



# BISON AS KEYSTONE HERBIVORES ON THE GREAT PLAINS: Can cattle serve as proxy for evolutionary grazing patterns?



By Samuel D. Fuhlendorf, Brady W. Allred  
and Robert G. Hamilton





**ABS WORKING PAPER NO. 4  
NOVEMBER 2010**

# **BISON AS KEYSTONE HERBIVORES ON THE GREAT PLAINS: CAN CATTLE SERVE AS PROXY FOR EVOLUTIONARY GRAZING PATTERNS?**

**By Samuel D. Fuhlendorf, Brady W. Allred, and Robert G. Hamilton**

Samuel D. Fuhlendorf  
Natural Resource Ecology & Management  
Oklahoma State University  
008C Ag. Hall  
Stillwater, OK 74078 USA  
[sam.fuhlendorf@okstate.edu](mailto:sam.fuhlendorf@okstate.edu)



American Bison Society Working Paper Series ISSN 2153-3008 (Print)  
American Bison Society Working Paper Series ISSN 2153-3016 (Online)

Copies of American Bison Society Working Papers are available for download from <http://www.americanbisonsocietyonline.org/Resources/ABSWorkingPapers>.

All photos © Stephen Winter

*Copyright:* The contents of this paper are solely the property of the authors, and cannot be reproduced without the permission of the authors.

The Wildlife Conservation Society saves wildlife and wild places worldwide. We do so through science, global conservation, education and the management of the world's largest system of urban wildlife parks, led by the flagship Bronx Zoo. Together these activities change attitudes towards nature and help people imagine wildlife and humans living in harmony. WCS is committed to this mission because it is essential to the integrity of life on Earth.

Over the past century, WCS has grown and diversified to include four zoos, an aquarium, over 100 field conservation projects, local and international education programs, and a wildlife health program. To amplify this diverse conservation knowledge, the WCS Institute was established as an internal "think-tank" to coordinate WCS expertise for specific conservation opportunities and to analyze conservation and academic trends that provide opportunities to further conservation effectiveness. The Institute disseminates WCS's conservation work via papers and workshops, adding value to WCS's discoveries and experience by sharing them with partner organizations, policy-makers, and the public. Each year, the Institute identifies a set of emerging issues that potentially challenge WCS's mission and holds both internal and external meetings on the subjects to produce reports and guidelines for the institution.

The American Bison Society (ABS), managed by the WCS Institute, works with a broad range of stakeholders to build the scientific and social bases for the long term ecological restoration of bison in North America. ABS and partners address information gaps by initiating research and papers on issues that require further exploration or synthesis, or where policy and guidelines are needed.

The ABS Working Paper Series, produced through the WCS Institute, is designed to share information with the conservation and bison stakeholder communities in a timely fashion. Working Papers address issues that are of immediate importance to helping restore bison and either offer new data or analyses, or offer new methods, approaches, or perspectives on rapidly evolving issues. The findings, interpretations, and conclusions expressed in this Paper are those of the author and do not necessarily reflect the views of the American Bison Society or the Wildlife Conservation Society.

# TABLE OF CONTENTS

<b>Introduction</b>	<b>1</b>
<b>Bison and cattle: a natural history</b>	<b>4</b>
<b>The role of grazing in the development of the Great Plains</b>	<b>6</b>
<b>How different are they? Evaluations of bison and cattle based on literature</b>	<b>8</b>
<b>The Tallgrass Prairie Preserve: a model for experimental design</b>	<b>12</b>
<b><i>Methods</i></b>	<b>13</b>
<b><i>Results</i></b>	<b>15</b>
<b><i>Conclusions from this study</i></b>	<b>16</b>
<b>How critical are bison to grassland conservation?</b>	<b>18</b>
<b>Conclusions for future comparisons between bison and cattle</b>	<b>20</b>
<b>References</b>	<b>22</b>
<b>Tables</b>	<b>27</b>
<b>Figures</b>	<b>29</b>
<b>ABS Working Paper Series</b>	<b>37</b>
<b>WCS Working Paper Series</b>	<b>37</b>
<b>WCS Canada Conservation Reports</b>	<b>40</b>

**Bison as Keystone Herbivores on the Great Plains: Can Cattle Serve as Proxy for Evolutionary Grazing Patterns?**

Samuel D. Fuhlendorf<sup>1\*</sup>, Brady W. Allred<sup>1</sup>, Robert G. Hamilton<sup>2</sup>

<sup>1</sup>Natural Resource Ecology & Management, Oklahoma State University, Stillwater, OK, USA

<sup>2</sup>The Nature Conservancy Tallgrass Prairie Preserve, Pawhuska, OK, USA

\*Corresponding author. Natural Resource Ecology & Management, Oklahoma State University, 008C Ag. Hall, Stillwater, OK 74078, USA. Tel.: +1-405-744-5437; fax.: +1-405-744-3530 email: sam.fuhlendorf@okstate.edu

---

# INTRODUCTION

The role of herbivores in grassland ecosystems is an important topic debated by ecologists and ecosystem managers for over a century. The Great Plains of North America are central to this discussion as most of the flora and fauna evolved with significant impact from large herbivores and other periodic disturbances. Until their near extirpation in the late 1800s, American bison (*Bison bison*) was the keystone herbivore on unfragmented landscapes, having shared them 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 in most places been replaced by fragmented agricultural lands where domestic cattle are the dominant grazers on prairie remnants and the few remaining large natural landscapes. Through the 1900s, restoration and conservation of bison was pursued by private citizens, conservation organizations, and government agencies. Since then, additional groups have become interested in the conservation and management of grassland ecosystems, with principle goals of restoring critical processes and functions.

Grazing is critical to restoration of grasslands. Too often, the effects of grazing within an ecosystem are viewed in isolation, removing all complexity and variation besides that caused by grazing (e.g., plant community response in homogeneous, grazed and ungrazed plots). Such work has resulted in tremendous amounts of knowledge gained, enhancing the management of grazed ecosystems. Grazing, however, is much more complex than traditional, small-scale experimental designs can replicate (Fuhlendorf et al. 2009); it is a dynamic process that interacts with complex landscapes to form disturbance patterns that are critical to biodiversity. Because of this, the effects of grazing can be confounded by many factors, including those associated with animals and the environment (**Figure 1**). While comparisons of cattle and bison may be interesting to conservation biologists, the species of animal alone is not the only determinant of grazing effects. Age, sex, number, and social organization all contribute to altering their behavior and ecological influences (e.g., one herbivore does not have the same effect as 100 herbivores). In addition to variation in the structure of the grazer community, environmental factors (e.g., predators, disturbances, climate, resources) will also alter the effects of

---

grazing (e.g., an arid system will respond differently than a mesic system). Central to both the grazing animals and the environment is the managerial objectives and actions at the social and ecological interface.

When discussing grazing effects or grazing behavior, a traditional reductionist approach is to focus on one factor without considering the complexity of other factors and their interactions. In the Great Plains of North America, for example, ecologists, conservationists, and land managers have studied and debated the effects of grazing by bison and domestic cattle (*Bos taurus*), often without including other relevant factors (Plumb and Dodd 1993; Hartnett et al. 1997; Steuter and Hidinger 1999). Studies that compare these two species are challenging because they could easily be confounded, as it would be expected that bison and cattle herds differ in number, age, sex, access to resources, or presence of disturbances unless they are evaluated in a carefully controlled experiment. The trade-off between recognizing the importance of complexity in nature and the desire to conduct well controlled experimental studies has been a persistent challenge for conservation ecologists.



Many previous studies of grazing were conducted through the discipline of rangeland management which was largely developed in response to the vast over-utilization of rangelands from the livestock industry in the early 1900s (Holechek et al. 2011). While the approach of this research has agronomic roots, many of the principles provide useful predictions of the effects of grazing on complex landscapes. Principles of grazing management on rangelands focus largely on managerial aspects on maintaining proper distribution of grazing pressure in time and space and selecting the appropriate animal for the environment (usually in reference to domestic livestock for commodity production purposes). The most important principle from this body of research is the consideration of the number of animals relative to the amount of forage available (stocking rate or grazing intensity). A well known meta-analysis (Milchunas and Lauenroth 1993) and range management textbooks (Holechek et al. 2011) suggest that the primary effects of grazing on vegetation and soils are largely dependent on grazing intensity, which is a function of animal numbers and biomass production. Animal numbers and distribution in space and time can be due to management or ecosystem dynamics, and are often primary drivers of animal behavior and the influence of grazing (**Figure 1**). The few comparisons of bison and cattle that hold grazing intensity and distribution constant have concluded that many of the differences between the species may actually be attributed to differences in the approach to their management (Towne et al. 2005).

The effects of species grazing behavior (bison and cattle) are difficult to separate from common managerial differences (e.g., grazing intensity) that may occur under various land management objectives. Questions focused on

---

the differences between species are very different from questions focused on how they are typically managed, yet, often these two questions lead to confounded conclusions. Cattle herds are typically associated with ranches that are managed for optimum commodity production. Operations commonly rely on herds where animals are separated for most of the year based on sex and age (e.g., cow-calf, stocker steers). Additionally, cattle ranches often employ general animal husbandry practices (e.g., supplemental feeding and minerals) and land management practices that homogenize the landscape. These landscapes are often heavily cross-fenced with extensive water development and potentially managed to increase the dominance of a few key forage species. Bison are often managed as production herds or as conservation-focused herds on preserves or refuges. Production/commodity systems with bison are often managed in a way similar to cattle systems, allowing for effective comparison in that simplified environment. Preserves focused on conservation may manage their bison herds as wildlife or livestock, but typically much less intensively than production systems. Cattle are rarely, if ever, managed as wildlife or with a conservation focus; consequently, many comparisons between bison and cattle may inevitably be confounded by differing land management approaches or alternatively, focus on comparing two similar production systems (i.e., small pastures intensively managed).

Very few studies comparing bison and cattle attempt to capture similar animal and environmental factors (Plumb and Dodd 1993; Towne et al. 2005). Even in these limited “head to head” studies, bison are most often placed in a cattle production environment. We argue that if there are important ecological differences between cattle and bison, they would best be studied on large and complex landscapes. It is unlikely, however, that one could ever compare these two species under all combinations of environmental and animal factors. Nonetheless, we suggest that using the conceptual framework presented in **Figure 1** will allow for a better and more accurate comparison of the ecological grazing effects between bison and cattle. From this framework, it is important to view studies in the context of other factors that could influence grazing behavior and effects on grasslands so that differences between species are not confounded by differences in management.

---

# BISON AND CATTLE: A NATURAL HISTORY

It is important to examine the life histories of bison and cattle to understand the selection pressures responsible for our current populations. Prior to European settlement of North America, there were over 10 million American bison (Freese et al. 2007). Ancestors of our modern bison arrived on the North American continent during the middle Pliocene (300,000 to 130,000 years ago) and reached their maximum distribution 100,000 to 12,000 years ago (Potter et al. 2010). Modern bison (*B. bison*), including plains and wood bison, ranged freely across most of North America for over 10,000 years. Early explorers, settlers, and hunters reported large herds and estimates that ranged from 10 to 100 million (Shaw 1995; Potter et al. 2010). Regardless of the broad range in population estimates, it is generally agreed that bison were the dominant herbivore throughout most of North America for thousands of years, capable of living in environments that ranged from the desert southwest to the boreal forest.

There is considerable debate over the taxonomy and nomenclature of American bison (Boyd et al. 2010). The genus name of *Bison* dates back to the early 1800s, but more recently taxonomists have argued that bison are not sufficiently distinct from bovines, resulting in a change to the genus *Bos* (Boyd et al. 2010). Similarities between bison and cattle and the adaptation of bison to rangelands of North America have led to many attempts to cross the two species and/or domesticate bison. Recent literature reviews have suggested that bison may be a more efficient range animal in North America because of their ability to digest low quality forage (Hawley et al. 1981; Plumb and Dodd 1993), defend against predators (Carbyn et al. 1993), survive harsh winter conditions, and have minimal calving difficulties (Haigh et al. 2001). Sections below will indicate that many of these claims have not been supported by experimental comparisons between bison and cattle, and while testable, would be very difficult to evaluate under all potential situations.

Domestication of cattle from aurochs occurred about 10,000 years ago, in the near east from *Bos taurus* and in Asia from *Bos indicus* (Loftus et al. 1994; Gotherstrom et al. 2005). Over the next 5,000 years, cattle dispersed over many

---

areas, becoming important economically, for both food and labor. There are currently over 250 recognized breeds of cattle and potentially hundreds more that are not recognized. There are as many as 80 breeds available for production in the United States. Each breed has distinctive characteristics that are used to develop herds that are best suited for certain objectives and environments. Most of the breeding efforts have been largely associated with the meat industry, although some are more focused on reproductive efficiency and relationships with specific environments. Selection traits include environmental adaptability, age-size relationships, milk production, rate and efficiency of weight gain, and meat quality. Recent studies have demonstrated that breeds of cattle will use rough terrain differently (VanWagoner et al. 2006) and have been suggested as a viable tool to obtain specific grazing effects (Rook et al. 2004). There is also concern over the loss of indigenous cattle breeds (Solti et al. 1999), with studies suggesting that these breeds are less selective and can be used to maintain biodiversity (Dumont et al. 2007). This is an indication that fairly subtle differences in animals may be important but also that there is substantial differences across breeds of cattle that make a comparison with bison difficult.

The evolutionary history of bison and cattle provides important insight on expected differences in behavior and ecosystem effects of the two species. In general, bison evolved from natural selection as a dominant grazer on complex landscapes, while cattle were selected for agricultural production and labor over thousands of years. It is a reasonable prediction that when these species are managed as wild populations on complex landscapes, there could certainly be differences in how they handle threats and limited resources. It is less reasonable to predict differences in ecological effects when both species are compared within an agricultural setting. Additionally, as cattle have been selectively bred for agriculture all over the world, it is not sufficient to discuss bison comparisons with the generic species *cattle*. Cattle can represent European beef breeds such as Hereford or Angus or the breeds more adapted to extreme environments such as Highlanders, Brahman, or Texas Longhorns. Many local breeds of cattle have lived as wild animals over the past century or more and are capable of surviving in complex landscapes with minimal support from human societies (e.g., Hernandez et al. 1999). We suggest that comparisons should be specific in their objectives, comparing bison to specific breeds of cattle or to local herds that are typical for production agriculture.

---

# THE ROLE OF GRAZING IN THE DEVELOPMENT OF THE GREAT PLAINS

In North America, herbivores were a strong driving factor in the establishment and maintenance of grasslands, but over at least the past 10,000–15,000 years, the effects of herbivore activity were largely controlled by an interaction between fire and grazing. This section summarizes the fire-grazing interaction, hereafter termed *pyric herbivory* (i.e., herbivory shaped by fire), that was recently published in *Conservation Biology* (Fuhlendorf et al. 2009). We have argued that grazing and fire may best be viewed as a single disturbance (pyric herbivory) that created a shifting mosaic of disturbance patches across a complex landscape (e.g., Fuhlendorf and Engle 2001; Salvatori et al. 2001; Hassan et al. 2008). This results from grazing animals freely selecting between burned and unburned portions of the landscape, and the dependence of fire occurrence on the removal of fuel by herbivores (e.g., Norton-Griffiths 1979; Fuhlendorf and Engle 2001). The mosaic pattern that results from this interaction of fire and grazing is critical for grassland biodiversity and suggest that these two disturbance processes are coupled.

Bison, cattle, and many other herbivores across rangelands throughout the world respond to patterns of fire (e.g., Fuhlendorf and Engle 2001; Archibald and Bond 2004; Archibald et al. 2005), preferentially selecting nutritious and available forages that grow in recently burned areas and avoiding unburned areas (Duvall and Whitaker 1964; Fuhlendorf and Engle 2004). Grazing patterns are also strongly influenced by the movement patterns of large carnivores (Ripple and Beschta 2006) and it is likely that when predators, fire, and grazing are considered collectively, grazing patterns would be very complex. Even if grazing pressure is moderate across the landscape, local areas that have burned recently may be heavily grazed, whereas other areas that did not burn over the past few years may receive little or no grazing pressure. This pattern of fire also interacts with complex landscape and rainfall patterns that drive grazing and biodiversity patterns. Recently burned areas that attract heavy grazing pressure would not have an accumulation of fine fuel, reducing

---

the likelihood and intensity of future fires completing the fire-grazing interaction (Fuhlendorf et al. 2008).

Pyric herbivory, with both cattle and bison, provides greater botanical and vegetation structural diversity across the landscape than when the same amount of grazing and fire is uniformly applied, as is done on most rangelands that are commonly managed for livestock production (Fuhlendorf and Engle 2004). Analyses of grassland birds, insects, and small mammals suggest that some species within these groups depend on recent disturbances, whereas other species depend on habitat without disturbance (**Figure 2**) (Fuhlendorf et al. 2006; Engle et al. 2008). For example, Henslow's Sparrows (*Ammodramus henslowii*) require dense litter and tall vegetation. Under pyric herbivory, this regionally rare bird was dominant in patches that had not been burned or grazed in two or more years. Upland Sandpipers (*Bartramia longicauda*) and Killdeer (*Charadrius vociferous*) were abundant in patches at the other end of the disturbance gradient (i.e., in areas with minimal litter and abundant bare ground) owing to recent application of fire and resulting focal grazing. Landscapes with variable patterns of interacting disturbances are critical for conservation of the full suite of grassland obligate species. Other studies illustrate that, in addition to species conservation, critical ecological processes (e.g., nutrient and water cycling) are also highly dependent upon this shifting mosaic of disturbance patterns (see Fuhlendorf et al. 2009). These studies of pyric herbivory exemplify the importance of heterogeneity and shifting mosaics associated with the interaction of fire and grazing.



Historically, fires and grazing with multiple herbivore species interacted across vast regions with climate patterns and predators to create heterogeneity at multiple scales. Recreating these patterns and scale with historical accuracy is both overwhelming and impractical, but it does not diminish the importance of restoring these disturbance processes as an interactive part of the landscape and of allowing the patterns that are critical for biodiversity to emerge from the interaction. The restoration of ecosystems involves critical processes such as fire and grazing, just as much as it involves restoring native plants and animals. Scaling limitations, societal issues, the existence of alternative disturbances on the landscape (e.g., cultivation), and lack of understanding of fire and grazing processes limit the widespread restoration of these processes. Understanding evolutionary patterns of grazing is critical to understanding the evolutionary context of bison in the Great Plains. It is clear that simplifying or ignoring fire grazing interactions leads to limited and incomplete understanding of this keystone process.



---

# HOW DIFFERENT ARE THEY? EVALUATIONS OF BISON AND CATTLE BASED ON LITERATURE

Examining the differences and similarities between bison and cattle is difficult due to the many confounding environmental factors (**Figure 1**). A title search within Web of Science (conducted December 10, 2009) revealed 87 papers with the terms “bison” and “cattle.” Of those, only nine contained an ecological focus, with several limited to conjecture and review. Two papers in particular attempted to control for confounding effects (Plumb and Dodd 1993; Towne et al. 2005). While such a literature search is not perfect, it is an adequate sample of information available for bison and cattle comparisons and reflects what is currently in the published literature. Due to the challenges of comparing these species, there are no peer-reviewed studies that directly compare bison and cattle on large complex landscapes (>300 ha). Because of this, dogma and casual opinions are often intermixed with experimental or observational conclusions (Fritz and Dodds 1999; Steuter and Hidingier 1999).

Some of the most commonly reported differences between bison and cattle are their use of riparian areas, plant selection/diet compositions, digestion, thermoregulation, energetic/metabolic rates, and foraging behavior (Hartnett et al. 1997). We used literature searches and citation indices to find studies that directly compared bison and cattle within these specific topics. While there are many studies of bison and cattle performed separately (e.g., one study examining bison diet in location A, one study examining cattle diet in location B), such studies are not well suited for a direct species comparison due to the potential variation of resources at different locations. These studies are useful in developing testable hypotheses but not useful for developing strong conclusions. We therefore limited our results to comparisons that were directly head to head, either observational or experimental.

---

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 and Dodds 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 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. This is the only study we found that directly compares use of water or riparian areas between bison and cattle and the lack of experimental control is likely one reason that it was not published in a peer-reviewed journal.

In contrast, it has been shown by direct comparison that cattle have greater plant selectivity and a lower composition of graminoids (grasses) in their diet than bison (Peden et al. 1974; Kautz and van Dyne 1978; Schwartz and Ellis 1981; van Vuren 1984; Plumb and Dodd 1993). Direct comparisons of digestibility found differences (Peden et al. 1974; Hawley et al. 1981; Schwartz and Ellis 1981) as well as no differences (Schaefer et al. 1978; Plumb and Dodd 1993) between bison and cattle (including Hereford and Scottish Highland breeds). Digestion retention time was also greater in bison than cattle (Schaefer et al. 1978). Additionally, many ruminal fermentation characteristics do not differ between bison and Hereford steers; bison, however, do average greater ruminal ammonia nitrogen concentrations, greater ciliate protozoal counts, and greater cell volume than cattle (Towne et al. 1988). While these differences are interesting they are not very informative about the actual influences of bison or their behavior in complex landscapes.

It is also commonly reported that bison may be able to cope with cold or heat stress better than cattle (Hartnett et al. 1997; Steuter and Hidinger 1999). Christopherson et al. (1979) examined metabolic rates of bison and Hereford calves in environments at 10, 0, and -30°C. Metabolic rate decreased with temperature in bison, while in cattle, metabolic rates were dependent upon temperature and age. Decreased metabolic rates were attributed to reduced activity of bison at lower temperatures. Heart rates and respiratory frequencies were not affected by temperature. Additionally, bison are estimated to have greater insulation and lower critical temperatures than Hereford and Scottish Highland breeds of cattle (Christopherson et al. 1978). It is likely that any differences in thermal regulation would be highly dependent upon the breed of cattle used in the comparison. Bison historically existed across a wide range of thermal conditions (Mexico to Alaska), while unique cattle breeds may only be dominant in local areas where they are best adapted (i.e., Scottish Highlanders may respond differently than Texas Longhorns).

There are many mechanisms that influence grazing behavior of large herbivores. Grazing patterns can be determined by abiotic (e.g., topography, temperature, distance to water, etc.) and biotic (e.g., forage quality/quantity,

---

predation, etc.) factors (Bailey et al. 1996). Abiotic factors primarily influence grazing behavior at larger scales, while biotic factors play a larger role at smaller scales (Senft et al. 1987). As it is out of the scope of this paper to summarize all mechanisms that influence grazing patterns of large herbivores, we refer the reader to the general literature for such information (e.g., Bailey et al. 1996). As with the use of riparian areas, direct comparisons of foraging ecology or behavior between bison and cattle have been minimal. Plumb and Dodd (1993) found differences among summer feeding behaviors of bison and cattle in South Dakota. In general, bison spent less time feeding with shorter grazing bouts than cattle, but had greater number of bouts per day. Aside from this study and the one non-peer reviewed study of the use of riparian areas, we found no other studies that directly compared bison and cattle behavior.

While differences and similarities between bison and cattle may exist, a more prevalent topic may be the ecological effects of the two species. The effects of species differences, however, are hard to separate from the two different management styles that often accompany them (Towne et al. 2005). In a direct comparison, where animals were managed similarly in small pastures, plant communities were 85% similar after 10 years of grazing (Towne et al. 2005). In the same experimental units, arbuscular mycorrhizal fungal root colonization and pasture reflectance characteristics did not differ between bison and cattle grazing (Villarreal et al. 2006). Forbs in tallgrass prairie are also affected differently by bison and cattle. Responses, however, are complex and dependent upon plant species, animal species, plant life history stages, and fire regimes (Damhoureyeh and Hartnett 1997). Studies that attempt to control all variation, except for the species differences, are difficult because ecosystems are variable and include interactive relationships. Studies have demonstrated that similar biodiversity effects can be achieved by cattle and bison as long as both species are allowed to interact with heterogeneous fire patterns (Fuhlendorf et al. 2006, 2009).

In addition to exaggerating differences between bison and cattle, both the scientific and lay literature contains speculation about the unique role of bison, much of which may be logical but is not supported by data. These speculations are likely due to the iconic nature and cultural history of bison. An example of this is the persistence of wallows in grassland ecosystems. While it is clear that bison, as well as other herbivores, wallow (McHugh 1958; Cabon-Raczynska et al. 1987; Momongan and Walde 1988), it is commonly believed that many circular depressions in prairies are relict wallows, and wallows have been cited as a long lasting ecological effect of bison that is important to biodiversity (Barkley and Smith 1934; Polley and Collins 1984; Collins and Barber 1985; Hartnett et al. 1997; Knapp et al. 1999). Critical study of relict wallows, however, simply revealed that they are unique landscape elements of pedogenic origin, which have also been described in many ecosystems throughout the world where bison do not occur (Coppedge et al. 1999). While grassland depressions, including bison wallows, are important, casual claims of their origin should be viewed skeptically.

---

There is limited peer-reviewed data to compare bison and cattle, both in their life history differences and ecological effects. Furthermore, nearly all of the bison and cattle comparisons do not attempt to account for both animal and environmental factors that can contribute to species differences (e.g., **Figure 1**). Doing such essentially simplifies differences and similarities between the two species. Reductionist science that eliminates all other variation except species may find differences but would be incapable of describing the relevance of such differences, particularly in complex landscapes. We located only two peer-reviewed studies that attempt to control for confounding effects (Plumb and Dodd 1993; Towne et al. 2005). Can we safely justify the differences between bison and cattle, particularly those regarding ecological effects, with such limited data? We recognize that comparisons of these species under all conditions or factors would be extremely difficult. We suggest an approach, however, for comparing bison and cattle that considers the context of comparisons based on our framework (**Figure 1**). Below we describe the design, results, and limitations of a current study within the Great Plains that incorporates factors found within complex landscapes. We present this study as an example of how bison and cattle can be more appropriately compared.



---

# 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. Topography is lightly variable, with rocky outcrops of both sandstone and limestone. It is one of a few large management areas in the United States that allows for fire grazing interactions (pyric herbivory) across large and complex landscapes (Fuhlendorf et al. 2009). The preserve is also unique as portions of the area are delegated to bison and cattle (mixed breeds) under similar conditions/management plans, allowing for a more effective bison/cattle comparison.

Within the property, there is one large bison unit (9532 ha) and seven smaller cattle units (430-980 ha) (**Figure 3**). Animals are free to roam within each unit, as only perimeter fences separate units. There is minimal handling of both bison and cattle and neither species receives supplemental feed, with the exception of salt and trace minerals to both species. Water is provided by natural streams and ponds constructed before ownership by The Nature Conservancy; water distribution is approximately equal for the two management areas (**Figure 3**). Bison are maintained in their respective unit all year, while cattle are only present April through September (similar to surrounding local management practice). 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 a way that fire and grazing are allowed to interact [i.e., fire influences grazing and vice versa; see Hamilton (2007) and Fuhlendorf et al. (2009)]. In the bison unit, approximately one third of the unit is burned each year (~3000 ha). Burns are variable in size (100-700 ha) and are located randomly across the landscape (no fixed burn units). The seasonality of fire varies with 80% of burns occur-

---

ring in the dormant season (40% in late spring, 40% in winter) and 20% occurring in the growing season (summer). Fire is managed similarly in the cattle units; burn units, however, are contiguous and vary in size relative to total unit size (e.g., burn area may be one half to one fourth of total unit size). Bison and cattle units are shifting mosaics with fire occurring in discrete portions of the landscape; animals are allowed to select between recently burned areas and those with greater time since fire (**Figure 4**).

In this study, bison and cattle units are managed similarly, but with important differences. The objective of bison management is to restore and maintain a large tract of functioning tallgrass prairie, while the objective of cattle management is to develop management tools that can be transferred to local working ranches. The differing objectives result in slightly different management scenarios. First, stocking rates are a little different because cattle units are designed to more closely represent preferred stocking by local landowners. Second, age, sex, and social organization are more complex with bison than the simplistic yearlings of cattle pastures (also chosen to represent local landowner preferences). Finally, the bison unit is one of the largest single pastures with free roaming bison within the Great Plains, while cattle units are large but more typical of local landowner size.

## Methods

Two of the most common reported differences between bison and cattle are their use of water/riparian areas and their ability to tolerate temperature stresses. To specifically examine these behaviors, we collared seven bison and seven cattle individuals (one per unit) at the Tallgrass Prairie Preserve with global positioning systems (GPS; GPS3300L and GPS7000MU, Lotek Wireless, Inc.) and recorded their location information at various frequencies (every 10 minutes – 1 hour). GPS collars also recorded temperature (underneath the neck of the animal) with every location. While this is not the same as internal animal temperature, it does provide a measure of temperature regulation. From these data we can evaluate whether animals are selecting different thermal conditions. All GPS location data were imported into a spatially enabled database (PostgreSQL/PostGIS). Bison data were reduced to match that of cattle (April – September). We mapped treatment unit perimeters, fire histories, and water sources with handheld GPS units (GeoXT, Trimble Navigation Ltd), aerial photographs, and United States Geological Survey 7.5 minute topographic maps.

We used Ivlev electivity indices (Ivlev 1961; Jacobs 1974) to evaluate the use of water/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 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 (20 and 40 m) using a t-test. Differences in temperatures would suggest that animals are selecting for cooler or warmer habitats. As cattle are only present during the growing season (late spring and summer), temperature regulation differences between bison and cattle would be most prominent during the heat of the day (1100-1600 hours). We calculated the mean and standard deviation of recorded temperature of each collared animal between 1100 and 1600 hours for a random selection of 15 days; we also included the days in which recorded temperature was lowest (May 17, 2009; 7°C) and highest (July 26, 2009; 52°C). The standard deviation of recorded temperature will show the variation in temperature regulation. Mean and standard deviation of temperature between bison and cattle were compared for each selected day using a t-test.

For a more detailed examination of the influence of environmental factors on the grazing behavior of bison and cattle, we estimated resource selection functions (used/available design; Boyce et al. 2002; Manly et al. 2002) using mixed-effect logistic regression models. To depict available habitat, we created five random locations for each observed location. Slope and aspect for all locations were calculated from digital elevation models for the area (United States Geological Survey). We transformed aspect data by simple trigonometric functions; two variables were created, northing = cosine(aspect) and easting = sin(aspect). We also calculated the amount of time since fire, distance to water, and distance to patch edge for all locations. Furthermore, we classified each location as herbaceous or woody vegetation using a GeoEye-1 satellite image acquired September 20, 2009. We examined variables for collinearity and found none. As we measured most environmental factors at a scale finer than that of time since fire (i.e., environmental factors are nested within fire patches), individual animals were nested within fire patch as a random intercept (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; Klop et al. 2007), we included interaction terms for this variable with all others individually (i.e., time since fire and distance to water, time since fire and 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 performed all analyses in R (R Development Core Team 2008) 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 ( $p < 0.01$ ; **Figure 5**). Cattle had a greater preference for ponds (**Figure 5A**), while bison avoided streams (**Figure 5B**). When water sources were combined (ponds and streams), bison had a small avoidance of water, while cattle had a greater preference (**Figure 5C**). These data show the predicted difference between bison and cattle in their use of water and riparian areas, when managed in a similar manner for a single year. Cattle had a stronger preference for water but the percent locations near water were still relatively minor (<20%) so it is difficult to determine the ecological significance of this difference. Neither species were strongly attracted to water sources, likely because this landscape has extensive watering with minimal areas far from water. On landscapes with less water it would likely change the distribution of these species, and based on these results bison may be more suited for such conditions.

Mean recorded temperature between 1100 and 1600 hours varied among the 17 days sampled (**Figure 6A**). No differences, however, were detected between bison and cattle with regards to thermal regulation ( $p > 0.05$ ) within randomly chosen days. Standard deviation of recorded temperature between 1100 and 1600 hours also varied, but did not show any differences between bison and cattle ( $p > 0.05$ ; **Figure 6B**). When managed in a similar manner, and on large landscapes, temperature regulation of the two species appears to be comparable during the growing season. However, these measurements are based on temperature sensors in the GPS collars and may not be the best approach for measuring temperature regulation.

Bison and cattle strongly preferred recently burned patches (**Figure 7**). Mean percentages of GPS locations in areas with six months or less since fire did not vary between bison and cattle (**Figure 8**;  $p > 0.05$ ). With bison, 71% of locations were found in recently burned areas, while cattle averaged 61%. The amount of areas burned within six months was approximately 25% (relative to total unit size) for both bison and cattle units.

Estimation of resource selection functions for both bison and cattle allowed for a more detailed examination of environmental factors that influence grazing behavior. Of models examined, the combination of interaction terms of time since fire with all variables (less northness and eastness) appeared to have the best fit for both bison and cattle (**Table 1**). Resource selection functions for bison revealed that time since fire had the strongest influence in determining site selection. Furthermore, bison tended to avoid steep slopes and wooded areas, while distance to water and patch edge did not limit selection (**Table 2**). Interactions of time since fire with other environmental factors indicate that

---

the influence of fire is complex but the dominant feature in driving selection patterns. The influence of time since fire will increase as slope, distance to patch edge, or woody vegetation increases; conversely, the influence of time since fire will decrease as distance to water increases. This decrease, however, is likely minimal, due to the strong influence of fire in general.

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 and patch edge, while bison did not (**Table 2**). As with bison, interactions of time since fire with other variables indicate the complexity of fire within the system. As slope, 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. One reason for a strong preference of woody cover for cattle is that woody vegetation was more limited in cattle pastures (<1-5%) than bison (6.5%). However, bison actually avoided woody cover when the entire summer was considered collectively.

## **Conclusions from this study**

Bison and cattle had similarities in many aspects of their behavior. Both species had a high preference for recently burned areas, corroborating separate studies of the individual species (Coppedge et al. 1998; Fuhlendorf and Engle 2004). Also, we were unable to detect any differences between recorded temperatures associated with these animals, suggesting that small scale studies of thermal regulation may not scale up to influence animal behavior. It is likely that thermal differences may alter animal performance, but a detailed examination was out of the scope of this study. 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 both bison and cattle. Selection for sites closer to water was also greater in cattle than bison; in fact, bison appeared to maximize their distance to water. In this particular landscape, bison spend less time near water than cattle. These differences occurred in a well watered landscape and may be even more important in landscapes with greater distance between ponds and streams.

The design of this study effectively permits comparisons between bison and cattle, both in examining differences between the two species (results presented here) and their ecological effects (e.g., plant response, water quality, etc.; no results presented). Our design incorporates more of the variability found in complex landscapes than most previous studies (e.g., Towne et al. 2005), allowing both species to interact and respond to variation and complexity. Admittedly, it is very difficult to account for the many factors that may create differences or similarities between bison and cattle, and our

---

study is not without limitations. While year round stocking rates are similar between bison and cattle units, cattle densities were higher but they were only present during the growing season (April – September), while bison densities were lower but remained throughout the year. A yearlong, cow-calf cattle operation would permit even better comparisons between the two species, allowing additional evaluation of winter thermal environments. Additionally, though treatment units were large and incorporated landscape complexity including fire, they were not of equal size. We could expect that animal behavior would be sensitive to the area available. There were differences in the social organizations of cattle and bison herds which may also confound any differences found.

This study compared bison to European cattle breeds (Angus and Hereford) that are typical for agrarian objectives on tallgrass prairies. There are other breeds of cattle that are likely to respond differently. Likewise, limited differences in the thermal environment may become more pronounced when greater climatic variation is included. This study provides minimal contribution to evaluation of differences in small pastures or in larger landscapes with less water available. We show, however, that both of these herbivores have a strong preference for recently burned areas. This would suggest that evaluation of differences between these species may be irrelevant to pre-settlement landscapes unless fire is incorporated. With regard to restoration and conservation, restoring the fire grazing interaction is perhaps more important than the specific species of large herbivore. In terms of regional conservation, cattle and bison are not identical but both species may be used to provide heterogeneity through pyric herbivory that is critical to biodiversity (Fuhlendorf et al. 2006, 2009). However, on large landscapes with less water development (currently rare within the Great Plains), bison may be better suited.



---

# HOW CRITICAL ARE BISON TO GRASSLAND CONSERVATION?

In the Great Plains of North America, bison are reintroduced for primarily two reasons. The first is to conserve bison as they were a dominant herbivore in the last 10,000 years (Anderson 2006). By the end of the 19<sup>th</sup> century, the species was nearly extinct with only a few hundred individuals remaining. 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 some areas. Indeed, conservation of this species is a unique success story that continues as more herds are developed each year. The second reason for reintroduction has been the focus of restoring the keystone impact that bison had within the Great Plains that may be important for the conservation of many species and entire ecosystems. Conservation groups and government agencies reintroduce bison to both small remnant preserves and large complex landscapes to restore historical disturbance patterns. In most cases, this is done without considering the many other factors that influence grazing effects or behavior (**Figure 1**). In some cases, complex and intensive grazing systems have been established to manage bison behavior and promote uniform utilization, counter to biodiversity objectives (Jackson et al. 2010). While the first reason for reintroduction can be accomplished by building wild bison herds throughout the Great Plains, the second objective is not possible without the consideration and reintroduction of other environmental factors.

With regard to the reasons for reintroducing bison, we developed a model to conceptualize the conservation value of different options (**Figure 9**). We define conservation value as the contribution to regional conservation efforts, including promotion of native plants, animals, and ecosystem processes. The simple 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 important factors such as species, diversity, origin, and social organization of the grazer community. Historically, bison were a keystone species within the landscape, but their impacts were depen-

---

dent upon how they interacted with the environment, disturbances, other small and large herbivores, carnivores, as well as their own complex social order. Increasing the complexity of grazers (more species diversity, more wild herbivores, etc.) increases the conservation value of a particular ecosystem. The simple replacement of domestic cattle with bison may contribute to bison conservation, but will have minimal impact on the broader conservation value of restored ecosystems. In an extreme example, replacing cattle with bison in a small, intensively managed, and simplified livestock production scenario has minimal conservation value. Restoring other important processes such as fire, predation, migrations, etc., are as critical as restoring the dominant grazer if the intent of restoration is focused on biodiversity.

Conservation value of a refuge or land holding is also highly dependent on the environmental complexity of the area, including landscape diversity, fire regime, and size. The majority of these factors are independent of the species of herbivore (bison or cattle), although in some situations there may be an interaction. Similar to the complexity of grazers, the simple replacement of cattle with bison without a restoration of fire regimes will not result in evolutionary disturbance patterns that are necessary for conservation and biodiversity. The interaction of herbivore and environmental complexity was vital to the evolution of the Great Plains and other ecosystems and therefore is also critical to restoration of these systems. In the study described above, time since fire was a primary variable influencing bison and cattle grazing behavior. Suppression of fire and the simplification of fire-grazing interactions have led to a simplified understanding of grazing on complex landscapes (Fuhlendorf et al. 2009). On lands with minimal environmental complexity, the differences between bison and cattle are minimal (Towne et al. 2005) and will contribute little to overall conservation value.

Grasslands are endangered worldwide (Hoekstra et al. 2005). While propositions to restore or conserve natural landscapes regularly focus on native herbivores (e.g., Sanderson et al. 2008), it is often overlooked that many natural landscapes are privately owned and used for domestic livestock production (Samson and Knopf 1994). It is important to state that low and high conservation values can be achieved with both bison and cattle. Though bison are the iconic symbol of the Great Plains of North America and it is critical that we conserve the species, there is not enough data to confidently state that landscapes with bison are inherently better for overall biodiversity than landscapes with cattle without considering the many other factors that interact with grazing. Both species can be mismanaged and cause degradation of habitat for other species as well as ecological processes, such as nutrient and water cycling. Indeed, in some cases it may be more practical, relevant, and convenient to use cattle for conservation purposes and ecological studies, because cattle currently make up the vast majority of herbivores in North American grasslands. As more studies effectively compare grazing effects and behavior between bison and cattle, incorporating environmental factors and variation, additional reliable conclusions will be made that may change conservation efforts or directions.

---

# CONCLUSIONS FOR FUTURE COMPARISONS BETWEEN BISON AND CATTLE

We argue that for future studies and comparisons between bison and cattle (as well as other species) it is critical that we qualify our conclusions with discussions of the abiotic, biotic, and managerial environments 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 tendency to over-infer. From a conservation perspective it is important that



we describe and understand effects of bison grazing along with the interaction of grazing with other disturbances. It is also important to understand the ecological effects of grazing cattle for livestock production and explore approaches to alter these patterns to more effectively achieve some conservation objectives. It is not productive to look for differences and similarities between these species to justify certain management objectives or agendas. Conservation of bison is important as they are an iconic species and a keystone herbivore that interacted with fire and other disturbances to create a shifting mosaic across

much of North America. However, from a broad context, conservation efforts should recognize that cattle will likely continue to be a dominant feature on the Great Plains, and that some conservation objectives can be met with cattle (e.g., restoring critical ecosystem processes such as fire grazing interactions). The conservation community should not allow research on cattle to be relegated strictly to a livestock production based enterprise.

---

The mystique and lore from historical accounts of millions of bison roaming freely across a vast landscape is fodder for many conservationists to direct their passions toward saving some of the most imperiled species and ecosystems in the world. It can be argued that this kind of passion is critical for radical changes that may be required for many aspects of conservation. A value laden approach to scientific questions, however, can also lead to the promotion of dogma that may not have been critically evaluated. There is a paucity of scientific evidence supporting many commonly described differences associated with bison and cattle comparisons in the peer-reviewed scientific literature. It is also important to note that there is even less evidence rejecting these differences. Evaluation of research literature demonstrates that there are actually many more studies demonstrating ecological differences in breeds of cattle than there are evaluating differences between bison and cattle, yet bison/cattle comparisons have become a dominant feature in grassland dogma. We argue that it is critical for us to understand grazing behavior and effects of both of these species in complex and simple landscapes relevant to conservation. There is an important place for species comparisons within this framework, but this is just one aspect of grassland conservation and it may not be the most important for future conservation of biodiversity.

---

# REFERENCES

- Anderson, R. C. 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., and W. J. Bond. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire* 13:377-385.
- Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. Shaping the landscape: fire-grazer interactions in an African savanna. *Ecological Applications* 15:96-109.
- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49:386-400.
- Barkley, F. A., and C. C. Smith. 1934. A preliminary study of buffalo wallows in the vicinity of Norman, Oklahoma. *Proceedings of the Oklahoma Academy of Science* 14:47-49.
- Bates, D., and M. Maechler. 2010. lme4: Linear mixed-effects models using Eigen and S4 classes. R package version 0.999375-33. <http://CRAN.R-project.org/package=lme4>
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281-300.
- Boyd, D. P., G. A. Wilson, and C. C. Gates. 2010. Taxonomy and Nomenclature. Pages 13-18 in C. C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors. *American Bison: Status Survey and Conservation Guidelines 2010*. IUCN, Gland, Switzerland.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- Cabon-Raczynska, K., M. Krasinska, Z. Krasinski, and J. Wojcik. 1987. Rhythm of daily activity and behavior of european bison in the Bialowieza forest in the period without snow cover. *Acta Theriologica* 32:335-372.
- Carbyn, L. N., S. Oosenbrug, and D. Anions. 1993. *Wolves, Bison, and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park*. Canadian Circumpolar Institute, Edmonton.
- Christopherson, R. J., R. J. Hudson, and M. K. Christophersen. 1979. Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Canadian Journal of Animal Science* 59:611-617.
- Christopherson, R. J., R. J. Hudson, and R. J. Richmond. 1978. Comparative winter bioenergetics of american bison, yak, scottish highland, and hereford calves. *Acta Theriologica* 23:49-54.
- Collins, S. L., and S. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64:87-94.

- 
- Coppedge, B. R., S. D. Fuhlendorf, D. M. Engle, B. J. Carter, and J. H. Shaw. 1999. Grassland soil depressions: Relict bison wallows or inherent landscape heterogeneity? *American Midland Naturalist* 142:382-392.
- Damhoureyeh, S. A., and D. C. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. *American Journal of Botany* 84:1719-1728.
- Dumont, B., A. J. Rook, C. Coran, and K. Röver. 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 2. Diet selection. *Grass & Forage Science* 62:159-171.
- Duvall, V. L., and L. B. Whitaker. 1964. Rotation burning: a forage management system of longleaf pine-bluestem ranges. *Journal of Range Management* 17:322-326.
- Engle, D. M., S. D. Fuhlendorf, A. Roper, and D. M. Leslie Jr. 2008. Invertebrate community response to a shifting mosaic of habitat. *Rangeland Ecology and Management*: 61:55-62.
- Freese, C. H., K. E. Aune, D. P. Boyd, J. N. Derr, S. C. Forrest, C. C. Gates, P. J. P. Goyan, S. M. Grassel, N. D. Halbert, K. Kunkel, and K. H. Redford. 2007. Second chance for the plains bison. *Biological Conservation* 136:175-184.
- Fritz, K. M., and W. K. Dodds. 1999. The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. *American Midland Naturalist* 141:253-265.
- Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* 41:604-614.
- Fuhlendorf, S. D., D. Engle, J. D. Kerby, and R. G. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23:588-598.
- Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16:1706-1716.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge; New York.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887-898.
- Götherström, A., C. Anderung, L. Hellborg, R. Elburg, C. Smith, D. G. Bradley, and H. Ellegren. 2005. Cattle domestication in the Near East was followed by hybridization with aurochs bulls in Europe. *Proceedings of the Royal Society B: Biological Sciences* 272:2345-2351.
- Hamilton, R. G. 2007. Restoring heterogeneity on the Tallgrass Prairie Preserve: applying the fire-grazing interaction model. Pages 163-169 in *Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems*. Tallahassee, Florida, USA.
- Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduced ungulates. Pages 72-101 in *Ecology and conservation of Great Plains vertebrates*. Springer, New York.
- Hassan, S. N., G. M. Rusch, H. Hytteborn, C. Skarpe, and I. Kikula. 2008. Effects of fire on sward structure and grazing in western Serengeti, Tanzania. *African Journal of Ecology* 46:174-185.
- Hawley, A. W. L., D. G. Peden, H. W. Reynolds, and W. R. Stricklin. 1981. Bison and cattle digestion of forages from the slave river lowlands, Northwest Territories, Canada. *Journal of Range Management* 34:126-130.
- Hernandez, L., H. Barral, G. Halffter, and S. S. Colon. 1999. A note on the behavior of feral cattle in the Chihuahuan Desert of Mexico. *Applied Animal Behaviour Science* 63:259-267.

- 
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8:23-29.
- Holechek, J.L., R.D. Piper, and C.H. Herbel. 2011. *Range Management: Principles and Practices*. Sixth Edition. Prentice Hall.
- Ivlev, V. S. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven.
- Jackson, R. D., L. K. Paine, and J. E. Woodis. 2010. Persistence of Native C4 Grasses under High-Intensity, Short-Duration Summer Bison Grazing in the Eastern Tallgrass Prairie. *Restoration Ecology* 18:65-73.
- Jacobs, J. 1974. Quantitative measurement of food selection: a modification of forage ratio and Ivlev's electivity index. *Oecologia* 14:413-417.
- Kautz, J., and G. van Dyne. 1978. Comparative analyses of diets of bison, cattle, sheep, and pronghorn antelope on shortgrass prairie in northern Colorado, USA. in *First International Rangeland Congress*. Society for Range Management, Denver, CO.
- Klop, E., J. van Goethem, and H. H. de Iongh. 2007. Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research* 34:77-83.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience* 49:39-50.
- Loftus, R. T., D. E. MacHugh, D. G. Bradley, P. M. Sharp, and P. Cunningham. 1994. Evidence for two independent domestications of cattle. *Proceedings of the National Academy of Sciences of the United States of America* 91:2757-2761.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erickson. 2002. *Resource selection by animals: Statistical design and analysis for field studies*. Kluwer Academic Publishers, Dordrecht ; Boston.
- Manning, R. 1995. *Grassland : the history, biology, politics, and promise of the American prairie*. Viking, New York.
- McHugh, T. 1958. Social behavior of the American buffalo (*Bison bison bison*). *Zoologica* 43:1-54.
- D. G. Milchunas, W. K. Lauenroth. 1993. Quantitative Effects of Grazing on Vegetation and Soils Over a Global Range of Environments. *Ecological Monographs*: 63: 327-366.
- Momongan, V. G., and G. Walde. (n.d.). Behavior of the endangered tamaraw (*Bubalus mindorensis*). *Asia Life Science* 2:241-250.
- National Park Service. 2009. Tallgrass Prairie National Preserve, Kansas, bison management plan, environmental assessment. National Park Service, United States Department of Interior.
- Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Pages 378-392 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, Illinois.
- Peden, D. G., G. M. Vandyne, R. W. Rice, and R. M. Hansen. 1974. Trophic ecology of *Bison bison* on shortgrass plains. *Journal of Applied Ecology* 11:489-497.
- Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecological Applications* 3:631-643.
- Polley, H. W., and S. L. Collins. 1984. Relationships of vegetation and environment in buffalo wallows. *American Midland Naturalist* 112:178-186.
- Potter, B. A., S. C. Gerlach, and C. C. Gates. 2010. History of Bison in North America. Pages 5-12 in C. C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors. *American Bison: Status Survey and Conservation Guidelines 2010*. IUCN, Gland, Switzerland.

- 
- R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Revolution Computing. 2009. foreach: Foreach looping construct for R. R package version 1.3.0. <http://CRAN.R-project.org/package=foreach>.
- Reynolds, H., C. Gates, and R. Glaholt. 2003. Bison. Pages 1009-1060 in *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, Md.
- Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* **230**:96-106.
- Rook, A. J., B. Dumont, J. Isselstein, K. Osoro, M. F. WallisDeVries, G. Parente, and J. Mills. 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. *Biological Conservation* **119**:137-150.
- Samson, F. B., and F. L. Knopf. 1994. Prairie conservation in North America. *Bioscience* **44**:418-421.
- Salvatori, R., F. Eguny, A. K. Skidmore, J. de Leeuw, and H. A. M. van Gils. 2001. The effects of fire and grazing pressure on vegetation cover and small mammal populations in the Maasai Mara National Reserve. *African Journal of Ecology* **39**:200-204.
- Sanderson, E. W., K. H. Redford, B. Weber, K. Aune, D. Baldes, J. Berger, D. Carter, C. Curtin, J. Derr, S. Dobrott, E. Fearn, C. Fleener, S. Forrest, C. Gerlach, C. Gates, J. E. Gross, P. Gogan, S. Grassel, J. A. Hilty, M. Jensen, K. Kunkel, D. Lammers, R. List, K. Minkowski, T. Olson, C. Pague, P. B. Robertson, and B. Stephenson. 2008. The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. *Conservation Biology* **22**:252-266.
- Schaefer, A. L., B. A. Young, and A. M. Chimwano. 1978. Ration digestion and retention times of digesta in domestic cattle (*Bos taurus*), american bison (*Bison bison*), and tibetan yak (*Bos grunniens*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **56**:2355-2358.
- Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology* **18**:343-353.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* **37**:789-799.
- Shaw, J. H. 1995. How Many Bison Originally Populated Western Rangelands? *Rangelands* **17**:148-150.
- Solti, L., E. Crichton, N. Loskutoff, and S. Cseh. 2000. Economical and ecological importance of indigenous livestock and the application of assisted reproduction to their preservation. *Theriogenology* **53**:149-162.
- Steuter, A. A., and Hidinger. 1999. Comparative ecology of bison and cattle on mixed-grass prairie. *Great Plains Research* **9**:329-342.
- Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications* **15**:1550-1559.
- Towne, G., T. G. Nagaraja, R. C. Cochran, D. L. Harmon, C. E. Owensby, and D. W. Kaufman. 1988. Comparisons of ruminal fermentation characteristics and microbial populations in bison and cattle. *Applied and Environmental Microbiology* **54**:2510-2514.
- VanWagoner, H. C., D. W. Bailey, D. D. Kress, D. C. Anderson, and K. C. Davis. 2006. Differences among beef sire breeds and relationships between terrain use and performance when daughters graze foothill rangelands as cows. *Applied Animal Behaviour Science* **97**:105-121.
- Villarreal, M., R. C. Cochran, D. E. Johnson, E. G. Towne, G. W. T. Wilson, D. C. Hartnett, and D. G. Goodin. 2006. The use of pasture reflectance characteristics and arbuscular mycorrhizal root colonization to predict pasture characteristics of tallgrass prairie grazed by cattle and bison. *Grass and Forage Science* **61**:32-41.

---

Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *American Midland Naturalist* 129:10-18.

van Vuren, D. 1982. Comparative ecology of bison and cattle in the Henry Mountains, Utah. Pages 449-457 in *Wildlife-Livestock Relationships Symposium* held at Coeur d'Alene, Idaho, April 20-22, 1981. Forest, Wildlife & Range Experiment Station, University of Idaho.

van Vuren, D. 1984. Summer diets of bison and cattle in southern Utah. *Journal of Range Management* 37:260-261.

Weston, S. 2009. doMPI: Foreach parallel adaptor for the Rmpi package. R package version 0.1-4. <http://CRAN.R-project.org/package=doMPI>.

Yu, H. 2010. Rmpi: Interface (wrapper) to MPI (Message-Passing Interface). R package version 0.5-8. <http://CRAN.R-project.org/package=Rmpi>.

# TABLES

**Table 1.** Varying models of resource selection for both bison and cattle at The Tallgrass Prairie Preserve, OK, USA. The difference in Akaike information criterion ( $\Delta$ AIC), log likelihood (LL), and the number of parameters (K) are shown. Model parameters include distance to water (*water*), distance to patch edge (*edge*), slope (*slope*), Northing (*north*), Easting (*east*; both derivatives of aspect), wooded area (*wood*), and time since fire (*tsf*). We included individual animals nested within fire patches as a random intercept in the mixed-effect logistic regression. We included main effects in all models with interaction terms.

	K	$\Delta$ AIC	LL
<b>Bison</b>			
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i> + <i>tsf</i> × <i>north</i> + <i>tsf</i> × <i>east</i>	16	3.75	-98234.51
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i> + <i>north</i> + <i>east</i>	14	0.00	-98234.63
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	6.56	-98239.92
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>wood</i>	12	66.33	-98270.80
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	493.77	-98484.52
<i>tsf</i> × <i>water</i> + <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	227.64	-98351.46
<i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	29.30	-98252.29
<i>tsf</i> + <i>water</i> + <i>slope</i> + <i>edge</i> + <i>wood</i>	8	855.56	-98668.42
<b>Cattle</b>			
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i> + <i>tsf</i> × <i>north</i> + <i>tsf</i> × <i>east</i>	16	5.14	-106418.90
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i> + <i>north</i> + <i>east</i>	14	0.00	-106413.40
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	1.41	-106414.70
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>wood</i>	12	12.04	-106422.50
<i>tsf</i> × <i>water</i> + <i>tsf</i> × <i>slope</i> + <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	85.89	-106459.40
<i>tsf</i> × <i>water</i> + <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	32.34	-106432.60
<i>water</i> + <i>tsf</i> × <i>slope</i> + <i>tsf</i> × <i>edge</i> + <i>tsf</i> × <i>wood</i>	11	497.62	-106665.20
<i>tsf</i> + <i>water</i> + <i>slope</i> + <i>edge</i> + <i>wood</i>	8	554.15	-106696.50

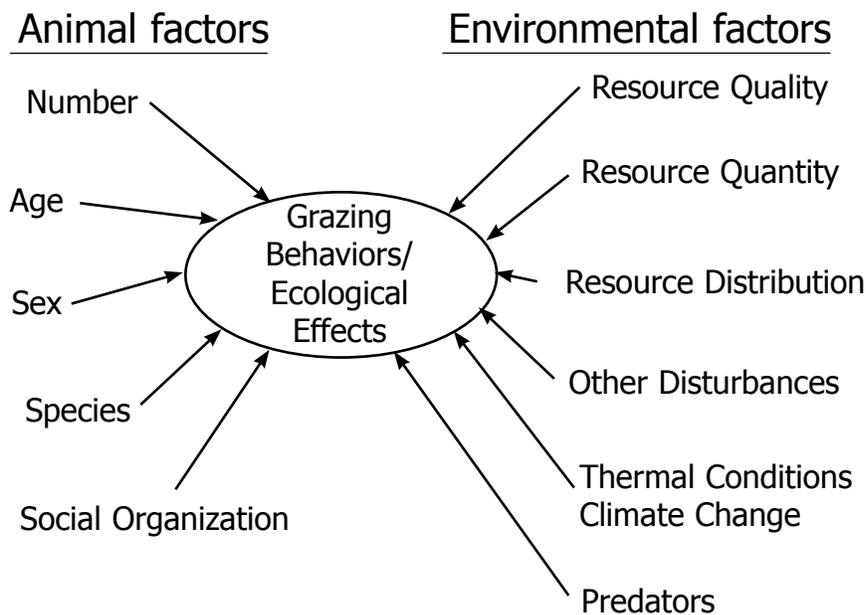
**Table 2.** Estimated resource selection function coefficients of the best model for bison and cattle at The Tallgrass Prairie Preserve, OK, USA. Standardized variables are shown for coefficient comparison.

	<b>Estimate</b>	<b>SE</b>	<b>Z value</b>	<b>P</b>
<b>Bison</b>				
intercept	-1.7148	0.2409	-7.12	<0.01
time since fire	-1.1277	0.0224	-50.26	<0.01
distance to water	0.1188	0.0069	17.17	<0.01
slope	-0.4309	0.0099	-43.19	<0.01
distance to patch edge	0.0252	0.0078	3.20	<0.01
woody vegetation	-0.5201	0.0570	-9.11	<0.01
northness	0.0088	0.0055	1.60	0.10
eastness	-0.0157	0.0055	-2.84	<0.01
time since fire × distance to water	0.0354	0.0070	5.01	<0.01
time since fire × slope	-0.1664	0.0116	-14.27	<0.01
time since fire × distance to patch edge	-0.1901	0.0088	-21.54	<0.01
time since fire × woody vegetation	-0.5031	0.0711	-7.07	<0.01
<b>Cattle</b>				
intercept	-0.1342	0.2694	-0.49	<0.01
time since fire	-0.2624	0.0316	-8.28	<0.01
distance to water	-0.1078	0.0063	-16.99	<0.01
slope	-0.2042	0.0065	-31.04	<0.01
distance to patch edge	-0.1145	0.0065	-17.50	<0.01
woody vegetation	0.7562	0.0382	19.77	<0.01
northness	0.0084	0.0053	1.57	0.11
eastness	-0.0017	0.0053	-0.31	0.74
time since fire × distance to water	-0.1521	0.0069	-21.95	<0.01
time since fire × slope	-0.0416	0.0070	-5.90	<0.01
time since fire × distance to patch edge	-0.0532	0.0057	-9.34	<0.01
time since fire × woody vegetation	0.1528	0.0386	3.95	<0.01

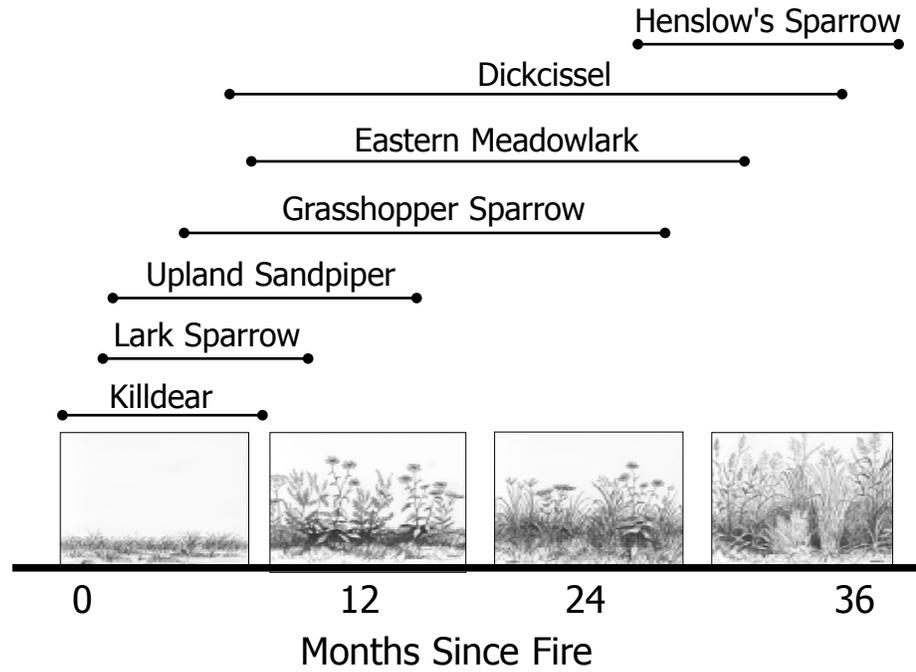
---

# FIGURES

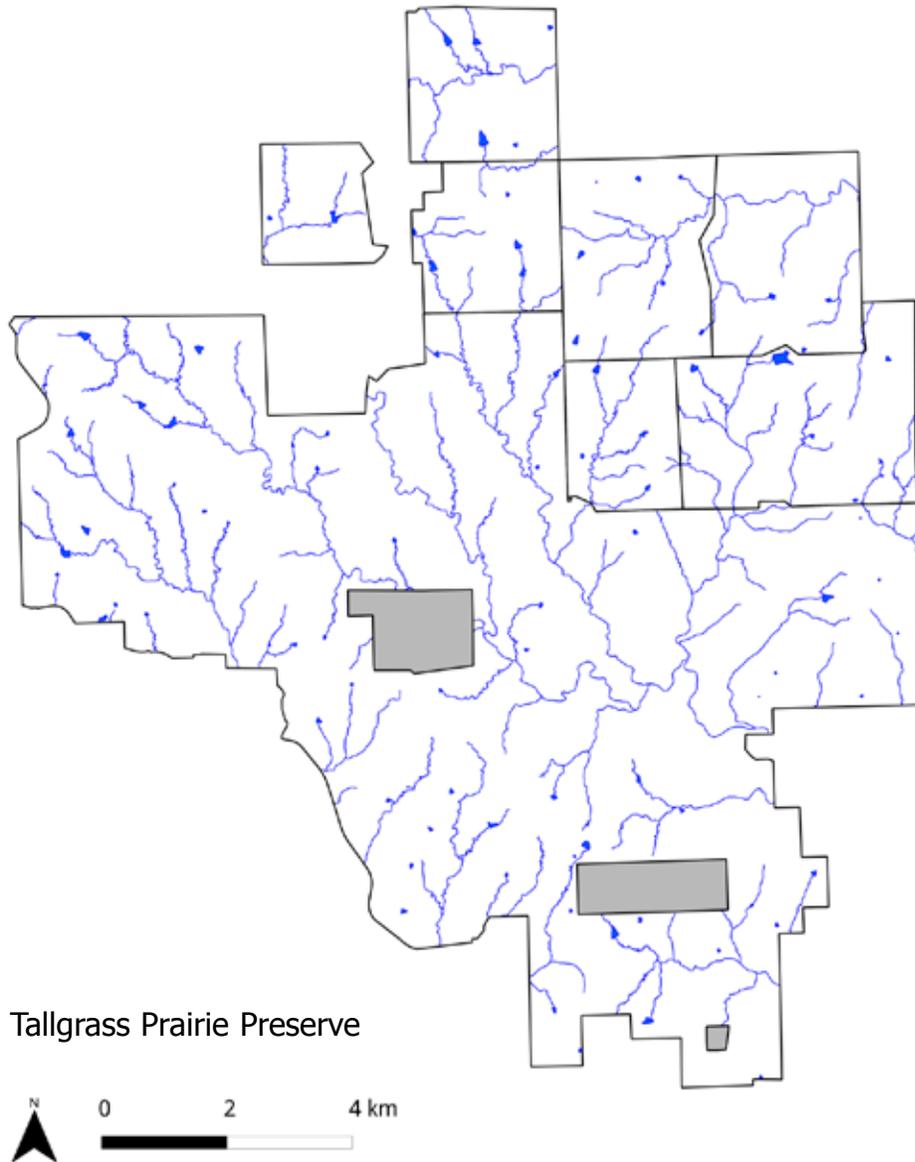
**Figure 1.** Examples of factors that affect grazing behavior and effects within grassland ecosystems. We focus primarily on animal and environmental factors. While species of herbivore is an important factor, it does not act alone in determining grazing effects. The interaction of many animal factors (sex, number, etc.) and environmental factors (resource distribution, disturbance, etc.) determine the effects of grazing.



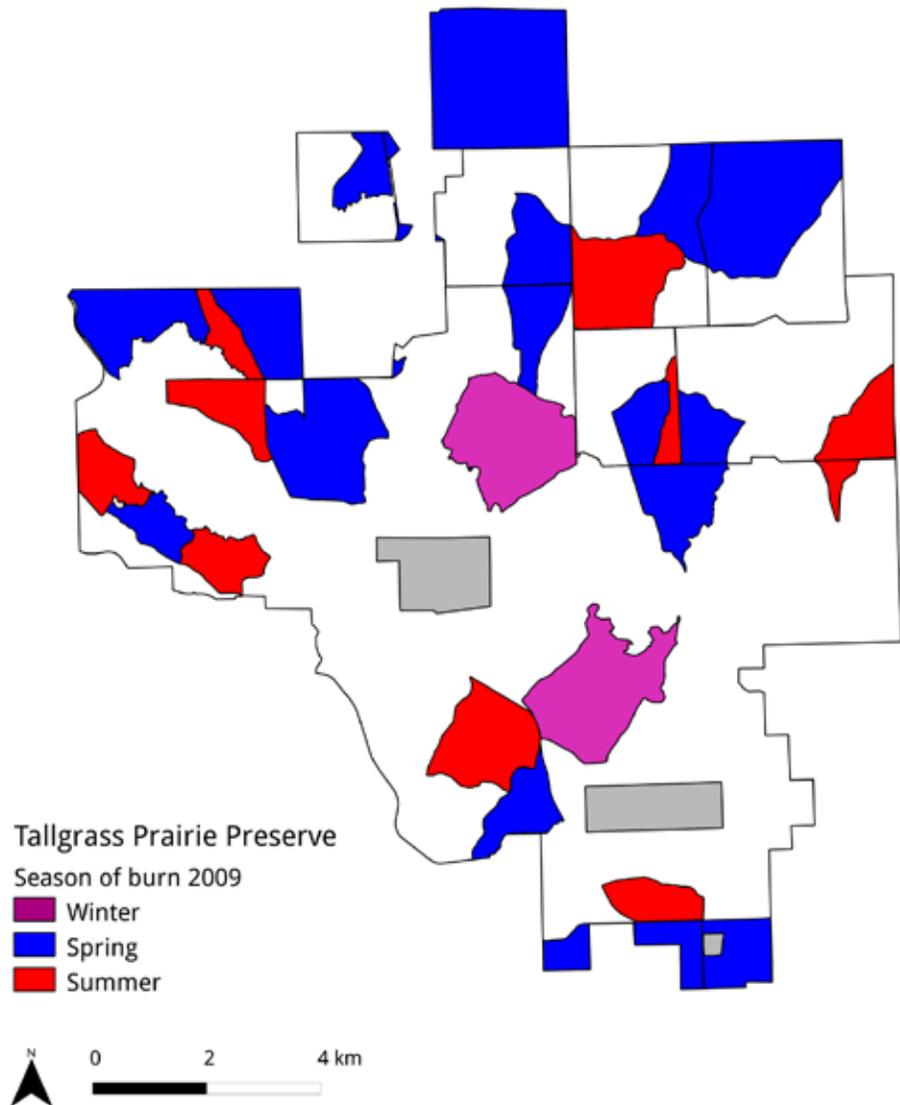
**Figure 2.** Response of grassland birds to time since focal disturbance by fire and grazing at the Tallgrass Prairie Preserve, Oklahoma, from 2001-2003 (Fuhlendorf et al. 2009). Some birds that are native to the area require recently burned patches that are currently heavily grazed while other birds require habitats that are relatively undisturbed for several years (Fuhlendorf et al. 2006). This research emphasizes that 1) the response of rangeland to fire is highly dependent upon the interaction of fire and grazing, and 2) fire management should not be considered in isolation from other environmental factors including grazing.



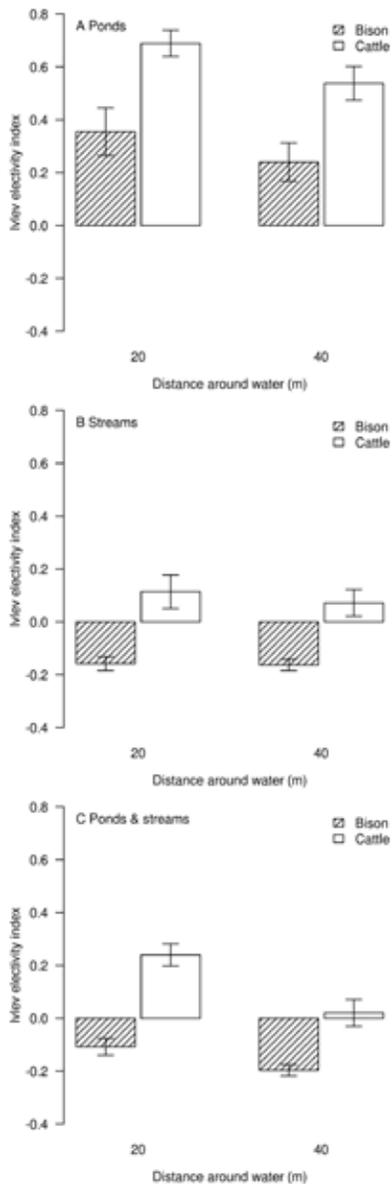
**Figure 3.** Map of bison and cattle units, and water distribution at The Nature Conservancy Tallgrass Prairie Preserve, north of Pawhuska, OK USA. The large southern unit is 9532 ha in size and holds approximately 2500 bison year round. The northern units are 430-980 ha in size and holds yearling cattle steers April-September. Solid black lines represent perimeter fences. Blue lines/areas represent water sources (streams or ponds). Gray areas represent inholdings which bison cannot access.



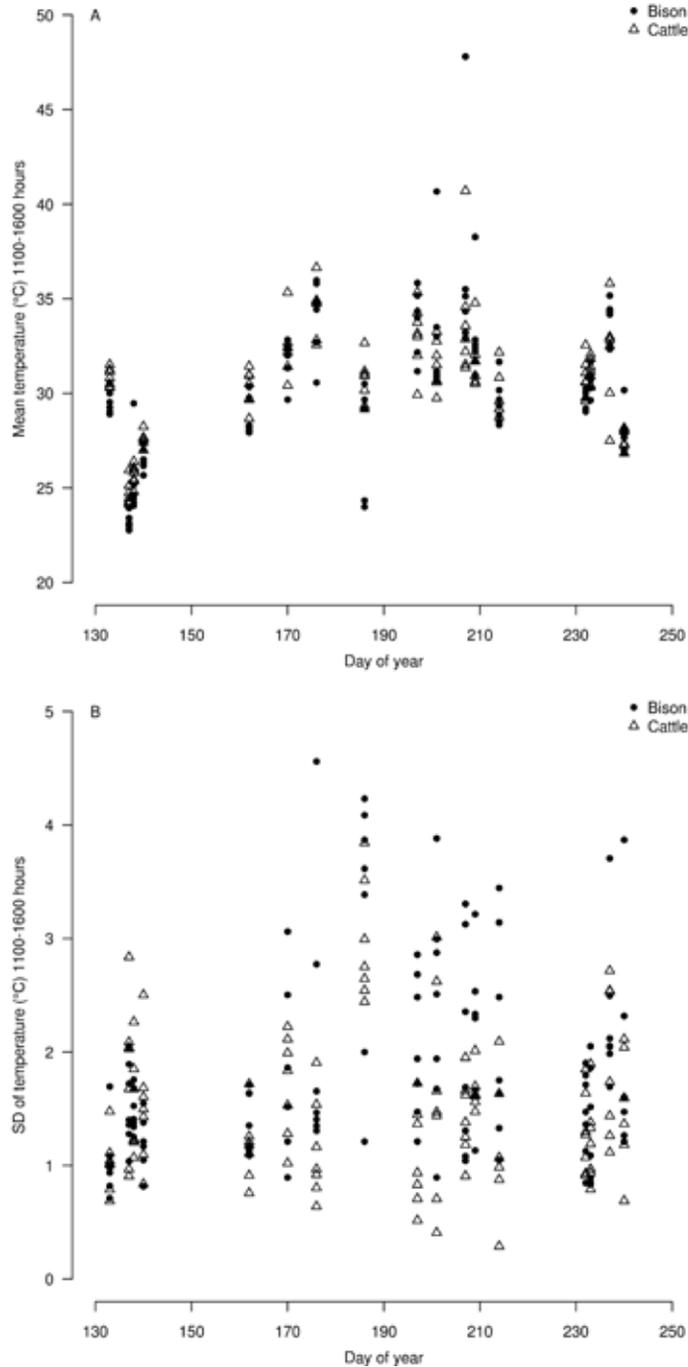
**Figure 4.** Map of prescribed fire in bison and cattle units at The Nature Conservancy Tallgrass Prairie Preserve, north of Pawhuska, OK USA. Differing colors represent season of burn for 2009. Grazing animals have free access to all burns (no internal fences present). Solid black lines represent perimeter fences. Gray areas represent inholdings which bison cannot access. Burn units within the bison unit (large, southernmost unit) are randomly applied each season (i.e. burn unit boundaries are not fixed, but rather dynamic through time); burn units within cattle units are fixed and occur at various frequencies.



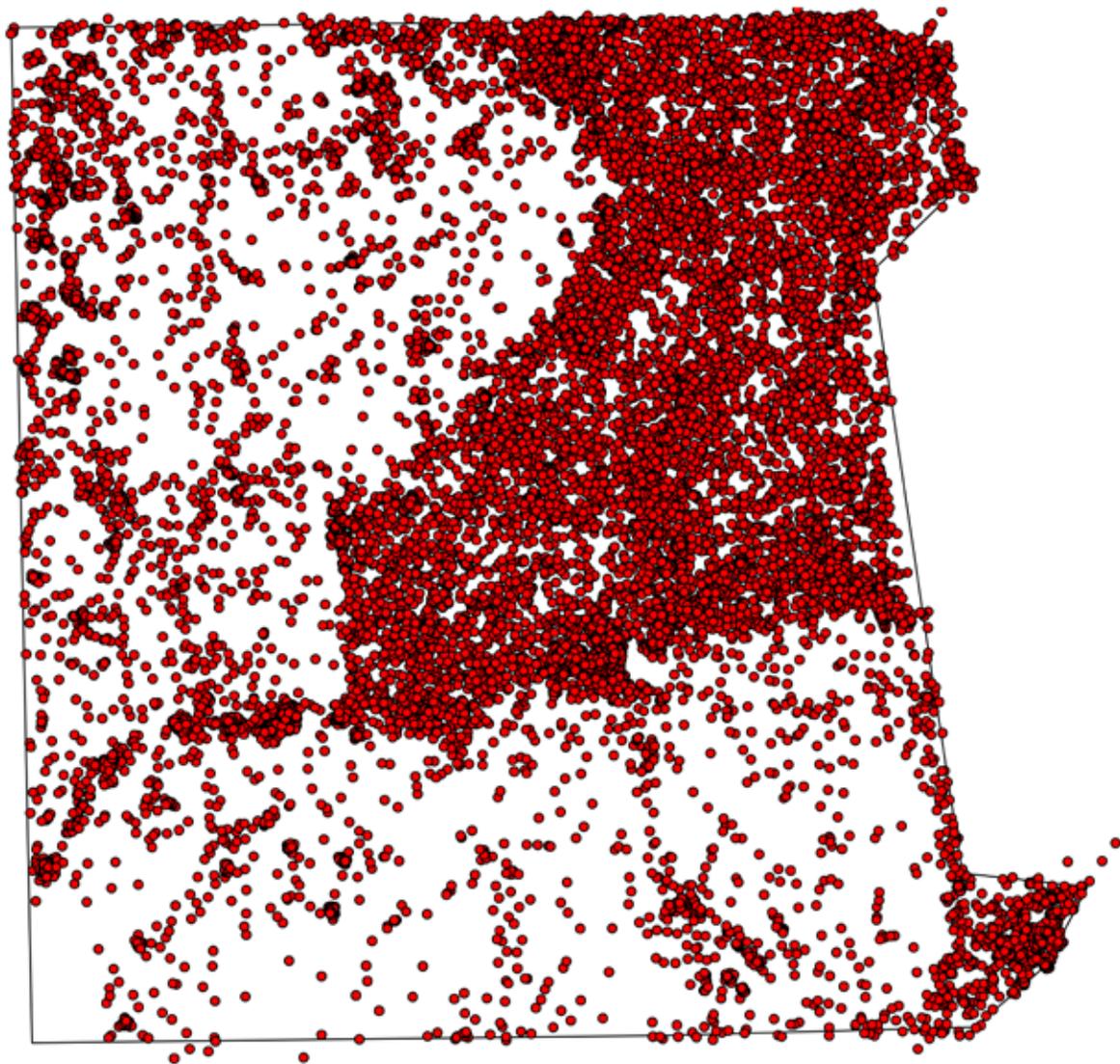
**Figure 5.** Ivlev electivity indices for riparian areas, separated by bison and cattle at the Tallgrass Prairie Preserve. Potential values range from -1 (complete avoidance) to +1 (complete preference). Distance around water indicates the size of buffer placed around riparian areas. A) Ivlev electivity 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 (ponds and streams combined) 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 ( $p < 0.01$ ). Error bars represent one standard deviation.



**Figure 6.** Mean (A) and standard deviation (B) of recorded temperature of bison and cattle at the Tallgrass Prairie Preserve, between 1100-1600 hours for a random selection of 15 days. Temperature regulation of both bison and cattle appeared similar. No significant differences were detected between mean or standard deviation bison and cattle temperatures within the randomly chosen days ( $p>0.05$ ).



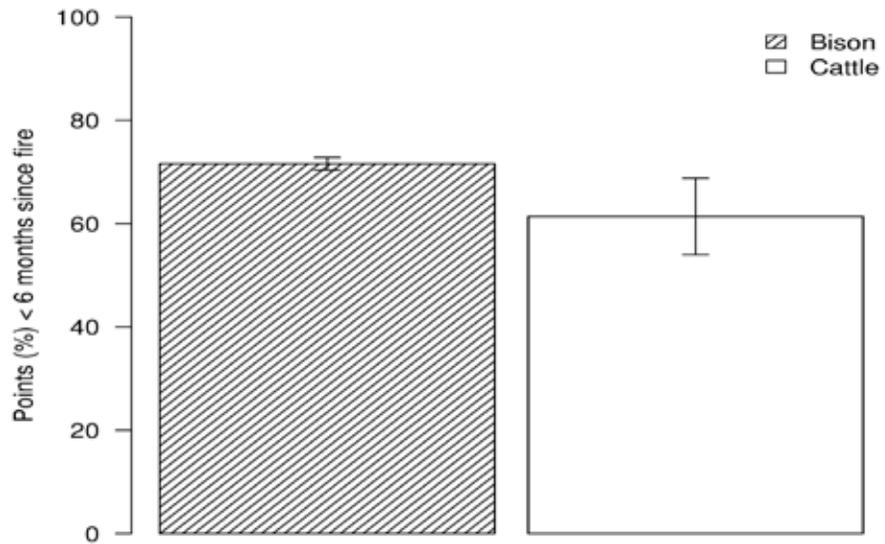
**Figure 7.** Map of recorded location information for one cattle individual at the Tallgrass Prairie Preserve, April – September 2009. Burn units (see Figure 3) can be easily inferred from cattle location information.



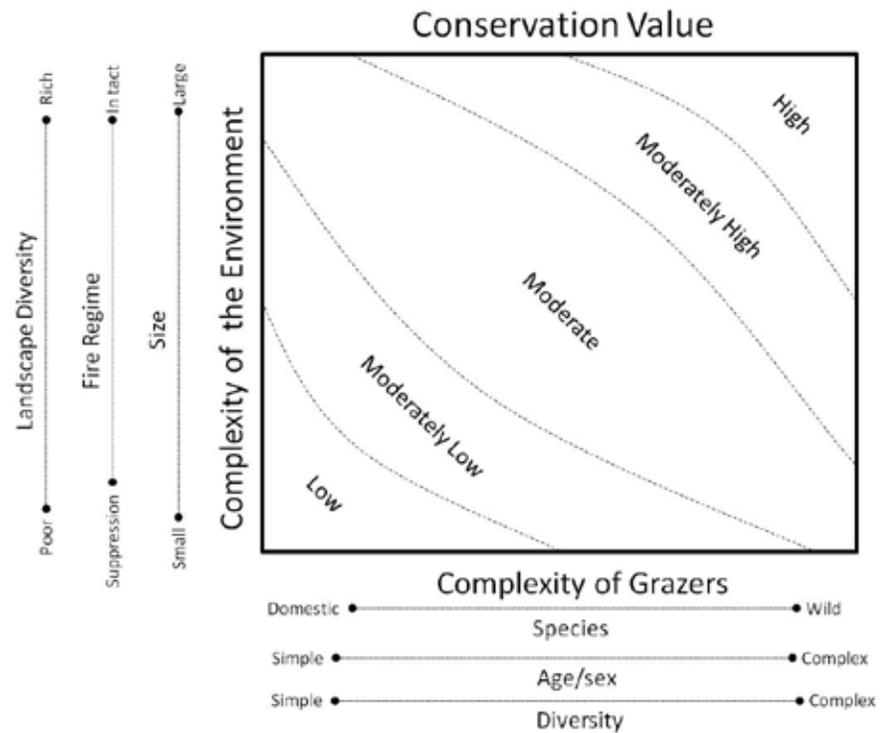
Tallgrass Prairie Preserve



**Figure 8.** Mean percentages of recorded location information for bison and cattle in areas with six months or less since fire. Both species are attracted to recently burned areas. Mean percentages did not differ between species ( $p>0.05$ ). Error bars represent one standard deviation.



**Figure 9.** Graphical 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. High conservation value can only be achieved by incorporating many animal and environmental factors, as well as their interactions.



---

# ABS WORKING PAPER SERIES

## **ABS Working Paper No. 1**

Redford, Kent H., and Eva Fearn, eds. (2007) Ecological Future of Bison in North America: A Report from a Multi-stakeholder, Transboundary Meeting. Previously published as WCS Working Paper No. 30.

## **ABS Working Paper No. 2**

Brodie, Jedediah F. (2008) A Review of American Bison (*Bos bison*) Demography and Population Dynamics. Previously published as WCS Working Paper No. 35.

## **ABS Working Paper No. 3**

Nishi, John S. (2010) A Review of Best Practices and Principles for Bison Disease Issues: Greater Yellowstone and Wood Buffalo Areas.

## **ABS Working Paper No. 4**

Fuhlendorf, Samuel D., Allred, Brady W., and Hamilton, Robert G. (2010) Bison as Keystone Herbivores on the Great Plains: Can Cattle Serve as Proxy for Evolutionary Grazing Patterns?

# WCS WORKING PAPER SERIES

## **WCS Working Paper No. 1**

Bleisch, William V. (1993) Management Recommendations for Fanjing Mountain Nature Reserve and Conservation at Guizhou Golden Monkey & Biodiversity.

## **WCS Working Paper No. 2**

Hart, John A. and Claude Sikubwabo. (1994) Exploration of the Maiko National Park of Zaire, 1989-1994, History, Environment and the Distribution and Status of Large Mammals.

## **WCS Working Paper No. 3**

Rumiz, Damian and Andrew Taber. (1994) Un Relevamiento de Mamíferos y Algunas Aves Grandes de la Reserva de Vida Silvestre Ríos Blanco y Negro, Bolivia: Situación Actual y Recomendaciones.

## **WCS Working Paper No. 4**

Komar, Oliver and Nestor Herrera. (1995) Avian Density at El Imposible National Park and San Marcelino Wildlife Refuge, El Salvador.

## **WCS Working Paper No. 5**

Jenkins, Jerry. (1995) Notes on the Adirondack Blowdown of July 15<sup>th</sup>, 1995: Scientific Background, Observations, and Policy Issues.

## **WCS Working Paper No. 6**

Ferraro, Paul, Richard Tshombe, Robert Mwinyihali, and John Hart. (1996) Projets Integres de Conservation et de Developpement: un Cadre pour Promouvoir la Conservation et la Gestion des Ressources Naturales.

---

**WCS Working Paper No. 7**

Harrison, Daniel J. and Theodore G. Chapin. (1997) An Assessment of Potential Habitat for Eastern Timber Wolves in the Northeastern United States and Connectivity with Occupied Habitat on Southeastern Canada.

**WCS Working Paper No. 8**

Hodgson, Angie. (1997) Wolf Restoration in the Adirondacks? The Question of Local Residents.

**WCS Working Paper No. 9**

Jenkins, Jerry. (1997) Hardwood Regeneration Failure in the Adirondacks: Preliminary Studies of Incidence and Severity.

**WCS Working Paper No. 10**

García Víques, Randall. (1996) Propuesta Técnica de Ordenamiento Territorial con Fines de Conservación de Biodiversidad en Costa Rica: Proyecto GRUAS.

**WCS Working Paper No. 11**

Thorbjarnarson, John and Alvaro Velasco. (1998) Venezuela's Caiman Harvest Program: A historical perspective and analysis of its conservation benefits.

**WCS Working Paper No. 12**

Bolze, Dorene, Cheryl Chetkiewicz, Qui Mingjiang, and Douglas Krakower. (1998) The Availability of Tiger-Based Traditional Chinese Medicine Products and Public Awareness about the Threats to the Tiger in New York City's Chinese Communities: A Pilot Study.

**WCS Working Paper No. 13**

O'Brien, Timothy, Margaret F. Kinnaird, Sunarto, Asri A. Dwiyahreni, William M. Rombang, and Kiki Anggraini. (1998) Effects of the 1997 Fires on the Forest and Wildlife of the Bukit Barisan Selatan National Park, Sumatra.

**WCS Working Paper No. 14**

McNeilage, Alistair, Andrew J. Plumtre, Andy Brock-Doyle, and Amy Vedder. (1998) Bwindi Impenetrable National Park, Uganda. Gorilla and Large Mammal Census, 1997.

**WCS Working Paper No. 15**

Ray, Justina C. (2000) Mesocarnivores of Northeastern North America: Status and Conservation Issues.

**WCS Working Paper No. 16**

Kretser, Heidi. (2001) Adirondack Communities and Conservation Program: Linking Communities and Conservation Inside the Blue Line.

**WCS Working Paper No. 17**

Gompper, Matthew E. (2002) The Ecology Northeast Coyotes: Current Knowledge and Priorities for Future Research

**WCS Working Paper No. 18**

Weaver, John L. (2001) The Transboundary Flathead: A critical Landscape for Carnivores in the Rocky Mountains

**WCS Working Paper No. 19**

Plumtre, Andrew J, Michel Masozera, Peter J. Fashing, Alastair McNeilage, Corneille Ewango, Beth A. Kaplin, and Innocent Liengola. (2002) Biodiversity Surveys of the Nyungwe Forest Reserve in South West Rwanda.

**WCS Working Paper No. 20**

Schoch, N. (2003) The Common Loon in the Adirondack Park: An Overview of Loon Natural History and Current Research.

---

**WCS Working Paper No. 21**

Karasin, Leslie N. (2003) All-Terrain Vehicles in the Adirondacks: Issues and Options

**WCS Working Paper No. 22**

Clarke, Shelley. (2002) Trade in Dried Asian Seafood: Characterization, Estimation and Implications for Conservation.

**WCS Working Paper No. 23**

Mockrin, Miranda H., E.L. Bennett, and D.T. LaBruna. (2005) Wildlife Farming: A Viable Alternative to Hunting in Tropical Forests?

**WCS Working Paper No. 24**

Ray, Justina C., Luke Hunter, and Joanna Zigouris. (2005) Setting Conservation and Research Priorities for Larger African Carnivores.

**WCS Working Paper No. 25**

Redford, Kent H. and Michael Painter. (2006) Natural Alliances Between Conservationists and Indigenous Peoples.

**WCS Working Paper No. 26**

Agrawal, Arun and Kent Redford. (2006) Poverty, Development, and Biodiversity Conservation: Shooting in the Dark?

**WCS Working Paper No. 27**

Sickler, Jessica, John Fraser, Sarah Gruber, Paul Boyle, Tom Webler, and Diana Reiss. (2006) Thinking About Dolphins Thinking.

**WCS Working Paper No. 28**

Castillo, Oscar, Connie Clark, Peter Coppolillo, Heidi Kretser, Roan McNab, Andrew Noss, Helder Quieroz, Yemeserach Tessema, Amy Vedder, Robert Wallace, Joseph Walston, and David Wilkie. (2006) Casting for Conservation Actors: People, Partnerships and Wildlife.

**WCS Working Paper No. 29**

Redford, Kent H., and Eva Fearn, eds. (2007) Protected Areas and Human Displacement: A Conservation Perspective.

**WCS Working Paper No. 30**

Redford, Kent H., and Eva Fearn, eds. (2007) Ecological Future of Bison in North America: A Report from a Multi-stakeholder, Transboundary Meeting.

**WCS Working Paper No. 31**

Smith, Brian D., Robert G. Shore, and Alvin Lopez. (2007) Status and Conservation of Freshwater Populations of Irrawaddy Dolphins.

**WCS Working Paper No. 32**

Redford, Kent H., and Eva Fearn, eds. (2007) Protected Areas and Human Livelihoods.

**WCS Working Paper No. 33**

Beckmann, J. P., L. Karasin, C. Costello, S. Matthews, and Z. Smith. (2008) Coexisting with Black Bears: Perspectives from Four Case Studies Across North America.

**WCS Working Paper No. 34**

Painter, Michael, Ana Rita Alves, Carolina Bertsch, Richard Bodmer, Oscar Castillo, AVECITA Chicchón, Félix Daza, Fernanda Marques, Andrew Noss, Lilian Painter, Claudia Pereira de Deus, Pablo Puertas, Helder Lima de Queiroz, Esteban Suárez, Mariana Varese, Eduardo Martins Venticinque, and Robert Wallace. (2008) Landscape Conservation in the Amazon: Progress and Lessons.

---

**WCS Working Paper No. 35**

Brodie, Jedediah F. (2008) A Review of American Bison (*Bos bison*) Demography and Population Dynamics.

**WCS Working Paper No. 36**

Redford, Kent H., and Catherine Grippio, eds. (2008) Protected Areas, Governance, and Scale.

**WCS Working Paper No. 37**

Estes, Richard D. and Rod East. (2009) Status of the Wildebeest (*Connochaetes Taurinus*) in the Wild 1967-2005

**WCS Working Paper No. 38**

Olupot, William, Alastair J. McNeilage and Andrew J. Plumptre (2009) An Analysis of Socioeconomics of Bushmeat Hunting at Major Hunting Sites in Uganda.

**WCS Working Paper No. 39**

O'Brien, Tim. (2010) Wildlife Picture Index: Implementation Manual Version 1.0.

# WCS CANADA CONSERVATION REPORTS

**WCS Canada Conservation Report #1**

BIG ANIMALS and SMALL PARKS: Implications of Wildlife Distribution and Movements for Expansion of Nahanni National Park Reserve. John L. Weaver. 2006.

**WCS Canada Conservation Report #2**

Freshwater fish in Ontario's boreal: Status, conservation and potential impacts of development. David R. Browne. 2007.

**WCS Canada Conservation Report #3**

Carnivores in the southern Canadian Rockies: core areas and connectivity across the Crowsnest Highway. Apps, Clayton D., John L. Weaver, Paul C. Paquet, Bryce Bateman and Bruce N. McLellan. 2007.

**WCS Canada Conservation Report #4**

Conserving Caribou Landscapes in the Nahanni Trans-Border Region Using Fidelity to Seasonal Ranges and Migration Routes. John L. Weaver. 2008.

**WCS Canada Conservation Report #5**

Strategic conservation assessment for the northern boreal mountains of Yukon and British Columbia. Reid, Donald, Brian Pelchat, and John Weaver. 2010.





**AMERICAN BISON SOCIETY**

American Bison Society  
c/o WCS Institute  
Wildlife Conservation Society  
2300 Southern Boulevard  
Bronx, NY 10460  
[www.americanbisonsocietyonline.org](http://www.americanbisonsocietyonline.org)  
[www.wcs.org](http://www.wcs.org)