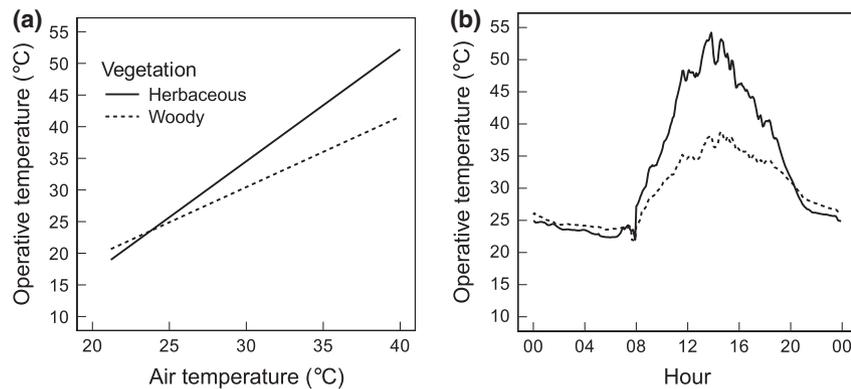


Fig. 1 Thermal representation of a tallgrass prairie ecosystem. Operative temperature as a function of (a), air temperature (T_{air}) separated by vegetation type, herbaceous ($\hat{y} = 1.91T_{air} - 22.33$; $r^2 = 0.72$, $P < 0.05$) and woody ($\hat{y} = 1.13T_{air} - 3.45$; $r^2 = 0.84$, $P < 0.05$) and (b), hour of day (values are averaged over summer sampling periods). Operative temperature is relatively more stable in woody than herbaceous vegetation. Woody vegetation is also significantly cooler at warmer air temperatures and during the heat of the day.

Table 2 Estimated resource selection coefficients for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA. Model parameters include time since fire (TSF), distance to water (Water), distance to woody vegetation (Woody), air temperature (T_{air}), and interactions with air temperature. Standardized variables are shown for coefficient comparison

Species	TSF	Water	Woody	T_{air}	TSF \times T_{air}	Water \times T_{air}	Woody \times T_{air}	Intercept
Bison	-0.134*	-0.009*	0.046*	0.00	-0.005*	-0.022*	-0.011*	0.249*
Cattle	-0.073*	-0.002*	-0.006*	0.00	-0.003*	-0.034*	-0.016*	0.248*

* $P < 0.005$.

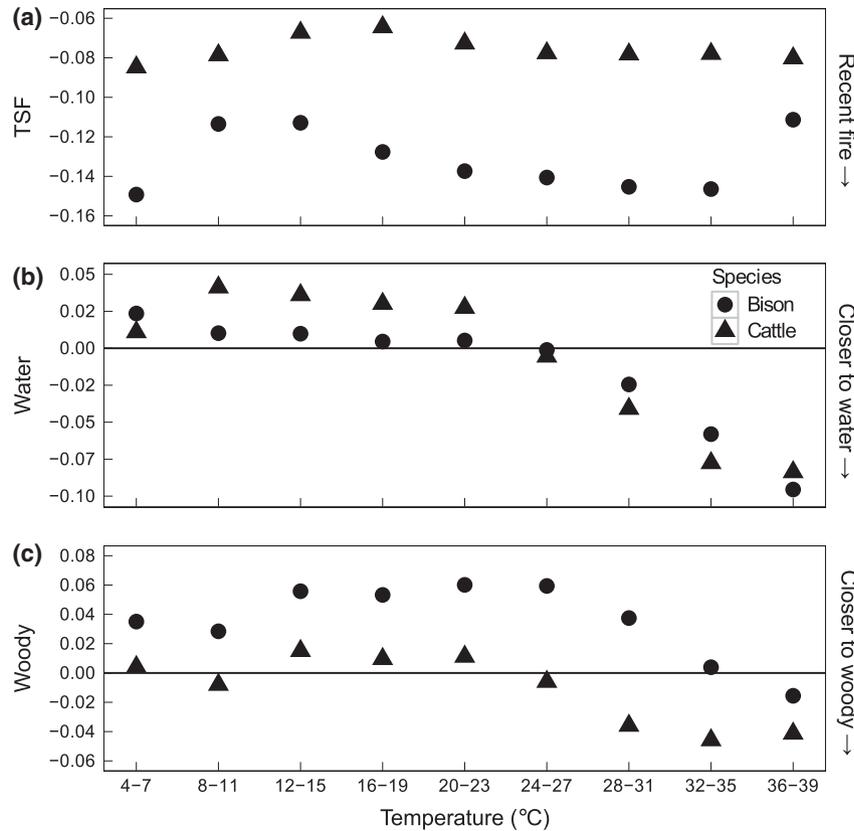


Fig. 2 Resource selection coefficients at varying air temperature classes for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA. Environmental factors include time since fire (TSF), distance to water (Water), and distance to woody vegetation (Woody). Standardized variables are shown for coefficient comparison. Text on right indicates the direction or preference of selection, i.e. animals prefer areas that are more recently burned, that are closer to water, or closer to woody vegetation. The crossing of the horizontal line at 0.00 indicates a change in preference. One resource selection function was estimated per animal species per temperature class. Confidence intervals (95%; calculated using bootstrapping procedures, 1000 iterations) did not overlap between species. Note scale differences for each graph.

woody vegetation until temperatures around 36 °C. The probability of bison use increased with distance to woody vegetation for all, but the warmest temperatures (Fig. 3c). The selection of areas closer to water also increased and became stronger as air temperature itself increased. At approximately 24 °C, both bison and cattle began to prefer areas closer to water; at 36 °C preferences had increased almost tenfold. In general, the preference for recently burned areas did not change with increasing temperature for bison or cattle. Both species continued to prefer recently burned areas to areas with greater time since fire.

As ambient air temperature increased, cattle generally sought cooler environments than those of bison. Temperature of GPS collars (as observed within the collar housing) for bison and cattle closely tracked air temperature, but deviated from a one-to-one relationship ($P < 0.05$; bison: $\hat{y} = 0.96T_{air} + 2.85$; cattle: $\hat{y} = 0.90T_{air} + 4.37$). As these relationships are simply dependent upon collar and air temperature, the

changing of physical location by animals altered collar temperature and caused deviations. The slope coefficient for cattle was smaller than bison (no overlap of 95% confidence intervals between species) and resulted in slightly cooler collar temperatures at warmer air temperatures. Although the magnitude of difference between bison and cattle was not large, it indicated a behavioral difference in response to temperature, corresponding with site selection results presented above.

Discussion

Understanding the behavioral responses of grazing animals to increasing temperature and consequent spatial distributions is critical to the future conservation of ecosystems goods and services. In tallgrass prairies, woody vegetation can provide a significantly cooler thermal environment than open herbaceous grassland, decreasing operative temperature by 2 °C in the morning and evening hours, and up to 16 °C in the heat of the day.

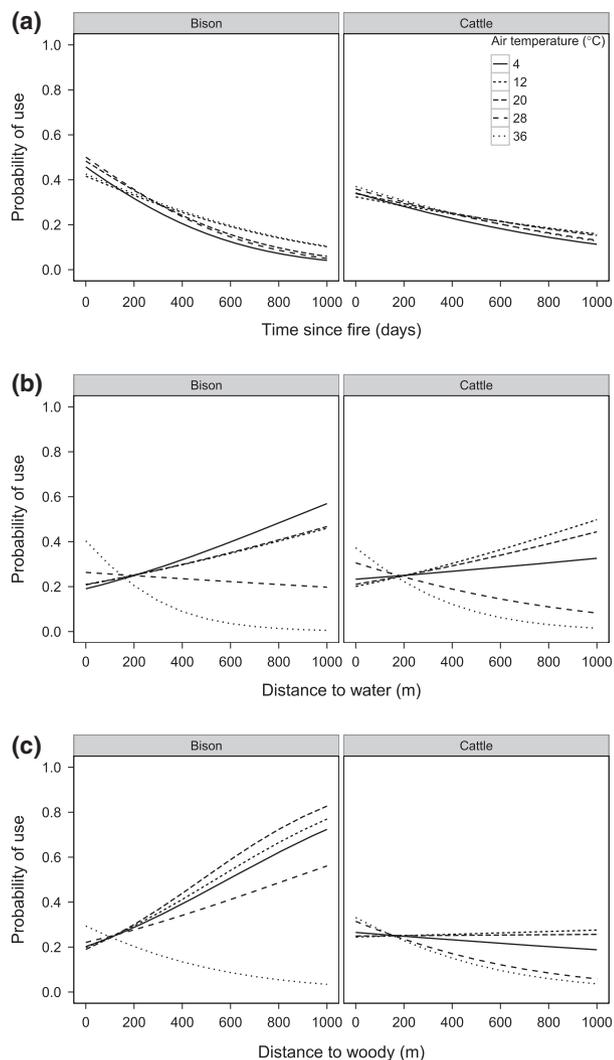


Fig. 3 Probability of use relative to selected air temperatures (differing lines; 4, 12, 20, 28, and 36 °C) for (a), time since fire, (b), distance to water, and (c) distance to woody vegetation as predicted by resource selection functions for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA. Air temperature has little effect on the influence of time since fire for both species, but heavily impacts the probability of use as related to distance to water and woody vegetation. Predicted mean July daytime temperatures (see Table 3) vary from 29 °C (low emission scenario, 2050s) to 36 °C (high emission scenario, 2080s). A mean daytime temperature of 29 °C would result in bison and cattle selecting areas closer to water, and cattle selecting areas closer to woody vegetation. A mean daytime temperature of 36 °C would result in bison and cattle selecting areas closer to water and woody vegetation.

Contrasting the similar behavioral preferences for water, there is a clear distinction between native bison (*Bison bison*) and introduced cattle (*Bos taurus*) in preferences for woody vegetation. Cattle stay away from woody vegetation at lower temperatures (4–23 °C), but

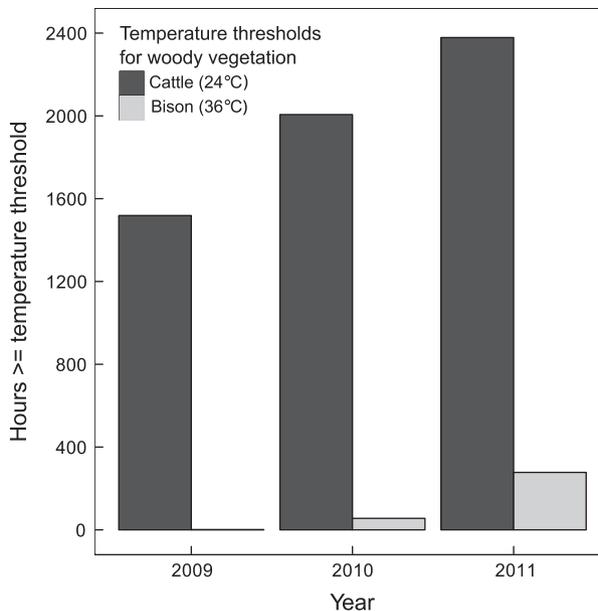


Fig. 4 Number of hours in which air temperature was greater than or equal to temperature thresholds representing attraction to woody vegetation for cattle (24 °C) and bison (36 °C) within the southern Great Plains, USA. Relative to cattle, the occurrence of conditions necessary for bison to be attracted to woody vegetation is extremely low, minimizing grazing or animal impacts in such environments. Temperature thresholds for being attracted to water sources were the same for cattle and bison, and equal to that of woody vegetation for cattle (24 °C; black bars). Increases in temperature will only result in greater time spent near or attracted to these landscape features.

switch preferences and select areas closer to woody vegetation at higher temperatures (>23 °C). In contrast, bison have greater avoidance of woody vegetation and do not select areas closer to woody vegetation until temperatures reach their highest levels (36–39 °C). Even in the hottest conditions, bison prefer woody vegetation less than cattle. In fact, the occurrence of such high temperature conditions is rare, making it less likely that bison will graze or rest in wooded areas, thus minimizing or removing any grazing effects therein. A lower threshold temperature for cattle results in a much greater proportion of time at which they are attracted to such areas (Fig. 4). Predicted future warming for the Great Plains suggests greater selection of woody vegetation. This attraction will be augmented if areas with woody vegetation contain water, increasing the potential for degraded water quality and bank stability (Trimble & Mendel, 1995; Belsky & Blumenthal, 1997). As the temperature threshold for woody vegetation attraction is much higher for bison, their use as grazers in place of introduced livestock may mitigate or lessen some of these adverse behavioral effects caused by increased temperature.

Table 3 Predicted mean July daytime (0600–2100 h) temperature (°C) by mid century (2050) and end of century (2080) for low, medium, and high emissions scenarios at the Tallgrass Prairie Preserve, USA. Temperature increases vary by general circulation model. Temperature increase data retrieved from the ClimateWizard (Girvetz *et al.* 2009) and added to base mean July daytime temperature (28.11 °C)

Model	Mid century (2050s)			End century (2080s)		
	Low	Medium	High	Low	Medium	High
CGCM3.1(T47)*	29.66	30.58	31.14	30.49	31.04	33.03
CSIRO-Mk3.0†	29.96	30.06	30.34	29.84	31.71	32.07
GISS-ER‡	29.99	30.05	30.99	30.60	31.21	32.49
ECHAM5/MPI-OM§	30.24	30.79	30.58	30.82	32.42	32.19
CCSM3¶	30.59	31.48	31.43	30.18	32.10	34.05
UKMO-HadCM3	32.48	33.15	32.88	33.14	34.65	36.34

*Canadian Centre for Climate Modeling and Analysis.

†CSIRO Atmospheric Research.

‡NASA/Goddard Institute for Space Studies.

§Max Planck Institute for Meteorology.

¶National Center for Atmospheric Research.

||Hadley Centre for Climate Prediction and Research.

Many riparian areas provide opportunities for both water and shade. Grazing animals, particularly cattle, gather in these areas to hydrate and thermoregulate within preferred temperature ranges (Bailey, 2005). In tallgrass prairie, both bison and cattle selected sites away from water (cattle more so than bison) at lower air temperatures (4–24 °C). At approximately 26 °C, both species switched preferences and began to move closer to water as temperature increased. When temperatures were hottest, preferences for water sources increased tenfold. These preferences occurred in a grassland landscape where water is not limited, and will likely be even more pronounced in arid or semiarid grasslands and rangelands, where distance between water sources is greater.

Vegetation and ecosystem changes are likely to result as grazing animals choose areas closer to water sources and woody vegetation. Grazing within riparian areas or areas near water reduces herbaceous cover, biomass, and productivity of vegetation (Kauffman *et al.*, 1983; Clary, 1995; Belsky *et al.*, 1999; DelCurto *et al.*, 2005). The concentration of grazing animals around water sources also increases nutrient concentration and can become a nonpoint pollution source (Pell, 1997; Belsky *et al.*, 1999; Ballard & Krueger, 2005). Predicted warming increases of 2.0–2.5 °C in mean annual temperature (IPCC, 2007) or 1.5–8.23 °C in July daytime temperature for the region (Table 3) suggest that animals will increase their selection of sites closer to water, regardless of origin (native or introduced). Bison may provide a small advantage in preventing riparian degradation and nonpoint source pollution with increased temperature, as they are less attracted to water sources than cattle. However, it is important to note that cattle may also

provide a similar advantage at cooler temperatures, as they tended to stay further from water sources than bison.

Altered behavior due to increased temperatures may impact grazer performance or productivity. Greater attraction to and more time spent near water sources and woody vegetation as a result of warming temperatures will likely translate to decreased grazing and weight gain. Furthermore, decreased forage quality and bison performance has been documented with increased temperature across regions (Craine *et al.*, 2010; J. Craine personal communication). Utilizing different breeds of cattle for conservation and livestock production may help mitigate behavioral effects of increased temperature. The management of cattle for this study is representative of that throughout much of the Great Plains in North America. In particular, European cattle breeds (e.g., Black angus, Hereford, etc.) are commonly used for livestock operations. These breeds originate from *Bos taurus* and have less thermoregulatory capability than the other primary species *Bos indicus* (Blackshaw & Blackshaw, 1994; Hansen, 2004), which includes Zebu and Brahman breeds. Performance by breeds accustomed to higher temperatures or more arid regions (e.g., Brahmans) will likely be more similar to native ungulates with increasing temperature. The size of the gastrointestinal tract associated with a specific breed also influences heat accumulation and, therefore, grazing behavior (Sprinkle *et al.*, 2000). In addition, hide color of specific breeds will affect behavioral responses to temperature, with dark hides (e.g., Angus) being more affected than light hides (Brown-Brandl *et al.*, 2006). To reach conservation or commercial production goals, land managers will need

to consider and incorporate appropriate breeds into livestock practices (Rook *et al.*, 2004).

The presence of bison throughout the Great Plains is primarily due to a) the intent to restore native ecological processes and disturbances to North American grasslands and b) their use as an agricultural commodity, i.e. meat production. Bison are labeled a keystone species of tallgrass prairie ecosystems due to their ability to increase habitat heterogeneity, increase biodiversity, and alter nutrient cycling processes through grazing and general disturbance patterns (Knapp *et al.*, 1999). For this reason, bison are often promoted for use in grassland restoration activities. Although useful in achieving conservation goals, it is important to recognize that bison (perhaps specifically bison grazing) are just one component of ecosystem restoration. Many other factors, including additional disturbance regimes and diversity of flora, fauna, and landscape, contribute significantly to overall conservation value. Although fire showed a dominating influence on grazing behavior, its impact varied surprisingly little with increasing temperature, illustrating the importance of other factors and interactions outside of species specific grazing. Although bison are often used as a restoration tool (Sanderson *et al.*, 2008; National Park Service, 2009), it is important to remember other grassland characteristics and properties which contribute to overall conservation goals.

Given the large amounts of privately owned land supporting a vast number of cattle and the economic industry of cattle ranching, the success of bison in United States grasslands is inherently linked to commercial livestock operations. Cultural, social, and economical barriers exist that limit the desire, incentive, and opportunity for landowners to replace introduced cattle with native bison (Freese *et al.*, 2007). Although we discuss the similarities and differences, and potential advantages and disadvantages for using native bison or introduced cattle in a changing climate, it is not likely that livestock producers will change from one species to the other, or change their overall land management strategy, in the near future due to the current barriers. Examining the dynamics and mechanisms associated with these barriers (e.g., social perception, economic dynamics and incentives, conservation values, etc.) is required to better understand the motivations necessary for ecosystem conservation. More importantly, improved communication, cooperation, and outreach are essential to inform landowners, agricultural organizations, and conservation agencies of conservation priorities and strategies. Federal cost-sharing programs (similar to the Conservation Reserve Program) may also aid in improving conservation related to livestock production. Further research examining the economic

valuation of ecosystem goods and services provided by native bison, and compared with introduced cattle, will help explain economic barriers that deter the use of bison in livestock operations.

Because of their dominant impact on grasslands, understanding how large grazing animals alter behavior in response to climatic events is necessary to realize the full effects of climate change. In the tallgrass prairies of the Great Plains, native bison and introduced cattle respond similarly in many ways to increasing temperature. Significant differences exist, however, that may potentially affect conservation efforts within this endangered ecosystem, particularly with regard to riparian areas and water sources. The use of bison or more heat-adapted livestock breeds, may mitigate adverse effects of overgrazing or loitering in or near riparian areas as air temperatures increase. In addition, the restoration of native bison along with other native grassland properties (e.g., fire, broad landscapes, biodiversity) will improve overall conservation value. Though bison are commonly used for conservation purposes (as well as small commercial livestock operations) and cattle for large commercial livestock operations, these can be and often are interchangeable options, i.e. bison for commercial purposes and cattle for conservation purposes. Recognizing that the commercial cattle industry is a dominant feature of the Great Plains, and developing or employing conservation practices compatible with livestock operations are the first steps to broadscale conservation in the face of climate change.

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References

- Allred BW, Fuhlendorf SD, Engle DM, Elmore RD (2011a) Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, **1**, 132–144.
- Allred BW, Fuhlendorf SD, Hamilton RG (2011b) The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere*, **2**, art26, doi: 10.1890/ES10-00152.1.
- Anderson RC (2006) Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *Journal of the Torrey Botanical Society*, **133**, 626–647.
- Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire-grazer interactions in an African savanna. *Ecological Applications*, **15**, 96–109.
- Axelrod DI (1985) Rise of the grassland biome, central North-America. *Botanical Review*, **51**, 163–201.
- Bailey DW (2005) Identification and creation of optimum habitat conditions for livestock. *Rangeland Ecology & Management*, **58**, 109–118.
- Bakken GS (1976) A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *Journal of Theoretical Biology*, **60**, 337–384.

- Ballard TM, Krueger WC (2005) Cattle and salmon I: cattle distribution and behavior in a northeastern Oregon riparian ecosystem. *Rangeland Ecology & Management*, **58**, 267–273.
- Belsky AJ, Blumenthal DM (1997) Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conservation Biology*, **11**, 315–327.
- Belsky AJ, Matzke A, Uselman S (1999) Survey of livestock influences on stream and riparian ecosystems in the western United States. *Journal of Soil and Water Conservation*, **54**, 419–431.
- Blackshaw J, Blackshaw A (1994) Heat stress in cattle and the effect of shade on production and behaviour: a review. *Australian Journal of Experimental Agriculture*, **34**, 285–295.
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.
- Brock FV, Crawford KC, Elliott RL, Cuperus GW, Stadler SJ, Johnson HL, Eilts MD (1995) The Oklahoma Mesonet: a technical overview. *Journal of Atmospheric and Oceanic Technology*, **12**, 5–19.
- Brown-Brandl TM, Nienaber JA, Eigenberg RA, Mader TL, Morrow JL, Dailey JW (2006) Comparison of heat tolerance of feedlot heifers of different breeds. *Livestock Science*, **105**, 19–26.
- Clary WP (1995) Vegetation and soil responses to grazing simulation on riparian meadows. *Journal of Range Management*, **48**, 18–25.
- Craine JM, Elmore AJ, Olson KC, Tolleson D (2010) Climate change and cattle nutritional stress. *Global Change Biology*, **16**, 2901–2911.
- DelCurto T, Porath M, Parsons CT, Morrison JA (2005) Management strategies for sustainable beef cattle grazing on forested rangelands in the Pacific Northwest. *Rangeland Ecology & Management*, **58**, 119–127.
- Dzialowski EM (2005) Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, **30**, 317–334.
- Freese CH, Aune KE, Boyd DP *et al.* (2007) Second chance for the plains bison. *Biological Conservation*, **136**, 175–184.
- Fritz KM, Dodds WK, Pontius J (1999) The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. *American Midland Naturalist*, **141**, 253–265.
- Fuhlendorf SD, Engle DM, Kerby JD, Hamilton RG (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, **23**, 588–598.
- Gates C, Ellison K, Gates CC (2010) Numerical and geographic status. In: *American Bison: Status Survey and Conservation Guidelines 2010* (eds Gates CC, Freese CH, Gogan PJP, Kotzman M), pp. 55–62. Switzerland, IUCN, Gland.
- Gelman A, Hill J (2007) *Data Analysis Using Regression And Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge; New York.
- Hamilton RG (2007) Restoring heterogeneity on the Tallgrass Prairie Preserve: applying the fire-grazing interaction model. *Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems*, pp. 163–169. Tallahassee, Florida, USA.
- Hansen PJ (2004) Physiological and cellular adaptations of zebu cattle to thermal stress. *Animal reproduction science*, **82–83**, 349–360.
- Hanson JD, Baker BB, Bourdon RM (1993) Comparison of the effects of different climate change scenarios on rangeland livestock production. *Agricultural Systems*, **41**, 487–502.
- Hartnett DC, Steuter AA, Hickman KR (1997) Comparative ecology of native and introduced ungulates. *Ecology and Conservation of Great Plains Vertebrates*, pp. 72–101. Springer, New York.
- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.
- Hornaday WT (1889) *The Extinction Of The American Bison, With A Sketch Of Its Discovery And Life History*. Washington, Smithsonian Institution.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge; New York.
- Joseph P, Suman SP, Li S, Beach CM, Steinke L, Fontaine M (2010) Characterization of bison (*Bison bison*) myoglobin. *Meat Science*, **84**, 71–78.
- Kauffman JB, Krueger WC, Vavra M (1983) Effects of late season cattle grazing on riparian plant communities. *Journal of Range Management*, **36**, 685–691.
- Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) The keystone role of bison in North American tallgrass prairie. *BioScience*, **49**, 39–50.
- Lohmann D, Tietjen B, Blaum N, Joubert DF, Jeltsch F (2012) Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing. *Journal of Applied Ecology*, **49**, 814–823.
- Loza HJ, Grant WE, Stuth JW, Forbes TDA (1992) Physiologically based landscape use model for large herbivores. *Ecological Modelling*, **61**, 227–252.
- Manning R (1995) *Grassland: The History, Biology, Politics, And Promise Of The American Prairie*. Viking, New York.
- McPherson RA, Fiebrich CA, Crawford KC *et al.* (2007) Statewide monitoring of the mesoscale environment: a technical update on the Oklahoma Mesonet. *Journal of Atmospheric and Oceanic Technology*, **24**, 301–321.
- Montana Legislature (2011) Clarify regulation of bison SB 207. 62nd Legislature.
- National Agricultural Statistics Service (2012) *Meat Animals Production, Disposition, And Income 2011 Summary*. NASS, USDA.
- National Park Service (2009) *Tallgrass Prairie National Preserve, Kansas, Bison Management Plan, Environmental Assessment*. United States Department of Interior, National Park Service.
- Pell AN (1997) Manure and microbes: public and animal health problem? *Journal of Dairy Science*, **80**, 2673–2681.
- Potter BA, Gerlach SC, Gates CC (2010) History of Bison in North America. In: *American Bison: Status Survey and Conservation Guidelines 2010* (eds Gates CC, Freese CH, Gogan PJP, Kotzman M), pp. 5–12. Switzerland, IUCN, Gland.
- R Development Core Team (2012) *R: A Language And Environment For Statistical Computing*. Austria, R Foundation for Statistical Computing, Vienna.
- Reynolds H, Gates C, Glaholt R (2003) Bison. *Wild Mammals Of North America: Biology, Management, And Conservation*, pp. 1009–1060. Maryland, Johns Hopkins University Press, Baltimore.
- Rook AJ, Dumont B, Isselstein J, Osoro K, WallisDeVries MF, Parente G, Mills J (2004) Matching type of livestock to desired biodiversity outcomes in pastures - a review. *Biological Conservation*, **119**, 137–150.
- Samson FB, Knopf FL (1994) Prairie conservation in North America. *BioScience*, **44**, 418–421.
- Sanderson EW, Redford KH, Weber B *et al.* (2008) The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. *Conservation Biology*, **22**, 252–266.
- Seton ET (1927) *Lives Of Game Animals*, 4 volumes. Doubleday, Doran & Co., Garden City, New York.
- Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB (2002) Grassland responses to global environmental changes suppressed by elevated CO₂. *Science*, **298**, 1987–1990.
- Shaw MR, Pendleton L, Cameron DR *et al.* (2011) The impact of climate change on California's ecosystem services. *Climatic Change*, **109**, 465–484.
- Signer C, Ruf T, Arnold W (2011) Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. *Functional Ecology*, **25**, 537–547.
- Smith MS (1988) *Modeling: Three Approaches To Predicting How Herbivore Impact Is Distributed In Rangelands*. New Mexico Agricultural Experiment Station Research, Report.. 628.
- Sprinkle JE, Holloway JW, Warrington BG, Ellist WC, Stuth JW, Forbes TD, Greene LW (2000) Digesta kinetics, energy intake, grazing behavior, and body temperature of grazing beef cattle differing in adaptation to heat. *Journal of Animal Science*, **78**, 1608–1624.
- Stuth JW (1991) Foraging behavior. In: *Grazing Management: An Ecological Perspective* (eds Heitschmidt RK, Stuth JW), pp.65–83. Timber Press, Portland, Or.
- Trimble SW, Mendel AC (1995) The cow as a geomorphic agent - a critical review. *Geomorphology*, **13**, 233–253.
- Wan S, Luo Y, Wallace LL (2002) Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology*, **8**, 754–768.