2012

Bison Conservation in the Northern Great Plains

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Recommended Citation

Kohl, Michel Thomas, "Bison Conservation in the Northern Great Plains" (2012). *Graduate Student Theses, Dissertations, & Professional Papers*. 153.
https://scholarworks.umt.edu/etd/153

BISON CONSERVATION IN THE NORTHERN GREAT PLAINS

By

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B.S., University of Montana, Missoula, Montana 2008, USA

Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife and Fisheries Biology

The University of Montana,
Missoula, Montana

June 2012

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Kohl, Michel, M.S., May 2012 *Wildlife Biology*

Bison Conservation in the Northern Great Plains

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Temperate grasslands are the least protected ecosystem in the world. In North America, only < 4% of tallgrass prairie, 64% of mixed-grass prairie, and 66% of shortgrass prairie are intact. Historically, grazing played an important role in maintaining prairie landscapes through nutrient cycling and the diversification of vegetation structure and composition. Within grasslands, the plains bison (*Bos bison*) was the most numerous and influential grazer. However, by 1900 bison were reduced to ≤ 1,000 animals throughout North America. Today, bison are scattered throughout their historical range, numbering > 500,000 individuals. Recent questions have surfaced regarding the success of this effort, however, because < 21,000 plains bison are managed as conservation herds ($n = 62$) and 8% of those herds are managed on areas of > 2,000 km^2. In addition, >100,000,000 cattle now graze rangelands in the U.S. and Canada leading to questions regarding the ecological significance of replacing bison with livestock. Our objectives were to increase knowledge regarding the ecological similarities between bison and cattle, and to determine how both species can be managed to mimic ecological patterns that approximate historical bison populations. We used behavioral observations, movement analyses, and Resource Selection Function (RSF) analyses too quantify similarities and differences between the bison and cattle in the Northern Great Plains. We observed a higher proportion of time spent grazing by cattle (45-49%) than bison (26-28%) and a greater amount of time spent at water. We used First-Passage-Time (FPT) analyses to compare the spatial scale of bison and cattle within pastures. We report selection of spatial scales by bison of 1.8 – 9.0 x greater than currently provided. Lastly, RSF analysis identified important resources including selection of water resources by bison. These results have implications when bison are used to meet grazing restoration objectives because water resources may alter grazing regimes important for prairie obligate species (i.e. grassland birds). For livestock, the time spent at water and grazing encourages grazing practices that increase grazing rotation and movement across the landscape. These may include changes in timing and intensity of grazing, and adjustable mineral and water resources.

ACKNOWLEDGMENTS

This project was a cooperative effort between groups and organizations. Kyran Kunkel was essential in the establishment of this project and allowed me to take the project in directions I envisioned. The staff at the American Prairie Reserve was always engaged with a positive outlook for the project. I thank Bryce Christensen, Damien Austin, and Ganay Johnson for advice and understanding of comments and concerns. The staff at the Northern Great Plains Program of World Wildlife Fund was exceptional. In particular, I thank Kristy Bly who played an important role in this project through her facilitation of internal politics, logistical assistance, and engaging questions. In addition, I had the pleasure of working with the incredible staff at Grasslands National Park that provided access, accommodations, and hospitality on trips to the North. Of them, I thank Rob Sissons for his logistical assistance. Also, I thank Wes Olson for providing his immeasurable knowledge of bison to this project and to him and his wife, Johanne, for their hospitality, encouragement, and thoughtfulness. I thank Keith Aune, of Wildlife Conservation Society, for his dedication to this project and to bison conservation as a whole. Lastly, this project would not be what it is without access to land and animals provide by the Barnard and Weiderrick Ranches. In addition, Gene Barnard, Jerry Mahan, and Chuck Mahan were incredible neighbors and hosts during my time in south Phillips County. Kenneth Plourde was instrumental in data collection, analysis, and providing needed conversation during the long wet summer months. Kristina Gunderson, Anna Derey-Wilson, and Taylor King assisted with volunteer and data entry work. Shawn Cleveland served as a sounding board for questions and concerns throughout the project. I thank the Boone and Crockett Program and Fellows for their companionship. In particular, Jerod Merkle was always available, assisting in coursework and research during the early years of this project. Accordingly, I would like to recognize my

committee, Kyran Kunkel, Kerry Foresman, and Mark Hebblewhite for their guidance and encouragement. Lastly, I thank 3 people that facilitated my research, my career, and my personnel life. Jeanne Franz made the day brighter, the path easier, and the lunch sweeter, thus, will always have my thanks. Second, none of this would be possible without my advisor, Dr. Paul R. Krausman. His guidance, understanding, and faith in a kid from north-eastern Montana cannot be overstated. Paul was a greater mentor in research, personal life, and attire and I will always carry this knowledge with me. Lastly, I thank my family who has encouraged and supported me throughout my education career. In particular, I thank my beautiful wife, Erin, who has struggled through distant summers and long winters with me over the past 3 years and I am eternally indebted to you. Research funding was provided by the American Prairie Reserve, the Boone and Crockett Wildlife Conservation Program at the University of Montana, the M. J. Murdock Charitable Trust, the Wildlife Conservation Society Research Fellowship Program, and the World Wildlife Fund- Northern Great Plains Program. Educational expenses were supported by the Alfred P. Sloan Foundation, the Boone and Crockett Wildlife Conservation Program at the University of Montana, the Montana Institute on Ecosystems, and the University of Montana.

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CHAPTER 1

INTRODUCTION

Grasslands historically encompassed ~30% (46,000,000 km^2) of Earth's landmass, comprising almost 42% of the planets plant cover (Anderson 2006). Today, temperate grasslands (~12,000,000 km^2) are the least protected biome in the world as a result of human-induced modification (Hoekstra et al. 2005). These include a host of human disturbances that result in habitat conversion and degradation. Nearly 46% of temperate grassland habitats have been converted from native grassland and < 5% of remaining temperate grasslands are protected (Hoekstra et al. 2005). In North America, temperate grassland, once covered 162,000 km^2, but conversion has now surpassed 50% (Hoekstra et al. 2005) leaving < 4% of tallgrass prairie, 64% of mixed-grass prairie, and 66% of shortgrass prairie intact (Samson and Knopf 1996).

Human modification and degradation has direct impacts on endemic populations as evidenced by the widespread and continuous population declines of grassland songbirds (Knopf 1996). Less intuitive are the cumulative effects caused by alterations to disturbance processes. Historically, prairie ecosystems were continuously in a state of flux, shifting by processes that include variable weather patterns and climatic conditions, and disturbance regimes (i.e. grazing, fire). Of these processes, grazing played a critical role in maintaining prairie landscapes through nutrient cycling (Coppock et al. 1983, McNaughton et al. 1997, Knapp et al. 1999), and the diversification of vegetation structure and composition (Hartnett 1996, Knapp et al. 1999, Fuhlendorf et al. 2006). In North America, historical estimates of large grazers are difficult to quantify (Shaw 1995), however it is assumed they were of substantial quantity to have significant effects on vegetation structure and composition. Of these grazers, bison (*Bos bison*) were the most numerous and influential herbivore (Samson and Knopf 1994, Shaw 1995).

The first bison (i.e., steppe bison; *Bos priscus*) appeared in North America during the middle Pleistocene (300,000 – 130,000 years ago) after crossing the Beringia land bridge from Asia (Shapiro et al. 2004). This species reached a maximum distribution during the last glacial period (Wisconsinan, 100,000-12,000 years B.P.) marking the southern expansion of bison into the grasslands of central North America. Recurrent glacial events forced rapid biological, taxonomic, and evolutionary differences in the steppe bison (van Zyell de Jong 1993) leading to multiple speciation. The subsequent speciation resulted in modern bison (*Bos bison*), which diverged around 5,000 years ago into the plains bison (*B. b. bison*) and the wood bison subspecies (*B. b. anthabascae*; Gates et al. 2010).

Plains bison (bison) ranged across North America from the eastern seaboard into Florida; westward to the Cascade and Rocky mountains, northward to mid-Alberta and Saskatchewan, and southward into Mexico (Reynolds et al. 1982, Danz 1997) encompassing the largest distribution of any indigenous large herbivore in North America (Gates et al. 2010). Throughout the Great Plains, bison functioned as a keystone species (Knapp et al. 1999) or foundational species (Soule et al. 2003) interacting with pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), deer (*Odocoileus* spp.), prairie dogs (*Cynomys* spp.), wolves (*Canis lupus*), grizzly bears (*Ursus arctos*) and grassland bird species through ecosystem alterations (Coppock et al. 19983, Krueger 1986, Knopf 1996, Freese et al. 2007). In addition, bison functioned as strong interactors within grassland systems through facilitation of vegetative heterogeneity (Knapp et al. 1999, Fuhlendorf et al. 2008). Wallowing activities resulted in standing water following rain or snowmelt (Knapp et al. 1999), in turn, supporting numerous plant species (Collins and Uno 1983, Polley and Wallace 1986), and providing habitat for amphibians (Bragg 1940, Corn and Peterson 1996). Vegetation communities were affected through grazing, physical disturbance, nutrient cycling, and seed dispersal (McHugh 1958, Knapp et al. 1999). These activities directed grassland heterogeneity that supported many prairie obligate species in the tall, mixed, and short-grass prairie (Powell 2006, Fuhlendorf et al. 2008 Gates et al. 2010).

Prior to the arrival of Europeans in North America, the estimates of bison numbers range from 15 – 100 million animals (Dary 1989, Shaw 1995), however most estimates range from 30-60 million bison (Seton 1929, McHugh 1972, Lott 2002), and most bison were located in the Great Plains region. Bison numbers declined rapidly following European settlement primarily due to subsistence and commercial hunting by Native Americans and European settlers for hides and meat (Hornaday 1887, Isenberg 2000) and competition with domestic livestock and domestic and wild horses (McHugh 1972, Dary 1989, Danz 1997, Isenberg 2000). As a result, <1,000 bison were in North American by 1890 (Hornaday 1887, Seton 1929) and wild, free-ranging bison were extirpated from Canada (Freese et al. 2007) and nearly extirpated from the U.S. (Meagher 1973).

The destruction of the bison herds led to the first major conservation movement in the U.S. to preserve a species on the brink of extinction (Coder 1975). These efforts were led predominantly by private individuals (e.g., Charles Goodnight, Walking Coyote, Michel Pablo, Charles Allard, and others) who established small herds throughout the Great Plains (Boyd 2003). Private herds would later form the foundation for most of the public and private plains contemporary herds (Boyd 2003). The second conservation effort was led by the American Bison Society (formed 1905) who influenced the U.S. Congress to establish public conservation herds at Wichita Mountains National Wildlife Refuge, Oklahoma, USA, the National Bison Range, Montana, USA, and Fort Niobrara National Wildlife Refuge, Nebraska, USA, (Coder

1975, Danz 1997). Federal conservation began in Canada with the 1907 purchase of plains bison for the Canadian Parks systems (Freese et al. 2007).

These conservation efforts resulted in a rapid increase in the bison population, doubling between 1888 and 1902 (Coder 1975). Bison were safe from extinction in 1909 (Coder 1975) and a conservation focus shifted to commercial production. Bison increased steadily through the 1970s to ~30,000 animals in North America (McHugh 1972), half of which resided in conservation herds (Freese et al. 2007). In the 1980s, commercial bison production further increased, resulting in >500,000 bison throughout North America (Boyd 2003) however, only 20,504 animals were located in 62 conservation herds (Gates et al. 2010). The International Union for Conservation of Nature (IUCN) Bison Specialist Group classified conservation herds according to numerical status, geographic status, population size, breeding competition, predator presence, diseases presence, and cattle gene introgression (Gates et al. 2010).

The ecological significance of losing bison has been questioned as conservation herds remain stagnant (Boyd 2003, Freese et al. 2007, Sanderson et al. 2008, Gates et al. 2010). Through a concerted effort, conservation organizations (e.g., The Nature Conservancy, World Wildlife Fund [WWF], Wildlife Conservation Society) and state and federal agencies (Utah Division of Wildlife, Montana Fish Wildlife & Parks, U.S. Fish and Wildlife Service, Parks Canada) are focusing their efforts toward preserving intact prairie habitat within the Great Plains. Bison, viewed as an important component of the historical grazing process, are thus being reestablished as wild, free-ranging bison herds throughout their historical habitat (Freese et al. 2007).

The objectives of these conservation efforts and similar initiatives occurring across North America are to restore bison to their historical range, thus conserving bison and returning an important ecological process to the landscape in an effort to maintain and restore the prairie landscape. Similar to these overall conservation objectives, I had 2 objectives. My first objective was to provide knowledge that leads toward landscape scale-prairie conservation. As exemplified by the current population data of bison and cattle, bison are no longer North America's dominant grazer, thus it is important to understand the similarities and differences between the species to understand whether cattle can serve as a proxy for evolutionary grazing patterns. My second objective was to determine how existing bison and cattle populations could use the landscape in similar ecological patterns to historical bison populations.

THESIS FORMAT

Chapter 1 is an overview of the entire thesis. Chapter 2 was written and formatted as an individual manuscript that will be submitted for publication in *The Journal of Rangeland Ecology and Management.* Because this is a collaboration among researchers, co-authors are included in the publications and I use we throughout the remainder of the thesis.

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CHAPTER 2

Bison Versus Cattle: Are They Ecologically Synonymous?

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Research was funded by the Alfred P. Sloan Foundation, American Prairie Reserve, Boone and Crockett Wildlife Conservation Program at the University of Montana, M.J. Murdock Charitable Trust, Montana Institute on Ecosystems by the National Science Foundation EPSCoR program grant EPS-1101342, The University of Montana, Wildlife Conservation Society Research Fellowship Program, and the World Wildlife Fund-Northern Great Plains Program.

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ABSTRACT

Historically, the plains bison (*Bos bison*) was the most numerous and influential grazer. Today, only 500,000 bison occupy North America amongst > 100,000,000 cattle leading to questions of the ecological significance of livestock replacing bison at a landscape scale. To restore historical grazing processes, bison are translocated onto landscapes manipulated for cattle use through water development. We hypothesized that bison would use these landscapes similarly to cattle, resulting in less heterogeneous grazing (primary objective of bison restoration). We quantified differences between bison populations at different locations and spatial scales and compared bison and cattle on similar locations and spatial. We used behavioral observations, movement analyses, and Resource Selection Functions (RSFs) to identify differences in ecologically significant activities of cattle and bison. Cattle spent a higher proportion of time grazing (45-49%) than bison (26-28%) and a greater amount of time at water. Bison moved at a greater rate than cattle. First Passage Time (FPT) movement analyses identified selection of a bison foraging patch (11,690 ha) 4.4 x larger than cattle (2665 ha). Similarly to cattle, bison selected water and riparian shrub communities; however species differed in selection of elevation and Normalized Difference Vegetation Index. This study has implications when bison and cattle are used to meet range restoration objectives, particularly if increased vegetation heterogeneity is a goal. For bison, large landscapes that include variation in topography and vegetation communities are required. Furthermore, limiting artificial water may facilitate bison grazing patterns that approximate historical bison use. For livestock, alterations to grazing practices such as changes in timing and intensity of grazing (i.e. duration, stocking level), and use of adjustable mineral and water resources may increase vegetation heterogeneity across spatial scales.

KEY WORDS

Behavior, first-passage time, grazing, resource selection functions, water

INTRODUCTION

The near extinction and subsequent recovery of plains bison (*Bos bison*) throughout North America was the first and greatest conservation success in North America. Today ~ 500,000 bison occupy North America because of the cooperation of private individuals, non-profit organizations, and the federal governments of the U.S., Canada, and Mexico. Despite the numerical recovery of the species, recent questions have surfaced regarding the success of these efforts because < 21,000 plains bison are managed as conservation herds ($n = 62$). Thirteen percent ($n = 8$) of conservation herds are outside of their historical range, 92% ($n = 57$) have < 1,000 individuals, and only 8% ($n = 5$) are managed on areas of > 2,000 km^2 (Boyd 2003, Gates et al. 2010). Thus, many conservation groups and state and federal agencies question the ecological significance of replacing bison with domestic cattle at a landscape scale.

Historically, bison were the dominant grazer throughout the Great Plains, affecting vegetation communities through grazing, physical disturbance, nutrient cycling, and seed dispersal (McHugh 1958, Knapp et al. 1999). These activities directed grassland heterogeneity that supported many prairie obligate species (e.g., grassland songbirds) in the tall, mixed, and short grass prairie (Powell 2006, Fuhlendorf et al. 2006, Gates et al. 2010). Following the reduction of the bison herds, they were replaced by domestic cattle and a significant shift occurred, resulting in overgrazing and then rotational grazing regimes that favor landscape-scale vegetation homogeneity (Holecheck 2006).

Cattle, which share a common ancestor with bison in *B. priscus*, are the result of wild aurochs (*B. primigenius*) domestication ~10,000 years ago in the Near East (Edwards et al.

2007). European cattle were introduced to Mexico by Hernando Cortez in 1515, and eventually the U.S. in 1540 (Holecheck et al. 2006). Cattle slowly expanded throughout the U.S. until the 1870s when the reduction in bison provided valuable rangeland for cattle in the northern and central Great Plains (Holecheck et al. 2006). Cattle numbers continued to rise throughout the 1900s expanding to 95% of the Great Plains grassland (Gates et al. 2010). Today, livestock numbers on rangelands in the U.S. and Canada are two times higher than historical bison estimates (Fig. 1), yet there is limited peer-reviewed data that compares the ecological similarities and differences between introduced livestock and bison, particularly when managed as wild populations on large, complex landscapes (Fuhlendorf et al. 2010).

Bison co-evolved with the grassland biome of North America whereas European cattle were domesticated on woodland-grassland-farmland landscapes for the past 10,000 years (Bailey et al. 1996) resulting in fundamental ecological differences. Bison groups generally consist of small bachelor groups and mixed groups consisting of females, calves, yearlings, and young males (McHugh 1958). These groups vary in size throughout the year (Lott and Minta 1983) ranging from a few individuals to >100 (Lott and Minta 1983, van Vuren 1983, Rutberg 1984) and are influenced by behavior (i.e., breeding season [Krueger 1986, Shaw and Meagher 2000]) and open habitats (van Vuren 1979). Cattle groups are dependent on specific range management techniques employed by operators.

Bison use higher elevation and steeper slopes than cattle when occupying the same range (van Vuren 1983). Additionally, burns (Coppedge and Shaw 1998, Knapp et al. 1999, Schuler et al. 2006), and prairie dog colonies (*Cynomys* spp.; Coppock et al. 1983, Krueger 1986, Wydeven and Dahlgren 1985), are selected. Bison generally use upland areas (Peden et al. 1974, van Vuren 1979, Philips 2000), whereas cattle use lowlands and riparian areas (Peden et al. 1974, Gillen et al. 1984, Smith et al. 1992). Within use areas, forage is a predictor (Phillips 2000), with bison primarily using areas consisting of warm-season gramminoids (Peden et al. 1974, Wydeven and Dahlgren 1985, Steuter et al. 1995). In the short-grass prairie, approximately 90% of bison diet consists of gramminoids (van Vuren 1979) and > 95% in the mixed-grass prairie (Wydeven and Dahlgren 1985, Krueger 1986). Cattle use cool-season grasses and forbs more than bison (Peden et al. 1974, Plumb and Dodd 1993). Cattle also spend more time grazing (Plumb and Dodd 1993) and near water and riparian areas than bison (Fuhlendorf et al. 2010). Specifically, cattle may spend half their time within 200 m of water (van Vuren 1979, Gillen et al. 1984, Porath et al. 2002), however, only Allred et al. (2011) have explicitly tested for water and riparian use differences between cattle and bison in a large landscape. They reported that cattle selected riparian areas and areas closer to water, whereas bison avoided them.

Water is a fundamental requirement of life and has often been listed as a limiting factor for wildlife and livestock in the western U.S. (Valentine 1947, Krausman 2002, Cain III et al. 2008). Since the 1940s, wildlife managers provided water for large ungulates including mule deer (*Odocoileus hemionus* [Elder 1954, Krausman and Etchberger 1995]), bighorn sheep (*Ovis canadensis* [Blong and Pollard 1968, Cain III et al. 2008]), and pronghorn (*Antilocapra americana* [Deblinger and Alldredge 1991]). Although controversial, (Krausman et al. 2006, Cain III et al. 2008) water availability may expand animal distribution, increase productivity, reduce mortality, and increase fitness (Rosenstock et al. 1999). Despite questionable benefits to wildlife (Rosenstock et al. 1999), water developments in the western U.S. are a necessity for livestock and have a direct bearing on livestock grazing capacity. Areas located <1.6 km from water are classified as high value, water distances between 1.6 km and 3.2 km are considered medium value, and areas >3.2 km are considered ungrazeable for cattle (Holecheck et al. 2006).

More importantly, heavy use of areas near water by cattle (van Vuren 1979, Gillen et al. 1984, Porath et al. 2002) may result in alterations to species composition, ecosystem structure, and disruptions of ecosystem functioning in riparian areas (Fleischner 1994). These effects are exacerbated during times of water scarcity such as drought, and hot, dry periods (James et al. 1999). In comparison to historical grazers such as bison, increased cattle use of areas near water sources can result in a more severe and larger animal impact zone (Steuter and Hidinger 1999). Regardless of the ecological implications, water sources have been developed for livestock across the western U.S. (Valentine 1947, Williams 1954) to increase forage use and grazing uniformity (Bailey 2004, 2005).

Despite the strong association between cattle and water, the importance of water to bison habitat selection has received little attention, but when addressed, the results vary across studies. For example, bison in Yellowstone National Park remain closer to water during drought, and will make daily round trips of up to 9.5 km to water (McHugh 1958). In concordance, bison at Prince Albert National Park, Saskatchewan, Canada, more strongly used meadows surrounded by water during summer (Fortin et al. 2003). However, these areas contained areas where snow or open water is readily available (Meagher 1973), thus, are not representative of historical water scarcity found in the Great Plains. Bison may have traveled several days without water (Hornaday 1887a) at distances up to 80 – 160 km in search of water (Dary 1989), which may explain the lack of relationship between water and bison in landscapes with limited water (van Vuren 1979, Phillips 2000, Babin 2009).

Data are available regarding the spatial and ecological use of bison and cattle, however direct comparisons between bison and cattle are difficult because of different management practices (i.e., pasture size, stocking densities, management priorities) and confounding environmental factors (Plumb and Dodd 1993, Towne et al. 2005, Fuhlendorf et al. 2010). Fuhlendorf et al. (2010) reported nine studies that compared bison and cattle with an ecological focus, only two of which attempted to control for confounding effects (Plumb and Dodd 1993; Towne et al. 2005). Recent work on the Tallgrass Prairie Reserve was the third study to control for confounding effects and the first to occur on pasture sizes > 300 ha (Allred et al. 2011).

Thus, our objectives were to compare the behavior, movement, and resource use of bison and cattle on large landscapes (>1,000 ha) within the Northern Great Plains. This area is the focus of a number of new and potential bison translocation efforts. These efforts have a high likelihood of occurring on landscapes manipulated for cattle through the use of water developments and fence construction. Because these translocation efforts are implemented alongside domestic livestock operations, we were provided opportunities for side-by-side comparisons of bison and cattle. Furthermore, with multiple bison populations within the region, we were able to compare landscapes used by bison across vegetation communities and spatial scales. We hypothesized that bison would use these landscapes similar to cattle, replacing historical bison use of the landscape resulting in less heterogeneous grazing. As such, we predicted bison and cattle on similar landscapes would demonstrate comparable ecological behaviors including resource use, movement, and grazing behaviors. We also predicted bison would differ in their ecological behaviors when under different management structures including pasture size and water density.

METHODS

Study Area

We conducted our bison-cattle comparison study on two study areas within the northwestern glaciated plain ecoregion (Forrest et al. 2004) of north-central Montana and southwestern Saskatchewan, Canada, in 2010 and 2011 (Fig. 2). In north-central Montana, we compared bison and cattle simultaneously on properties owned and leased from the Bureau of Land Management (BLM) by private ranchers and the American Prairie Reserve (APR). The APR is located 74 km south of Malta, Montana (Philips County) on Regina Road. The area borders C.M. Russell and U.L. Bend National Wildlife Refuges. To compare bison across spatial scales, vegetation communities, and water availability, a second bison site was selected 150 km north in Grasslands National Park (GNP).

Dominant plant species on APR are representative of a sagebrush steppe system that include blue grama (*Bouteloua gracilis*), needlegrass (*Stipa* spp.), crested wheatgrass (*Agropyron cristatum*), silver sagebrush (*Artemsia cana*), and Wyoming big sagebrush (*Artemisia tripartita*). Sedges (*Carex* spp.), cacti, and forb species are also common in the area. Dominant plant species in GNP are representative of the mixed-grass prairie ecosystems and include blue grama (*Bouteloua gracilis*), needlegrass (*Stipa* spp.), western wheatgrass (*Pascopyrum smithii*), and silver sagebrush (*Artemsia cana*).

Large ungulates on APR and GNP include mule deer, white-tail deer (*Odocoileus virginianus*), and pronghorn. Elk (*Cervus elaphus*) are also on APR. Black-tailed prairie dogs (*Cynomys ludovicianus*) and coyotes (*Canis latrans*) are common in both areas. Greater sage grouse (*Centrocecus urophasinus*), Baird's sparrows (*Ammodramus bairdii*), and mountain plover (*Charadrius montanus*) are grassland bird species of conservation concern found throughout the area.

The APR lies in a semi-arid region consisting of upland flats intersected by coulees and ephemeral streams flowing toward the Missouri River. Yearly precipitation ranges from 25.4 – 27.9 cm; however 2010 and 2011 were 150-200% above normal (45.6 cm, 57.1 cm respectively).

Mean annual temperature is 6.5°C and ranges from -8.4°C in January to 20.8°C in July. Elevation lies between 700 and 825 m. Soil primarily contains heavy clay loams with moderate amounts of salt resulting in high imperability by water. Thus, most water developments remain full throughout the year. Reynolds Hill Road passes through the eastern section of the pasture and receives low to moderate levels (~30 vehicles/day) of use throughout the summer with heavier use (~ 250 vehicles / day) during hunting season (1 September – 25 November).

Grasslands National Park also lies in a semi-arid region and consists of similar topographic features as APR. The Frenchman River runs through the southern section of the park with consistent, regulated flow throughout the year. Annual precipitation ranges from 30-33 cm, however 2010 and 2011 were 140-200% above normal (46.5 cm, 53.1 cm respectively). Mean annual temperature is 3.4°C and ranges from -13.4°C in January to 18.8°C in July. Elevation lies between 750 and 900 m. The main ecotour road passes through the center of the park (~ 6,000 visitors / year) from north to south and receives low to moderate levels of use throughout the summer, however recreational use is rare in the core summer range.

Bison on APR were contained within a 3,555 ha electrified pasture from 1 May through 31 October of each year (Fig. 3). The pasture is leased from the BLM and contains 15 artificial reservoirs. An ephemeral stream maintained small remnant pools during the study. Bison on GNP were in an 18,153 ha pasture containing 26 reservoirs (Fig. 4). Importantly, bison typically used only the north-east portion of the park (4,200 ha; average 95% kernel monthly home range estimate). This area contained five reservoirs (three of which were permanent throughout summer), one large depression, and three ephemeral channels which contained remnant pools during the study. In addition to reservoirs, the Frenchman River provides water throughout the year, except when frozen.

Two cattle herds adjoined the APR bison herds. The Weiderrick Ranch grazed 100 cow/calf pairs (red and black Angus) from 1 July – 15 October on 2 rotational pastures (1,090 and 1,408 ha) administered by BLM which contained 5 – 7 reservoirs / pasture (Fig. 3). The Barnard Ranch grazed ~140 cow/calf pairs (red Hereford and red Angus) on two rotational pastures (777 and 1,000 ha) that contained 6 – 8 reservoirs / pasture and were partially administered by BLM and owned by the Barnard Ranch. One pasture was bisected by Reynolds Hill Road. Topography of all cattle pastures was similar to APR and all cattle pastures contained ephemeral streams similar to APR. Stocking density was similar across bison and one cattle pasture (Table 1).

GPS Data Collection

We deployed Global Positioning System (GPS) radiocollars (Lotek 3300, Lotek 4400, Lotek Wireless Fish and Wildlife Monitoring, Newmarket, Ontario, Canada and NSG-LD2, North Star Science and Technology, LLC, Kind George, Virginia, USA) on adult female bison and cattle. Bison were immobilized (carfentanil [4-8 µg/kg, IM] and xylazine [0.05-0.1 mg/kg, IM], A3080, or butrphanol, atipamezole medetomidine [BAM], and reversed with naltrexone and tolazine [for carfentanil and xylazine], K. Kunkel, American Prairie Reserve, personnel communication) by air powered darts (Pneu-Dart Inc, Williamsport, PA, USA) fired from the ground. Cattle were physically restrained in a cattle squeeze-shoot. Collars were scheduled to obtain locations every 1, 2, or 3 hours from 1 June – 31 August (or until collar failure) in 2010 and 2011 (Table 2). The GPS locations were censored from analysis when bison moved outside of study pastures. This research was approved by The University of Montana Animal Care and Use Board (Animal Use Protocol# 014-10PKWB) and Parks Canada (Permit #: GRA-2010-5415).

Landscape Variables

Abiotic variables (i.e., aspect, slope, and elevation) were developed from the 30 m^2 Montana Digital Elevation Model. Biotic variables included vegetation community and 250 m^2 Normalized Difference Vegetation Index data (NDVI [Moderate Resolution Imagine Spectroradiometer {Huete et al. 2002}]). Vegetation classifications on GNP were based on field work completed by ground sampling (R. Sissons, GNP, unpublished data). Landcover type was classified on APR using remotely sensed data and was designed to allow for comparison between vegetation communities on GNP. We delineated 10 vegetation communities (e.g., eroded, upland grassland, disturbed, sloped grassland, shrub/riparian, valley grassland, treed, unclassified, sage-brush, water bodies). We use a dynamic measure of vegetation productivity by estimating primary productivity from mid-month NDVI estimates (Tucker and Sellers 1986). We analyzed anthropogenic variables using Euclidiean distance estimates (km) for fence, water, and roads. We located permanent water sources using Bureau of Land Management (Malta Field Office, Malta, MT, USA) and Parks Canada (GNP Headquarters, Val Marie, Canada) topographic maps. We inspected water developments monthly to confirm water availability throughout summer. Additional water sources (i.e., hardpans, rainfall, coulees) are generally semi-permanent (< 1 week), thus we assumed they were homogenous throughout the landscape and did not influence overall movement patterns of bison and cattle relative to permanent water sources.

Behavior

To understand how bison and cattle differ in behaviors, we conducted behavioral observations. Observations occurred near semi-permanent to permanent water sources because water is an anthropogenic alteration that is largely homogenous throughout the western U.S., whereas cross fencing is determined by grazing practices and goals. Observations occurred for one week/month/study group from 1 June – 1 October. Observations ($\leq$4 hours) occurred during daylight hours twice per day and were focused on periods of high movement periods identified from previous observations. Behavior of mixed groups (female, calf, subadult males) was determined using instantaneous scan sampling (15 min. intervals; Altmann 1974) from distances >100 m (Komers et al. 1992). A sampling unit consisted of a group of > 2 animals separated from other groups by $\geq$ 100 m (Fortin et al. 2003). Observation periods began when a watering event (i.e., the start of an adult animal drinking water) was not occurring, at which point we recorded behavior (e.g., moving, feeding, nursing, bedded, wallowing, social activities). When a watering event occurred, the observation period ceased and weather data (i.e., temperature, cloud cover, wind speed) and time spent at water (TSW [i.e., time from initial drinking activity to time when animal was > 1 body length from water source]) was recorded in seconds.

We calculated proportional differences in ecological significant behaviors (i.e. moving, grazing). We used ANOVA to compare differences in TSW between species and study locations. Lastly, a multiple analysis of variance (MANOVA) was used to calculate the influence of temperature on TSW. Statistical analyses were conducted using the Rcmdr package in R (Fox 2005).

Movement

We predicted that bison movement rates (MR) to be larger than cattle on similar landscapes because of their expected requirement for landscapes at orders of magnitudes larger than domestic cattle. We also predicted bison on APR would have smaller movement rates than bison on GNP due to restricted landscape availability, thus inability to move across the landscape in search of additional resource patches. Movement rates, calculated as distance (*d*) in meters divided by time (*t*) in seconds, has a non-normal distribution, thus we used a negative binomial regression to test this hypothesis. Negative binomial regression, a type of generalized linear model (GLM), uses the log link function to, in this case, calculate MR differences between species and study groups. Coefficients are interpreted according to a one unit change in the predictor variable. Thus, the difference in the log of the response variables expected counts is expected to change by the respective regression coefficient, given other predictor variables are held constant. Analyses were performed in R and negative binomial regression was performed using the MASS package (Venables and Ripley 2002).

To calculate the effect of landscape on movement rates, we used First Passage Time (FPT) analyses that measure the search effort along a pathway (Fauchald and Tveraa 2003) to identify the spatiotemporal scale of a biologically relevant move (Turchin 1998, Morales et al. 2005). Specifically, FPT incorporates step-length, turning angles and tortuosity (Fauchald and Tveraa 2003) to estimate the spatial scale at which the consumer perceives a resource. Variance in FPT, calculated by the time it takes an animal to travel across a circle of a specified radius (Fauchald and Tverra 2003), allows ecologists to identify area-restricted search (ARS) behavior from movement behavior between patches. Unlike many ungulates (including cattle) in which ARS behavior is assumed to include bedding and feeding sites (Fryxell et al. 2008), we assumed bison ARS behavior consist of bedding sites and calving areas and movement behaviors consisted of foraging bouts.

First-passage time analyses were conducted in the adehabitatLT package of R (Calenge 2006). Circles of radii between 50 – 15,000 m, increasing at 25 m increments, were applied to each GPS location along an individual movement path for bison and 50-10,000 m, increasing at 25 m increments, for cattle. Location data (GPS) was used from the focal sampling period (June

– August 2010, 2011) except for 2011 for APR bison (Table 2). The omission of 2011 for APR bison was due to temporary bison movements outside of the designated study pasture which necessitated data censoring, thus resulting an inadequate sample size for FPT analysis. Where a circle intersected the path between GPS locations, the FPT ($t(r)_i$) was calculated by estimating the absolute value of forward movement ($FPTF_i$) plus the backward movement ($FPTB_i$) in seconds. First Passage times were not calculated in instances of missed locations which created breaks along the path (Williams et al. 2012). Furthermore, variation in FPT increases with increasing circles radii, thus variance in FPT was divided by the area of the circle (Frair et al. 2005, Williams et al. 2012). Combined, peaks in the variance of FPT per unit area (varFPT/area) identified the spatial scale of resources across 2010 and 2011 summers for each individual.

Resource Selection

We used a resource selection function (RSF) framework to compare resource use of bison and cattle during summer (1 June – 31 August; Manly et al. 2002). Our specified covariates were vegetation community, water availability, and additional abiotic, biotic, and anthropogenic covariates. However, RSFs assume independence among observations (Hosmer and Lemeshow 2000) leading to increased Type I error rates (Gillies et al. 2006). This issue is of importance when identifying resource use in grouping species such as bison and cattle and when comparing resource selection across locations that differ in available resources. Random effects can accommodate temporal and spatial autocorrelation among individuals and groups (Breslow and Clayton 1993) and correct for unbalanced number of locations among individuals (Bennington and Thyane 1994, Gillies et al. 2006). As a result, the inclusion of a random effect for individuals allowed for identification of individual variability in resource selection and resulted in a population estimate of resource selection (Neter et al. 1996).

We used generalized linear mixed-models (GLMM) with a random-intercept for each animal to allow for interpretation of selection among different populations and species (Hebblewhite and Merrill 2008, Bolker et al. 2009). Furthermore, we treated each animal month as an individual (i.e. Animal1_June2010, Animal2_June2010, Animal1_July2010, etc.) to provide a population estimate across the summer months while taking into account changing availability in our dynamic measure of vegetation productivity, NDVI. The form of the mixed-effects model for individual animal (j) with a random intercept (Skrondal and Rabe-Hesketh 2004) is given as:

$$\omega(x) = \beta_{oj} + \gamma_{oj} + \beta_1 x_{\mathrm{j}} + \beta_2 x_{2\mathrm{j}} + \ldots + \beta_n x_{nj} + \varepsilon_j$$

where $\omega(x)_{\mathrm{n}}$ is proportional to the predicted probability of use as a function of covariates with fixed regression coefficients $x_{1\ldots n}$, and $\beta_{1\ldots n}$ are the selection coefficients estimated from fixed-effects logistic regression (Manly et al. 2002). Because the fixed and random intercepts $\beta_{oj} + \gamma_{oj}$ are meaningless in a use-available design, they are often dropped, resulting in a predicted relative probability. Although β_{oj} is dropped when estimating the RSF, the addition of a random intercept can improve model fit and change coefficients dramatically because of the correlation within groups (Skrondal and Rabe-Hesketh 2004).

Due to the 10-fold increase in pasture size from APR to GNP, we estimated RSFs at the third order scale (Johnson 1980) on APR and in GNP. On APR, we randomly sampled monthly availability (*n* = 1,000) across individual months within a given pasture for bison and cattle. In GNP, we randomly sampled monthly availability (*n* = 1,000) within a 95% fixed kernel monthly home range (third order) using Geospatial Modeling Environment 6.0 (Beyer 2012). In GNP, we also estimated RSFs at a constrained second order scale to understand whether resource selection differed across spatial scales in GNP. We define this as constrained second order resource selection because the area is used throughout the year, however we cannot explicitly state whether this area would encompass the bison's annual population range if no peripheral fence existed. We estimated the constrained second order selection by randomly sampling monthly availability (*n* = 2,000) across the entire park. A GLMM was estimated using the lme4 package (Bates et al. 2011) for R 2.14.2 (R Development Core Team 2008) and included our covariates (described above) that influenced bison and cattle resource selection in previous studies. For categorical covariates, we selected shrub communities as the reference category for vegetation due to previous relationships between shrub and riparian communities and bison and cattle reported in the literature. East facing slopes were selected as a reference category in relation to other cardinal direction because of perceived heat exposure. We assumed that north facing slopes were cooler, and west and south facing slopes were warmer than east facing slopes, thus influence the selection of aspect. All variables were screened for collinearity by calculating the Pearson's correlation between variables and using $|r| > 0.6$ as the threshold for removing a covariate (Hosmer and Lemeshow 2000). Because analysis coefficients are relative to all other model variables, no model selection technique was used, thus allowing a direct comparison of covariates across location and species.

RESULTS

Behavior

We collected 87 behavioral observations spanning 155.3 hours across all study areas from 22 May – 23 August 2010 and 2011. Observations resulted in 544 watering events across 2010 and 2011. We were unable to collect observation data and watering events for 1.5 months on the Barnard Ranch in 2010 due to grazing rotation. Access was limited to Weiderrick Pastures in 2010 and 2011 due to weather conditions. Cattle spent proportionately more time grazing than bison (Table 3). Bison demonstrated similar behavior in APR and GNP for grazing (26.2, 27.5% respectively) and movement (11.1, 7.6% respectively). Cattle on the Barnard and Weiderrick Ranches were similar to one another but differed from bison in grazing (49.1, 45.0% respectively) and movement (1.7, 5.0% respectively). Analysis of TSW followed our prediction that cattle and bison differed in TSW ($F_1 = 75.07$, $P < 0.01$). Cattle populations did no differ in TWS ($F_1 = 2.29$, $P < 0.13$), however bison populations were statistically different in their TSW ($F_1 = 19.68$, $P < 0.01$). Furthermore, temperature ($F_5 = 9.12$, $P < 0.01$), location ($F_2 = 31.58$, $P < 0.01$), and the interaction between temperature and location (e.g., GNP, APF, Cattle [$F_5 = 9.12$, $P < 0.01$]) were important in explaining TSW.

Movement

Bison moved at a significantly faster rate than cattle ($\beta = 0.62 \pm 0.08$ SE, $P = < 0.001$). Cattle did not statistically differ in their movement rates across locations ($\beta = -0.17 \pm 0.27$ SE, $P = < 0.206$), however, bison differed across locations with bison moving at faster rates on APR ($\beta = 0.41 \pm 0.11$ SE, $P = < 0.001$) and GNP ($\beta = 0.69 \pm 0.0822$ SE, $P = < 0.0005$) than cattle (combined). Thus, bison on APR and GNP moved at a rate 51 and 99% faster than cattle, respectively, following our prediction that bison would demonstrate higher movement rates than cattle.

Variance in FPT was maximized at 5,162 ± 17.7 (patch area = 8,368 ha) and 6,100 ± 457.1 (patch area = 11,690 ha) m radii for bison in APR and GNP (Fig. 5), respectively, whereas cattle on Barnard and Weiderrick Ranches were maximized at 2,785 ± 230.1 (area = 2,435 ha) and 3,040 ± 568.1 (area = 2,901 ha) m radii, respectively (Fig. 5). Bison in GNP also showed increased variance in FPT at 9,904 ± 914.9 m radii, however no large scale response was found on APR (Fig. 5). Cattle on the Barnard Ranch showed hierarchical selection at a smaller scale located at 395 ± 118.0 m radii (Fig. 5). Cattle on Weiderrick Ranch also appeared to select resources at a fine scale (1,400 ± 636.4) in 2011 but no selection was obvious in 2010.

Resource Selection

We obtained > 9,000 GPS telemetry locations of bison on APR ($n = 2$) and GNP ($n = 3.5$) encompassing 28 animal months during summer (June – August 2010, 2011). We obtained > 7,000 GPS telemetry locations of cattle on Barnard ($n = 2.5$) and Weiderrick ($n = 2.5$) Ranches encompassing 24 animal months during the same period (Table 2).

Bison. Resource selection by Bison on APR (Table 4) was similar across years except for distance to fencing and sagebrush communities, which were selected in 2010 and avoided in 2011. Aspect showed no clear statistically significant trends across years. Bison selected higher elevation and water sources and avoided roads and steeper slopes. Resource selection by bison in GNP within the constrained second order (within full pasture [Table 4]) and third order (within summer range [Table 4]) showed large similarities for some covariates across time and space, particularly in selection of higher elevations and water. Avoidance of steep slopes occurred at both scales and avoidance occurred for most vegetation communities, including sagebrush, upland grassland, and disturbed communities across time and space. Bison demonstrated a quadratic response to NDVI (Fig. 6) except on APR in 2011. Lastly, avoidance of fence varied across years and spatial scale.

Cattle. Resource selection by cattle on the Barnard Ranch (Table 4) and Weiderrick Ranch (Table 4) were nearly identical across time and space. All cattle demonstrated strong selection for water resources except cattle on the Barnard Ranch in 2011, however that result was not significant (0.42, $P = 0.27$). Cattle on both ranches selected low elevations and cattle on the Barnard Ranch selected areas closer to roads, however no comparison to cattle on the Weiderrick

Ranch could be made because of the lack of major roads in the area. Cattle avoided steep slopes and avoided all vegetation types in relation to riparian shrub communities. Contrary to bison, cattle demonstrated a linear response to NDVI except on the Barnard Ranch in 2010 (Fig. 6).

DISCUSSION

Interest in bison and prairie conservation has been renewed with range and wildlife managers questioning the impacts of and differences between domestic and native grazers on the landscape. In particular, bison and cattle share a common ancestry, however evolutionary changes which have taken place over the past 600,000 years (MacHugh et al. 1997), lead to questions of whether the two species are, or can, serve as ecological synonyms of one another. Furthermore, complications arise when addressing these questions due to different management strategies between bison and cattle (Plumb and Dodd 1993, Towne et al. 2005, Allred et al. 2011).

In addition, bison are effectively extinct at what is thought be ecologically relevant scales (Freese et al. 2007). However, a definition of this spatial scale for bison has, until recently, been subjective. For example, Lott (2002) approximated an ecological functional scale for a bison herd within a sustainable prairie ecosystem to be as large as 1,300,000 ha. In support of large areas, Sanderson et al. (2008) stated that landscapes > 200,000 ha are exceptional contributors to the ecological recovery of bison, yet no quantitative work has demonstrated the true scale that bison operate at until this study.

Behavior

Water developments are the primary tool used on public and private lands to improve grazing uniformity. In the U.S., ~34,000 water development projects have been implemented on Bureau of Land Management lands since 1936 (L. Pack, Bureau of Land Management, personnel communication). Despite the ecological impacts of cattle around water (Fleischner 1994), the beneficial impacts of livestock water development on wildlife species are controversial and many times unsubstantiated (Broyles 1995, Krausman et al. 2006). In particular, only Allred et al. (2011) have directly compared the influence of water resources on bison and cattle while accounting for management and environmental factors. Through the use of resource selection analyses, they were able to quantify selection (cattle) and avoidance (bison) of riparian areas and water resources, however the inclusion of behavioral observations, allows for a stronger understanding of bison physiology and thus, bison requirement of water resources on the landscape.

Similarly to Plumb and Dodd (1993), we report bison spending less time grazing than cattle. Grazing is an important ecological process for maintaining and restoring prairie landscapes through nutrient cycling (Coppock et al. 1983, Knapp et al. 1999) and increased vegetation structure and composition (Hartnett 1996, Knapp et al. 1999, Fuhlendorf et al. 2006). As a result, increased grazing time by cattle in combination with stocking levels 2 x historic bison estimates may further exacerbate homogenous grazing across the landscape resulting in a continued decline of prairie obligate species (Knopf 1996).

Historical accounts state that bison would graze for multiple days before attaining water (Dary 1979), at which time they would drink heavily (Hornaday 1887a, Dary 1979) which was exemplified by van Vuren (1979) who calculated bison water events to last 21.3 minutes in a desert landscape. Based on this information and the evolutionary adaptation of bison to the Great Plains, we predicted bison would spend less time at water than cattle. We also predicted bison in GNP would spend increased time at water than APR due to GNP's decreased water availability in the north-east corner of the park, thus imitating a historic water landscape. We report, however, shorter watering periods in GNP which may be due to high precipitation levels during the study which permitted water acquisition from temporary water sources during bison grazing periods. Even in the event of a dry year, bison TSW in GNP may not be highly influenced by water availability because water is always available within 5km, thus providing greater water availability than historical periods.

Movement

Due to differing evolutionary histories and approximations of bison space use (above), we predicted bison and cattle would show differences in the spatial scale at which they perceive their resources. As predicted, bison identified larger patch scales than cattle according to the FPT analysis. In fact, we report bison on APR identifying resource patches at a spatial scale 1.8 x that of currently available areas given fence constriction. Similarly, FPT identified resource patches for bison in GNP at 2.7 and 5.50 – 9.0 x greater than their seasonal kernel home range estimate. Interestingly, cattle selected patch sizes 2.4 – 3.5 x greater than their available pasture unit.

If FPT truly identifies the ecological resource size of bison (5,162 ± 17.7– 6,100 ± 457.1 m radii), then this may be the first quantitative evidence that bison require larger landscapes than currently provided by managers. In addition, FPT identifies a single resource patch, implying that multiple patches are necessary, particularly when considering long temporal scales which bison may have operated at historically (Seton 1929). It is important to note, however, that variance in FPT is a function of area which may be influenced by the incorporation of a defined boundary (i.e., fencing), a factor that no previous FPT study has dealt with. Specifically, area calculations would incorporate space that is unavailable for use leading to inconclusive findings.

The FPT analysis appeared to be strongly influenced by pasture size, with the largest FPT peaks coinciding with the largest transversable distance across pastures for cattle and bison on

APR (Fig. 7). Similarly, the largest scale of selection by bison in GNP coincides with the largest seasonal use of bison (Fig. 8). More importantly, the selection by cattle of spatial scales smaller (2,785 ± 230.1 - 3,040 ± 568.1 m radii) than their available pasture unit provides support to the possibility that bison spatial scales are larger than their current pasture availability on APR (Fig. 7). If this is the case, the peak in FPT by bison in GNP at ~6,100 m radii may in fact represent that spatial scale of selection by bison during the summer months. Contrary to previous FPT work in which selection has occurred within spatial scales, FPT analysis of bison may identify temporal scales, in which bison use a single patch at ~6,100 m radii (11690 ha) until overgrazed, upon which they move to another region of similar scale in the following year. This further encourages larger landscapes because the probability of increased heterogeneity increases with larger spatial scopes (Morrison 2002), thus allowing for temporal selection of resources.

Resource Selection

Cattle located on the Weiderrick and Barnard ranches demonstrated strong selection for riparian areas, lowlands, and water resources as predicted by other studies (van Vuren 1983, Gillen et al .1984, Porath et al. 2002, Allred et al. 2011). Furthermore, we report maximum areas of use to be ≤ 3 km from water for cattle (Fig. 9). Similar to previous research, we report selection of higher elevations for bison (van Vuren 1979, Phillips 2000); however we report avoidance of most vegetation communities by bison populations on APR and GNP in relation to shrub/riparian areas, a finding contrary to previous literature. These riparian areas were generally found within steep drainage areas where water availability may exist, thus explaining the selection of these areas. We were, however, unable to quantify all available water in these locations due to its semi-permanent nature.

We also report variance in selection of bison on APR for fencing. We predicted electrical fencing would result in a negative stimulus that would increase fence avoidance by bison, however avoidance varied across years. This may be a result of biotic factors across the landscape that outweighs the impact of electrical fencing. Similarly, we did not expect fencing to have an impact in GNP at any spatial scale, thus the selection of fencing at the second order may be a result of selection for other biotic factors.

We report selection for water resources by bison across location and spatial scale, a finding contrary to other work throughout the literature (van Vuren 1979, Phillips 2000, Babin 2009, Allred et al. 2011). However, our findings, similar to McHugh (1958), do support use of areas only up to 10 km from water sources (Fig. 9). Due to significant precipitation, we predicted increased avoidance of permanent water resources resulting in a decrease in water selection. Despite adjusted spatial estimates of water resources used for the RSF analysis, it is likely we underestimated the total water available for bison, which would predict greater avoidance of water due to decreased necessity to seek permanent water sources. It may be possible, however, that bison populations were located in areas consisting of high water densities which prevented avoidance if bison were unable to leave areas of significant water.

In terms of grazing, NDVI explains a linear estimate of the plant canopy cover (Tucker and Sellers 1986) allowing identification of tradeoffs between forage quality and quantity (Fryxell 1991). As a result, maximum net intake occurs at intermediate biomass where daily energy intake and forage biomass intersect (Hebblewhite et al. 2008), but this selection may be scale dependent (Wilmshurst et al. 1999, Fortin et al. 2002, Fortin et al. 2003). We report differing selection relationships in relation to NDVI by bison and cattle (Fig. 6). A quadratic relationship was fit to each species to maintain consistency within the study; however it is evident that cattle may be maximizing intake rate by selecting areas of higher forage biomass (Fig. 6). Previous work has varied across studies with cattle selecting for maximum intake (Distel et al. 1995), previously grazed areas (Silvia Cid and Brizuela 1998), higher forage quality (Bailey 1995), or areas of intersecting forage quantity and quality (Senft et al. 1985). Similar to other studies (Coppock et al. 1983, Coppedge and Shaw 1998, Bergman et al. 2001), bison selected for intermediate biomass except at the third order scale in 2011 on APR and GNP (Fig. 6). We hypothesize these differences in 2011 are due to abundant rainfall throughout the year which may have resulted in areas of high biomass with abnormally high nutrient quality, thus reducing the relationship between forage quality and quantity.

IMPLICATIONS

Current range management techniques have been designed to maximize livestock production through the use of cross fencing and uniformly distributed stock reservoirs, effectively rescaling the grazing process across the landscape in a homogenous fashion (Fuhlendorf and Engle 2001, Derner et al. 2009). However, if increased vegetation heterogeneity leading to landscape scale prairie conservation is a goal, particularly when maintaining domestic livestock as the dominant grazer, then alteration of grazing rotations may reduce the impact of increased grazing periods and localized use areas by livestock (Fuhlendorf and Engle 2001). This may be implemented through alterations to rotational grazing practice timing, duration, and intensity across spatial and temporal scales (S. Cleveland, The Nature Conservancy, personnel communication) or transportable water and mineral sources (Ganskopp 2001, Porath et al 2002, Bailey 2004).

If increased vegetation heterogeneity through bison grazing is an objective, then we have demonstrated that large landscapes may be required to facilitate bison movement and resource selection that approximate historical bison use. Although we have not quantified the pasture scale that would permit historical landscape use, we have provided the first quantitative support for the contribution of large landscape to the ecological recovery of bison. Due to the limited area of availability for bison in this study, we encourage movement analyses of these types to be adapted to non-constricted populations which may provide additional insight into the scale of bison use across time and space. Within bison conservation areas, we have identified resources of value including variable vegetation communities that occur across upland and lowland areas. Within these areas, we recommend testing the minimum spatial requirements of water by bison through water source reductions, thus encouraging long distance movements across the landscape that facilitate grazing heterogeneity similar to historic use (Hornaday 1887b).

ACKNOWLEDGMENTS

We thank the private landowners who provided access to their property and technicians K. Plourde, K. Gunderson, A. Derey-Wilson, and T. King. This material is based on work supported by the Alfred P. Sloan Foundation, American Prairie Reserve, Boone and Crockett Wildlife Conservation Program at the University of Montana, M.J. Murdock Charitable Trust, Montana Institute on Ecosystems funded through the National Science Foundation EPSCoR grant EPS-1101342, The University of Montana, Wildlife Conservation Society Research Fellowship Program, and the World Wildlife Fund-Northern Great Plains Program.

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FIGURES

Figure 1. Inventory of bison and cattle numbers from historic to current periods in North America. Bison historic estimates are estimated from commonly accepted literature on historic bison numbers. Bison estimates from 1890 to present were collected by Boyd 2003 and Gates et al. 2010. Conservation herds denote bison herds that are not managed for commercial purposes. Cattle inventory numbers were provided by U.S. Department of Agriculture and Statistics Canada.

Figure 2. Location of bison and cattle study sites. Bison herds were located at American Prairie Reserve (diamond) and Grasslands National Park (star). Two cattle herds are located in pastures adjacent to APR bison herd. The GNP is located 20 km southeast of Val Marie, SK, Canada and other sites are located 74 km south of Malta, MT, USA.

Figure 3. Location of bison and cattle pastures for bison-cattle study on and adjacent to American Prairie Reserve. White identifies artificial stock reservoirs and remnant pools within ephemeral streams.

Figure 4. Location of Grasslands National Park bison pasture for bison-cattle study. White identifies perimeter of artificial stock reservoirs and remnant pools within ephemeral streams. Dashed line identifies main ecotour route through the park.

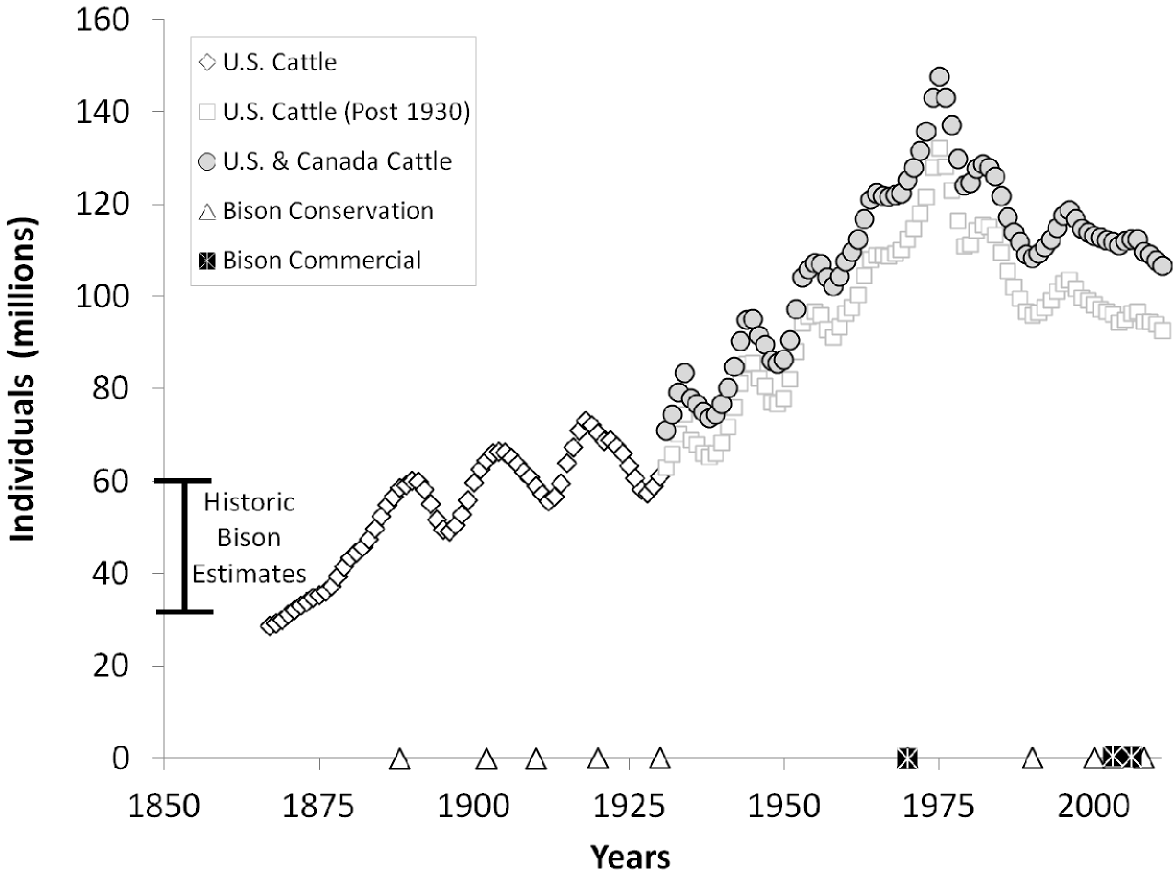
Figure 5. Results of First Passage Time (FPT) analysis for 1 female bison during summer 2010 on American Prairie Reserve (A) and in Grasslands National Park (B) and for one domestic female during summer 2010 on Barnards Ranch (C) and on Weiderrick's Ranch (D. Peaks in variance of FPT identify the spatial scale at which consumers perceive their resources. X-axis is a measure of a circles radius.

Figure 6. Probability of use for intermediate green vegetation (NDVI values) for bison on Grasslands National Park (GNP) and American Prairie Reserve (APR) and cattle on APR. Selection of NDVI was compared across entire pasture (Ann) and within summer range (Sum) on GNP. Selection was fit to a quadratic relationship for both species to identify whether selection was occurring for intermediate forage biomass.

Figure 7. Visual comparison of fence effect of First Passage Time analysis (FPT) for bison and cattle on Grasslands National Park (GNP) and American Prairie Reserve (APR). Dotted lines represent average transversable distance across pastures. Cattle on Barnard Ranch (A) demonstrate a small-scale selection within their pasture (circle). Bison on GNP (B) do not identify scales under 5,000 m radii, however, average transferable distance across the pasture coincides with secondary peaks at ~10,000 m radii supporting areas around 6,100 m radii as the scale of selection by bison in a large pasture.

Figure 8. Graphical representation of transversable distance across Grasslands National Park bison. Kernel density home range estimate (95%) overlayed on GPS locations from 2010 and 2011. Measurement lines (12 km) of transversable distance provides support to hypothesis that seasonal use is identified by FPT analysis at scales >10,000 m radii, thus ~6,000 m radii represent spatial scale use.

Figure 9. Probability of use for bison and cattle in relation to distance to water. Calculated using averaged values from RSF across years and locations for bison and cattle on GNP and APR.



◇ U.S. Cattle
□ U.S. Cattle (Post 1930)
● U.S. & Canada Cattle
△ Bison Conservation
☒ Bison Commercial
Historic Bison Estimates
Individuals (millions)
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120
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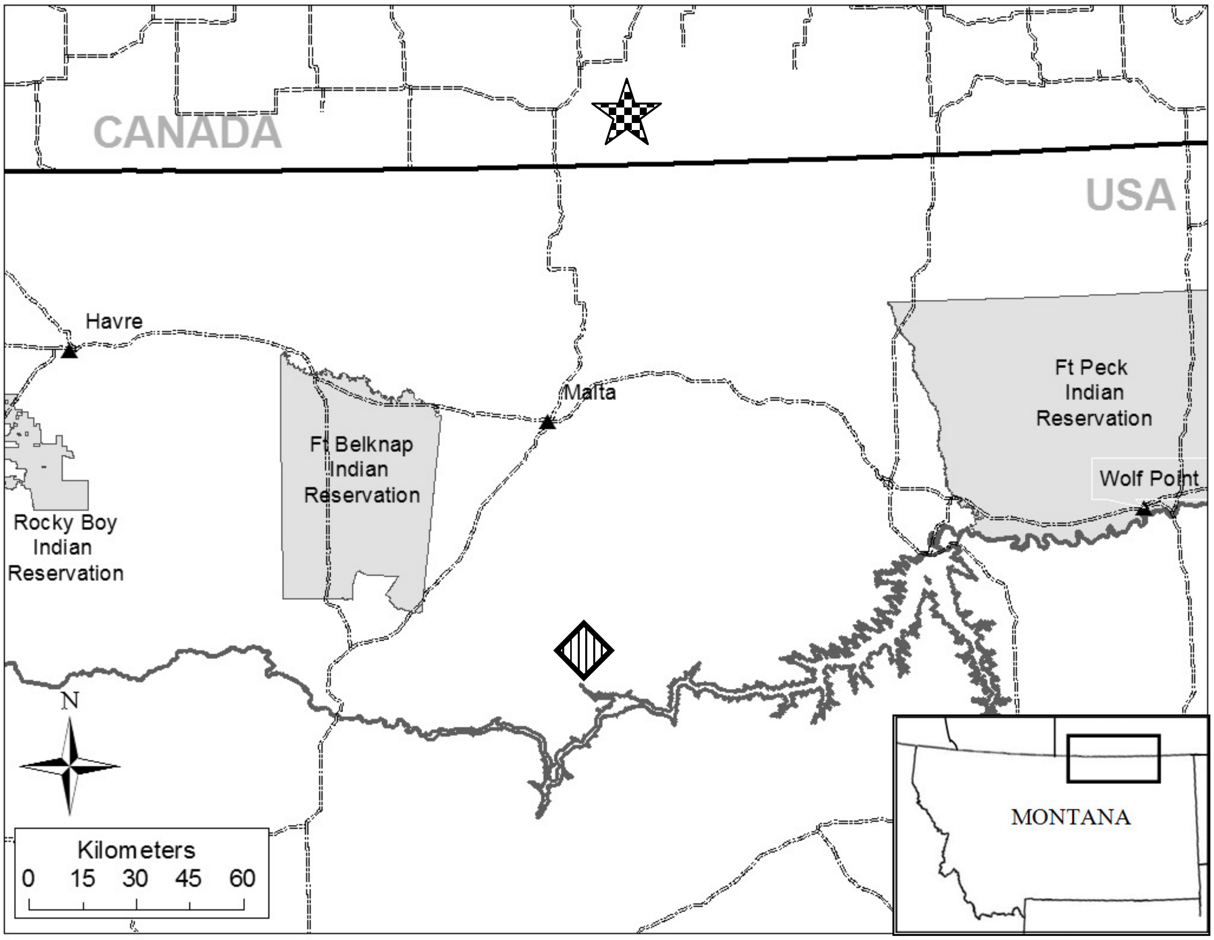
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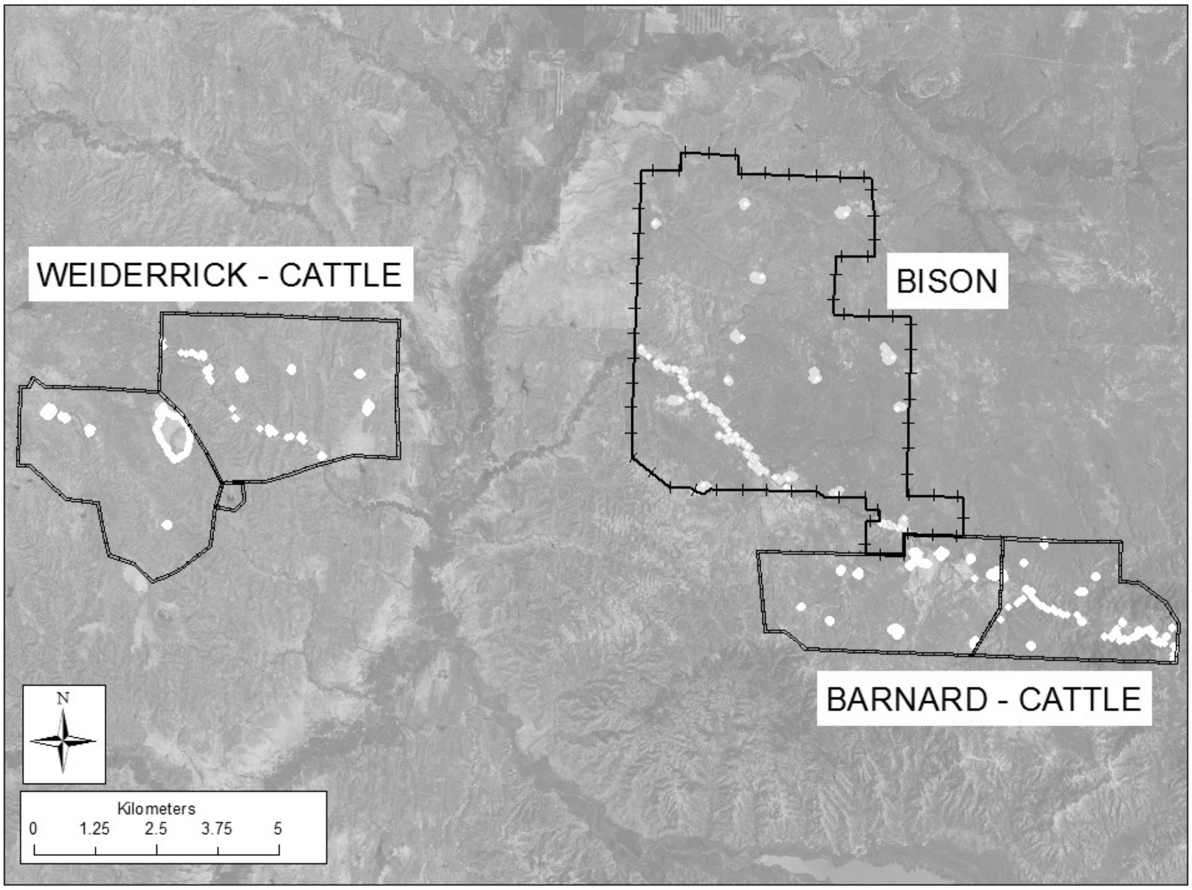
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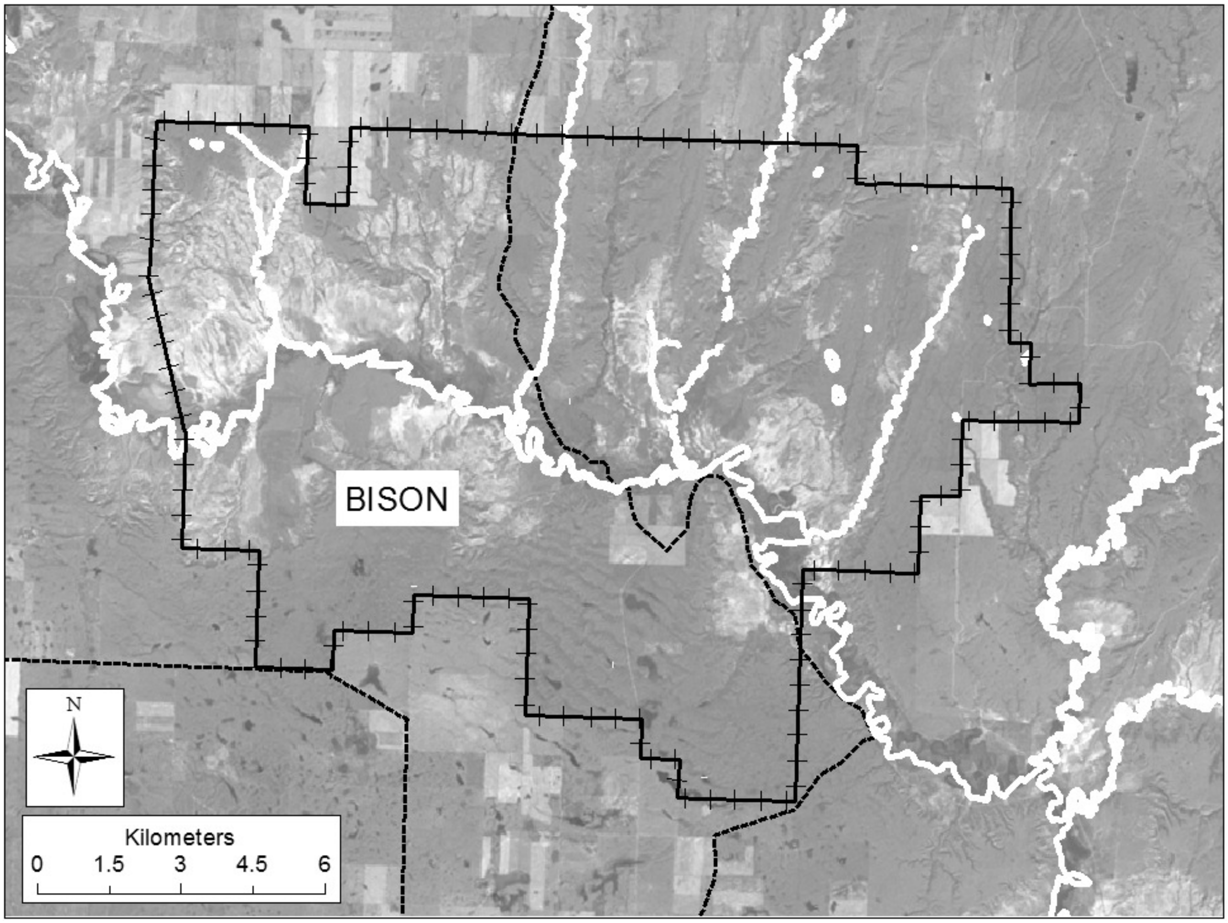
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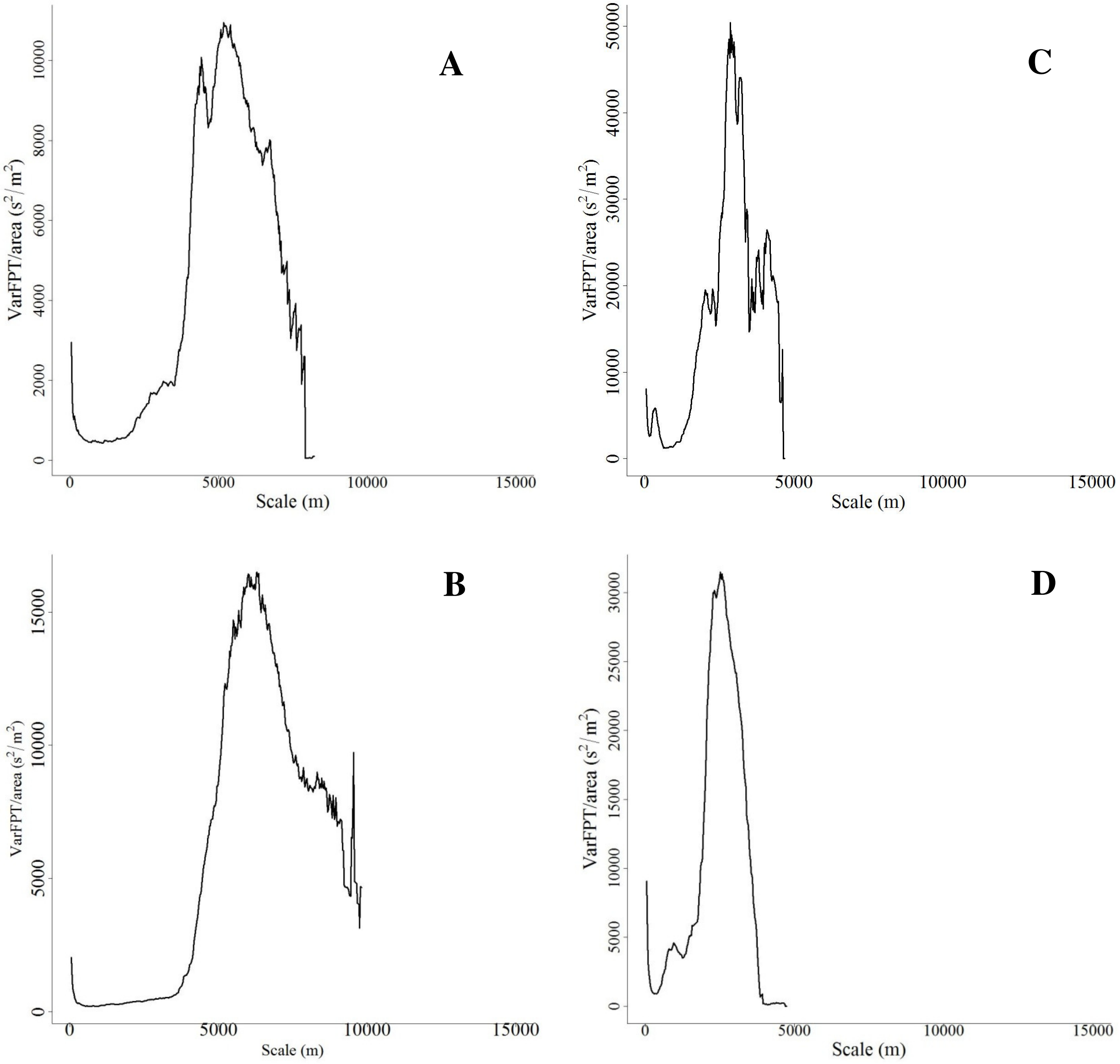
4.5
6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4000
6000
8000
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Scale (m)
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10000
15000
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0
10000
20000
30000
40000
50000
Scale (m)
0
5000
10000
15000
B
VarFPT/area (s^2/m^2)
0
5000
10000
15000
Scale (m)
0
5000
10000
15000
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30000
Scale (m)
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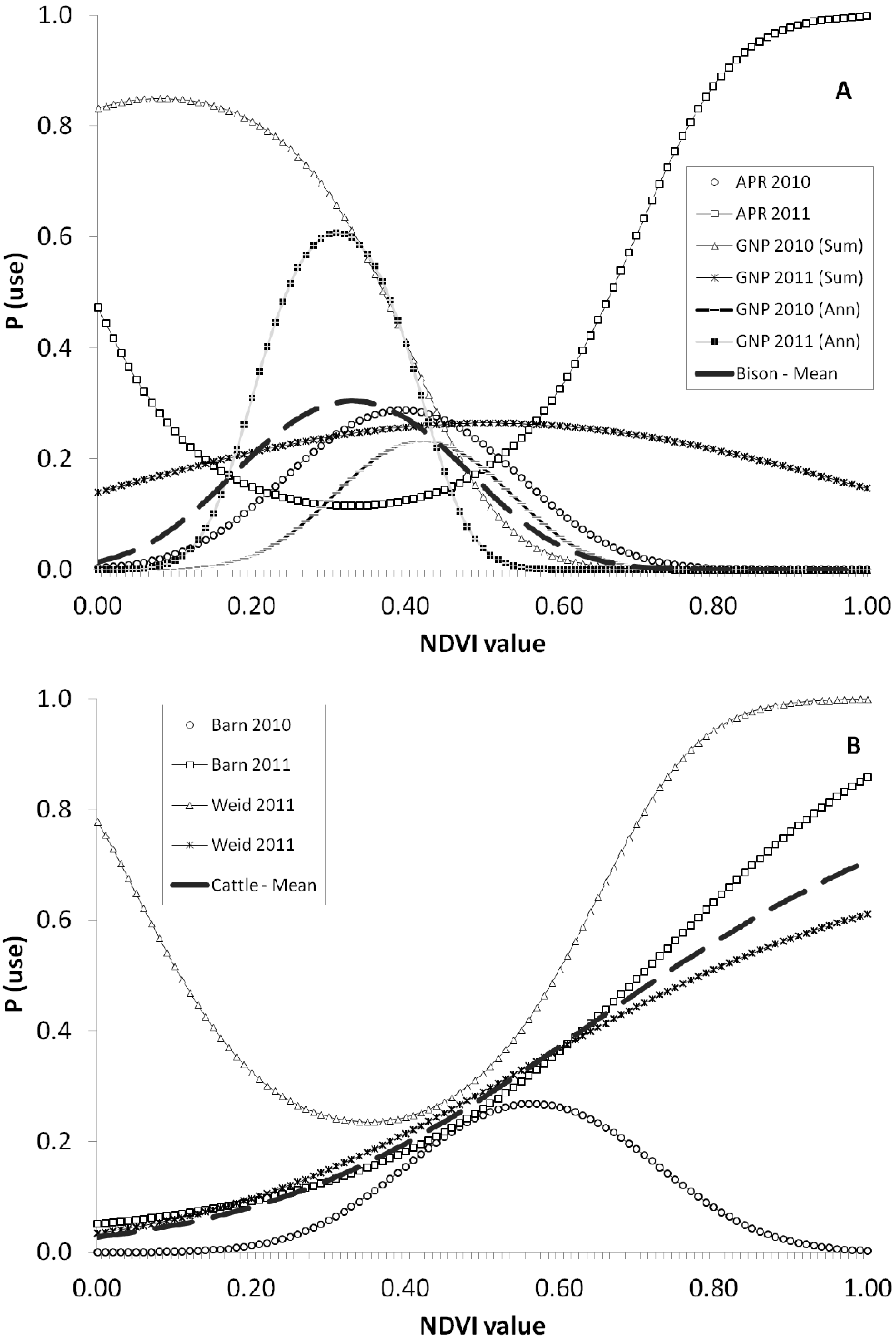
10000
15000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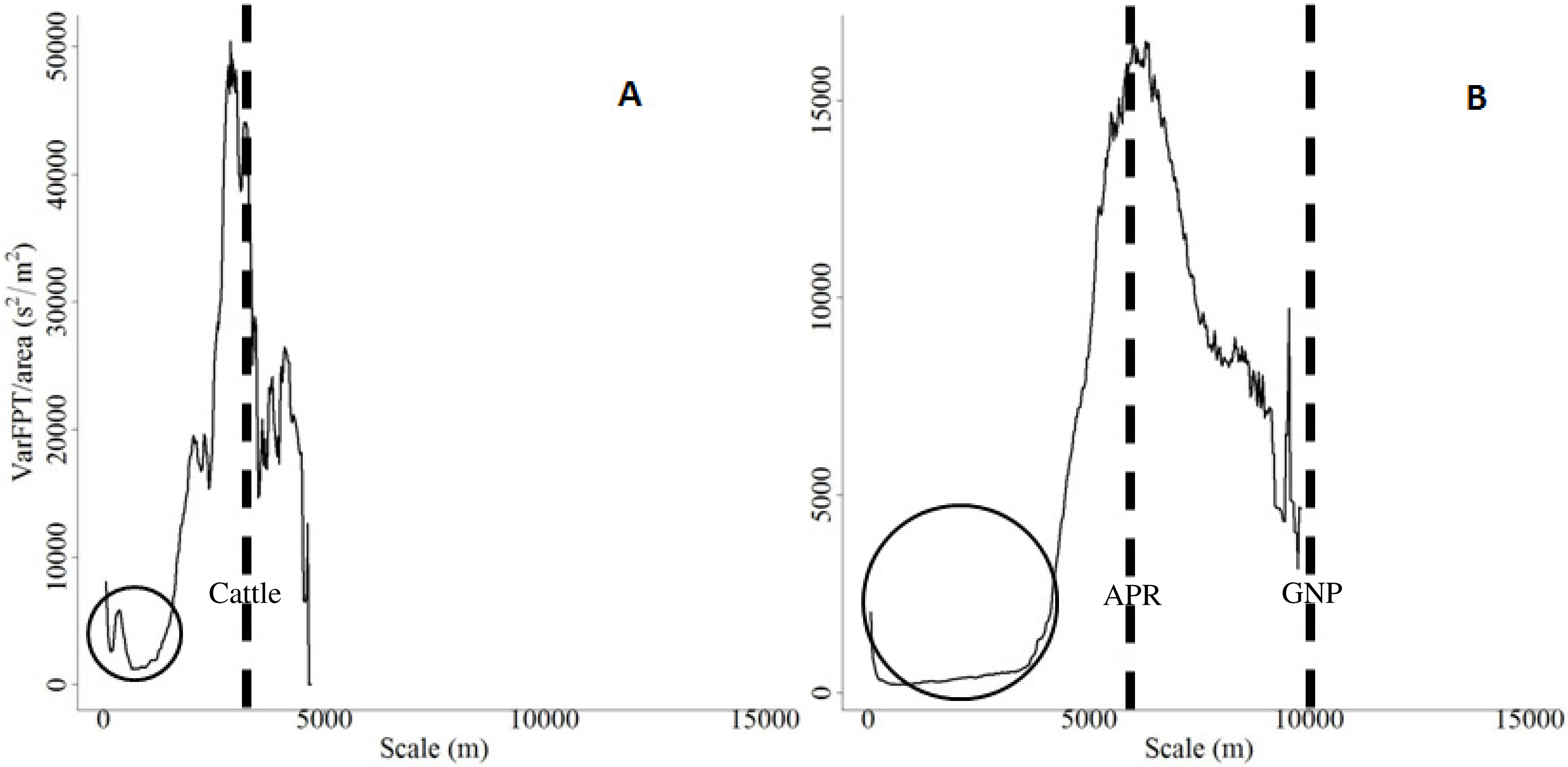
0.4
0.2
0.0
P (use)
0.00
0.20
0.40
0.60
0.80
1.00
NDVI value
A
APR 2010
APR 2011
GNP 2010 (Sum)
GNP 2011 (Sum)
GNP 2010 (Ann)
GNP 2011 (Ann)
Bison - Mean
B
Barn 2010
Barn 2011
Weid 2011
Weid 2011
Cattle - Mean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B
VarFPT/area (s²/m²)
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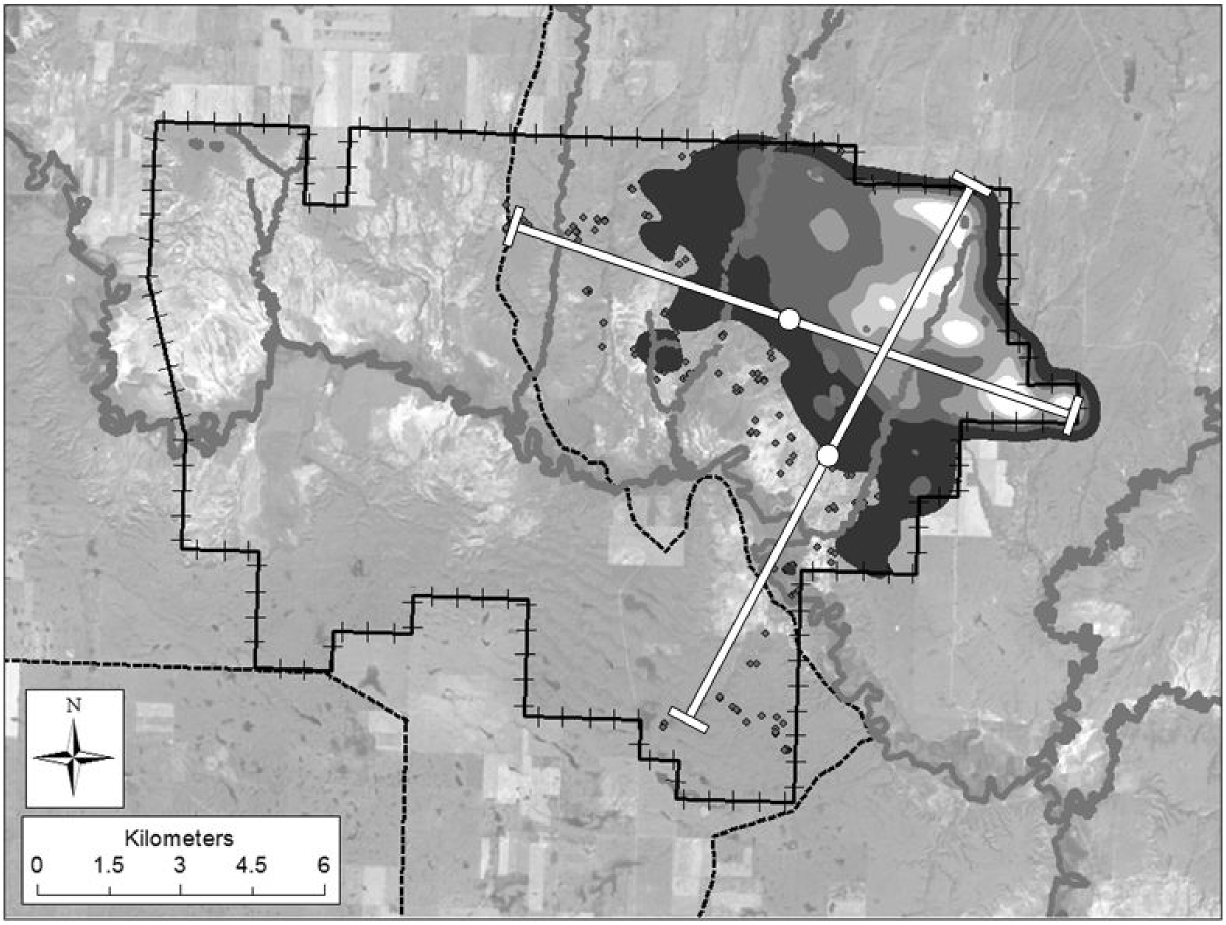
15000
Scale (m)
Cattle
APR
GNP


N
Kilometers
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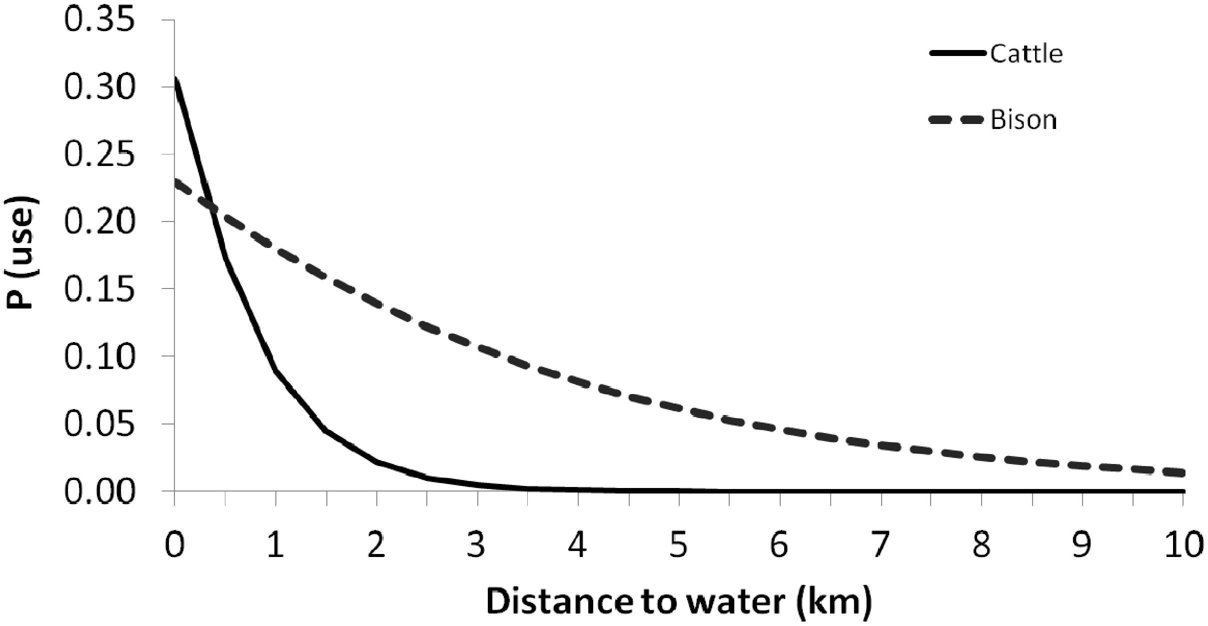
4.5
6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0.30
0.25
0.20
0.15
0.10
0.05
0.00
P (use)
0
1
2
3
4
5
6
7
8
9
10
Distance to water (km)
Cattle
Bison

Table 1. Description of grazing pastures and stocking densities for animals owned by American Prairie Reserve (APR), Parks Canada (PC), Weiderrick Ranch (WR) and Barnard Ranch (BR). Analysis was performed on annual bison range (Park) and within summer home range (NE Corner) in Grasslands National Park (GNP). The GNP is located 20 km southeast of Val Marie, SK, Canada and other sites are located 74 km south of Malta, MT, USA.

Year	Species	Owner	Pasture Name	AUM/ha
2010	Bison	APR	Box Elder	0.25
2011	Bison	APR	Box Elder	0.18
2010	Bison	PC	GNP - Park	0.11
2011	Bison	PC	GNP - Park	0.14
2010	Bison	PC	GNP - NE Corner	0.14
2011	Bison	PC	GNP - NE Corner	0.18
2010	Cattle	WR	Telegraph North	0.14
2011	Cattle	WR	Telegraph North	0.09
2011	Cattle	WR	Telegraph West	0.16
2010	Cattle	BR	Kill Woman	0.36
2011	Cattle	BR	Box Elder	0.39
2011	Cattle	BR	Kill Woman	0.49

Table 2. Collar ID, fix interval, and collection dates for female bison in Grasslands National Park (GNP) and American Prairie Reserve (APR) and collection dates for female cattle on Barnard Ranch (Br) and Weiderrick Ranch (WR).

Study Site	Collar ID	Company	Fix-Interval (hr)	Data Start	Data End	Fixes	Data Start	Data End	Fixes
				2010			2011		
GNP	1	Lotek	1	1-Jul	31-Aug	1194	1-Jun	23-Aug	1966
	2	Lotek	1	1-Jul	31-Aug	1374	--	--	--
	3	Northstar	3	1-Jul	31-Aug	479	1-Jun	31-Aug	621
	4	Northstar	3	1-Jul	31-Aug	473	1-Jun	31-Aug	610
APR	1	Lotek	2	1-Jun	31-Aug	1071	9-Jun	31-Aug	705
	2	Northstar	2	1-Jun	30-Jul	651	2-Jun[1,2]	31-Aug[1,2]	253
BR	1	Lotek	2	1-Jun	16-Jul [3]	533	18-Jun	31-Aug	535
	2	Lotek	2	--	--	--	10-Jun	31-Aug	881
	3	Lotek	2	--	--	--	10-Jun	31-Aug	855
	4	Lotek	2	--	--	--	10-Jun	31-Aug	750
WR	1	Lotek	2	9-Jul	31-Aug	642	6-Jul	31-Aug	660
	2	N / L [4]	2	9-Jul	31-Aug	716	6-Jul	31-Aug	672
	3	Lotek	2	--	--	--	6-Jul	31-Aug	663

[1] Locations were censored in cases of bison movement outside of designated study pastures: June 1 – 9, 11 – 22, July 27 – Aug. 2, Aug. 22 – 29.

[2] Collar intermittent failure occurred: July 11 – Aug. 19. Collar Replacement Aug 19.

[3] Animals moved to non-comparable rotational grazing pasture.

[4] Northstar collar (N) used in 2010, Lotek (L) in 2011

Table 3. Proportion of time of behavioral activities observed from 1 June – 31 August (2010, 2011) of bison on American Prairie Reserve (APR) and Grasslands National Park (GNP) and cattle on Barnard Ranch (BR) and Weiderrick Ranch (WR).

Behavior (%)	Bison		Cattle	
	APR	GNP	BR	WR
Grazing	0.26	0.28	0.45	0.49
Standing	0.15	0.18	0.24	0.20
Bedded	0.46	0.46	0.23	0.29
Moving	0.11	0.08	0.05	0.02
Tending	0.01	0.01	0.00	0.00
Other	0.01	0.01	0.02	0.00

Table 4. Coefficient estimates from Resource Selection Functions of summer 2010 and 2011 bison use on American Prairie Reserve (APR) and Grasslands National Park (GNP). Analysis was calculated within summer range (summer) and within annual range (annual) in GNP. Coefficient values were calculated for cattle on Barnard and Weiderrick Ranches. Dashes identify non-significant values. Variables unavailable for calculation are identified by NA. Significance at > 0.05.

	Bison						Cattle			
	APR		GNP (Summer)		GNP (Annual)		Barn		Weid	
Variables	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
North Aspect	0.2262	--	--	-0.1892	-0.3833	-0.2953	--	0.2435	--	--
South Aspect	--	--	--	--	NA	-0.2882	--	0.3922	0.4299	0.2667
West Aspect	0.2135	--	--	--	NA	0.2608	--	0.2472	0.4456	--
Distance to fence	0.3388	--	-0.5995	--	0.1921	-0.6575	--	--	--	-0.3461
Distance to road	0.1706	0.1089	0.1383	0.112	0.6053	--	--	1.6972	NA	NA
Distance to water	-0.4416	-0.5284	-0.1219	--	-0.4284	-0.3973	-0.5649	0.4258	-0.9565	-1.4969
Elevation	16.0968	11.95	5.4866	6.0146	18.3053	33.146	--	--	26.8354	--
NDVI	25.6805	9.666	-17.228	--	37.6806	--	--	--	--	17.963
NDVI^2	-32.38	--	--	--	-43.355	55.0786	--	--	--	--
Slope	-0.1373	-0.0617	-0.0739	-0.0574	-0.0445	--	-0.0832	0.1554	-0.0728	-0.0455
Vegetation										
Disturbed	NA	--	-1.3217	-1.2518	-1.8345	-1.5641	NA	NA	NA	NA
Eroded	0.8378	--	-0.3617	-0.5754	-1.6471	-3.4417	--	0.9504	-1.616	14.1033
Upland grassland	NA	--	--	-0.4645	-0.2817	--	--	--	-0.743	-1.1259
Sloped grassland	--	--	-0.3539	-0.4743	-0.2692	--	--	1.4182	--	-0.8715
Sagebrush	0.3814	-1.073	--	-0.5006	--	-1.679	--	0.9429	--	-0.7111
Treed	NA	NA	NA	NA	--	--	-1.1957	1.7603	NA	NA
Water bodies	--	--	NA	NA	NA	NA	NA	--	--	0.9442
Valley grassland	NA	NA	-0.3328	--	0.5064	-0.4314	NA	NA	NA	NA
Unknown	--	--	2.3274	--	-1.1978	-5.7184	--	--	--	--

Appendix A

Vegetation Classification

Vegetation classifications on GNP were based on field work completed by ground sampling (R. Sissons, GNP, unpublished data). Vegetation classifications on APR were designed to allow for comparison between vegetation communities on GNP and were achieved through contracted service. We delineated 10 vegetation communities (e.g., eroded, upland grassland, disturbed, sloped grassland, shrub/riparian, valley grassland, treed, unclassified, sage-brush, and water bodies). Classification was achieved using aerial photo interpretation of 1 m resolution true-color ortho-imagery acquired in 2009. Guiding this classification was the 30m resolution Gap Analysis Program (U.S. Geological Survey 2011), Landsat imagery (NASA 2009) and field site visits (M. Kohl, unpublished data). Class delineations were further enhanced using Landsat spectral signatures derived from field sites and 250 m^2 Normalized Difference Vegetation Index (NDVI [Moderate Resolution Imagine Spectroradiometer {Huete et al. 2002}]) time series, from 2009 and 2010, to define habitat specific phenology patterns.

Appendix B

Grazing Time and Intensity

Description of stocking densities for animal owned by American Prairie Reserve (APR), Parks Canada (PC), Weiderrick Ranch (WR) and Barnard Ranch (BR). Analysis was performed on annual bison range (Park) in Grasslands National Park (GNP; 20 km southeast of Val Marie, SK, Canada; other sites are 74 km south of Malta, MT, USA) and within summer range (NE Corner).

Year	Species	Owner	Pasture Name	Pasture Size (ha)	Start Date	End Date	Months	Number*	AUMs*	AUM/ha
2010	Bison	APR	Box Elder	3555	15-May	15-Oct	5.0	215	900	0.25
2011	Bison	APR	Box Elder	3555	15-May	15-Oct	5.0	147	650	0.18
2010	Bison	PC	GNP - Park	18,153	1-Jan	31-Dec	12.0	147	1965	0.11
2011	Bison	PC	GNP - Park	18,153	1-Jan	31-Dec	12.0	195	2575	0.14
2010	Bison	PC	GNP - NE Corner	4,200	15-May	1-Sep	3.5	147	573	0.14
2011	Bison	PC	GNP - NE Corner	4,200	15-May	1-Sep	3.5	195	751	0.18
2010	Cattle	WR	Telegraph North	1408	1-Jul	2-Sep	2.0	100	200	0.14
2011	Cattle	WR	Telegraph North	1408	1-Jul	9-Aug	1.3	100	130	0.09
2011	Cattle	WR	Telegraph West	1090	9-Aug	1-Oct	1.7	100	170	0.16
2010	Cattle	BR	Kill Woman	777	15-May	15-Jul	2.0	140	280	0.36
2011	Cattle	BR	Box Elder	1000	15-May	11-Aug	2.8	140	392	0.39
2011	Cattle	BR	Kill Woman	777	11-Aug	15-Oct	2.7	140	378	0.49

[1] Cattle Population Estimated at Pasture Release (May 1) - Total Cow/Calf Pairs

[2] Animal Unit Month Values were calculated for bison as follows:

Cow (lactating): 1:00
Cow (adult non-lactating): 0.90
Cow (dry, 12-36 months): 0.80
Bull (12-36 months): 1.20
Bull (Adult): 1.50

Appendix C

Resource Selection Function - APR

Resource Selection Function models incorporating all abiotic, biotic, and anthropogenic variables for female bison from 1 June – 31 August (2010, 2011) on American Prairie Reserve. Bold identify statistically significant variables. Asterisks identify similar significant responses across years and underlines identify differing significant responses across years.

	2010			2011		
Variables	β	SE	*p*	β	SE	*p*
Intercept	**-19.0516**	**2.2703**	**<0.0005**	**-12.9700**	**2.9820**	**<0.0005**
North aspect	**0.2262**	**0.1078**	**0.0358**	-0.0081	0.1317	0.9510
South aspect	0.1464	0.1074	0.1729	0.0656	0.1326	0.6209
West aspect	**0.2135**	**0.1018**	**0.0361**	0.1071	0.1213	0.3771
Distance to fence	**0.3388**	**0.0551**	**<0.0005**	-0.1354	0.0754	0.0728
Distance to road *	**0.1706**	**0.0363**	**<0.0005**	**0.1089**	**0.0475**	**0.0219**
Distance to water *	**-0.4416**	**0.1078**	**<0.0005**	**-0.5284**	**0.1336**	**<0.0005**
Elevation *	**16.0968**	**2.5866**	**<0.0005**	**11.9500**	**3.3900**	**<0.0005**
NDVI *	**25.6805**	**4.4944**	**<0.0005**	**9.6660**	**4.8570**	**0.0466**
NDVI^2	**-32.3796**	**5.4012**	**<0.0005**	-6.8040	5.6980	0.2324
Slope *	**-0.1373**	**0.0184**	**<0.0005**	**-0.0617**	**0.0201**	**0.0021**
Vegetation						
Disturbed	--	--	--	1.62E+01	3.48E+03	0.9963
Eroded	**0.8378**	**0.1792**	**<0.0005**	0.0924	0.1750	0.5976
Upland grassland	--	--	--	1.61E+01	2.85E+03	0.9955
Sloped grassland	0.1389	0.1561	0.3736	-0.2501	0.1391	0.0722
Sagebrush	**0.3814**	**0.1159**	**0.0010**	**-1.0730**	**0.1047**	**<0.0005**
Treed	--	--	--	--	--	--
Water bodies	-0.2262	0.5268	0.6676	-0.0706	0.3858	0.8549
Valley grassland	--	--	--	--	--	--
Unknown	-0.4827	0.4062	0.2347	-14.8100	324.8000	0.9636

Appendix D

Resource Selection Function – GNP (Summer)

Resource Selection Function models incorporating all abiotic, biotic, and anthropogenic variables for female bison within their summer home range from 1 June – 31 August (2010, 2011) on Grasslands National Park. Bold identify statistically significant variables. Asterisks identify similar significant responses across years and underlines identify differing significant responses across years.

	2010			2011		
Variables	β	SE	p	β	SE	p
Intercept	**3.3270**	**1.3680**	**0.0150**	**-7.0878**	**1.3829**	**<0.0005**
North aspect	0.0347	0.0822	0.6727	**-0.1892**	**0.0757**	**0.0125**
South aspect	-0.0351	0.0666	0.5983	-0.0368	0.0598	0.5377
West aspect	0.0098	0.0599	0.8705	-0.0050	0.0552	0.9283
Distance to fence	**-0.5995**	**0.0335**	**<0.0005**	0.0384	0.0281	0.1711
Distance to road *	**0.1383**	**0.0203**	**<0.0005**	**0.1120**	**0.0220**	**<0.0005**
Distance to water	**-0.1219**	**0.0562**	**0.0301**	0.0885	0.0556	0.1113
Elevation *	**5.4866**	**0.9147**	**<0.0005**	**6.0146**	**0.9679**	**<0.0005**
NDVI	**-17.2281**	**4.7120**	**<0.0005**	4.7289	4.5902	0.3029
NDVI^2	-5.6198	5.3237	0.2911	-5.9859	4.5929	0.1925
Slope *	**-0.0739**	**0.0077**	**<0.0005**	**-0.0574**	**0.0069**	**<0.0005**
Vegetation						
Disturbed *	**-1.3217**	**0.1968**	**<0.0005**	**-1.2518**	**0.1651**	**<0.0005**
Eroded *	**-0.3617**	**0.1520**	**0.0174**	**-0.5754**	**0.1321**	**<0.0005**
Upland grassland	-0.1902	0.1064	0.0737	**-0.4645**	**0.0999**	**<0.0005**
Sloped grassland *	**-0.3539**	**0.1103**	**0.0013**	**-0.4743**	**0.0997**	**<0.0005**
Sagebrush	-0.1319	0.1328	0.3206	**-0.5006**	**0.1202**	**<0.0005**
Treed	--	--	--	--	--	--
Water bodies	--	--	--	--	--	--
Valley grassland	**-0.3328**	**0.1464**	**0.0230**	-0.0872	0.1279	0.4957
Unknown	**2.3274**	**0.8215**	**0.0046**	0.4875	0.6569	0.4581

Appendix E

Resource Selection Function – GNP (Annual)

Resource Selection Function models incorporating all abiotic, biotic, and anthropogenic variables for female bison within their annual range from 1 June – 31 August (2010, 2011) on Grasslands National Park. Bold identify statistically significant variables. Asterisks identify similar significant responses across years and underlines identify differing significant responses across years.

	2010			2011		
Variables	β	SE	p	β	SE	p
Intercept	**-24.2664**	**1.5555**	**<0.005**	**21.8502**	**1.6601**	**<0.005**
North aspect *	**-0.3833**	**0.0777**	**<0.005**	**-0.2953**	**0.1251**	**0.0182**
South aspect	-0.0312	0.0659	0.6359	**-0.2882**	**0.0999**	**0.0039**
West aspect	0.0623	0.0609	0.3068	**0.2608**	**0.0948**	**0.0059**
Distance to fence	**0.1921**	**0.0285**	**<0.005**	**-0.6575**	**0.0488**	**<0.005**
Distance to road	**0.6053**	**0.0191**	**<0.005**	-0.0097	0.0230	0.6726
Distance to water *	**-0.4284**	**0.0550**	**<0.005**	**-0.3973**	**0.0759**	**<0.005**
Elevation *	**18.3053**	**0.9264**	**<0.005**	**33.1460**	**1.4462**	**<0.005**
NDVI	**37.6806**	**3.5613**	**<0.005**	11.9903	6.3138	0.0576
NDVI^2	**-43.3549**	**4.1541**	**<0.005**	**-55.0786**	**7.2307**	**<0.005**
Slope	**-0.0445**	**0.0076**	**<0.005**	-0.0088	0.0111	0.4256
Vegetation						
Disturbed *	**-1.8345**	**0.1857**	**<0.005**	**-1.5641**	**0.2247**	**<0.005**
Eroded	**-1.6471**	**0.1429**	**<0.005**	**-3.4417**	**0.1784**	**<0.005**
Upland grassland	**-0.2817**	**0.1075**	**0.0088**	0.2053	0.1650	0.2136
Sloped grassland	**-0.2692**	**0.1106**	**0.0149**	0.1622	0.1682	0.3349
Sagebrush	-0.0263	0.1228	0.8307	**-1.6790**	**0.1750**	**<0.005**
Treed	-12.8528	184.6161	0.9445	-14.1364	332.9162	0.9661
Water bodies	--	--	--	--	--	--
Valley grassland	**0.5064**	**0.1438**	**<0.005**	**-0.4314**	**0.1930**	**0.0254**
Unknown *	**-1.1978**	**0.3622**	**0.0009**	**-5.7184**	**0.5052**	**<0.005**

Appendix F

Resource Selection Function – Barnard Ranch

Resource Selection Function models incorporating all abiotic, biotic, and anthropogenic variables for female cattle from 1 June – 31 August (2010, 2011) on Barnard Ranch. Bold identify statistically significant variables. Asterisks identify similar significant responses across years and underlines identify differing significant responses across years.

	2010			2011		
Variables	β	SE	p	β	SE	p
Intercept	5.1889	6.3004	0.4102	4.8875	1.7845	0.0062
North aspect	0.4212	0.1606	0.0087	**-0.2435**	**0.0571**	**<0.005**
South aspect	-0.1453	0.1482	0.3270	**0.3922**	**0.0707**	**<0.005**
West aspect	0.2431	0.1553	0.1175	**0.2472**	**0.0619**	**<0.005**
Distance to fence	0.0978	0.2302	0.6709	0.1396	0.0804	0.0825
Distance to road	0.4235	0.3813	0.2666	**-1.6972**	**0.1188**	**<0.005**
Distance to water *	**-0.5649**	**0.0933**	**<0.005**	**-0.4258**	**0.0322**	**<0.005**
Elevation	-16.3355	5.1045	0.0014	-6.5159	1.9764	0.0010
NDVI	22.9438	21.7654	0.2918	-1.3184	3.0504	0.6656
NDVI^2	-9.2069	23.4070	0.6941	9.2915	3.6125	0.0101
Slope *	**-0.0832**	**0.0171**	**<0.005**	**-0.1554**	**0.0124**	**<0.005**
Vegetation						
Disturbed	--	--	--	--	--	--
Eroded	0.2154	0.2649	0.4162	**-0.9504**	**0.0866**	**<0.005**
Upland grassland	-0.4100	0.5788	0.4788	-1.5994	0.7328	0.0291
Sloped grassland	-0.6679	0.2809	0.0174	**-1.4182**	**0.0996**	**<0.005**
Sagebrush	-0.3051	0.1337	0.0225	**-0.9429**	**0.0720**	**<0.005**
Treed *	**-1.1957**	**0.2198**	**<0.005**	**-1.7603**	**0.2753**	**<0.005**
Water bodies	--	--	--	0.4945	0.3756	0.1879
Valley grassland	--	--	--	--	--	--
Unknown	-0.1432	1.1333	0.8994	0.6246	0.4612	0.1756

Appendix G

Resource Selection Function – Weiderrick Ranch

Resource Selection Function models incorporating all abiotic, biotic, and anthropogenic variables for female cattle from 1 June – 31 August (2010, 2011) on Weiderrick Ranch. Bold identify statistically significant variables. Asterisk identify similar significant responses across years and underlines identify differing significant responses across years.

	2010			2011		
Variables	β	SE	p	β	SE	p
Intercept	**18.0206**	**2.1093**	**<0.005**	-0.9051	1.3898	0.5149
North aspect	0.2636	0.0976	0.0070	0.2274	0.0738	0.0021
South aspect *	**0.4299**	**0.0886**	**<0.005**	**0.2667**	**0.0674**	**<0.005**
West aspect	**0.4456**	**0.0967**	**<0.005**	-0.0829	0.0845	0.3268
Distance to fence	-0.0856	0.1018	0.4002	**-0.3461**	**0.0841**	**<0.005**
Distance to road	--	--	--	--	--	--
Distance to water *	**-0.9565**	**0.1395**	**<0.005**	**-1.4969**	**0.1081**	**<0.005**
Elevation	**26.8354**	**2.4980**	**<0.005**	-5.1135	1.7647	0.0038
NDVI	3.9713	8.1755	0.6271	**17.9630**	**2.5820**	**<0.005**
$NDVI^2$	5.2424	12.6459	0.6785	11.2836	3.7787	0.0028
Slope*	**-0.0728**	**0.0156**	**<0.005**	**-0.0455**	**0.0128**	**<0.005**
Vegetation						
Disturbed	--	--	--	--	--	--
Eroded	**-1.6160**	**0.3759**	**<0.005**	14.1033	272.0897	0.9587
Upland grassland *	**-0.7430**	**0.1370**	**<0.005**	**-1.1259**	**0.1287**	**<0.005**
Sloped grassland	-0.3343	0.1220	0.0061	**-0.8715**	**0.0949**	**<0.005**
Sagebrush	-0.2816	0.1635	0.0851	**-0.7111**	**0.1079**	**<0.005**
Treed	--	--	--	--	--	--
Water bodies	0.5608	0.3289	0.0882	**0.9442**	**0.1888**	**<0.005**
Valley grassland	--	--	--	--	--	--
Unknown	0.0664	0.7055	0.9251	-0.9346	0.5058	0.0646

Appendix H

Summary of Results

	Bison		Cattle	
Activity	**APR**	**GNP**	**Barnard**	**Weiderrick**
Behavior				
Grazing (% time)	26.2	27.5	49.1	45.0
Movement (% time)	11.1	7.6	1.7	5.0
Time spent at water (s)	132.3	84.3	193.7	266.4
Movement				
Movement rate (m/s)	0.045	0.111	0.029	0.035
Movement rate (relative to cattle)	151%	199%		
Large spatial scale (radii km)	--	9.904	2.785	3.040
Small spatial scale (radii km)	5.162	6.100	0.395	1.400
Resource Selection (Selection/Avoidance)				
Elevation	-	-	-	-
Slope	-	-	-	-
Grassland vegetation	+	-	-	-
Sagebrush vegetation	Unknown	-	-	-
Fence (distance to)	Unknown	Unknown	+	-
Road (distance to)	+	+	Unknown	
Water (distance to)	-	-	-	-

Appendix I

Spatial Use

Kernel density home range estimation of bison and cattle use on American Prairie Reserve (APR; top) and bison use in Grasslands National Park (GNP; bottom). Kernels (e.g, 95, 75, 50, 25, 10%) are overlayed on GPS locations from summer (2010, 2011). Water (e.g, ephemeral streams, artificial reservoirs) is represented in white on APR and grey on GNP.