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THE SPATIAL ECOLOGY OF BISON (BISON BISON) IN MULTIPLE  
CONSERVATION HERDS ACROSS THE AMERICAN WEST

A Thesis Presented to the  
Graduate Faculty of the Biology Department  
and the  
Faculty of the Graduate College  
University of Nebraska

In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science  
University of Nebraska at Kearney


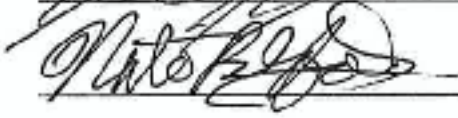
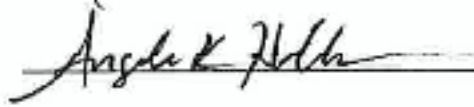
By  
Robert J Ritson Jr.

April 2019

## THESIS ACCEPTANCE

Acceptance for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree Biology, University of Nebraska at Kearney.

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## ABSTRACT

Historically, American bison (*Bison bison*) occupied one of the largest ranges and widest niches of any North American mammal and are considered to play a keystone role in the ecosystem. Though spared from complete extinction due to overhunting and habitat loss, bison are considered by some to be ecologically extinct. Contemporary management paradigms (e.g. fencing, artificial feeding, and frequent human interaction) heavily influence spatial patterns of today's bison but has yet to be accounted for in their conservation. We assessed space-use patterns of two free-ranging bison herds and three captive herds at two spatial scales, using autocorrelated kernel density estimated home range and radius of maximum variance in first-passage time, over three temporal scales (annual, growing, and non-growing). We also calculated resource selection functions to assess annual habitat preferences. Free-range bison had significantly larger home ranges across seasons than the captive bison ( $p < 0.05$ ), but no differences were apparent for first-passage time between herd categories or seasons. Landscape covariates seemed to explain home range patterns but not first-passage times. In the order of decreasing resource selection strength, we found that bison generally preferred areas which had gentle slopes, higher elevations, and greater vegetation productivity. However, the free-range herds notably differed in road and vegetation productivity preferences by selecting for farther proximities to roads and intermediate levels of NDVI compared to captive bison. Our results suggest that management practices may prevent bison from responding to seasonal landscape changes, which may have ecological consequences for this historically nomadic herbivore. Understanding the general patterns in resource use of bison and

accounting for differences influenced by management practices can help to improve bison conservation efforts. Although sociopolitical realities currently prevent bison restoration at a continental scale, managers should strive towards increasing available space for bison where possible in order to replicate historical ecological processes.

## DEDICATION

I would like to dedicate this work to my parents, Robert Ritson Sr. and Sharon Ritson, for instilling in me a passion for the outdoors and learning about the natural world. You have always encouraged me in all of my pursuits. Your love and support mean more to me than you can ever know.

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I would like to thank the following people and organizations who provided the bison location which made my research possible. I would like to thank Kent Hersey and Justin Shannon at the Utah Department of Natural Resources, Division of Wildlife Resources for providing the Henry Mountains and Book Cliffs bison data, The Nature Conservancy and Kate Schoenecker with the United States Geological Service for the Medano-Zapata Ranch data, a'Lisa McAnally at Texas State University and Donald Beard with Texas Parks & Wildlife for the Texas State Bison Herd data at Caprock Canyons State Park, as well as Damien Austin and Kyran Kunkel at the American Prairie Reserve and World Wildlife Fund for making their bison GPS data available for this project.

My deepest love and thanks go to my amazing fiancée Cindy. Though we are not strangers to distance, this chapter has been one of our most challenging to date. You are the voice that gives me confidence and the hand that helps me when I fall. Our shared love for each other, science, and the natural world makes every day an adventure.

Robert J Ritson Jr.



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## Chapter 1: Introduction

Upon the arrival of Europeans, North America was home to an estimated 30 million bison (*Bison bison*) from Alaska to northern Mexico (Bates and Hersey 2016). Overhunting dwindled the population of known animals to 1,644 by the year 1903. Most of the survivors existed in privately owned herds and zoos. Bison endured in two wild populations which included Yellowstone National Park in Wyoming, USA and Wood Buffalo National Park in Alberta, Canada (Meagher 1986). Since then, bison have slowly been reintroduced to parts of their former range. Due to the efforts of numerous private individuals, conservation organizations, and government and tribal agencies, there are approximately 500,000 bison in the United States today (Sanderson et al. 2008). However, the majority of these are in commercially raised herds while fewer than 11,000 bison exist on public lands for the purpose of conservation (Bates and Hersey 2016). There are two major types of bison conservation herds: free-range and captive. Free-range bison typically occur in large tracts of relatively contiguous habitat which are not enclosed by fences, thus allowing for more natural movement patterns. The term captive bison will refer to herds which live completely within fenced areas which encompass either a single pasture or are moved between multiple pastures, consequently restricting movements and pre-defining available space and habitat. This diversity of management strategies has allowed for the continued development of additional bison conservation herds which further bolsters their population.

Although they are no longer in danger of numeric extinction and widely celebrated as a conservation success (Sanderson et al. 2008), the future of bison in North

America is far from certain. The population crash over a century ago reduced bison genetic variation, which could lead to inbreeding depression. Several remaining bison herds were crossbred with cattle during their recovery, which has resulted in cattle gene introgression in bison genomes (Kolipinski et al. 2014). In fact, very few bison conservation herds are free from introgression (Ranglack et al. 2015). An association between mitochondrial cattle DNA and reduced body size in bison has been detected (Douglas et al. 2011). Furthermore, anthropomorphic selection of larger, more docile bison in commercial herds may also negatively alter bison genetics (Kolipinski et al. 2014). Herds raised for markets are intentionally bred for meat production and ease of handling which may reduce evolutionary and ecologically favorable behaviors (Freese et al. 2007). While the objectives of conservation herds are different from commercial production, management similarities could inadvertently alter the natural tendencies of bison within their historic ecosystems.

Local circumstances of bison occurrence may also influence how they use space and resources. The former range of bison in North America encompassed a diversity of ecoregions, each with unique vegetation communities and climatic conditions (Omernik 1987) which may influence bison habitat preferences. For example, bison seem to prefer close proximities to water in northern Montana (Kohl et al. 2013a) but not in southern Utah (Van Vuren 1979). However, other habitat features may be universally important to bison such as reduced woody vegetation (Ranglack and du Toit 2015a; Schoenecker et al. 2015) and gentle terrain slopes (Van Vuren 2001; Kohl et al. 2013a). In addition to influencing preference strength, availability of resources could also affect the amount of

space bison will require. The home range sizes of bison seem to decrease when more forage is locally available (Van Vuren 1983; Larter and Gates 1994; Krasińska et al. 2000). Bison have also been documented to respond to temporal variations in forage availability by increasing their range during the winter relative to summer (Merkle, Cherry, et al. 2015). However, movement can also become more difficult in the winter for bison when snow accumulation, is high which could lead to relative decreases in space use (Krasińska et al. 2000). Understanding the ecological features of bison spatial patterns is important for their conservation, but the influence of anthropogenic characteristics must also be considered.

Following their near extinction, ranching, agriculture and urbanization fragmented the former range of bison. Though bison populations are increasing in number, land-use conflict is likely to constrain their spatial patterns. When unrestricted, bison are seasonally migratory and can travel as far as 240 km between habitats (Meagher 1986) which could require an estimated 2,000 km<sup>2</sup> or more of continuous space (Sanderson et al. 2008). The effect of fences on the space use of captive herds is illustrated by their correlation with reserve size (Kohl et al. 2013a). Vehicles and other human presences have also been documented to increase daily movements of bison when disturbances were frequent (Fortin and Andruskiw 2003). However, studies of bison spatial patterns often focus on either captive bison or free-range bison but seldom compare the impacts of management type on the extent of space use or selection of habitat. An assessment of bison spatial patterns across these management types and over a variety of landscape

features is necessary to further our understanding of the abiotic, biotic, and anthropogenic influences of space and resource use.

### *Study Areas*

In order to address the multitude of influences on bison space use, it was necessary to acquire location data from herds with a diversity of local environmental characteristics and management restrictions. This study examined five bison conservation herds which occurred in four distinct ecoregions spanning approximately 1,600 km of a north-south latitudinal gradient. These were comprised of two free-range and three captive herds, including the fenced Texas State Bison Herd at Caprock Canyon State Park in Texas, Medano-Zapata Ranch at San Luis Valley in Colorado, and the American Prairie Reserve in Montana, as well as the free-ranging Henry Mountains and Book Cliffs bison herds in Utah. The ecoregions included Southwestern Tablelands (Caprock Canyon), Northwestern Great Plains (American Prairie Reserve), Colorado Plateau (Book Cliffs and Henry Mountains), and Arizona/New Mexico Plateau (Medano-Zapata Ranch; Omernik 1987)

#### Caprock Canyons, TX

Captive

The Texas State Bison Herd (34°26'N, 101°3'W; Figure 1.1) at Caprock Canyon State Park was established with 36 bison descended from five wild bison captured in the 1880s and currently consists of approximately 150 individuals which are managed by the Texas Parks and Wildlife Department. They occupy a completely fenced pasture encompassing about 44.5 km<sup>2</sup> in north-central Texas. Since these individuals have not



been crossed with other bison herds, some consider this to be remnants of a unique Southern Plains bison subspecies. Although the herd has suffered from severe inbreeding and were previously crossed with cattle, genetic analysis suggests these bison hold a mitochondrial type separate from plains (*B. b. bison*) or wood bison (*B. b. athabasca*) but there has been no formal recognition of this distinction (Halbert et al. 2004). Though habitat was historically comprised of short and tall grasses, woody vegetation is encroaching the native vegetation (McAnally 2018). There are no large predators present and the bison are vaccinated annually (Halbert et al. 2005).

#### San Luis Valley, CO

Captive

The Medano-Zapata Ranch bison herd located in the San Luis Valley of south-central Colorado (37°39'N, 105°35'W; Figure 1.1) is privately managed by The Nature Conservancy and is surrounded by public lands including Baca National Wildlife Refuge and Great Sand Dunes National Park and Preserve. It was established in 1986 for meat production with source animals from ranches in Montana and purchased by The Nature Conservancy in 1999 to be managed as a conservation herd. The herd is currently maintained at a lower population size than it was for production in order to promote species diversity and reduce grazing pressure, however the density of the herd is still fairly high with approximately 1,500 bison occurring within the 153 km<sup>2</sup> fenced boundary. The bison are managed through annual round-ups which remove half of the yearling males and some mixed age females. The landscape is comprised primarily of shrublands, sand sheets and salt flats with adjacent wetlands and desert (Schoenecker et al. 2015). This area does not support predators capable of affecting adult bison, but calves

may be susceptible to coyotes (Schoenecker et al. 2015). Genetic analysis indicates cattle gene introgression in this population (Schoenecker et al. 2015).

#### American Prairie Reserve, MT

Captive

The American Prairie Reserve bison herd in the Upper Missouri River Breaks of Montana (47°45'N, 107°41'W; Figure 1.1) was established in 2005 with 16 bison from Wind Cave National Park on less than 0.5 km<sup>2</sup> of land. Additional individuals from Broken Kettle Grassland Preserve in Iowa and Elk Island National Park in Alberta were added intermittently until 2014 (Austin and Kunkel 2015). Today nearly 860 animals occupy about 1,616 km<sup>2</sup> of deeded and leased properties stewarded by the American Prairie Reserve (Freese et al. 2017). The herd is currently disease free and genetically pure (Austin and Kunkel 2015). The area does not currently support major predators. The major habitat type of the region are sage-steppe and mixed grass prairie (Kunkel et al. 2005). To control population growth in order to ensure grazing sustainability, bison have been regularly translocated to other herds beginning in 2008. Hunting at APR began in 2018 to simulate natural predation by targeting specific age classes, totaling six individuals (2018a).

#### Henry Mountains, UT

Free-range

The Henry Mountains bison herd is located in southern Utah (38°5'N, 110°50'W; Figure 1.1) and was established with 18 individuals (3 males and 15 females) in 1941 from Yellowstone National Park. The herd established near the release site on the San Rafael Desert, but dispersing animals necessitated an addition of 5 bulls the next year.

There have been no additional introductions since. Following the capture and vaccination of the herd in 1963 against brucellosis, the bison dispersed south into the Henry Mountains where they have remained ever since (Jeffrey et al. 2007). There are currently about 325 bison in the Henry Mountains which occupy approximately 1,250 km<sup>2</sup> (Ranglack and du Toit 2015) of public land managed by the Utah Department of Wildlife Resources. Public hunting of this herd began in 1950 and is located primarily on public land managed by the Bureau of Land Management and Utah Department of Wildlife Resources. The terrain is characterized by deserts, canyons, and mesas with elevations between 1,500-3,540 m. Habitat composition ranges from arid to subalpine (Koons et al. 2017) which correlates with elevation, typically containing pinyon-juniper woodlands in the lower areas and higher areas establishing coniferous forest and aspen parkland (Van Vuren 1979). Cougars and coyotes occur in the Henry Mountains and are known to predate on bison but are not a considerable threat. Although occasional dispersing wolves are expected from neighboring states, they are not anticipated to establish in this area (Jeffrey et al. 2007).

#### Book Cliffs, UT

Free-range

The Book Cliffs (BC) are located in eastern Utah (39°23'N, 109°30'W; Figure 1.1). The herd was established in 2008 on public land managed by the Utah Department of Wildlife Resources with 15 bison from Ute Tribe, which were originally sourced from National Bison Range, and supplemented with 71 additional individuals from the Henry Mountains between 2009 and 2010. This herd regularly mixes with the neighboring Ute

Tribal herd which is introgressed with cattle genes, but the Book Cliffs are estimated to consist of approximately 200 animals excluding animals in the Ute herd (Bates and Hersey 2016). The Book Cliffs herd is considered to be free of diseases. Hunting began in 2012 with a total harvest of 35 bulls and 5 cows to date. The total area available to the herd, including tribal land, is 5,665 km<sup>2</sup> (Bates and Hersey 2016). Although predators are not currently present in the Book Cliffs, one study predicts dispersing wolves from the Greater Yellowstone Ecosystem have the potential to colonize and thrive in this area if tolerated (Switalski et al. 2002). Habitat characteristics of the Book Cliffs are similar to the Henry Mountains with a gradient of arid biotic communities at lower elevations to sub-alpine at higher elevations, including conifer and aspen forests (Sexton et al. 2006).

### *Objective*

The objectives of this study were to evaluate the variations in bison space use and habitat selection between free-range and captive bison occurring over a gradient of ecological characteristics within their historic range. Although environmental factors vary between each of the herds, this analysis aims to identify factors which are universally important to bison in addition to understanding how both management and the landscape contribute to variations in spatial patterns. Assessment of space use will involve calculating the sizes of home range and foraging patches for individuals from each herd and modeling their relationship to local ecological variables. Habitat preferences will be analyzed using resource selection functions.

### *Literature Cited*

- American Prairie Reserve. 2018. Bison Harvest. <<https://www.americanprairie.org/bison-harvest>>.
- Austin D, Kunkel K. 2015. 2015 Bison Report. <[https://www.americanprairie.org/sites/default/files/APR-Bison-Report\\_2015.pdf](https://www.americanprairie.org/sites/default/files/APR-Bison-Report_2015.pdf)>.
- Bates B, Hersey K. 2016. Lessons Learned from Bison Restoration Efforts in Utah on Western Rangelands. *Rangelands*. 38(5):256–265. doi:10.1016/j.rala.2016.08.010.
- Douglas KC, Halbert ND, Kolenda C, Childers C, Hunter DL, Derr JN. 2011. Complete mitochondrial DNA sequence analysis of Bison bison and bison-cattle hybrids: Function and phylogeny. *Mitochondrion*. 11:166–175. doi:10.1016/j.mito.2010.09.005.
- Fortin D, Andruskiw M. 2003. Behavioral response of free-ranging bison to human disturbance. *Wildl Soc Bull*. 31(3):804–813.
- Freese CH, Aune KE, Boyd DP, Derr JN, Forrest SC, Cormack Gates C, Gogan PJP, Grassel SM, Halbert ND, Kunkel K, et al. 2007. Second chance for the plains bison. *Biol Conserv*. 136:175–184. doi:10.1016/j.biocon.2006.11.019.
- Halbert ND, Grant WE, Derr JN. 2005. Genetic and demographic consequences of importing animals into a small population: A simulation model of the Texas State

Bison Herd (USA). *Ecol Modell.* 181:263–276.

doi:10.1016/j.ecolmodel.2004.02.022.

Halbert ND, Raudsepp T, Chowdhary BP, Derr JN. 2004. Conservation genetic analysis of the Texas State Bison Herd. *J Mammal.* 85(5):924–931.

Jeffrey T, LeFever D, Grayson S, Smalley L, Hall G, Christensen C, Keeler J, Torgerson R, Hallows G, Dalton S, et al. 2007. Bison Unit Management Plan Unit #15 Henry Mountains. <[https://wildlife.utah.gov/hunting/biggame/pdf/bison\\_15.pdf](https://wildlife.utah.gov/hunting/biggame/pdf/bison_15.pdf)>.

Kohl MT, Krausman PR, Kunkel K, Williams DM. 2013. Bison versus cattle: are they ecologically synonymous? *Rangel Ecol Manag.* 66(6):721–731.  
doi:10.2111/REM-D-12-00113.1.

Kolipinski M, Borish S, Scott A, Kozłowski K, Ghosh S. 2014. Bison: yesterday, today, and tomorrow. *Nat Areas J.* 34(3):365–375. doi:10.3375/043.034.0312.

Koons DN, Terletzky P, Adler PB, Wolfe ML, Howe FP, Hersey K, Paskett W, Toit JT, Koons DN, Terletzky P, et al. 2017. Climate and density-dependent drivers of recruitment in plains bison. *J Mammal.* 93(2):475–481. doi:10.1644/1.

Krasińska M, Krasiński ZA, Bunevich AN. 2000. Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Białowieża Forest. *Acta Theriol (Warsz).* 45(3):321–334.

- Kunkel K, Forrest S, Freese C. 2005. Reintroducing Plains Bison (*Bos bison*) to American Prairie Foundation lands in Northcentral Montana: 5-year conservation and management plan.
- Larter NC, Gates CC. 1994. Home-range size of Wood bison: effects of age, sex, and Forage Availability. *J Mammal*. 75(1):25.
- McAnally AM. 2018. Evaluating bison seasonal resource selection within Caprock Canyons State Park. Tarleton State University. Master's Thesis.
- Meagher M. 1986. Bison. *Mamm Species*. 16(266):1–8.
- Merkle JA, Cherry SG, Fortin D, Kotler BP. 2015. Bison distribution under conflicting Foraging strategies: Site fidelity vs. Energy maximization. *Ecology*. 96(7):1793–1801. doi:10.1890/14-0805.1.
- Omernik JM. 1987. Map supplement ecoregions of the conterminous United States. *Ann Assoc Am Geogr*. 77(1):118–125.
- Ranglack DH, Dobson LK, du Toit JT, Derr J. 2015. Genetic analysis of the Henry Mountains bison herd. *PLoS One*. 10(12):1–11. doi:10.1371/journal.pone.0144239.
- Ranglack DH, du Toit JT. 2015. Habitat selection by free-ranging bison in a mixed grazing system on public land. *Rangel Ecol Manag*. 68(4):349–353. doi:10.1016/j.rama.2015.05.008.

- Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr J, Dobrott S, et al. 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conserv Biol.* 22(2):252–266. doi:10.1111/j.1523-1739.2008.00899.x.
- Schoenecker KA, Nielsen SE, Zeigenfuss LC, Pague CA. 2015. Selection of vegetation types and density of bison in an arid ecosystem. *J Wildl Manage.* 79(7):1117–1128. doi:10.1002/jwmg.940.
- Sexton JO, Douglas Ramsey R, Bartos DL. 2006. Habitone analysis of quaking aspen in the Utah Book Cliffs: Effects of site water demand and conifer cover. *Ecol Modell.* 198:301–311. doi:10.1016/j.ecolmodel.2006.04.024.
- Van Vuren D. 1979. Ecology and behavior of bison in the Henry Mountains, Utah. Oregon State University. Master's Thesis.
- Van Vuren D. 1983. Group dynamics and summer home range of bison in Southern Utah. *J Mammal.* 64(2):329–332.
- Van Vuren DH. 2001. Spatial relations of American bison (*Bison bison*) and domestic cattle in a montane environment. *Anim Biodivers Conserv.* 24(1):117–124.



## Chapter 2: Seasonal space use patterns of American bison across multiple management regimes

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**ABSTRACT** Plains bison (*Bison bison*) were spared from numerical extinction but have been considered by some to be ecologically extinct, partially due to spatial restrictions in their former range. In order to understand how management and local environmental conditions influence space-use patterns, we calculated home range using autocorrelated kernel density estimators (95% UD) and foraging patch size with first-passage time at three temporal scales (annual, growing, and non-growing seasons) for two free-ranging and three captive bison herds. Management and seasonal differences in home range and foraging patch sizes were determined using Kruskal-Wallis tests and Wilcoxon pairwise comparison of medians. The influence of landscape characteristics were modeled for each spatial scale using generalized linear mixed models. Free-range bison had significantly larger home ranges across seasons than the captive bison ( $p < 0.05$ ), but no significant differences were apparent for first-passage time. Mean precipitation significantly explained variations in home range size across seasons ( $p < 0.05$ ), but distance to roads

was the most important factor annually ( $\beta=-7.33$ ,  $p<0.05$ ), reserve size was most important during the growing season ( $\beta=3.55$ ,  $p<0.05$ ) and ruggedness was most important during the non-growing season ( $\beta=-9.42$ ,  $p<0.05$ ). First-passage time variations were explained better by herd than landscape patterns. Our results suggest that fences may prevent bison from using the landscape seasonally, which could have ecological consequences for this historically nomadic herbivore. Although sociopolitical realities currently prevent bison restoration at a continental scale, increasing the amount of space available to bison where possible has the potential to replicate previous ecological processes. Further research is necessary to evaluate the influence of local environmental conditions on seasonality of bison space-use.

Key words: autocorrelated kernel density estimation, *Bison bison*, first-passage time, home range, seasonality, space-use

### *Introduction*

American plains bison (*Bison bison*) were once the most numerous large vertebrate in North America. By the turn of the 20<sup>th</sup> Century, their estimated population of over 30 million individuals dwindled to ~1,000 from the collective impacts of overhunting and habitat loss (Bates and Hersey 2016). Though conservation efforts ultimately prevented the numerical extinction of bison, lack of space remains one barrier to their restoration (Freese et al. 2007; Sanderson et al. 2008). While there are over half a million bison alive in the United States today, fewer than 2% exist outside of commercial production and are generally relegated to small, isolated herds (Freese et al. 2007; Sanderson et al. 2008;

Gates et al. 2010). Intensive management of bison distributions over the past 100 years has obscured the underlying temporal and ecological influences of their spatial patterns (Freese et al. 2007; Sanderson et al. 2008). Although current management practices enabled bison to persist into the present day, today's management regimes may induce divergent patterns of space use.

When unencumbered by management restrictions, ecological and evolutionary characteristics are expected to be the primary influence of bison space use. Population attributes like density (Van Vuren 1983; Fortin et al. 2009; Merkle, Cherry, et al. 2015), social and individual tendencies (Daleszczyk 2007; Merkle et al. 2014; Merkle, Sigaud, et al. 2015; Sigaud et al. 2017), and predation risk (Laundré et al. 2001; Hernández and Laundré 2005; Harvey and Fortin 2013) can affect distributions and foraging decisions at localized scales. However, broader space use patterns tend to be influenced by abiotic and biotic landscape features. Biotic characteristics such as vegetation productivity fluctuate with temperature, water availability, and other seasonal changes which influence space use of bison (Steuter et al. 1995; Fortin et al. 2002; Dancose et al. 2011; Bergmann et al. 2015; Ranglack and du Toit 2015b). Bison movement can also be affected by abiotic attributes like terrain. Since bison coevolved with these environmental factors, they are expected to be consistent in the face of disturbances. Bison prefer to graze areas with abundant and high quality forage which leads to frequent shifts to new sites (Frank et al. 2016; Merkle et al. 2016). Although topography is sometimes related to forage quality (Van Vuren 2001), frequent extreme changes (i.e. ruggedness) can affect the ability of animals to efficiently move through the landscape (Sappington et al. 2007).

While certain features like steep slopes are avoided throughout the year (Van Vuren 1983, Steenweg et al. 2016) others may be influenced by season such as preference for aspect with low snow accumulation during the winter and areas close to water when temperatures are warm (Van Vuren 2001). Landcover type may also affect bison space use including avoidance of dense over-story canopy cover given their reliance on grasses (Kohl et al. 2013; Ranglack and du Toit 2015a; Schoenecker et al. 2015). While biotic and abiotic environmental components are strong drivers of bison spatial patterns, anthropogenic influences could manipulate these relationships.

Based on their body mass, bison should have the largest spatial requirements of any North American mammal (Ofstad et al. 2016), yet they are among the most geographically restricted due to current management regimes (Gates et al. 2010). More than half of bison herds managed for conservation are confined to fenced pastures encompassing areas less than 16 km<sup>2</sup>, which is ~80 times smaller than the expected minimum space use of free-range bison (Bailey 2013). Anthropogenic restrictions like this render bison incapable of responding to seasonal changes in landscape characteristics, including shifts in forage productivity (Merkle et al. 2016), resulting in increasingly intensive use of existing patches (Frank et al. 2016). Movement and diet patterns of European bison (*Bison bonasus*) are impacted by similar practices such as supplemental feeding (Kowalczyk et al. 2011; Ramos et al. 2016) and other human disturbances, including settlements and roads (Kuemmerle et al. 2018). Bison are also known to increase their daily movements when disturbed by humans (Fortin and Andruskiw 2003). At worst, bison may be induced to fall into ecological traps resulting

from human alterations (Sigaud et al. 2017). Multiple landscape factors influence bison space use but their relative strengths may differ across seasons and management types.

Accounting for management restrictions and temporal variations in landscape features is necessary to understand the influences of bison spatial patterns. Although European bison space use has been assessed across multiple herds (Kuemmerle et al. 2018), no such investigation has yet been made for American bison. The objective of our study was to examine the seasonal spatial patterns of five bison herds at multiple scales under different management regimes, including two free-ranging and three captive herds of varying numerical and spatial size. To assess total space use, we calculated annual and seasonal home ranges for individuals within each herd and used first-passage time (FPT) analysis to determine fine scale space use (i.e. foraging patch). We also examined the influence of local ecological characteristics on these spatial patterns. We expected home ranges of intensively managed captive bison to be smaller than those of free-range bison but anticipated FPT to be smaller when local conditions supported higher forage productivity. Space use at each scale was also predicted to be highest during the most limiting season for each herd.

### *Study Area*

The five bison conservation herds we assessed included the Henry Mountains (HM) in southern Utah (38°5'N, 110°50'W), Book Cliffs (BC) in eastern Utah (39°23'N, 109°30'W), American Prairie Reserve (APR) in northern Montana (47°45'N, 107°41'W), Medano-Zapata Ranch (MZR) in southern Colorado (37°39'N, 105°35'W), and the Texas

State Bison Herd (TSBH) at Caprock Canyons State Park in northern Texas (34°26'N, 101°3'W; Figure 1.1). The amount of space available to each herd varied between 13-1,250 km<sup>2</sup> and total population sizes ranged from 150-1,500 bison (Table 1.1). The HM and BC bison are considered to be free-ranging, as there are no boundary fences restricting their movements (Bates and Hersey 2016; Ranglack and du Toit 2016). The remaining herds undergo more intensive management, including fenced pastures, round-ups, and regular vaccinations (Halbert et al. 2005; Kohl et al. 2013; Schoenecker et al. 2015). While restricted to single contiguous pastures throughout the year at both MZR and TSBH, APR bison occurred in five separate pastures ranging in size from 13-114 km<sup>2</sup> (Table 1.1). The highest average temperatures are experienced by TSBH at Caprock Canyons while the lowest mean temperatures are found at APR. The HM bison experience on average the lowest precipitation and highest elevations of the herds we looked at while TSBH experienced the highest precipitation and lowest elevations overall (Table 1.2).

### *Methods*

Location data was collected from GPS (n= 59) and VHF (MZR only, n=14) collared bison between the years 2005-2018 (Table 1.1). The locations were collected daily for GPS collars at intervals ranging from 1-13 hours over a period of at least 3 months while VHF collar locations were only recorded 1-3 times per week over a single month. All location data were transformed to UTM coordinates prior to analyses and screened to remove outlying points. For captive bison, outlying points were defined as locations which occurred outside of their fenced pastures. If an individual was transferred to a new

pasture within a particular season, only the area where the majority of points were recorded was considered. For free-range bison, locations which occurred close to settlements or other areas known to be unused by the herds were considered outliers.

We defined the growing season for each study area by calculating the average day measurable photosynthesis, as indicated by normalized difference vegetation index (NDVI), began and ended using the zonal statistics tool in ArcMap 10.6.1 (2018). The remainder of the year was designated as the non-growing season (Table 1.2). The bison with VHF collars were only included in annual home range calculations since the data were insufficient for seasonal home range assessment and inappropriate for FPT analysis. For bison with GPS collars, we defined the annual period as at least 10 months of regularly collected location data over a single year while those collected within the locally defined designations were used to identify seasonal space use. Individuals with multiple years of data were included as separate observations to supplement sample size.

### Spatial Calculations

Individual home ranges were estimated using autocorrelated kernel density estimates (AKDE) following the methods of Fleming and Calabrese (2017) with the ‘ctmm’ package in R version 3.5.1 (RStudio Team 2016; Fleming and Calabrese 2018). This relatively new development for assessing animal home ranges accounts for the inherent autocorrelation structure of relocation data by fitting continuous time movement models to estimate space use, giving this method improved accuracy over traditional techniques (Fleming et al. 2018; Noonan et al. 2019). This approach relaxes assumptions

of independence and enables a greater comparability of individuals with different location sampling schedules than standard kernel density estimators. Our AKDE's were specified to incorporate smooth error distributions, area-corrected estimates of model fit (Fleming and Calabrese 2017), and defined a target probability error of 0.001 using a 95% utilization distribution.

First-passage time was estimated following the methods of Fauchald and Tveraa (2003) and conducted using the R package 'adehabitatLT' (Calenge 2006). Prior to calculations, the movement path of each bison was interpolated with additional locations every 500 m to remove spatial bias. Our assessment considered circles of radii between 50 to 150,000 m at 100-m intervals. The variance of log-transformed first-passage times were then calculated for each individual. The radius of the circle corresponding with the maximum variance was considered to be the approximate area which the bison perceived a foraging patch (Fauchald and Tveraa 2003; Kohl et al. 2013). We reported this area in  $\text{km}^2$  to facilitate comparison with the individual's home range size.

We evaluated 10 ecological covariates as potentially influencing home range and foraging patch size for bison, including precipitation, elevation, ruggedness (Sappington et al. 2007), time integrated and amplitude of NDVI (2018), distance and density of roads, distance and density of water, and percentage of overhead canopy cover (Table 1.3). NDVI amplitude is the maximum increase from the baseline NDVI, and time integrated NDVI accounts for photosynthetic activity across the entire growing season (2018). Since many individuals had GPS data for multiple years, we used averaged NDVI



values across the years 2001-2015. Distance from roads and water was calculated using Euclidean distance, and density of roads and water was calculated using line density in ArcMap 10.6.1 from TIGER line features (United States Census Bureau 2018).

Ruggedness was calculated using the Vector Ruggedness Measure (VRM) tool in ArcMap 10.6.1 following the methods of Sappington et al. (2007). The mean value for each covariate was extracted for each home range using zonal statistics in ArcMap 10.6.1 and R version 3.5.1 (RStudio Team 2016).

### Statistical Analyses

We assessed differences of home range and foraging patch sizes between free-range and captive herds within each season as well as seasonal differences within each management type using nonparametric Kruskal-Wallis tests in R version 3.5.1 (RStudio Team 2016). This test was used instead of a one-way ANOVA due to violation of normality and equal variance assumptions. Significance was defined *a priori* as  $\alpha=0.05$  for each comparison. Medians were compared using Wilcox pairwise comparisons test with a correction factor for multiple comparisons (Benjamini and Hochberg 1995).

We then examined how ecological covariates influenced the sizes of home ranges and foraging patches using generalized linear mixed models with gamma errors using log link functions. Gamma distributed errors were used as measures of home range and FPT contained skewed and non-negative continuous values (Anderson et al. 2012), while the log link functions accounted for their expected asymptotic responses to landscape characteristics (McCullagh and Nelder 1991). This also prevented negative estimates for

space usage in model predictions. The fixed effects contained the mean values for the covariates precipitation, elevation, ruggedness, NDVI, road proximity, linear water proximity, and canopy cover. To control for the effect of local variations and management, we included study area as random effect. We modeled home range size and first-passage time separately for each individual season. In order to scale our comparisons on the effect of environmental characteristics on space use, we standardized all covariate values by taking the difference from the mean and dividing by twice the standard deviation before the analysis (Gelman 2008). We also accounted for potential nonlinear relationships by fitting pseudothreshold functional forms using natural log transformation (Franklin et al. 2000) and quadratic functional forms using square transformation.

We followed a multi-tiered approach to model selection to reduce the number of competing models (Burnham and Anderson 2002). For the first tier, we created univariate models to evaluate the most explanatory functional forms for each covariate and ranked using Akaike's Information Criterion corrected for small samples (AICc). As road, water, and NDVI were each represented by two landscape covariates, their model functional forms were ranked against each other in order to select the best version of the variable. Pearson's correlation coefficients were calculated for each covariate to ensure candidate models only included combinations of variables which were not collinear ( $<|0.6|$ ). For the second tier, we combined all covariates from models within 2 AICc units of the top ranked models in the first tier for each covariate in all possible combinations, while accounting for collinearity, to determine the best overall model. The best overall model in second tier was evaluated for uninformative parameters (Arnold 2010). This was repeated

for each season for both home range and foraging patch, totaling six overall models. We used the functions ‘glmer’ in package ‘lme4’ (Bates et al. 2015) to create our generalized linear mixed effects models and ‘dredge’ in package ‘MuMIn’ (Barton 2018) for selecting the top models.

## *Results*

### Home Range

A total of 224 home ranges were calculated, including 57 annual ranges, 84 during the growing season, and 83 during the non-growing season (Table 1.4). The free-range bison had larger home ranges than captive individuals across all seasons (Figure 1.2). Only the free-range bison displayed significant changes in home range size between seasons, using larger areas in the growing than non-growing season (Figure 1.2). Though captive bison tended to use more space in the non-growing season, the relationship was not significant (Figure 1.2). Overall, total space use of captive bison appeared to be consistent with the amount of space available (Table 1.4).

From the generalized linear mixed models, the top model for annual home ranges included, in order of relative importance, average distance from roads, mean precipitation, and mean percentage of canopy cover (AICc=658.2, wt.=0.95, Table 1.5). Increasing distance from roads and percentage of canopy cover tended to decrease annual home range size but seemed to be maximized when mean precipitation was about 283 mm (Figure 1.3). The top model for growing season home ranges included reserve size, mean precipitation, and average landscape ruggedness (AICc=1026.2, wt.=0.44, Table

1.5). Home range sizes during the growing season tended to increase with reserve size and ruggedness, but decreased with mean precipitation (Figure 1.3). The top model during the non-growing season included average landscape ruggedness, mean precipitation, and mean percentage of overhead canopy cover ( $AIC_c=1064.6$ ,  $wt.=0.58$ , Table 1.5). Non-growing season home ranges tended to increase with ruggedness and decrease with canopy cover, but was maximized when mean precipitation was about 333 mm (Figure 1.3). Annual and growing season home range models each included anthropogenic landscape features while the non-growing season home range models did not (Table 1.5, Figure 1.3).

#### First-Passage Time

A total of 210 foraging patches were calculated from first-passage times, including 43 annual patch sizes, 84 during the growing season, and 83 during the non-growing season (Table 1.6). Although the free-range bison tended to have slightly larger foraging patches than captive bison there were no statistical differences ( $p=0.39$  for growing season,  $p=0.9$  for non-growing season; Figure 1.2). Foraging patches also tended to be smallest during the growing season on average for both free-range and captive bison but these differences were also not significant (Figure 1.2). Overall, the area of captive bison foraging patches tended to be similar to their pasture size (Figure 1.2).

There was no distinguishable relationship between annual or non-growing foraging patches and landscape characteristics given the high ranking of the null models during model selection ( $\Delta AIC_c < 2$ ; Table 1.7). Similar to the home range model, growing

season patch size was best predicted by average landscape ruggedness and mean precipitation in order of relative importance ( $AICc=640.6$ ,  $wt.=0.363$ ). Foraging patch size appeared to be maximized when average landscape ruggedness was 0.616 on a scale from 0-1 and mean precipitation was 408 mm (Figure 1.4).

### *Discussion*

Our comparison of free-range and captive bison spatial patterns indicates fences may have a larger influence on their space use than local environmental characteristics, manifested by the lack of seasonal variations in space-use. Local characteristics of movement and selection are generally emphasized as major influences of bison spatial distributions (Fortin 2003; Dancose et al. 2011; Merkle et al. 2014; Merkle, Cherry, et al. 2015; Merkle, Sigaud, et al. 2015; Raynor et al. 2017), but understanding the emergent properties of these patterns across the modern landscape is important for bison conservation. Only recently has research begun to address the incompatibility of small scale management for ungulates with large spatial requirements (Meisingset et al. 2018). Our models of home range suggest anthropogenic features heavily impact bison home range sizes. The amount of space available to bison in the study areas we examined was the most important explanatory factor for the size of growing season home ranges. Overall, free-ranging bison used nearly 40 times more space than captive bison during the equivalent season while space use of captive bison predictably concurred with their pasture size (i.e., available space). We also found that proximity to roads significantly described trends in annual home ranges. Space use tended to be greater in areas closer to roads on average, which may be related to frequent human disturbances leading to

increased bison movement rates (Fortin and Andruskiw 2003). However, due to the large portion of the bison sampled for these models coming from the Henry Mountains, interpretation should proceed with caution.

Our estimates of annual home range reflected those of wood bison (*Bison bison athabasca*) in Canada which averaged 1,240 km<sup>2</sup> (Larter and Gates 1994). However, the same study attributed decreased forage availability to larger home range sizes. As forage tends to become scarcer during the winter, it is expected that space use would increase during the non-growing season. Surprisingly, we found that free-range plains bison actually used more space during the growing season than the non-growing season, at least those in the Henry Mountains. While no significant differences were detected in the captive bison or the free-ranging Book Cliffs bison, the remaining four herds did tend to have larger non-growing season home ranges. It is worth noting though that the average non-growing season home range of American Prairie Reserve bison may have been larger due to transfer of individuals to new pasture during this time which would expand their typical available space (Table 1.3; Figure 1.3). Regardless, increased space use through seasons with limited resources has also been noted in the free-ranging bison of Prince Albert National Park in Canada, which had a winter range of 693 km<sup>2</sup> and summer range of 140 km<sup>2</sup> (Merkle, Cherry, et al. 2015). A similar trend has also been identified in European bison but found that periods of deep snow actually saw contractions in total space used (Krasińska et al. 2000). Snow can decrease mobility and reduce search efficiency of foragers (Courant and Fortin 2012), which could explain its negative effect on home ranges. Similarly, we found that mean precipitation was significantly related to

home range size across all seasons (Figure 1.4). While landscape ruggedness also influences mobility (Frair et al. 2005), the amount of space bison used in this study actually tended to increase when terrain was rougher. This could be related to individuals circumventing obstacles rather than expending energy traversing them.

It is well established that large ungulates use space at multiple spatial scales (Anderson et al. 2005; van Beest et al. 2010; Northrup et al. 2016) including bison (Fortin et al. 2003). In our study, free-range bison tended to have first-passage times nearly twice that of captive bison across seasons on average, however, there was considerable variation within herds and none of the observed differences were statistically significant (Table 1.5; Figure 1.2), suggesting bison may use similarly sized foraging patches regardless of local ecological characteristics. Nonetheless, captive bison seemed to use foraging patches approaching or exceeding that of their home range estimates (Figure 1.2), a pattern also detected in previous studies (Williams, A.C. Dechen Quinn, et al. 2012). Kohl et al. (2013) suggested that the similarity between summer FPT and pasture size supported the need to manage bison at a larger spatial scale. While these patterns could be an artifact of large grazers being confined to fixed areas, FPT of domestic cattle was detected to be consistently smaller than the total pasture extent (Kohl et al. 2013; Larson-Praplan et al. 2015). However, we only focused on the absolute maximum variance in FPT to calculate size of foraging patches, but several individuals did appear to have two peaks in variance which would indicate a multi-scaled area-restricted search (Le Corre et al. 2008; Pinaud 2008). This may explain the relatively small FPT values at the Medano-Zapata Ranch (Table 1.6), which could be the focus of future work.

However, a study with roe deer (*Capreolus capreolus*) suggests that the first identified patch size in multi-patch detection tended to be the most heavily used (Le Corre et al. 2008). It is possible that MZR differences in FPT could be related to their relatively high population density positively influencing intense use at foraging patches (Courant and Fortin 2012).

Though our findings and previous studies suggest free-range bison vary their space use temporally at the scale of home range, we found little statistical support for this pattern at the foraging patch scale. However, we did see a slight increase in foraging patch size during the non-growing season relative to the growing season (Figure 1.2). Although we are not the first to attempt modeling FPT as a function of environmental variables (Cleveland et al. 2012; Williams, A. Dechen Quinn, et al. 2012; Williams, A.C. Dechen Quinn, et al. 2012; Byrne et al. 2014; Henry et al. 2016), the patterns of bison FPT we detected tended to be explained best by the random effect on study area as opposed to particular landscape factors during the annual and non-growing seasons. The high AICc value of the null model, which contained only the random effect of study area to model FPT, indicated that the fixed effects of the ecological covariates were no better than random at explaining the observed patterns during these seasons ( $\Delta AICc < 2$ ). Our top-ranked model for growing season FPT was better than random and suggested a nonlinear relationship between foraging patch size and the fixed effects of average landscape ruggedness and mean precipitation, but had a relatively low model weight. However, the values for the ecological covariates we used in the FPT models were



calculated at the home range scale which may explain their poor fit. Future studies should investigate these patterns using finer scale habitat characteristics.

Despite the strides made in the last century to conserve bison, practices deemed necessary to prevent their extinction may have actually removed essential spatial components of their evolutionary history and contributed to their possible ecological extinction (Freese et al. 2007; Sanderson et al. 2008). The vast extents required by bison necessitates a landscape approach to their conservation (Gates et al. 2010). Although restoring their influence to the entirety of North America is not viable, nor are small scale efforts less important, our findings indicate that future efforts may need to allocate more space for bison conservation (Knapp et al. 1999; Sanderson et al. 2008). We suggest that sufficient space could positively contribute to the long-term success of bison and may not be at odds with minimizing conflict with humans on public land (Ranglack and du Toit 2016). Further investigations into encouraging temporally relevant bison spatial patterns within the limitations of current land uses is an essential step forward in bison conservation.

### *Management Implications*

Our multi-scale assessment of bison spatio-temporal patterns suggest that fencing may inhibit bison from responding to seasonal landscape variations. While sociopolitical influences preclude bison from returning to their entire historic range and population levels, more space may be necessary to replicate ecologically beneficial behaviors. As innately intensive grazers, bison have a natural tendency to move frequently to avoid

overgrazing patches. This work can be used by managers to help identify spatial extents for future bison restoration which allow for temporal variations in space use.

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### *Literature Cited*

- Anderson CJ, Verkuilen J, Johnson T. 2012. Applied generalized linear mixed models: continuous and discrete data. Springer. <[https://education.illinois.edu/docs/default-source/carolyn-anderson/edpsy587/GLM\\_GLMM\\_LMM.pdf](https://education.illinois.edu/docs/default-source/carolyn-anderson/edpsy587/GLM_GLMM_LMM.pdf)>.
- Anderson DP, Forester JD, Turner MG, Frair JL, Merrill EH, Fortin D, Mao JS, Boyce MS. 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landsc Ecol.* 20:257–271. doi:10.1007/s10980-005-0062-8.

- Arnold TW. 2010. Uninformative parameters and model selection using Akaike's information criterion. *J Wildl Manage.* 74(6):1175–1178. doi:10.1111/j.1937-2817.2010.tb01236.x.
- Bailey JA. 2013. American plains bison rewilding an icon. Helena: Sweetgrass Books.
- Barton K. 2018. MuMIn: Multi-Model Inference. R package version 1.42.1.
- Bates B, Hersey K. 2016. Lessons learned from bison restoration efforts in Utah on western rangelands. *Rangelands.* 38(5):256–265. doi:10.1016/j.rala.2016.08.010.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67(1):1–48. doi:doi:10.18637/jss.v067.i01.
- van Beest FM, Mysterud A, Loe LE, Milner JM. 2010. Forage quantity, quality and depletion as scale- dependent mechanisms driving habitat selection of a large browsing herbivore. *J Anim Ecol.* 79:910–922. doi:10.1111/j.1365-2656.2010.01701.x.
- Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc Ser B.* 57(1):289–300.
- Bergmann GT, Craine JM, Robeson MS, Fierer N. 2015. Seasonal Shifts in Diet and Gut Microbiota of the American Bison (*Bison bison*). *PLoS One.* 10(11):e0142409. doi:10.1371/journal.pone.0142409.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer.

- Byrne ME, Guthrie JD, Hardin J, Collier BA, Chamberlain MJ. 2014. Evaluating wild turkey movement ecology: an example using first-passage time analysis. *Wildl Soc Bull.* 38(2):407–413. doi:10.1002/wsb.404.
- Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Modell.* 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017.
- Cleveland SM, Thompson M, Henderson R. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. *Wildl Soc Bull.* 36(4):658–668. doi:10.1002/wsb.182.
- Le Corre M, Pellerin M, Pinaud D, Van Laere G, Fritz H, Saïd S, Sai Le Corre S, Laere V. 2008. A multi-patch use of the habitat: testing the First-Passage Time analysis on roe deer *Capreolus capreolus* paths. *Wildlife Biol.* 14(3):339–349. doi:10.2981/0909-6396(2008)14[339:AMUOTH]2.0.CO;2.
- Courant S, Fortin D. 2012. Search efficiency of free-ranging plains bison for optimal food items. *Anim Behav.* 84:1039–1049. doi:10.1016/j.anbehav.2012.08.003.
- Daleszczyk K. 2007. Habitat structure, climatic factors, and habitat use by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Białowieża Forest, Poland. *Can J Zool.* 85(2):261–272. doi:10.1139/Z06-209.
- Dancose K, Fortin D, Xulin GUO. 2011. Mechanisms of functional connectivity: The case of free-ranging bison in a forest landscape. *Ecol Appl.* 21(5):1871–1885.

doi:10.1890/10-0779.1.

Fauchald P, Tveraa T. 2003. Using First-Passage Time in the analysis of area-restricted search and habitat selection. *Ecology*. 84(2):282–288.

Fleming CH, Calabrese JM. 2017. A new kernel density estimator for accurate home-range and species-range area estimation. *Methods Ecol Evol*. 8:571–579.

doi:10.1111/2041-210X.12673.

Fleming CH, Calabrese JM. 2018. ctmm: Continuous-Time Movement Modeling.

Fleming CH, Sheldon D, Fagan WF, Leimgruber P, Mueller T, Nandintsetseg D, Noonan MJ, Olson KA, Setyawan E, Sianipar A, et al. 2018. Correcting for missing and irregular data in home-range estimation. *Ecol Appl*. 28(4):1003–1010.

doi:10.1002/eap.1704.

Fortin D. 2003. Searching Behavior and Use of Sampling Information by Free-Ranging Bison (*Bos bison*). *Behav Ecol Sociobiol*. 54(2):194–203.

Fortin D, Andruskiw M. 2003. Behavioral response of free-ranging bison to human disturbance. *Wildl Soc Bull*. 31(3):804–813.

Fortin D, Fortin M-E, Beyer HL, Duchesne T, Courant S, Dancose K. 2009. Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology*. 90(9):2480–2490. doi:10.1890/08-0345.1.

Fortin D, Fryxell JM, O ’brodovich L, Frandsen D. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization

- principles. *Oecologia*. 134:219–227. doi:10.1007/s00442-002-1112-4.
- Fortin D, Fryxell JM, Pilote R. 2002. The Temporal Scale of Foraging Decisions in Bison. *Ecology*. 83(4):970–982.
- Frair JL, Merrill EH, Visscher DR, Fortin D, Beyer HL, Morales JM. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc Ecol*. 20(3):273–287. doi:10.1007/s10980-005-2075-8.
- Frank DA, Wallen RL, White PJ. 2016. Ungulate control of grassland production: grazing intensity and ungulate species composition in Yellowstone Park. *Ecosphere*. 7(11):e01603. doi:10.1002/ecs2.1603.
- Franklin AB, Anderson DR, Gutiérrez RJ, Burnham KP. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecol Monogr*. 70(4):539–590.
- Freese CH, Aune KE, Boyd DP, Derr JN, Forrest SC, Cormack Gates C, Gogan PJP, Grassel SM, Halbert ND, Kunkel K, et al. 2007. Second chance for the plains bison. *Biol Conserv*. 136:175–184. doi:10.1016/j.biocon.2006.11.019.
- Gates C, Freese CH, Gogan PJP, Kotzman M. 2010. American Bison: Status Survey and Conservation Guidelines 2010. Gland, Switzerland. IUCN.
- Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. *Stat Med*. 27:2865–2873. doi:10.1002/sim.3107.
- Halbert ND, Grant WE, Derr JN. 2005. Genetic and demographic consequences of

- importing animals into a small population: A simulation model of the Texas State Bison Herd (USA). *Ecol Modell.* 181:263–276.  
doi:10.1016/j.ecolmodel.2004.02.022.
- Harvey L, Fortin D. 2013. Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in wolf country. *PLoS One.* 8(9):e73324. doi:10.1371/journal.pone.0073324.
- Henry DAW, Ament JM, Cumming GS. 2016. Exploring the environmental drivers of waterfowl movement in arid landscapes using first-passage time analysis. *Mov Ecol.* 4(8):1–18. doi:10.1186/s40462-016-0073-x.
- Hernández L, Laundré JW. 2005. Foraging in the ‘landscape of fear’ and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biol.* 11(3):215–220. doi:10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2.
- Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999. The keystone role of bison in North American tallgrass prairie bison increase habitat heterogeneity processes. *Bioscience.* 49(1):39–50.
- Kohl MT, Krausman PR, Kunkel K, Williams DM. 2013. Bison Versus Cattle: Are They Ecologically Synonymous? *Rangel Ecol Manag.* 66(6):721–731. doi:10.2111/REM-D-12-00113.1.
- Kowalczyk R, Taberlet P, Coissac E, Valentini A, Miquel C, Kamiński T, Wójcik JM.

2011. Influence of management practices on large herbivore diet—Case of European bison in Białowieża Primeval Forest (Poland). *For Ecol Manage.* 261(4):821–828. doi:10.1016/J.FORECO.2010.11.026.
- Krasińska M, Krasiński ZA, Bunevich AN. 2000. Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Białowieża Forest. *Acta Theriol (Warsz)*. 45(3):321–334.
- Kuemmerle T, Levers C, Bleyhl B, Olech W, Perzanowski K, Reusch C, Kramer-Schadt S. 2018. One size does not fit all: European bison habitat selection across herds and spatial scales. *Landsc Ecol.* 33(9):1559–1572. doi:10.1007/s10980-018-0684-2.
- Larson-Praplan S, George MR, Buckhouse JC, Laca EA. 2015. Spatial and temporal domains of scale of grazing cattle. *Anim Prod Sci.* 55(3):284–297. doi:10.1071/an14641.
- Larter NC, Gates CC. 1994. Home-Range Size of Wood Bison: Effects of Age, Sex, and Forage Availability. *J Mammal.* 75(1):25.
- Laundré JW, Hernández L, Altendorf KB. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Can J Zool.* 79:1401–1409. doi:10.1139/cjz-79-8-1401.
- McCullagh P, Nelder JA. 1991. *Generalized Linear Models*. 2nd ed. New York: Chapman & Hall.
- Meisingset EL, Leif |, Loe E, Brekkum Ø, Bischof | Richard, Rivrud IM, Unni |, Lande S,



- Zimmermann B, Veiberg V, et al. 2018. Spatial mismatch between management units and movement ecology of a partially migratory ungulate. *J Appl Ecol.* 55:745–753. doi:10.1111/1365-2664.13003.
- Merkle JA, Cherry SG, Fortin D, Kotler BP. 2015. Bison distribution under conflicting Foraging strategies: Site fidelity vs. Energy maximization. *Ecology.* 96(7):1793–1801. doi:10.1890/14-0805.1.
- Merkle JA, Fortin D, Morales JM. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecol Lett.* 17:924–931. doi:10.1111/ele.12294.
- Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, Oates BA, Sawyer H, Scurlock BM, Kauffman MJ. 2016. Large herbivores surf waves of green-up during spring. *Proc R Soc B.* 283(1833):20160456. doi:10.1098/rspb.2016.0456.
- Merkle JA, Sigaud M, Fortin D. 2015. To follow or not? How animals in fusion-fission societies handle conflicting information during group decision-making. *Ecol Lett.* 18(8):799–806. doi:10.1111/ele.12457.
- Noonan MJ, Tucker MA, Fleming CH, Akre TS, Alberts SC, Ali AH, Altmann J, Antunes PC, Belant JL, Beyer D, et al. 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol Monogr.* 0(0):e01344. doi:10.1002/ecm.1344.

- Northrup JM, Anderson CR, Hooten MB, Wittemyer G. 2016. Movement reveals scale dependence in habitat selection of a large ungulate. *Ecol Appl.* 26(8):2746–2757. doi:10.1002/eap.1403.
- Ofstad EG, Herfindal I, Solberg EJ, Saether B-E. 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proc R Soc B Biol Sci.* 283:20161234. doi:10.1098/rspb.2016.1234.
- Pinaud D. 2008. Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: Effect of the structure of environment and tracking systems. *J Appl Ecol.* 45(1):91–99. doi:10.1111/j.1365-2664.2007.01370.x.
- Ramos A, Petit O, Longour P, Pasquaretta C, Sueur C. 2016. Space Use and Movement Patterns in a Semi-Free-Ranging Herd of European Bison (*Bison bonasus*). *PLoS One.* 11(2):e0147404. doi:10.1371/journal.pone.0147404.
- Ranglack DH, du Toit JT. 2015b. Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. *Ecol Indic.* 56:145–151. doi:10.1016/j.ecolind.2015.04.009.
- Ranglack DH, du Toit JT. 2015a. Habitat Selection by Free-Ranging Bison in a Mixed Grazing System on Public Land. *Rangel Ecol Manag.* 68(4):349–353. doi:10.1016/j.rama.2015.05.008.
- Ranglack DH, du Toit JT. 2016. Bison with benefits: towards integrating wildlife and ranching sectors on a public rangeland in the western USA. *Oryx.* 50(3):549–554.

doi:10.1017/S0030605314001197.

Raynor EJ, Beyer HL, Briggs JM, Joern A. 2017. Complex variation in habitat selection strategies among individuals driven by extrinsic factors. *Ecol Evol.* 7:1802–1822. doi:10.1002/ece3.2764.

Remote Sensing Phenology. 2018. USGS. doi:<https://doi.org/10.5066/F7PC30G1>. [accessed 2018 Sep 18]. [https://phenology.cr.usgs.gov/get\\_data\\_250w.php](https://phenology.cr.usgs.gov/get_data_250w.php).

RStudio Team. 2016. RStudio: Integrated Development for R.

Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr J, Dobrott S, et al. 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conserv Biol.* 22(2):252–266. doi:10.1111/j.1523-1739.2008.00899.x.

Sappington JM, Longshore KM, Thompson DB. 2007. Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. *J Wildl Manage.* 71(5):1419–1426. doi:10.2193/2005-723.

Schoenecker KA, Nielsen SE, Zeigenfuss LC, Pague CA. 2015. Selection of vegetation types and density of bison in an arid ecosystem. *J Wildl Manage.* 79(7):1117–1128. doi:10.1002/jwmg.940.

Sigaud M, Merkle JA, Cherry SG, Fryxell JM, Berdahl A, Fortin D. 2017. Collective decision-making promotes fitness loss in a fusion-fission society. *Ecol Lett.* 20:33–40. doi:10.1111/ele.12698.

- Steenweg R, Hebblewhite M, Gummer D, Low B, Hunt B. 2016. Assessing potential habitat and carrying capacity for reintroduction of plains bison (*Bison bison bison*) in Banff National Park. *PLoS One*. 11(2):1–23. doi:10.1371/journal.pone.0150065.
- Steuter AA, Steinauer EM, Hill GL, Bowers PA, Tieszen LL. 1995. Distribution and Diet of Bison and Pocket Gophers in a Sandhills Prairie. *Ecol Appl*. 5(3):756–766.
- United States Census Bureau. 2018. TIGER/Line Shapefiles. [accessed 2018 Sep 18]. <https://www.census.gov/geo/maps-data/data/tiger-line.html>.
- Van Vuren D. 1983. Group Dynamics and Summer Home Range of Bison in Southern Utah. *J Mammal*. 64(2):329–332.
- Van Vuren DH. 2001. Spatial relations of American bison (*Bison bison*) and domestic cattle in a montane environment. *Anim Biodivers Conserv*. 24(1):117–124.
- Williams DM, Dechen Quinn A, Porter WF. 2012. Impact of Habitat-Specific GPS Positional Error on Detection of Movement Scales by First-Passage Time Analysis. *PLoS One*. 7(11):e48439. doi:10.1371/journal.pone.0048439.
- Williams DM, Dechen Quinn AC, Porter WF. 2012. Landscape effects on scales of movement by white-tailed deer in an agricultural-forest matrix. *Landsc Ecol*. 27:45–57. doi:10.1007/s10980-011-9664-5.

## Tables

Table 1.1. Summary of characteristics for each bison herd assessed in this study. This includes type of management, approximate area of the reserve, estimated total population, number of individuals analyzed from each herd, the years during which data was collected, and the fix-rate interval for GPS relocations.

Herd	Type	Reserve Size* (km <sup>2</sup> )	Population Size	Sample Size	Years	GPS Fix-Rate (hours)
Henry Mountains	Free-range	1250	325	25	2011-2014	6
Book Cliffs	Free-range	5665	200	2	2014	6
American Prairie Reserve	Captive	13-114 <sup>a</sup>	860	10	2012-2017	2 & 13 <sup>b</sup>
Medano- Zapata Ranch	Captive	153	1500	16 <sup>c</sup>	2005-2007	1
Caprock Canyons	Captive	44.5	150	4	2015-2018	2

\* Reserve size for the free-range herds are approximated by the area of their management unit, but they are free to move beyond these boundaries. Although American Prairie Reserve owns over 1616 km<sup>2</sup>, these properties are not yet contiguous, restricting portions of their herd to variously sized pastures.

<sup>a</sup> Bison were in different pastures during different years, so amount of available space varied

<sup>b</sup> Some of the bison had GPS collars set to different sampling schedules

<sup>c</sup> Sample included 2 individuals with GPS and 14 with VHF collars

Table 1.2. Summary of habitat characteristics for each of the bison herds we assessed. This includes average maximum and minimum temperatures, mean precipitation and elevation, as well as average day the growing season started and ended according to measures of NDVI.

Herd	Mean Temperature (°C)		Mean Precipitation (cm)	Mean Elevation (m)	Growing Season	
	Max	Min			Start	End
Henry Mountains	21.4	2.2	14.4	2,500	14 Mar	5 Oct
Book Cliffs	19.2	0.1	16.0	1,600	13 Apr	4 Nov
American Prairie Reserve	12.4	-1.1	48.3	930	27 Mar	31 Oct
Medano-Zapata Ranch	14.3	-1.1	28.2	2,300	6 May	23 Nov
Caprock Canyons	24.4	9.0	55.0	745	12 May	19 Nov

Table 1.3. Landscape characteristics and functional forms used for models of home range size and first-passage time.

Raster Layer	Functional Forms	Description	Resolution (m)	Units
Precipitation <sup>1</sup>	Linear, pseudothreshold, quadratic	30 year average measured precipitation	800	Millimeters
Elevation <sup>2</sup>	Linear, pseudothreshold, quadratic	Digital elevation model	30	Meters
Ruggedness <sup>2</sup>	Linear, pseudothreshold, quadratic	Vector ruggedness measure (Sappington et al 2007)	30	index
Canopy Cover <sup>3</sup>	Linear, pseudothreshold, quadratic	Percentage of upper canopy cover	30	Percent
Roads <sup>4</sup> (distance & density)	Linear, pseudothreshold	Euclidean distance & Line density	30	Meters & Kilometer per square kilometer
Water <sup>4</sup> (distance & density)	Linear, pseudothreshold, quadratic	Euclidean distance & Line density	30	Meters & Kilometer per square kilometer
NDVI <sup>5</sup> (amplitude & time integrated)	Linear, pseudothreshold, quadratic	Average amplitude & time integrated NDVI	250	Index

<sup>1</sup> PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 4 Feb 2004.

<sup>2</sup> U.S. Geologic Survey: <https://viewer.nationalmap.gov/advanced-viewer/>

<sup>3</sup> Multi-Resolution Land Characteristics Consortium- National Land Cover Database: [https://www.mrlc.gov/nlcd11\\_data.php](https://www.mrlc.gov/nlcd11_data.php)

<sup>4</sup> U.S. Census Bureau: <https://www.census.gov/geo/maps-data/data/tiger-line.html>

<sup>5</sup> U.S. Geologic Survey: <https://doi.org/10.5066/F7PC30G1>.

Table 1.4. Summary of mean home range sizes for each during each season across the study areas. N indicates the number of bison home ranges calculated for each study area. The only bison herd which showed a significant difference in home range size between seasons was the Henry Mountains, which also had the largest sample size and is free-range. Available space and home range size are reported in square kilometers.

Study Area	Available Space	Annual		Growing		Non-growing	
		N	HR ( $\pm$ SE)	N	HR ( $\pm$ SE)	N	HR ( $\pm$ SE)
Henry Mountains	1250	25	1204.36 ( $\pm$ 96.50)	57	1270.36 ( $\pm$ 56.67)	47	823.37 ( $\pm$ 79.38)
Book Cliffs	5665	2	467.91 ( $\pm$ 169.09)	3	267.28 ( $\pm$ 57.08)	3	690.17 ( $\pm$ 89.22)
American Prairie Reserve	114	10	109.05 ( $\pm$ 23.95)	14	117.10 ( $\pm$ 21.47)	22	353.61 ( $\pm$ 142.25)
Medano-Zapata Ranch	153	16	143.78 ( $\pm$ 5.95)	2	107.09 ( $\pm$ 4.94)	2	183.66 ( $\pm$ 25.04)
Caprock Canyons	44.5	4	32.01 ( $\pm$ 3.29)	8	31.87 ( $\pm$ 3.61)	9	25.92 ( $\pm$ 2.94)
<i>All</i>	<i>1445.3*</i>	<i>57</i>	<i>601.04</i> ( $\pm$ 83.37)	<i>84</i>	<i>896.68</i> ( $\pm$ 71.10)	<i>83</i>	<i>525.84</i> ( $\pm$ 60.09)

\*Average space available to the herds



Table 1.5. Top bison home range models for each season. Ecological covariates are ranked by their significance as measured by the absolute value of their  $\beta$  coefficient estimates. P-values of covariates less than 0.05 were considered to be statistically significant (bolded). Coefficients with 'ln()' were natural log transformed for the model (psuedothreshold functional form) and those with '<sup>2</sup>' were square transformed (quadratic functional form).

Season/Models	Intercept	$\beta$	SE	p
<b>Annual</b>	4.947		1.590	<b>0.002</b>
Road Distance		-7.329	1.699	<b>&lt;0.001</b>
Canopy Cover		-1.182	0.320	<b>&lt;0.001</b>
Canopy Cover <sup>2</sup>		0.162	0.137	0.238
Precipitation		-0.622	0.211	<b>0.003</b>
Precipitation <sup>2</sup>		-2.231	0.632	<b>&lt;0.001</b>
<b>Growing</b>	6.183		0.679	<b>&lt;0.001</b>
ln(Reserve Size)		3.550	0.200	<b>&lt;0.001</b>
ln(Precipitation)		-1.230	0.100	<b>&lt;0.001</b>
Ruggedness		0.877	0.235	<b>&lt;0.001</b>
<b>Non-growing</b>	2.692		2.040	0.187
Ruggedness		-9.418	2.211	<b>&lt;0.001</b>
Precipitation		-0.017	0.302	0.955
Precipitation <sup>2</sup>		-2.771	0.646	<b>&lt;0.001</b>
ln(Canopy Cover)		-1.113	0.171	<b>&lt;0.001</b>

Table 1.6. Summary of mean radii at maximum variance in first-passage time during each season across study areas. N indicates the number of bison home ranges calculated for each study area. None of the seasonal FPT comparisons were significant. Available space and FPT are reported in square kilometers.

Study Area	Available Space	Annual		Growing		Non-growing	
		N	FPT ( $\pm$ SE)	N	FPT ( $\pm$ SE)	N	FPT ( $\pm$ SE)
Henry Mountains	1250	25	203.73 ( $\pm$ 93.61)	57	101.08 ( $\pm$ 63.17)	47	202.54 ( $\pm$ 58.16)
Book Cliffs	5665	2	143.83 ( $\pm$ 124.97)	3	93.02 ( $\pm$ 68.34)	3	154.91 ( $\pm$ 86.09)
American Prairie Reserve	114	10	155.68 ( $\pm$ 95.96)	14	68.43 ( $\pm$ 30.76)	22	109.56 ( $\pm$ 35.99)
Medano-Zapata Ranch	153	2	0.95 ( $\pm$ 0)	2	0.48 ( $\pm$ 0.47)	2	0.48 ( $\pm$ 0.47)
Caprock Canyons	44.5	4	49.11 ( $\pm$ 48.16)	8	24.52 ( $\pm$ 22.77)	9	43.22 ( $\pm$ 18.86)
<i>All</i>	<i>1445.3*</i>	<i>43</i>	<i>165.96 (<math>\pm</math>59.03)</i>	<i>84</i>	<i>85.67 (<math>\pm</math>43.23)</i>	<i>83</i>	<i>150.70 (<math>\pm</math>34.89)</i>

\* Average space available to the herds

Table 1.7. Top bison first-passage time models for each season. Both annual and non-growing season models are 'NA' because the proximity of the null model ( $\Delta AIC_c < 2$ ) to the top ranked model indicates none of the covariates were explanatory. The ecological covariates for the growing season model are ranked by their significance as measured by the absolute value of their  $\beta$  coefficient estimates. P-values of covariates less than 0.05 were considered to be statistically significant (bolded). Coefficients with '<sup>2</sup>' were square transformed (quadratic functional form).

Season/Models	Intercept	$\beta$	SE	p
<b>Annual</b>	NA	NA	NA	NA
<b>Growing</b>	7.196		0.724	<b>&lt;0.001</b>
Ruggedness		-6.159	1.042	<b>&lt;0.001</b>
Ruggedness <sup>2</sup>		-13.644	2.873	<b>&lt;0.001</b>
Precipitation		2.575	0.838	<b>0.002</b>
Precipitation <sup>2</sup>		-2.636	0.778	<b>&lt;0.001</b>
<b>Non-growing</b>	NA	NA	NA	NA

Figures

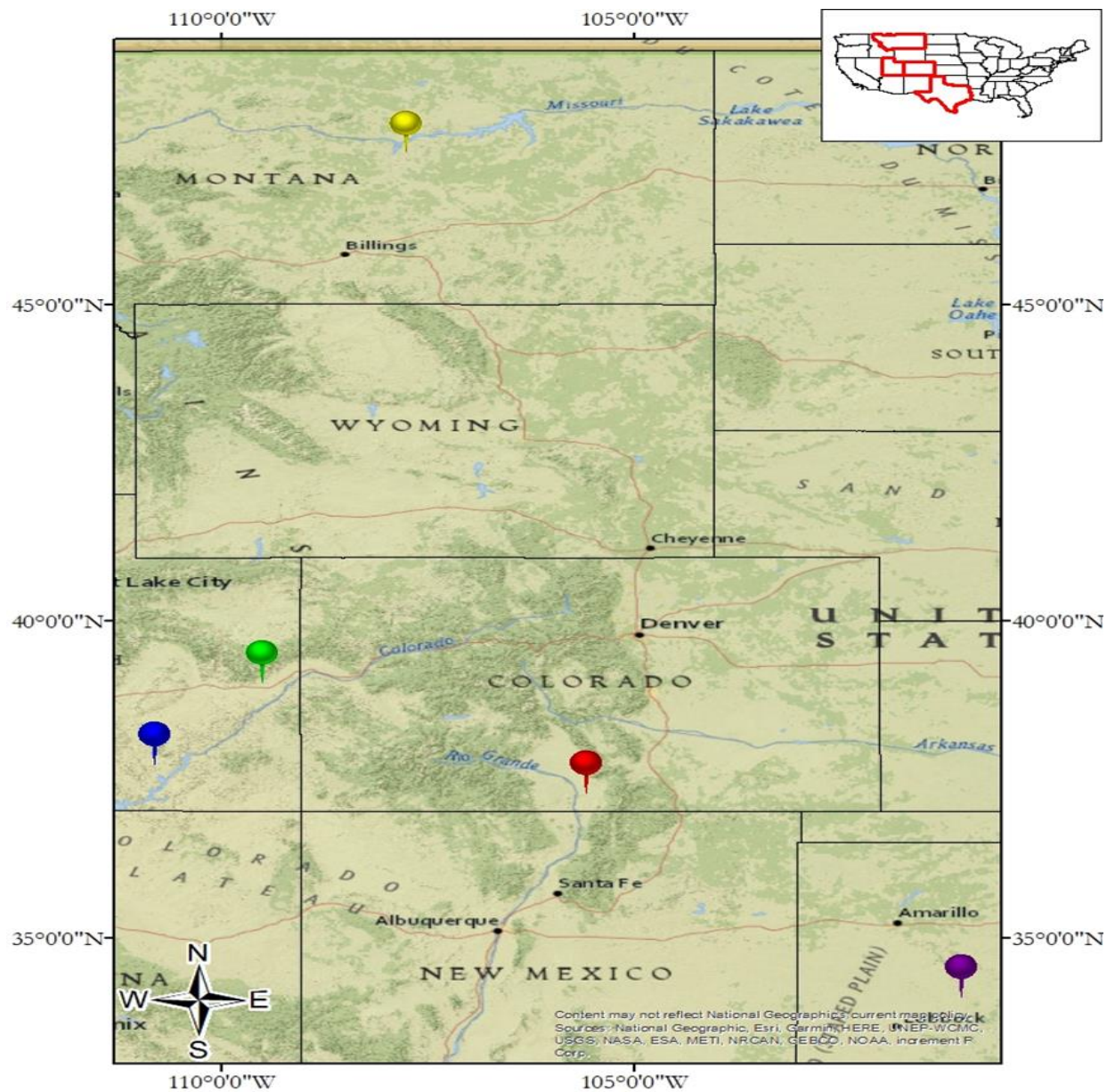


Figure 1.1. Map of the herd locations we assessed for this study. The yellow pin indicates American Prairie Reserve, green is the Book Cliffs, blue is the Henry Mountains, red is Medano-Zapata Ranch, and purple is the Texas State Bison Herd.

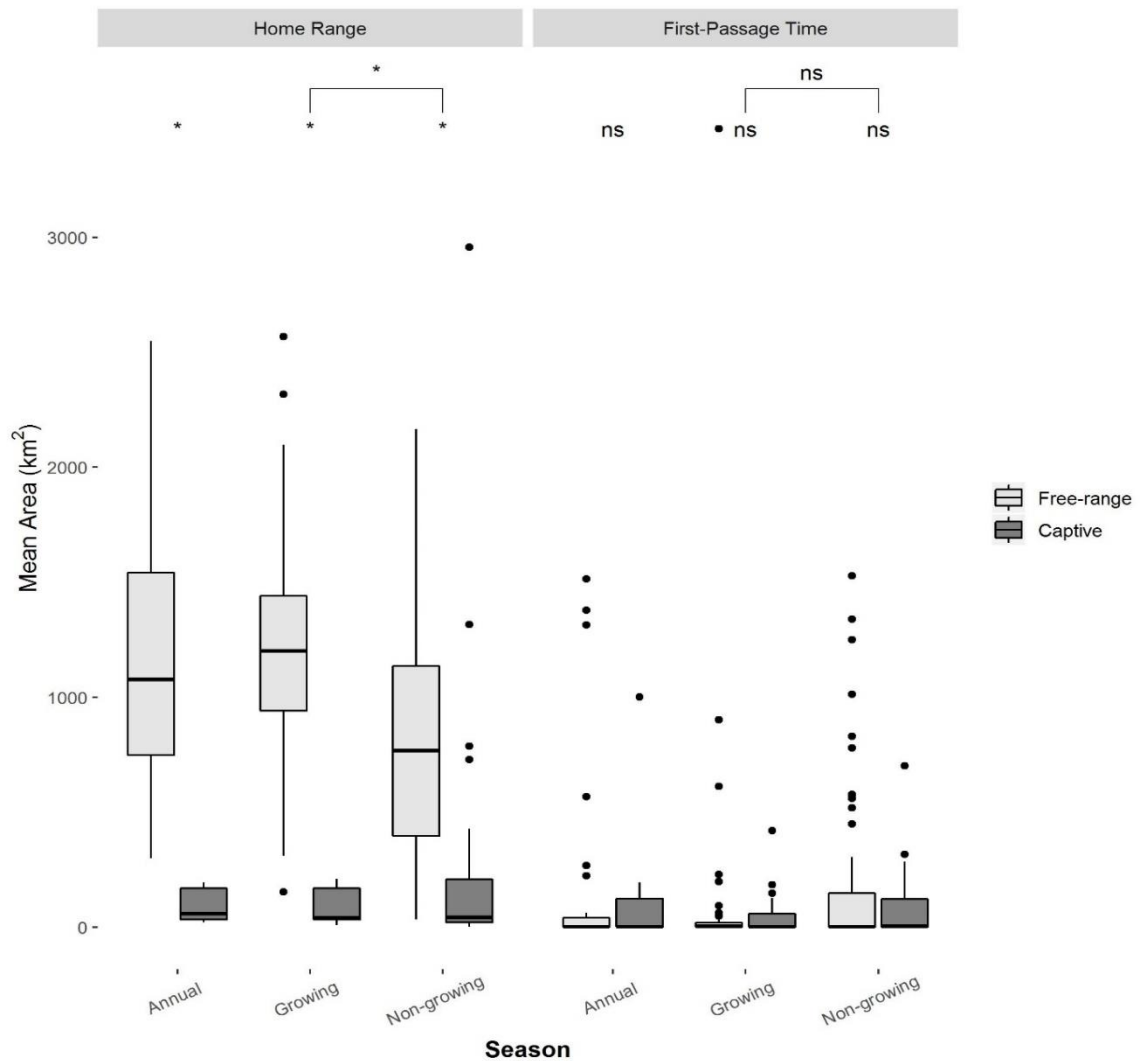


Figure 1.2. Mean home range size and first-passage times for each management type within each season. Free-range bison (HM and BC) had larger home ranges than captive herds (APR, MZR, CC) within each season and had significantly larger home ranges during the growing season than non-growing season ( $p < 0.05$ ). Although first-passage time tended to be larger for free-range herds within each season and greatest during the non-growing season for each management type, none of the comparisons were significant ( $p > 0.05$ ).

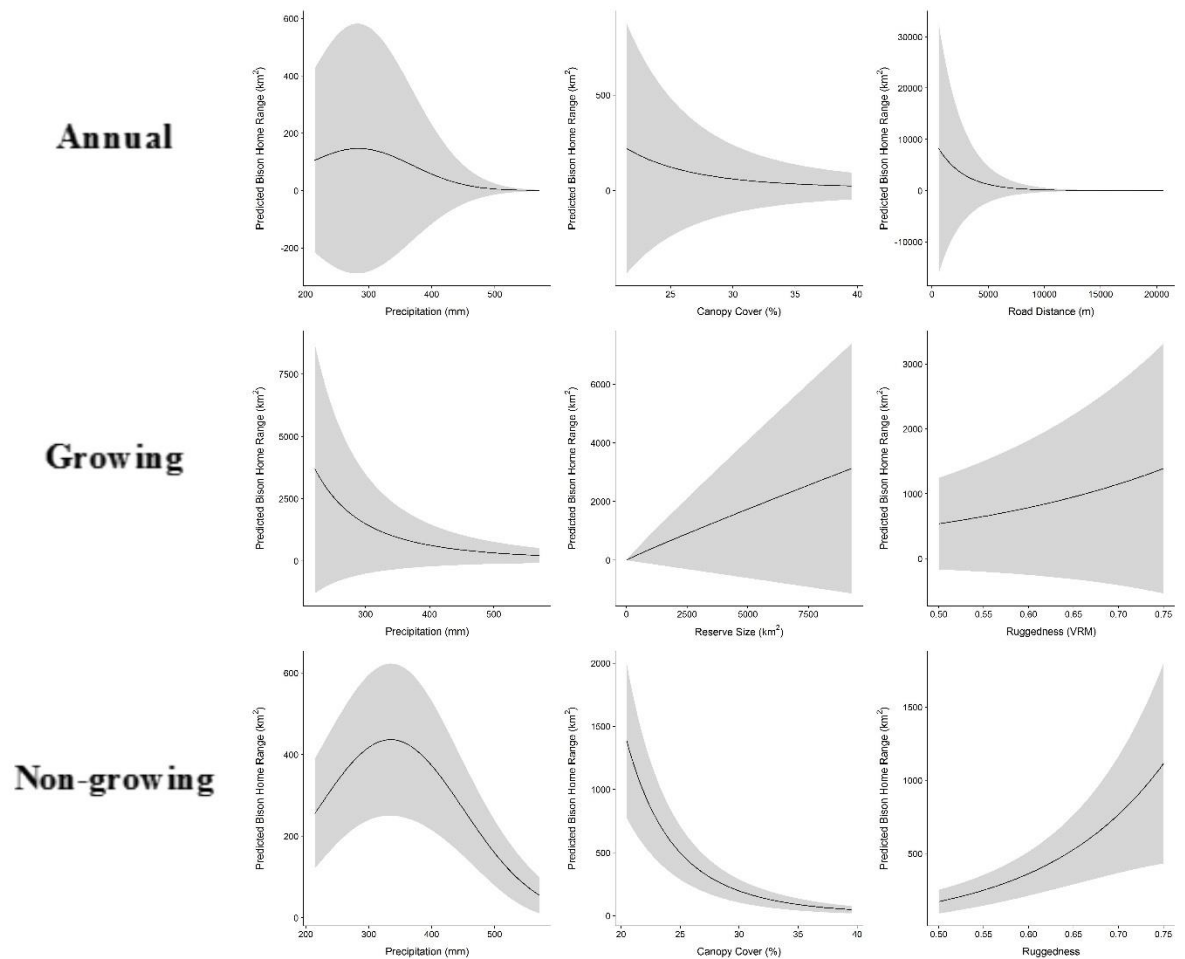


Figure 1.3. Home range sizes were estimated with the top ranked model for each season using simulated values for each ecological correlate while the remaining covariates were held at their means. The black line indicates the home range prediction at each simulated covariate value and the gray ribbons represent the 95% confidence intervals (of the predictions). All simulated values were derived within the range of the measured values.

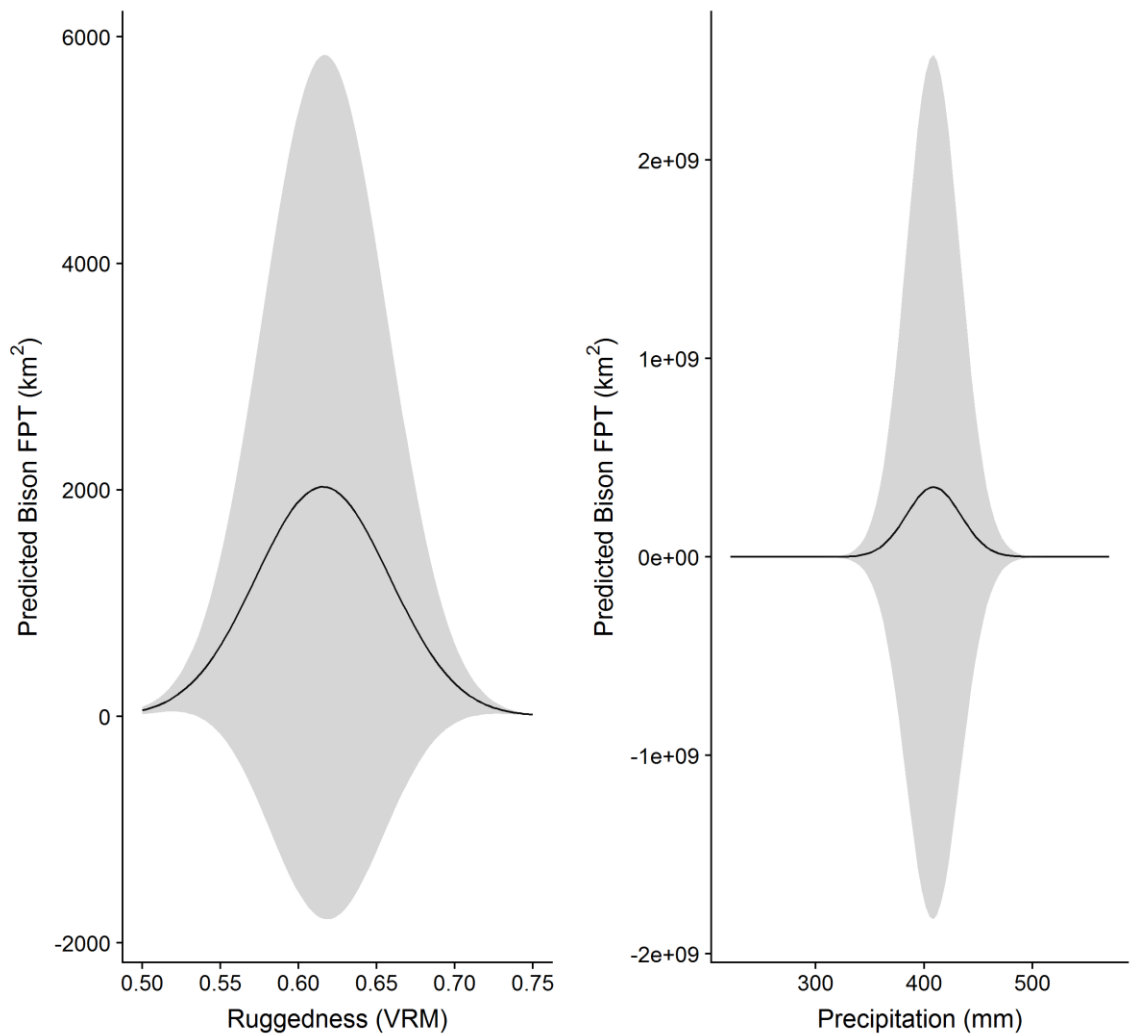


Figure 1.4. Estimated foraging patch size as indicated by first-passage time during the growing season using the top ranked model with simulated values for each ecological correlate. The black line indicates the first-passage time prediction at each simulated covariate value and the gray ribbons represent the 95% confidence intervals of the predictions. All simulated values were derived within the range of the measured values.

**Chapter 3: Terrestrial castaway as a competing hypothesis to the refugee concept:  
an example using American bison habitat selection**

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**Abstract:** The establishment of multiple bison (*Bison bison*) conservation herds across their former range offers a unique natural experiment to assess the relative importance of management constraints and habitat suitability on their future restoration. Despite their broad niche, fencing may offer a barrier to bison resource selection. Differences in selection patterns may indicate a fundamental lack of suitability, as explained by the refugee species concept, while a high level of agreement could suggest barriers themselves are more limiting to their long-term survival, which we term “terrestrial castaways.” We propose testing these competing hypotheses by assessing patterns of habitat selection between separate herds. We used resource selection functions (RSFs) to compare the preferences of bison in five different conservation herds, including two free-range and three fenced herds, occurring over an ecological gradient of their prior range, to assess the relative importance of eight continuous measures of biotic (NDVI and canopy cover), abiotic (elevation, ruggedness, slope, solar radiation, and water), and anthropogenic (roads) landscape characteristics. Bison generally preferred areas which had gentle slopes, higher elevations, greater vegetation productivity, were closer to linear water features, had lower intensity of solar radiation, sparse canopy cover, homogenous terrain, and were generally close to roads. However, the two free-range herds had notable



differences from the fenced herds. Bison in the Henry Mountains noticeably preferred to use areas farther from roads while those in the Book Cliffs selected areas with intermediate vegetation productivity. The overall high level of resource selection agreement between the herds suggest that bison may be a “terrestrial castaway” rather than “refugee species” which could indicate bison require more *continuous* instead of better *quality* habitat. This important distinction may help conservationists to prioritize potential bison restoration areas within their historic range. Future assessments can improve this framework by incorporating more detailed investigations of diet and fitness relative to spatial availability.

Keywords: *Bison bison*, fencing, habitat preference, refugee species, resource selection function, terrestrial castaway

Article impact statement: Comparing habitat preferences of spatially isolated bison herds may suggest factors limiting their conservation.

### *Introduction*

The American plains bison (*Bison bison*) has a long history of conservation challenges. While overhunting nearly led to their extinction towards the end of the 19<sup>th</sup> Century, habitat loss has been an ongoing barrier to their restoration (Freese et al. 2007; Aune et al. 2017). Today, most of the range historically occupied by bison has been converted to either agriculture, urbanization, or reserved for livestock grazing (Sanderson et al. 2008; Gates et al. 2010). Despite their broad niche size (Plumb and McMullen 2018), many bison managed for conservation purposes are occupying areas considered to be the

periphery of their former range such as intermountain mixed-forest (Meagher 1973) and arid steppe ecosystems (Ranglack and du Toit 2015). The potential of these regions for decreased conflicts with humans makes them attractive locations for restoration due to the sociopolitical limitations (Freese et al. 2007; Gates et al. 2010), but whether such areas are optimal for their long-term recovery is not explicit. Ignoring habitat suitability of this once widely distributed species may be restricting them to environments which inhibit their fitness, putting them in danger of becoming a ‘refugee species’ and continuing their extinction risk (Kerley et al. 2012). Bison are particularly susceptible due to the anthropogenic influences of their range contraction (Sanderson et al. 2008) and the fact that the remaining wild herds were only found in remote areas away from humans (Meagher 1973). If disturbances are causing bison to take refuge from humans by choosing secluded habitats, those areas may not have optimal resources for their long-term survival.

Currently, the best suggested approach to test the refugee species hypothesis is experimental species reintroductions into diverse habitats to discern which habitats result in higher overall fitness (Kerley et al. 2012). The presence of multiple bison conservation herds across their former range with known management histories offers a unique natural experiment following this framework. However, it remains unclear how management and environmental features interact to influence bison conservation. Given the spatial restrictions on bison (see Chapter 2), it is possible space itself, rather than habitat, has the greater influence on their conservation. We propose an alternate hypothesis to the refugee species concept (Kerley et al. 2012) in which a wide ranging species, such as bison, are

restricted to suitable habitats but of limited size and isolated from other populations, which negatively affects their conservation in the long-term. We are referring to this concept as “terrestrial castaways.”

In order to test whether bison should be classified as a refugee species or terrestrial castaway, we put forth comparing habitat selection within different bison herds to investigate if variations in use are related to particular herds or overall ecological characteristics. Though we would expect bison habitat preferences to vary across local environmental conditions (Kuemmerle et al. 2018), management practices can artificially manipulate selection by either restricting or supplementing access to resources (Ramos et al. 2016). Previous studies of bison habitat selection indicate preferences for vegetation types consistent with forage quality (Ranglack and du Toit 2015; Schoenecker et al. 2015) and tendency to avoid woody species (Allred et al. 2011). If a specific herd deviates from the expectations of past studies, then such habitat may be not be optimal and could suggest classification as a refugee. However, if habitat selection remains consistent across reintroduction sites, then isolation may have a stronger influence on their long-term conservation, suggesting a terrestrial castaway.

Though an ideal experiment would survey multiple parameters of successful conservation (Kerley et al. 2012), comparing habitat use across multiple reintroduced herds is an important first step. Bison conservation herds are often compared with adjacent or co-occurring cattle (Van Vuren 1979; Fuhlendorf et al. 2010; Allred et al. 2011; Kohl et al. 2013) but less frequently compared across their historic distribution

(Kuemmerle et al. 2018). Since there are so few ‘wild’ bison herds (Bates and Hersey 2016), it is important to assess habitat selection patterns over a diversity of historically available habitat to account for ecological variations in addition to differences potentially related to management. Individually assessed herds do seem to have consistent patterns, such as variation in strength of resource selection across seasons (Ranglack and du Toit 2015; Schoenecker et al. 2015; McAnally 2018) and between sexes (Berini and Badgley 2017). However, herds which are more actively managed, such as those restricted by fencing, have ambiguous conservation value (Hayward et al. 2015) and may use resources differently (Lea et al. 2016). There have been no comparisons of habitat use between bison herds occupying different habitats in North America. Examining broad patterns in resource selection to identify whether bison are a refugee or terrestrial castaway can further conservation efforts by determining the factors which are most limiting to their restoration.

The objective of this research was to assess the habitat selection patterns of five bison conservation herds occurring from northern Montana to northern Texas to ascertain if herd characteristics were more consistent with the expectations of a refugee species or a terrestrial castaway. We calculated resource selection functions (RSFs) for two free-range bison herds and three captive herds with varying spatial availability. A high level of agreement in resource selection patterns across the herds was expected if bison conservation is taking place in suitable areas, which would support classification as a terrestrial castaway, while inconsistencies may indicate potentially suboptimal locations, suggesting a refugee species.

## *Methods*

### Study Area and Data Collection

We examined resource selection patterns for a total of 90 bison, including 47 from the Henry Mountains (HM) in south-central Utah (38°5'N, 110°50'W), 5 from the Book Cliffs (BC) in eastern Utah (39°23'N, 109°30'W), 17 at the American Prairie Reserve (APR) in northern Montana (47°45'N, 107°41'W), 16 at the Medano-Zapata Ranch (MZR) in the San Luis Valley of south-central Colorado (37°39'N, 105°35'W), and 5 from the Texas State Bison Herd at Caprock Canyons State Park (CC) in north-central Texas (34°26'N, 101°3'W; Table 2.1; Figure 2.1). Location data was collected between the years 2005-2018 using both GPS and VHF collars, however, VHF was only used at MZR. We calculated the extent of available space for the free-range herds (HM and BC) using 99% minimum convex polygons with the R package 'adehabitatHR' (Calenge 2006) of all relocations within the study area and buffered it by median step-length of the observed individuals. The captive herds were considered to be completely bound by the pastures they occurred in, so available space was defined as their non-buffered fenced extent. As bison occasionally escaped or are transferred between pastures, we removed any locations which occurred outside the fenced extents.

### Landscape Characteristics

We evaluated eight continuous landscape variables (Table 2.2) as potentially influencing bison habitat selection. Digital elevation models (DEM, U.S. National Map) were used to create the elevation, ruggedness, slope, and solar radiation rasters for each area.

Ruggedness was calculated following the methods of Sappington et al. (2007) with the Terrain Ruggedness (VRM) tool for ArcMap. Topographic slope (degrees) was calculated using the ‘raster’ package in program R (Hijmans 2018). Solar radiation was used as a proxy for aspect and calculated in R package ‘insol’ (Corripio 2019) by averaging solar insolation ( $J \cdot m^{-2}$ ) during the spring equinox, summer solstice, fall equinox, and winter solstice for each study area. Distance to roads and water (m) rasters were developed from vector layers (TIGER) using the Euclidean distance tool with ArcMap 10.6.1 (ESRI 2018). We also acquired normalized difference vegetation index (NDVI) amplitude (USGS Remote Sensing Phenology) and canopy cover (National Land Cover Database) rasters for each study area.

#### Resource Selection Functions

We calculated third-order resource selection functions following a use-available framework (Johnson et al. 2006). The GPS locations collected from each herd were the used sample. We ran a simulation to identify the number of available points necessary in each study area to accurately represent the distribution of values for each landscape characteristic (Lowrey et al. 2017). The minimum ratio necessary to accurately represent the variation of each covariate on the landscape was defined and used for each herd. As such, we randomly generated available points within the extents of each study area at a 1:5 ratio of used to available locations. The values of each landscape characteristic were then extracted for each point and standardized for each study area by subtracting it from the mean and dividing by twice the standard deviation (Gelman 2008). We calculated two

additional functional forms for each covariate to account for possible nonlinear relationships, including psuedothreshold using natural log transformation (Franklin et al. 2000) and quadratic using square transformation.

Our model selection approach followed a multi-tiered framework for reducing the number of competing models (Burnham and Anderson 2002). In the first tier, we evaluated univariate mixed-effect logistic regressions with a random effect for individual animal of each covariate to identify the most explanatory functional form ranked by Akaike's Information Criterion (AICc). We then calculated Pearson's correlation coefficients for each covariate to ensure candidate models only included combinations of variables which were not collinear ( $<|0.6|$ ). In the second tier, we combined all covariates in the first tier which were within 5 AICc units of the top ranked models in all possible combinations, with consideration for collinearity, in order to find the best overall model. We then evaluated the best models from the second tier for uninformative parameters (Arnold 2010). This was completed for each herd, totaling five herd-specific best models. We also created an additional pooled model which used the data from all five herds and included an additional random effect for study area following this multi-tiered approach. The packages 'lme4' (Bates et al. 2015) and 'MuMIn' (Barton 2018) were used to fit and select these models in RStudio version 3.5.1 (RStudio Team 2016). In order to compare the resource preferences between each herd-specific model and the pooled model, we looked at the relative selection strength for each landscape covariate and ranked relative importance of each covariate by the absolute magnitude of their beta-coefficient.

## *Results*

In total, 144,320 used points and 721,600 randomly generated available points were analyzed (Table 2.1). Overall, the topographical features (i.e., elevation, slope, ruggedness, and solar radiation) were the most variable at HM, while APR had the highest mean NDVI amplitude and CC had the highest average percentage of canopy cover (Table 2.1). Bison at HM used areas farther from roads on average while those at MZR were farthest from linear water on average (Table 2.1).

In general, bison resource selection was fairly consistent across the landscape characteristics we assessed (Figures 6 and 7). Steep slopes and heterogeneous terrain were consistently avoided in all the study areas while higher elevations and close proximity to linear water was typically sought out (Figure 2.2 and 7). NDVI amplitude and ruggedness were the only covariates not included in all of the models due to collinearity (Table 2.3). Specifically at the HM, bison relative selection for proximity to water was minimized at ~1,200 m, after which selection strength began to increase, while farther distances from roads and open canopy cover were steadily preferred (Figure 2.2). These preferences seemed to generally agree with the pooled model, except for roads which had higher relative selection strength for farther distances from roads. NDVI amplitude was not modeled for HM as it was collinear with elevation. Higher elevations were preferred by bison at HM but selection strength appeared to be maximized at ~3,000 m, while lower levels of solar radiation were preferred, minimizing at  $\sim 2.0 \times 10^8 \text{ J} \cdot \text{m}^{-2}$ , however, gentle slopes and low terrain ruggedness were preferred consistently (Figure 2.3). Preference for these covariates generally agreed with the pooled model. At BC,



bison preferred areas further than 1,500 m from water, but preferred to be close to roads. Selection for NDVI amplitude was greatest at the index value of 20 for BC, while open canopy cover was steadily preferred. The pooled model tended to predict greater selection for these variables, but was fairly consistent for canopy cover (Figure 2.2). Selection for elevation at BC was maximized at ~2,200 m and solar radiation at  $\sim 1.6 \times 10^8 \text{ J} \cdot \text{m}^{-2}$ , while lower values for slope and ruggedness were generally preferred (Figure 2.3). These preferences were generally consistent with the pooled model, except for solar radiation which tended to be overestimated relative to the herd model.

However, the captive herds (APR, MZR, and CC) seemed to be more similar in their resource selection patterns to each other than the free-rang herds mentioned above (HM and BC). APR bison preferred to be close to water and roads, as well as in areas with open canopies, but preferred for areas with high NDVI amplitude (Figure 2.2). While NDVI preference agreed with the pooled model, the other covariates tended to be overestimated relative to the herd models. Preference for slope and solar radiation were maximized at  $\sim 5^\circ$  and  $\sim 2.2 \times 10^8 \text{ J} \cdot \text{m}^{-2}$  respectively, while elevation preference was minimized at ~775 m (Figure 2.3). Ruggedness preference was not significantly predicted at APR. Slope preference was slightly overestimated and elevation preference slightly underestimated in the pooled model relative to the herd model while solar radiation predictions were dissimilar (Figure 2.3). At MZR, selection for proximity to water was predicted to be minimized at ~3,500 m, while closer distances to roads and higher values of NDVI were preferred (Figure 2.2). Selection for canopy cover was not significantly predicted. Preference for distance to water agreed with the pooled model, while selection

for proximity to roads and NDVI amplitude were generally overestimated (Figure 2.2). Selection for elevation at MZR was maximized at ~2,320 m, while gentle slopes and higher values of solar radiation were preferred, however ruggedness preference was not modeled as it was collinear with slope (Figure 2.3). Elevation and slope predictions generally agreed with the pooled model but tended to be overestimated relative to the herd models while solar radiation estimates were entirely dissimilar (Figure 2.3). Finally, at CC close proximity to both water and roads were preferred, while selection for NDVI amplitude was minimized at an index of ~12, and preference for canopy cover increased slightly at higher percentages of density (Figure 2.2). Selection for distance to water and roads were generally overestimated in the pooled model and underestimated for NDVI amplitude. Preference of canopy cover density at CC was dissimilar from the pooled model (Figure 2.2). Elevation preference was maximized at ~850 m, while lower values of slope and ruggedness were selected at CC, but higher values of solar radiation tended to be preferred (Figure 2.3). Slope predictions agreed with the pooled model however preference for elevation and ruggedness tended to be overestimated while predictions for solar radiation were dissimilar (Figure 2.3).

All of the covariates fit in the pooled model were significant ( $p < 0.05$ ), but the most important were slope and elevation while the weakest predictor was road distance (Table 2.3). It seems captive bison tended to prefer more productive areas while BC bison seemed to select intermediate productivity as indicated by NDVI amplitude. Interestingly, HM bison preference for farther distances from roads was entirely opposite of the remaining four herds (Figure 2.2). Also, most of the herds selected for sparse canopy

cover while bison at CC seemed to slightly prefer denser canopies. In general, the pooled model seemed to agree the most with HM selection strengths across the covariates

### *Discussion*

We compared the resource selection between each bison conservation herd to a pooled model of all the data in order to assess similarities in habitat preferences across local ecological conditions. The amount of consistency in selection between herds may indicate whether bison are ‘refugees’ in suboptimal habitat or simply ‘terrestrial castaways’ isolated to small tracts of suitable habitat. Our results appear to suggest the latter, given the relatively high degree of agreement in resource selection patterns between the herds we examined. Particularly, topographic features were used very similarly across the study areas regardless of habitat type or available space. Steep slopes and heterogeneous terrain ruggedness are expected to reduce landscape permeability which explains the tendency of bison to avoid such areas. Their generally high selection for areas with greater NDVI, lower density of canopy cover, and increased elevations may be related to their preference for productive vegetation (Allred et al. 2011; Merkle et al. 2015). This has been previously found to be the case in other studies of bison resource selection which also suggest a tendency for preferring productive habitats (Kohl et al. 2013; Ranglack and du Toit 2015; Schoenecker et al. 2015). Given a sufficient space, free-range herbivores may actually track forage quality during vegetation maturation to maximize their energy consumption (Merkle et al. 2016). However, there were some minor differences in habitat selection between the herds.

The preference of the free-range HM bison for farther distances from roads suggests the possibility of a different influence on this particular herd, as the others tended to select areas closer to roads. Since bison at HM generally have a greater capacity to move than the fenced herds, the observed dissimilarities may be due in part to their greater spatial availability, allowing them to move farther from roads in general. However, it is more likely due to the fact that HM bison have received greater annual hunting pressure (Ranglack and du Toit 2016) than the remaining herds which have been hunted for only a short period of time (BC and APR; Bates and Hersey 2016, Austin et al. 2017) or not at all (MZR and CC). Elk (*Cervus canadensis*) have been previously found to avoid motorize routes during hunting seasons compared to the summer season (Ranglack et al. 2017). Although, proximity to roads can also be confounded by their tendency to follow water courses and natural topography (Bruggeman et al. 2006; Bruggeman et al. 2007). While it may be an important explanation of the differences in bison habitat selection between herds, we do not believe road proximity selection to be useful in distinguishing refugee species from terrestrial castaways. There was also a marked difference in their selection for solar radiation. Captive bison preferred higher levels of solar radiation than free-range bison, consistent with south and west aspect preference for fenced bison and north and east aspect preference in the Henry Mountains. Previous studies of the HM bison also detected a propensity for foraging on north facing slopes, relative to cattle, which was attributed to the relative proximity of water to these locations (Van Vuren 1979). Aspect preference was inconsistent in a previous assessment of resource selection at APR (Kohl et al. 2013). Since preferences for this habitat

characteristic are inconsistent in the literature and may vary across seasons, we also do not consider it helpful for identifying suitable areas for bison.

The overall resource selection similarities we detected between bison herds across their former range suggests they do not fit the definition of refugee species (Kerley et al. 2012) but rather what we term a ‘terrestrial castaway.’ That is, current bison habitat appears suitable and individuals tend to prefer similar environmental characteristics, which may be explained by their broad niche and adaptability (Plumb and McMullen 2018). The differences we observed appear to be a function of management influences such as fences and hunting rather than landscape features. Spatial limitations of available habitat within their highly fragmented former range is widely regarded as a major barrier to bison conservation (Sanderson et al. 2008; Gates et al. 2010; Aune et al. 2017). The isolation of these herds is similar to that of island species, which are constrained by a fixed amount of space and genetic diversity (Frankham 2003). However, instead of oceans, bison conservation herds are separated by sociopolitical restrictions. We believe that framing the restoration challenges of bison as a castaway species can help to improve their management. By thinking of bison as terrestrial castaways, strategies such as improving connectivity between herds become more apparent in their ability to both minimize conflict with humans and encourage genetic diversity (Gates et al. 2010). While identifying areas suitable for future bison herds is an important long-term goal (Sanderson et al. 2008), maintaining connections between current herds may be a more immediate concern.

This research shifts the focus away from improving habitat quality of bison to simply increasing connectivity of existing habitat. The historically large ecological niche and historical range bison once occupied suggests their adaptability and potential resilience (Gunderson 2000). By taking advantage of these characteristics, managers can improve the conservation future of bison while minimizing the conflicts which are responsible for their current isolation. Our ‘terrestrial castaway’ concept may also be useful for other species at risk which are strongly limited by sociopolitical influences but ecologically adaptable.

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#### *Literature Cited*

Allred BW, Fuhlendorf SD, Hamilton RG. 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere*. 2(3):1–17.

doi:10.1890/ES10-00152.1.

Arnold TW. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *J Wildl Manage.* 74(6):1175–1178. doi:10.1111/j.1937-2817.2010.tb01236.x.

Aune K, Jorgensen D, Gates C. 2017. The IUCN Red List of Threatened Species. [accessed 2019 Mar 5]. <http://dx.doi.org/10.2305/IUCN.UK.2017->.

Austin D, Anderson L, Anderson E, Heidebrink S, Kunkel K, Holder B. 2017. Bison Report 2016-2017.

Barton K. 2018. MuMIn: Multi-Model Inference. R package version 1.42.1. Available from <https://cran.r-project.org/package=MuMIn>.

Bates B, Hersey K. 2016. Lessons Learned from Bison Restoration Efforts in Utah on Western Rangelands. *Rangelands.* 38(5):256–265. doi:10.1016/j.rala.2016.08.010.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67(1):1–48. doi:doi:10.18637/jss.v067.i01.

Berini JL, Badgley C. 2017. Diet segregation in American bison (*Bison bison*) of Yellowstone National Park (Wyoming, USA). *BMC Ecol.* 17(27):1–10. doi:10.1186/s12898-017-0137-9.

Bruggeman JE, Garrott RA, Bjornlie DD, White PJ, Watson FGR, Borkowski J. 2006. Temporal variability in winter travel patterns of Yellowstone bison: the effects of road grooming. *Ecol Appl.* 16(4):1539–1554. doi:10.1890/1051-

0761(2006)016[1539:TVIWTP]2.0.CO;2.

- Bruggeman JE, Garrott RA, White PJ, Watson FGR, Wallen R. 2007. Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecol Appl.* 17(5):1411–1423. doi:10.1890/06-0196.1.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer.
- Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Modell.* 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017.
- Corripio JG. 2019. insol: Solar Radiation. R package version 1.2. Available from <https://cran.r-project.org/package=insol>.
- ESRI. 2018. ArcGIS Desktop: Release 10.6.1. Environmental Systems Research Institute, Redlands, CA, USA.
- Frankham R. 2003. Genetics and conservation biology. *C R Biol.* 326:22–29. doi:10.1016/S1631-0691(03)00023-4.
- Franklin AB, Anderson DR, Gutiérrez RJ, Burnham KP. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecol Monogr.* 70(4):539–590.
- Freese CH, Aune KE, Boyd DP, Derr JN, Forrest SC, Cormack Gates C, Gogan PJP, Grassel SM, Halbert ND, Kunkel K, et al. 2007. Second chance for the plains bison.



- Biol Conserv. 136:175–184. doi:10.1016/j.biocon.2006.11.019.
- Fuhlendorf BSD, Allred BW, Hamilton RG. 2010. Bison as keystone herbivores on the Great Plains : Can cattle serve as proxy for evolutionary grazing patterns ? (4).
- Gates C, Freese CH, Gogan PJP, Kotzman M. 2010. American Bison: Status Survey and Conservation Guidelines 2010. Gland, Switzerland. IUCN.
- Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. Stat Med. 27:2865–2873. doi:10.1002/sim.3107.
- Gunderson LH. 2000. Ecological resilience- in theory and application. Annu Rev Ecol Syst. 31:425–39.
- Hayward MW, Child MF, Kerley GIH, Lindsey PA, Somers MJ, Burns B. 2015. Ambiguity in guideline definitions introduces assessor bias and influences consistency in IUCN Red List status assessments. Front Ecol Evol. 3:1–12. doi:10.3389/fevo.2015.00087.
- Hijmans RJ. 2018. raster: Geographic Data Analysis and Modeling.
- Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS. 2006. Resource Selection Functions Based on Use-Availability Data: Theoretical Motivation and Evaluation Methods. J Wildl Manage. 70(2):347–357. doi:10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2.
- Kerley GIH, Kowalczyk R, Crooms J. 2012. Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a

- marginal habitat? *Ecography (Cop)*. 35:519–529. doi:10.1111/j.1600-0587.2011.07146.x.
- Kohl MT, Krausman PR, Kunkel K, Williams DM. 2013. Bison Versus Cattle: Are They Ecologically Synonymous? *Rangel Ecol Manag*. 66(6):721–731. doi:10.2111/REM-D-12-00113.1.
- Kuemmerle T, Levers C, Bleyhl B, Olech W, Perzanowski K, Reusch C, Kramer-Schadt S. 2018. One size does not fit all: European bison habitat selection across herds and spatial scales. *Landsc Ecol*. 33(9):1559–1572. doi:10.1007/s10980-018-0684-2.
- Lea JM, Kerley GI, Hrabar H, Barry TJ, Shultz S. 2016. Recognition and management of ecological refugees: A case study of the Cape mountain zebra. *Biol Conserv*. 203:207–215. doi:10.1016/j.biocon.2016.09.017.
- Lowrey B, Garrett RA, Miyasaki HM, Fralick G, Dewey SR. 2017. Seasonal resource selection by introduced mountain goats in the southwest Greater Yellowstone Area. *Ecosphere*. 8(4):e01769. doi:10.1002/ecs2.1769.
- McAnally AM. 2018. Evaluating Bison Seasonal Resource Selection within Caprock Canyons State Park. Tarleton State University. Master's Thesis.
- Meagher M. 1973. The Bison of Yellowstone National Park.
- Merkle JA, Cherry SG, Fortin D, Kotler BP. 2015. Bison distribution under conflicting Foraging strategies: Site fidelity vs. Energy maximization. *Ecology*. 96(7):1793–1801. doi:10.1890/14-0805.1.

- Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, Oates BA, Sawyer H, Scurlock BM, Kauffman MJ. 2016. Large herbivores surf waves of green-up during spring. *Proc R Soc B*. 283(1833):20160456.  
doi:10.1098/rspb.2016.0456.
- Plumb G, McMullen C. 2018. Bison on the Southwest Colorado Plateau: Conservation at the Edge. *Southwest Nat*. 63(1):42–48. doi:10.1894/0038-4909-63.1.42.
- Ramos A, Petit O, Longour P, Pasquaretta C, Sueur C. 2016. Space Use and Movement Patterns in a Semi-Free-Ranging Herd of European Bison (*Bison bonasus*). *PLoS One*. 11(2):e0147404. doi:10.1371/journal.pone.0147404.
- Ranglack DH, Proffitt KM, Canfield JE, Gude JA, Rotella J, Garrott RA. 2017. Security areas for elk during archery and rifle hunting seasons. *J Wildl Manage*.  
doi:10.1002/jwmg.21258.
- Ranglack DH, du Toit JT. 2015. Habitat Selection by Free-Ranging Bison in a Mixed Grazing System on Public Land. *Rangel Ecol Manag*. 68(4):349–353.  
doi:10.1016/j.rama.2015.05.008.
- Ranglack DH, du Toit JT. 2016. Bison with benefits: towards integrating wildlife and ranching sectors on a public rangeland in the western USA. *Oryx*. 50(3):549–554.  
doi:10.1017/S0030605314001197.
- Remote Sensing Phenology. 2018. USGS. doi:<https://doi.org/10.5066/F7PC30G1>.  
[accessed 2018 Sep 18]. [https://phenology.cr.usgs.gov/get\\_data\\_250w.php](https://phenology.cr.usgs.gov/get_data_250w.php).

RStudio Team. 2016. RStudio: Integrated Development for R.

Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr J, Dobrott S, et al. 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conserv Biol.* 22(2):252–266. doi:10.1111/j.1523-1739.2008.00899.x.

Sappington JM, Longshore KM, Thompson DB. 2007. Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. *J Wildl Manage.* 71(5):1419–1426. doi:10.2193/2005-723.

Schoenecker KA, Nielsen SE, Zeigenfuss LC, Pague CA. 2015. Selection of vegetation types and density of bison in an arid ecosystem. *J Wildl Manage.* 79(7):1117–1128. doi:10.1002/jwmg.940.

Van Vuren D. 1979. Ecology and Behavior of Bison in the Henry Mountains, Utah. Oregon State University. Master's Thesis.

Tables

Table 2.1. Summary of herd information for bison resource selection functions. The bison herds include the Henry Mountains (HM), Book Cliffs (BC), American Prairie Reserve (APR), Medano-Zapata Ranch (MZR), and Caprock Canyons (CC) as well as pooled model containing all of the data. The number of individual bison sampled from each herd is indicated as well as the area of available extent, which is reported in square kilometers. The units for landscape covariates can be found in Table 1.2. Standard deviation for each covariate means is reported below each value in parentheses.

Herd	No. Bison	Extent Area	Used Pts	Available Pts	Mean at Used Points							
					Elevation	Slope	Ruggedness	Solar Radiation	Road Distance	Water Distance	NDVI Amplitude	Canopy Cover
HM	47	1,212	77,959	389,795	2094 (±405)	9.94 (±7.56)	5.27e <sup>-3</sup> (±9.67e <sup>-3</sup> )	2.31e <sup>8</sup> (±1.57e <sup>7</sup> )	1287 (±1091)	389 (±326)	13.97 (±9.08)	6.91 (±13.82)
BC	5	586	4,436	22,180	2211 (±106)	3.76 (±3.40)	1.28e <sup>-3</sup> (±4.47e <sup>-3</sup> )	2.27e <sup>8</sup> (±6.17e <sup>7</sup> )	452 (±571)	451 (±281)	19.13 (±3.93)	2.05 (±7.86)
APR	17	161	30,355	151,775	739 (±37)	1.92 (±2.16)	4.75e <sup>-4</sup> (±1.16e <sup>-3</sup> )	2.07e <sup>8</sup> (±4.53e <sup>6</sup> )	1164 (±1378)	416 (±378)	29.32 (±6.33)	0.26 (±2.15)
MZR	16	154	9,310 (484 VHF)	46,550	2309 (±10)	0.57 (±0.55)	5.55e <sup>-5</sup> (±1.41e <sup>-4</sup> )	2.34e <sup>8</sup> (±1.39e <sup>6</sup> )	686 (±560)	1055 (±1334)	23.76 (±10.08)	0.01 (±0.43)
CC	5	57	22,260	111,300	778 (±33)	2.50 (±2.89)	1.13e <sup>-3</sup> (±2.86e <sup>-3</sup> )	2.42e <sup>8</sup> (±4.78e <sup>6</sup> )	256 (±248)	391 (±287)	19.15 (±4.85)	12.00 (±14.30)
Pooled	90	2,170	144,320	721,600	1624 (±725)	6.31 (±7.01)	3.16e <sup>-3</sup> (±7.56e <sup>-3</sup> )	2.28e <sup>8</sup> (±1.66e <sup>7</sup> )	1038 (±1110)	440 (±494)	18.80 (±10.05)	5.07 (±12.38)

Table 2.2. Landscape variables evaluated in resource selection functions, including the source and analysis tool (if derived from another layer).

Variable	Units	Resolution	Source/Tool
Elevation	Meters	30 meters	US National Map (DEM)
Vector Ruggedness Measure	Index	30 meters	DEM/Terrain Ruggedness (VRM) <sup>a</sup>
Road distance	Meters	30 meters	TIGER/Euclidean distance <sup>a</sup>
Water distance	Meters	30 meters	TIGER/Euclidean distance <sup>a</sup>
NDVI Amplitude	Index	250 meters	USGS Phenology
Canopy Cover	Percent	30 meters	National Land Cover Database
Slope	Degrees	30 meters	DEM/‘raster’ package <sup>b</sup>
Solar Radiation	Joules per square meter	30 meters	DEM/‘insol’ package <sup>b</sup>

<sup>a</sup> ArcMap 10.6.1

<sup>b</sup> RStudio version 3.5.1

Table 2.3. Coefficient estimates for landscape covariates of bison resource selection

functions in the American west. Bolded beta coefficients indicate p-values less than 0.05

and standard errors of estimates appear in parentheses below the coefficient. ‘NA’

indicate a covariate was not included in the top model.

Covariates	Study Areas					Pooled Model
	Henry Mountains	Book Cliffs	American Prairie Reserve	Medano-Zapata Ranch	Caprock Canyons	
Intercept	<b>-1.6457</b> (±0.0098)	<b>-2.1187</b> (±0.0553)	<b>-1.9108</b> (±0.0684)	<b>-1.8017</b> (±0.0228)	<b>-2.4351</b> (±0.0279)	<b>-1.7181</b> (±0.0235)
Elevation	<b>1.6486</b> (±0.0141)	<b>0.1193</b> (±0.0565)	<b>-0.5883</b> (±0.0191)	<b>0.3773</b> (±0.0344)	<b>1.1772</b> (±0.0301)	<b>0.8120</b> (±0.0088)
	<b>-0.5119<sup>sq</sup></b> (±0.0150)	<b>-0.8317<sup>sq</sup></b> (±0.0861)	<b>0.9116<sup>sq</sup></b> (±0.0315)	<b>-0.6747<sup>sq</sup></b> (±0.0512)	<b>-0.9942<sup>sq</sup></b> (±0.0345)	<b>-0.6341<sup>sq</sup></b> (±0.0106)
Ruggedness	<b>-0.2784</b> (±0.0184)	<b>-0.8446<sup>ps</sup></b> (±0.0799)	0.0084 <sup>ps</sup> (±0.0203)	NA	<b>-1.0545<sup>ps</sup></b> (±0.0384)	<b>-0.2750<sup>ps</sup></b> (±0.0091)
	0.0129 <sup>sq</sup> (±0.0078)					
Road distance	<b>0.3338<sup>ps</sup></b> (±0.0096)	<b>-0.1446<sup>ps</sup></b> (±0.0311)	<b>-0.2565<sup>ps</sup></b> (±0.0117)	<b>-0.1864</b> (±0.0269)	<b>-0.7202</b> (±0.0217)	<b>-0.0135<sup>ps</sup></b> (±0.0056)
Water distance	<b>-0.5103</b> (±0.0109)	-0.0985 (±0.0551)	<b>-0.4009</b> (±0.0186)	<b>-1.1091</b> (±0.0440)	<b>-0.5344<sup>ps</sup></b> (±0.0176)	<b>-0.5015</b> (±0.0081)
	<b>0.2277<sup>sq</sup></b> (±0.0135)	<b>0.1937<sup>sq</sup></b> (±0.0556)	<b>-0.1178<sup>sq</sup></b> (±0.0239)	<b>0.8634<sup>sq</sup></b> (±0.0442)		<b>0.1605<sup>sq</sup></b> (±0.0101)
NDVI Amplitude		<b>-0.2229</b> (±0.0649)	<b>0.3164</b> (±0.0195)	<b>0.5784<sup>ps</sup></b> (±0.0280)	<b>0.8459</b> (±0.0196)	<b>0.6906</b> (±0.0064)
	NA	<b>-0.8049<sup>sq</sup></b> (±0.1004)	<b>0.1054<sup>sq</sup></b> (±0.0189)		<b>0.5096<sup>sq</sup></b> (±0.0139)	
Canopy Cover	<b>-0.1538</b> (±0.0210)	<b>-1.9777</b> (±0.0720)	<b>-0.1073</b> (±0.0339)	-0.0544 (±0.0311)	<b>0.0417<sup>ps</sup></b> (±0.0194)	<b>-0.4596</b> (±0.0077)
	<b>-0.2244<sup>sq</sup></b> (±0.0206)		-0.0058 <sup>sq</sup> (±0.0059)			<b>0.0207<sup>sq</sup></b> (±0.0010)
Slope	<b>-1.2528</b> (±0.0160)	<b>-2.1454</b> (±0.1275)	<b>0.1469</b> (±0.0282)	<b>-0.4302</b> (±0.0458)	<b>-2.2582</b> (±0.0670)	<b>-1.0258</b> (±0.0129)
	<b>-0.7421<sup>sq</sup></b> (±0.0253)	<b>-0.7972<sup>sq</sup></b> (±0.2394)	<b>-0.3781<sup>sq</sup></b> (±0.0259)	0.0042 <sup>sq</sup> (±0.0284)	-0.0891 <sup>sq</sup> (±0.1141)	<b>-0.1289<sup>sq</sup></b> (±0.0156)
Solar Radiation	<b>0.5914</b> (±0.0184)	<b>-0.3378</b> (±0.1000)	<b>0.0537</b> (±0.0157)	<b>0.0707</b> (±0.0287)	<b>0.5911</b> (±0.0503)	<b>0.4633</b> (±0.0087)
	<b>0.3389<sup>sq</sup></b> (±0.1457)	-0.2487 <sup>sq</sup> (±0.1466)	<b>-0.0291<sup>sq</sup></b> (±0.0136)	-0.0038 <sup>sq</sup> (±0.0193)	<b>-0.4509<sup>sq</sup></b> (±0.1067)	<b>0.1324<sup>sq</sup></b> (±0.0084)

<sup>ps</sup> Pseudothreshold, <sup>sq</sup> Quadratic

## Figures

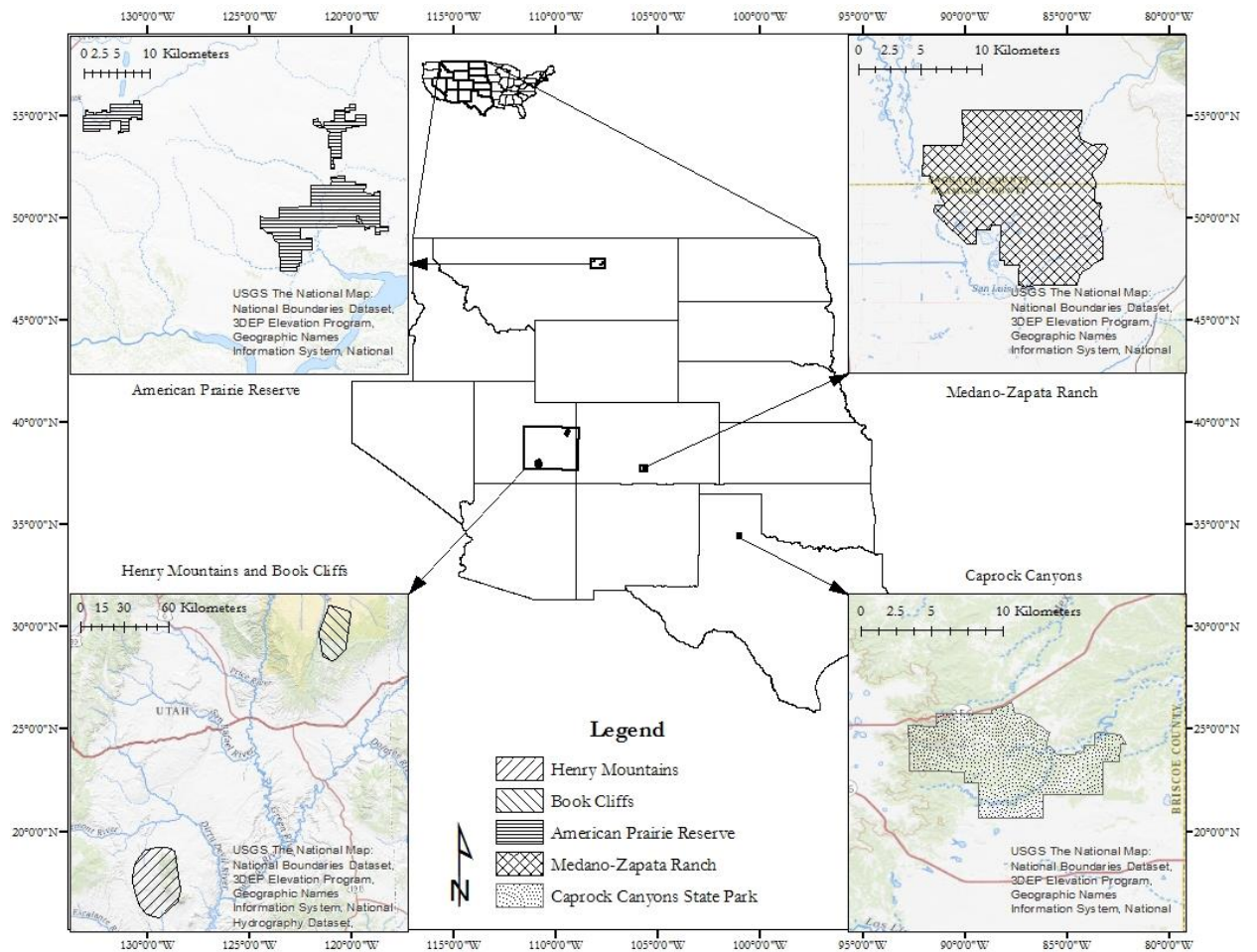


Figure 2.1. Available extents of five bison herds across the American west. The extents of the free-range herds (Henry Mountains and Book Cliffs) herds are defined by 99% minimum convex polygons buffered by the median individual step lengths and were calculated using all of the individual locations for each herd. The extents of the captive herds (American Prairie Reserve, Medano-Zapata Ranch, and Caprock Canyons) are defined by their fenced pastures.



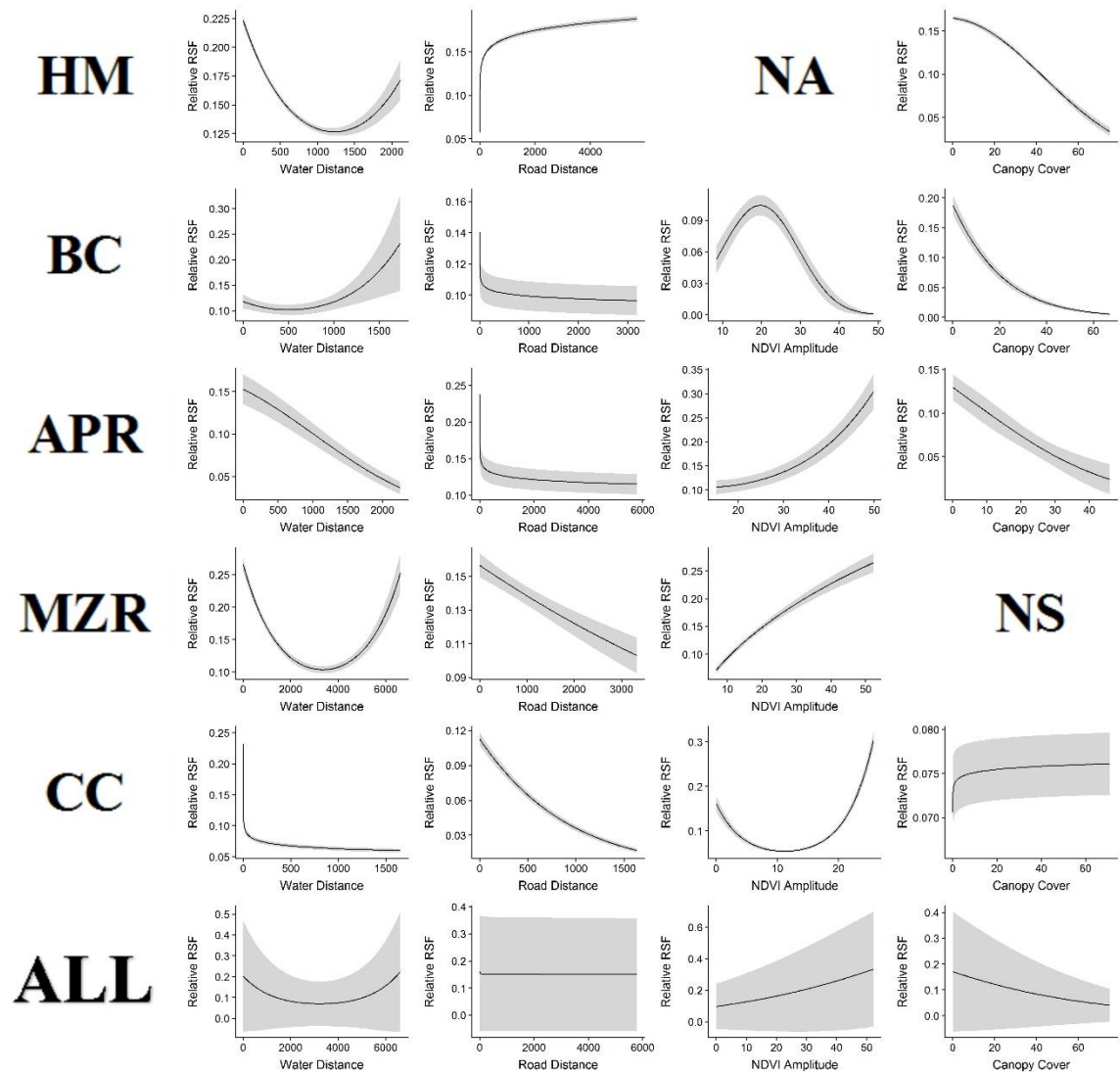


Figure 2.2. Predicted relative resource selection functions (RSF) of biotic and anthropogenic covariates by study area using the original values. ‘HM’ indicates the Henry Mountains, ‘BC’ is the Book Cliffs, ‘APR’ is American Prairie Reserve, ‘MZR’ is Medano-Zapata Ranch, ‘CC’ is Caprock Canyons, and ‘ALL’ indicates the pooled model. ‘NA’ indicates a covariate was not included in the model for a herd and ‘NS’ indicates the covariate was included in the model but not a significant predictor ( $p < 0.05$ ).

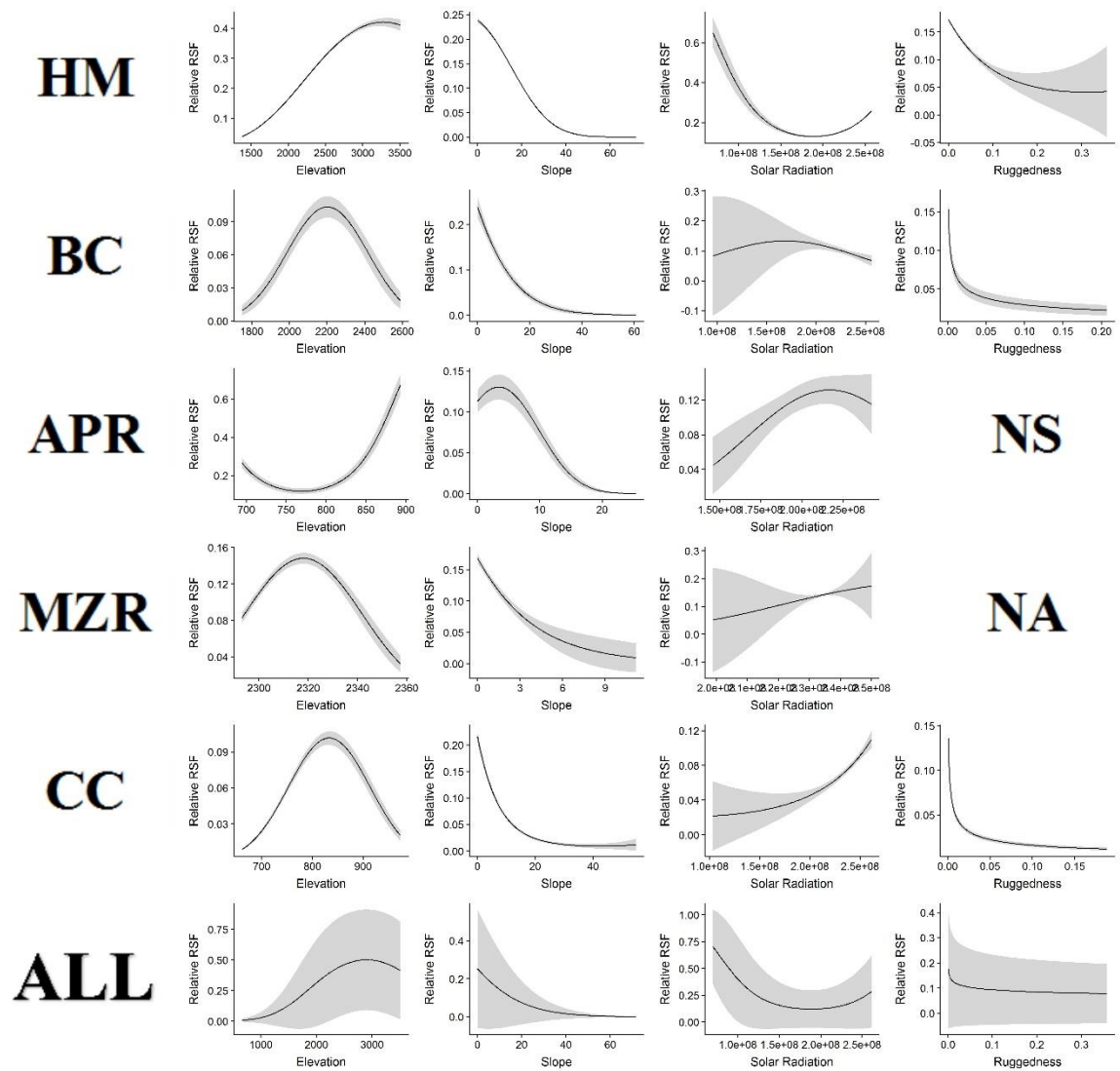


Figure 2.3. Predicted relative resource selection functions (RSF) of biotic and anthropogenic covariates by study area using the original values. ‘HM’ indicates the Henry Mountains, ‘BC’ is the Book Cliffs, ‘APR’ is American Prairie Reserve, ‘MZR’ is Medano-Zapata Ranch, ‘CC’ is Caprock Canyons, and ‘ALL’ indicates the pooled model. ‘NA’ indicates a covariate was not included in the model for a herd and ‘NS’ indicates the covariate was included in the model but not a significant predictor ( $p < 0.05$ ).

## **Chapter 4: Summary**

Despite the diversity of habitats once occupied by bison (Plumb and McMullen 2018) and recommendations of landscape-level management for their conservation (Sanderson et al. 2008), there has been little emphasis on examining variations in bison spatial ecology across their former range, particularly between free-range and captive herds. This research contributes towards understanding the relative influences of both ecological conditions and management on bison space use patterns. In Chapter 2, I focused on how these influences affected the total area bison occupied (home range) and the extent of intensive space use (first-passage time) across seasons. At the home range scale, bison which were constrained by fences used significantly less space than individuals from free-ranging herds overall. While this finding was expected and appears intuitive, restrictions on bison movements could be influencing additional differences between these herds. We detected seasonal variation in the size of free-range bison home ranges, but not in captive bison, which suggests that management limitations may affect the ability of bison to respond to landscape changes and has possible consequences on their fitness. Temporal fluctuations in resource availability influence spatial requirements, especially in herbivores (Merkle et al. 2016). As the majority of bison exist in commercially raised herds (Bates and Hersey 2016), it is important that the few populations managed for the purposes of conservation maintain their suitability for achieving this goal. Preventing bison from altering their movements to suit ecological conditions may encourage maladaptive behaviors, which could decrease their value for future conservation efforts.

We did not detect temporal differences in foraging patch size as indicated by first-passage time between herds or across seasons. This was surprising, as we expected local vegetation productivity to have a greater impact on the amount of space necessary for bison to fulfill their energy requirements (Plumb et al. 2009; Raynor et al. 2016). However, this could be an innate characteristic of bison which allows them to be successful over their wide ecological niche. An interesting pattern we saw was the similarity of captive bison foraging patch sizes to their overall home range extent, a marked difference from free-range bison, which had home ranges at least four times greater than their foraging patch. This has ramifications for the potential number of foraging patches available to captive and free-range bison. It is possible that number rather than size of foraging patches could be related to ecological features, however, the fact that foraging patch size is similar to home range size only for captive bison is suggestive that this pattern is influenced mostly by their movement limitations. In the context of bison conservation, decreased access to foraging patches may discourage their natural feeding patterns and result in individuals less similar to their wild ancestors.

Restricting the natural space use tendencies of bison could have cascading effects on their long-term conservation. While the physiological needs of captive bison are likely being fulfilled by the pastures they occur in (Kohl et al. 2013, Schoenecker et al. 2015), it may not be adequate for the large-scale biological interactions bison have as a keystone species (Knapp et al. 1999; Freese et al. 2007; Fuhlendorf et al. 2010). These results support previous recommendations for managing bison at a larger spatial scale by allocating more space for their conservation. Though the sociopolitical challenges of

bison conservation cannot be overlooked (Sanderson et al. 2008; Ranglack and du Toit 2016), this work suggests that future areas for bison restorations which account for seasonal space use may address their ecological needs while necessarily reducing the potential for land use conflict. Future research can use this to identify a threshold of bison space use which minimizes conflict with humans but permits spatially relevant ecological interactions at a broader spatial scale.

In Chapter 3, I examined patterns of bison resource selection across various habitats within their historic range under the hypothesis that differences in habitat preference attributable to ecological characteristics would indicate the possibility that bison were occupying suboptimal habitat (refugee species), while differences in habitat use that were related to management could suggest spatial isolation as a greater limiting factor (terrestrial castaway). I found considerable consistency in resource selection between the bison herds we examined despite the great variation in total available space and environmental characteristics. Considering my findings from Chapter 2 suggesting management limitations decrease bison space use, it makes sense that resource selection could also be influenced. Particularly, free-range herds seemed to prefer different road and NDVI characteristics. The unencumbered movement ability of free-range bison could enable their response to anthropogenic disturbance (Fortin and Andruskiw 2003) while captive individuals may be restrained from such responses. Continued restriction of natural responses to disturbance may lead to captive bison becoming desensitized to humans, a characteristic selected in commercially raised herds but maladaptive for bison conservation (Freese et al. 2007; Sanderson et al. 2008).

Free-range bison also seemed to select areas with vegetation productivity (NDVI) consistent with their grazing foraging strategy, while captive bison used areas with greater productivity than expected. Selection for intermediate NDVI is adaptive for bison because it maximizes their instantaneous intake of energy, but this necessitates intensive grazing and frequent movement to new foraging patches (Babin et al. 2011; Raynor et al. 2017). Since constraints on captive bison movements possibly limit the number of available foraging patches, as suggested by my Chapter 2 findings, it makes sense that areas of higher vegetation productivity would be selected to fulfill their energy requirements. The observed differences in resource selection patterns seemed to be grouped by management characteristics rather than environmental features, which led to our classification of bison as terrestrial castaways as opposed to a refugee species. This suggests that spatial isolation is a greater issue for bison conservation than suitability of habitat and is complemented by our findings in Chapter 2, indicating differences in spatial patterns which could have negative impacts on adaptive behaviors in bison.

Overall, the variations we observed in spatial patterns of bison seemed most related to management constraints rather than ecological characteristics. The bison space use restrictions and inability to respond to temporal variations detected in Chapter 2 are likely to contribute to the differences in resource selection observed in Chapter 3. These findings suggest the possibility that limitations on bison movement might result in behaviors unsuitable for long-term evolutionary fitness, as well as capacity for ecological interactions, working against the conservation goals of these herds. However, the reality of current land use across their former range is a reminder that space is also the most

limiting factor for the long-term conservation of bison (Aune et al. 2017). The limitation of management approaches (i.e., fencing) on bison space use suggests the need for a more spatially integrative approach to their conservation. Ensuring the continued value of bison conservation herds for their long-term viability as a species can be supported by allocating enough space for temporal variation in space use as well as promoting connectivity between existing herds. These strategies encourage the need for bison conservation to take place at a landscape scale instead of local management of isolated herds.

#### *Literature Cited*

- Aune K, Jorgensen D, Gates C. 2017. The IUCN Red List of Threatened Species™. [accessed 2019 Mar 5]. <http://dx.doi.org/10.2305/IUCN.UK.2017->.
- Babin J-S, Fortin D, Wilmschurst JF, Fortin M-E. 2011. Energy gains predict the distribution of plains bison across populations and ecosystems. *Ecology*. 92(1):240–252. doi:10.1890/10-0252.1.
- Bates B, Hersey K. 2016. Lessons Learned from Bison Restoration Efforts in Utah on Western Rangelands. *Rangelands*. 38(5):256–265. doi:10.1016/j.rala.2016.08.010.
- Fortin D, Andruskiw M. 2003. Behavioral response of free-ranging bison to human disturbance. *Wildl Soc Bull*. 31(3):804–813.
- Freese CH, Aune KE, Boyd DP, Derr JN, Forrest SC, Cormack Gates C, Gogan PJP, Grassel SM, Halbert ND, Kunkel K, et al. 2007. Second chance for the plains bison. *Biol Conserv*. 136:175–184. doi:10.1016/j.biocon.2006.11.019.

- Fuhlendorf BSD, Allred BW, Hamilton RG. 2010. Bison as keystone herbivores on the Great Plains : Can cattle serve as proxy for evolutionary grazing patterns ? (4).
- Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999. The keystone role of bison in North American tallgrass prairie bison increase habitat heterogeneity processes. *Bioscience*. 49(1):39–50.
- Kohl MT, Krausman PR, Kunkel K, Williams DM. 2013. Bison Versus Cattle: Are They Ecologically Synonymous? *Rangel Ecol Manag*. 66(6):721–731.  
doi:10.2111/REM-D-12-00113.1.
- Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, Oates BA, Sawyer H, Scurlock BM, Kauffman MJ. 2016. Large herbivores surf waves of green-up during spring. *Proc R Soc B*. 283(1833):20160456.  
doi:10.1098/rspb.2016.0456.
- Plumb G, McMullen C. 2018. Bison on the Southwest Colorado Plateau: Conservation at the Edge. *Southwest Nat*. 63(1):42–48. doi:10.1894/0038-4909-63.1.42.
- Plumb GE, White PJ, Coughenour MB, Wallen RL. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. *Biol Conserv*. 142(11):2377–2387.  
doi:10.1016/J.BIOCON.2009.05.019.
- Ranglack DH, du Toit JT. 2016. Bison with benefits: towards integrating wildlife and ranching sectors on a public rangeland in the western USA. *Oryx*. 50(3):549–554.  
doi:10.1017/S0030605314001197.



- Raynor EJ, Beyer HL, Briggs JM, Joern A. 2017. Complex variation in habitat selection strategies among individuals driven by extrinsic factors. *Ecol Evol.* 7:1802–1822. doi:10.1002/ece3.2764.
- Raynor EJ, Joern A, Nippert JB, Briggs JM. 2016. Foraging decisions underlying restricted space use: effects of fire and forage maturation on large herbivore nutrient uptake. *Ecol Evol.* doi:10.1002/ece3.2304.
- Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr J, Dobrott S, et al. 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conserv Biol.* 22(2):252–266. doi:10.1111/j.1523-1739.2008.00899.x.
- Schoenecker KA, Nielsen SE, Zeigenfuss LC, Pague CA. 2015. Selection of vegetation types and density of bison in an arid ecosystem. *J Wildl Manage.* 79(7):1117–1128. doi:10.1002/jwmg.940.