Influence of nutrition on the habitat selection of the Ronald Lake wood bison (*Bison bison athabascae*) herd

by

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Abstract

Acquiring food is a key component of what it means to be an animal. A significant portion of any animal's life is spent locating, acquiring, consuming, and digesting food. Nearly every aspect of their life is influenced by it. The nutritional quality varies depending on foraging strategy and is a key component of what has led to the diversity of modern physiologies. The key factors influencing habitat selection are quantity, quality, and distribution of food, avoiding becoming food (i.e., predation), and competing with others for food. For wildlife managers, understanding how habitat selection results from making tradeoffs between these factors is key to making effective management decisions. In this dissertation, I explored how the nutritional components of food influence the habitat selection of an ungulate, wood bison, within a heterogeneous landscape to inform their management and conservation. The Ronald Lake wood bison (*Bison bison athabascae*) are a genetically distinct and disease-free wild population that are culturally significant to local Indigenous communities. They are located at the northern edge of Alberta's oil-sands region subjecting their range to natural resource exploration and extraction. Since the herd's diet is not well understood I started by conducting a review of the literature on bison diets and explored geographic trends in diet composition and macro-nutrition. I showed that at higher latitudes bison consume more woody plants and acquire more proteins and lipids. I then used this information to make predictions about the Ronald Lake bison's diet and nutritional targets. The results demonstrate a seasonal switching from grazing in the winter and spring to more browsing during summer. Bison were able to maintain a specific nutrient composition between spring and summer despite differences in diet, demonstrating an ability to maintain nutritional targets. Next, I examined how selecting habitats for different behaviors is influenced by nutrition. Bison selected foraging sites with plants that had more crude protein and more digestible energy and while traveling they selected locations with plants that have more protein. Lastly, I assessed phenological factors motivating females to migrate to a distinct meadow during spring. This period likely aligns with parturition, which suggests the bison may be migrating to a calving site. I compared the non-mutually exclusive hypotheses that migration is a result of the green-up of vegetation (i.e., green-wave hypothesis) or that migration is a tactic to avoid predation pressure. I found support for the green-wave hypothesis as the timing of migration and habitat selection during migration were both influenced by the vegetation's phenology. The start of migration to the meadow was most closely tied to peak of spring green-up and bison arrived at the meadow close to the end of green-up. Additionally, habitats selected during migration were closer to the peak of green-up at that location, suggesting selection for habitats with more readily digestible plants that contain more protein. Collectively, the results of my dissertation will inform the management of the Ronald Lake bison and help to mitigate the influence of future natural resource extraction on their range. Further, my work highlights the importance of considering the influence of nutrition on multiple components of an animal's life, not just their foraging habits.

Preface

This dissertation is an original work by Lee Hecker.

Chapter 2 has been published as: Hecker, L.J., S.C.P. Coogan, S.E. Nielsen, and M.A. Edwards. 2021. Latitudinal and seasonal plasticity in American bison *Bison bison* diets. *Mammal Review*. 51(2):193-206. L.J. Hecker conceptualized the research questions, collected the data, conducted analyses, and wrote the original manuscript. S.C.P. Coogan was involved with research design, assisted with analyses, and provided significant edits to the manuscript. S.E. Nielsen and M.A. Edwards acquired and provided funding, contributed to research design, and provided significant edits to the manuscript.

Chapter 3 has been published as: Hecker, L.J., M.A. Edwards, and S.E. Nielsen. 2021. Assessing the nutritional consequences of switching foraging behavior in wood bison. *Ecology & Evolution*. 11(22):16165-16176. L.J. Hecker conceptualized the project, acquired supporting funding, collected the data, conducted the analyses, and wrote the original manuscript. M.A. Edwards and S.E. Nielsen acquired primary funding, contributed to project conceptualization, contributed to research design, and provided significant feedback to the manuscript.

Chapter 4 has been submitted for publication as: Hecker, L.J., S.E. Nielsen, and M.A. Edwards. Migration leads to nursery herd formation in wild wood bison (*Bison bison athabascae*). *Behavioral Ecology*. Submitted on March 18, 2022. L.J. Hecker conceptualized the project, acquired supporting funding, collected the data, conducted the analyses, and wrote the original manuscript. M.A. Edwards and S.E. Nielsen acquired primary funding, contributed to project conceptualization, contributed to research design, and provided significant feedback to the manuscript.

Two additional papers were published during my doctoral program that contributed to my understanding of nutritional ecology and the study population but were not central to the investigation of nutrition's influence on the population's habitat selection. Therefore, they are not included in this document, but are listed below:

Shrestha, T.K., L.J. Hecker, A. Aryal, and S.C. Coogan. 2020. Feeding preferences and nutritional niche of wild water buffalo (*Bubalus arnee*) in Koshi Tappu Wildlife Reserve, Nepal. *Ecology and Evolution*. 10:6897-6905.

Sheppard, A.H.C., L.J. Hecker, M.A. Edwards, and S.E. Nielsen. 2021. Determining the influence of snow and temperature on the movement rates of wood bison (*Bison bison athabascae*). *Canadian Journal of Zoology*. 99:489-496.

As part of our obligations to our funders and the Ronald Lake Bison Herd Technical Team, I also co-authored nine semi-annual technical reports. For brevity, I have listed the three that I was lead author on below, but the rest are publicly available on Dr. Nielsen's website.

Hecker, L.J., L.T. Dewart, R.J. Belanger, S.E. Nielsen, and M.A. Edwards. 2019a. Ronald Lake wood bison research program: Semi-annual progress report 2019. University of Alberta, Edmonton, Alberta, Canada, T6G 2H1. 19 pp.

Hecker, L.J., L.T. Dewart, D. Epperson, M.A. Edwards, and S.E. Nielsen. 2019b. Ronald Lake wood bison research program: 2019 annual report. University of Alberta, Edmonton, Alberta, Canada, T6G 2H1. 46 pp.

Hecker, L.J., L.T. Dewart, D.M. Epperson, G.J. Rawleigh, A.C. Sheppard, S.E. Nielsen, and M.A. Edwards. 2020a. Ronald Lake wood bison research program: 2020 semi-annual report. University of Alberta, Edmonton, Alberta, Canada, T6G 2H1. 37 pp.

Dedication

This dissertation is dedicated to my grandfather, Dr. Lee Edward Stickles (May 2, 1928 – July 27, 2022).

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I would first like to thank my supervisors Mark Edwards and Scott Nielsen for creating this opportunity and providing me with mentorship throughout my time at the University of Alberta. They successfully applied for and received funding to support my doctoral studies from the Natural Sciences and Engineering Research Council, which was matched in-kind by Teck Resources Limited. They always kept me in mind when opportunities to teach or representing our research with the communities we work in. I greatly appreciate their patience and support throughout.

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This project would not have been possible without the support and contributions of the Ronald Lake Bison Herd Technical Team and local Indigenous communities: Treaty 8 First Nations - Athabasca Chipewyan First Nation, Mikisew Cree First Nation, Fort McMurray First

Nation #468, and Fort McKay First Nation; Métis Indigenous groups - Fort Chipewyan Métis Local 125, Fort McMurray Métis Local 1935, Fort McKay Métis 63, and Lakeland Métis Local 1909. There are many members of each of these communities that have contributed more knowledge on the ecology of the Ronald Lake wood bison herd than this project ever will and I appreciate their support. The advice and direction provided by Petr Komers, Karen Halwas, Neil Sandstrom, Martin Jalkotzy, Troy Hegel, Joann Skilnick, and Craig Dockrill were critical to the success of this project. Shauna Young and Sophia Graine are valuable members that welcomed me with kindness and made sure discussions were on topic.

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Field work would not have been possible without the support of local experts who live or trap near Ronald Lake. Roy Ladouceur, James Ladouceur, Gerry Ladouceur, Mike Martin, and Cuck Shovelup all assisted during various phases on my fieldwork either showing us and clearing trails, letting us borrow equipment, guiding us down the Athabasca River, and providing a roof and a warm drink on a cold and/or rainy day. Also, integral to the completion of field work were Aidan Sheppard, Adam Scharnau, Alex Coley, and Neil Josephs the field technicians that shared the mud, blood, and tears with me over three field seasons. Josh Balak and Lynsey Bent also put in many hours of lab work drying and processing vegetation and fecal samples, which I am extremely grateful for.

I also would like to thank my family. My grandfather, Dr. Lee Stickles, was a pediatrician in Fredericton, NB for over 50 years. He was convinced my supervisor and a fellow Fredericton native, Mark Edwards, was a former patient. So, when I mentioned off hand that I had applied for this position he called Mark, and while it turns out Mark was not a former patient, he convinced Mark to pull my CV out of the pile and the rest is history. Both of my grandmothers have shown me a work ethic and kindness towards others that I truly believe is unmatched. My parents and sister were always there to provide their love and support, even traveling out to Edmonton. And finally, my wife Melissa Kimble who was there with me (at least in spirit) every step on the way. When I started we were dating and she endured 3.5 years of a long-distance relationship pursuing her own doctoral program at the University of Maine. From encouraging me to apply to spending two weeks in Edmonton before my candidacy exam to gently pushing me to keep writing this dissertation. The lengths she went to give me encouragement, support, and love are extraordinary and I will forever be indebted.

Lastly, I would like to thank the wood bison of the Ronald Lake region.

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Chapter 1: Introduction

1.1 Animal nutrition and habitat selection

One of the defining attributes of the kingdom Animalia is heterotrophy (i.e., the consumption of food; Pough and Janis 2019). Given the vital importance to all animal life, investigations into food acquisition and nutrition have become an interdisciplinary field encompassing animal health, bioenergetics, morphology, habitat selection, and effects of climate change under the umbrella of ecology. The interdisciplinary nature also makes it difficult to synthesize information that draws from various fields with unique analytical methods, but provides the opportunity to integrate information and frameworks to provide a more holistic understanding of animal ecology (Raubenheimer et al. 2009). The apparent foraging decisions made by animals change when examined at differing spatial and temporal scales (Fortin et al. 2015). These factors influence the distribution, quantity, and quality of available foods for all animals regardless of diet or foraging strategy (Develey et al. 2000, Cleland et al. 2006, Ordiz et al. 2017). For herbivores, the seasonal variability in available forage has led to seasonal selection of different forage materials to optimize gains of energy and limiting nutrients forcing the integration of traditional nutritional studies with studies of spatial variability influencing habitat selection (Moen et al. 1997, Craine et al. 2015). Understanding these nuanced mechanisms that influence how nutrition effects herbivore's use of their range are invaluable to wildlife managers as it allows for the prediction of the spatial distribution of individuals and populations, assessment of competing mechanisms, and estimation of nutritional carrying capacity on the landscape.

The effective management of any population is contingent upon a thorough understanding of how and why that population selects habitats available to them (Kerr and

Deguise 2004). The process of selection results from generations of fitness benefits gained from learned or innate behaviors (Holbrook et al. 2019). Habitat selection by herbivores is influenced by a number of ecological processes, including: forage availability, quantity and quality (i.e., bottom-up), predation (i.e., top-down), and intra- and/or interspecific competition (Coulson et al. 2001, Nielsen et al. 2010). However, the cumulative consequences of these processes on the habitat selection of individuals and populations are not well understood (Sutherland et al. 2013). Development of mechanistic habitat selection models has been an important tool for wildlife managers (Guisan and Thuiller 2005). These methods get at the root of selection by decoupling the tradeoffs between forage quality, predation risk, and competition. For example, Bergman et al. (2001) examined the foraging strategies of a large herbivore to evaluate if they foraged in a manner that minimized the time they were exposed to predators or maximized the energy gained. Therefore, decoupling the tradeoffs between forage quality and predation risk. These methods are important because the knowledge gained from the outputs allows managers to predict the spatial distributions of individuals and populations. Further, they allow for estimation of where, when, and how long an individual with occupy a particular habitat within their range. These predictions are improved when appropriate mechanistic tradeoffs are previously identified and appropriately incorporated into analyses (Beck et al. 2006, Holbrook et al. 2019).

These decisions become further convoluted when a species exists on a multiple-use landscape subject to both natural and anthropogenic disturbances (Schneider et al. 2011). Natural disturbances, such as wildfires, and anthropogenic disturbances, like cut-blocks and seismic lines (i.e., linear openings in the landscape created during oil exploration), change the physical structure of the landscape, which results in changes to the vegetative community setting successional processes into motion, and can influence an animal's ability to move around the landscape. Habitat selection modeling has been effectively used to identify regions that are critical to a population's persistence (Guisan et al., 2013) and predict how disturbances will influence a population's use of habitat (Harju et al., 2011). The rate of recovery within disturbances is variable. In cut-blocks, recovery rates can be similar to those of wildfires, but along linear disturbances (i.e., seismic lines and winter roads) the ground can remain covered in herbaceous vegetation for 35 years and even longer if there is heavy vehicle use (Nguyen-Xuan et al. 2000, Lee and Boutin 2006, Pigeon et al. 2016). Correspondingly, the availability, quality, and quantity of habitat including forage is highly variable depending on the disturbance and the species' ecology. For example, early successional processes typically generate more graminoid and herbaceous plant biomass, which grazers prefer, but opening the habitats with linear disturbances can increase the accessibility to prey for predators (Redburn et al. 2008, Latham et al. 2011). Slash and other debris created by timber harvesting or forest fires can have long lasting counterproductive effects on herbivores such as increasing energetic costs of movement (Parker et al. 1984). Therefore, modeling habitat selection can be improved by incorporating the factors that encourage or discourage the use of disturbance areas especially on multiple use landscapes.

1.2 American bison and the Ronald Lake wood bison herd

American bison (*Bison bison*) have been a focal species for ecological management in North America for over a century (Allen 1877, Freese et al, 2007). Once spanning from Mexico to Alaska and the Northwest Territories, and from Washington to Maine, they numbered in the tens of millions. Colonialists headed west reported spending days traveling through a continuous herd (Allen 1877). However, by 1900 they had been reduced to just a few hundred individuals due to changing climatic conditions reducing preferred habitat, competition with reintroduced and expanding wild horse (*Equus ferus*) populations, but primarily, overexploitation due to market demand for hides and pemmican (Cunfer and Waiser 2016). Ecologically, American bison are widely recognized as a keystone species in prairie ecosystems influencing plant distributions, soil composition, insect communities, and other ecosystem processes (Knapp et al. 1999, McMillian et al. 1999, Barber et al. 2019, McMillan et al. 2019). There are two subspecies of American bison: plains bison (*B. b. bison*) and wood bison (*B. b. athabascae*). Wood bison are larger, darker in color, have a larger hump, and longer hair on their heads. Wood bison occupy boreal and parkland habitats in northern Canada and Alaska, whereas plains bison inhabit prairie habitats throughout the United States and Canada with the traditional confluence of the two subspecies located near present day Edmonton, Alberta (Cunfer and Waiser 2016).

Currently, the International Union for Conservation of Nature (IUCN) lists American bison as *Near Threatened* (IUCN 2021). In the United States, neither American bison nor either of its subspecies are currently listed under the Endangered species Act (ESA), but petitions to list the species or specific populations have been put forward as recently as 2018 (Buffalo Field Campaign v. Zinke, 289 F. Supp. 3d 103, D.D.C. 2018). In Canada, plains bison have been listed as *Threatened* under the Species at Risk Act (SARA) since 2004 and wood bison have been listed as a subspecies of *Special Concern* since 2013 (COSEWIC 2013). Only three large (>300 individuals) and wild populations of wood bison currently exist in Canada.

One wood bison population in particular has come to the forefront as being of particular conservation and management concern in Canada over the past decade; the Ronald Lake wood bison herd. The population is named after a large lake at the center of its range, Ronald Lake, in northeastern Alberta just south of Wood Buffalo National Park (WBNP). The population is estimated to contain 272 individuals (pers. comms. Alberta Environment and Parks [AEP] 2021).

The herd was long thought by government officials to have broken away from the much larger (~3000 individuals) WBNP population, which contains a mixture of wood bison, plains bison, and hybrids due to the introduction of plains bison into the native wood bison population in the 1920's (AEP and ACA, 2017). However, the persistent insistence of local Indigenous community members that Ronald Lake bison had always been present in the region prompted AEP to conduct a study on the genetic make-up of the herd and other herds in northern Alberta and the Northwest Territories. The study revealed the Ronald Lake bison were genetically distinct from all other herds in the region with significantly less genetic introgression with plains bison than all other herds except the Wabasca herd (Ball et al. 2016). Further, when plains bison were transferred into WBNP they carried with them the livestock-borne diseases bovine tuberculosis and brucellosis, which have been a concern for the population ever since. These diseases have not been found in the Ronald Lake bison (Shury et al. 2016). These unique traits and the recognized cultural significance of the Ronald Lake bison to First Nations and Métis communities in the region make this population of significant conservation concern (Noseworthy 2016). The Government of Alberta lists the wood bison as *At Risk* under the provincial Wildlife Act (AEP 2021). This designation excludes hunting by all individuals who are not Indigenous.

In 2011, Teck Resources Limited submitted a proposal to develop an oil sands open-pit mine, the Frontier project, which would be the most northern surface mine in Alberta's oil sands region. The mine would overlap partly with the range of the Ronald Lake bison. This proposal prompted the formation of the Ronald Lake Wood Bison Herd Technical Team (RLBHTT), which is comprised of representatives from local Indigenous communities, industry, non-government organizations, and provincial and federal government agencies, with the mandate to "identify the knowledge necessary for the conservation and management of the Ronald Lake wood bison herd and its habitat" (RLBHTT, 2020). The RLBHTT identified a series of knowledge gaps related to the herd's ecology that needed to be addressed to meet their mandate. Teck Resources Limited withdrew their development proposal in 2019, but still hold the lease to the land and the RLBHTT has not abandoned their mandate. This dissertation addresses a number of the RLBHTT's knowledge gaps.

1.3 Scope and objective of dissertation

The purpose of my dissertation is to understand how the nutritional ecology of the Ronald Lake wood bison influences their habitat selection. I use a combination of field-based methods and modern technologies that allow for monitoring and analysis to address this fundamental knowledge gap in the population's ecology. Seasonal differences and the influence of recent and historic disturbances are touched on and explored. Each chapter has been designed to address a specific knowledge gap identified by the RLBHTT and build off the knowledge gained from previous chapter(s). Throughout this dissertation I explore multiple predictions and hypotheses by utilizing multiple lines of evidence to make robust conclusions. This is an applied ecological dissertation. I begin by reviewing the diets and the nutritional composition of those diets for American bison populations across North America (Chapter 2). Next, I use this information to make predictions about the seasonal diets and their nutritional content for the Ronald Lake wood bison before quantifying the population's diet and its nutritional content during three seasons (Chapter 3). Then, I apply this information to assess the bottom-up mechanisms influencing habitat selection during different behavior states (Chapter 4). Finally, I take a closer look at the unique migratory behavior the population exhibits each spring to compare and contrast non-mutually exclusive hypotheses related to the mechanisms encouraging the bison to migrate

(Chapter 5). The following paragraphs highlight the specific predictions, hypotheses, and analyses used in each chapter:

In chapter 2 (published in *Mammal Review*; Hecker et al. 2021a), I reviewed the available literature on bison diet composition across North America. Specifically, I examined 1) the composition of three function forage groups (graminoids, forbs, and browse) and three macronutrients (carbohydrates, protein, and lipids) in each population's diet, 2) assessed how the composition of the forage groups and macronutrients changed seasonally, 3) investigated how environmental variation between ranges related to changes in forage groups and macronutrients, and 4) tested for differences in diet and nutrient composition between plains bison and wood bison. I predicted diets would generally be dominated by graminoids and carbohydrates throughout the year, but there would be an expansion in the diversity of forage groups and macronutrients during the growing season compared to winter. I also predicted that diet composition would shift along a latitudinal gradient, which would be supported by the comparison of subspecies. I applied nutritional geometry techniques, linear models, ordinal analyses, and simple significance tests to assess my predictions.

In chapter 3 (published in *Ecology & Evolution*; Hecker et al. 2021b), I analyzed the diet composition, and macronutrient and fiber content of the Ronald Lake wood bison during winter, spring, and summer to explore seasonal changes of each. I predicted that the population's diet would switch from that of a typical grazer in winter and spring to that of an intermediate feeder during summer. I considered two competing hypotheses to explain the predicted switch in forage selection: 1) switching is a behavioral mechanism to maximize the consumption of limited macronutrients (i.e., protein), or 2) switching is a response to changes in plant nutrient composition and is an effort to maintain a particular macronutrient composition. I used nutritional geometry, quantified and compared dietary niche breadth and overlap for each season, and assessed differences in specific nutrients between seasons and forage groups.

In chapter 4, I explored the behavioral habitat selection of the bison during the growing season. In the field, I quantified physical attributes, quantity of forage, and quality of forage at bison locations labeled as either a foraging, traveling, or bedding site. I used resource selection functions (RSFs) to compare a suite of variable known to influence bison habitat selection between bison locations subset by each behavior state and random locations. Additionally, I assessed differences in these variables between bison locations representing each behavioral state. I predicted both the strength, significance, and direction of selection for each variable would change between behavioral states.

In chapter 5 (submitted to *Behavioral Ecology*), I compared how bottom-up and top-down mechanisms influence the bison to migrate and influenced their habitat selection during migration. Additionally, I explored the use of linear disturbances (i.e., seismic lines) during migration and the validity of calving as a mechanism motivating migration. I used remote sensing techniques to explore the timing of migration compared to the green-up of vegetation and assess the green-wave hypothesis. I also used data from collared wolves to quantify their habitat use while the bison were migrating. Camera traps were deployed along migration corridors to determine the validity of the migration leading to calving grounds.

Chapter 2: Latitudinal and seasonal plasticity in American bison (*Bison bison*) diets

Abstract

In niche theory, diet is a trait frequently used to place species along a continuum from specialists to generalists. A multidimensional approach to investigating species niches has been developed to incorporate nutrition. Here, we apply the concepts of multidimensional nutritional niche theory to the dietary patterns of a widespread megaherbivore, American bison (*Bison bison*), at various levels of their nutritional niche. Specifically, we seek to estimate dietary niches for female bison at the level of the forage items they consume and the macronutrients they acquire from those forage items. We assessed how these dietary niches changed seasonally and explored physical and climatic mechanisms that contribute to observed differences in the dietary niches. We also examined dietary differences between the two bison subspecies: wood bison (*B. b. athabascae*) and plains bison (*B. b. bison*). We compiled data for 16 bison subpopulations in North America using 26 peer-reviewed publications, government reports, conference proceedings, and graduate theses that described dietary composition of female bison for analysis of dietary niches. We found that female bison diets were expectedly dominated by graminoids throughout the year, but during the growing season dietary niches had greater breadth. Their diets were also relatively high in carbohydrate, but the proportion of dietary lipid and protein increased during the growing season. Further, we found significant increases in the consumption of browse items, lipids, and proteins with latitude, and between American bison subspecies. Our study provides insight into the fundamental macronutrient niche for American bison providing a framework for the nutritional targets of bison. We show that bison are able to adapt to the

availability of local forages, and that they may consume different items in different proportions to actively regulate the nutritional composition of their diet.

Introduction

The ecological niche is a foundational concept in ecological and evolutionary theory. In the context of niche theory, diet is a trait consistently used to place species along a scale of niche breadth from specialists to generalists (Terraube et al. 2014). A multidimensional approach known as nutritional geometry has been advanced to incorporate dietary nutrition in ecological niche theory (Machovksi-Capuska et al. 2016). This approach allows for the characterization of a species' dietary niche within different functional (i.e., adaptive; Bateson & Laland 2013) levels, which are defined as: the food exploitation niche, food composition niche, realized macronutrient niche, and fundamental macronutrient niche. The food exploitation niche explores the physical and ecological traits of food items (e.g., food type, part of food item, or seasonal availability). For example, foods with hard exteriors (e.g., nuts) may not be available for consumption by some species due to their physical characteristics, while foods that occur below ground (e.g., roots) may not be ecologically available to non-digging species. The food composition niche characterizes the macronutrient composition of food items, whereas the realized macronutrient niche characterizes the macronutrient composition of a species diet in a particular space and time based on factors such as food availability, competition, and other ecological constraints. The fundamental macronutrient niche estimates the range of macronutrient compositions in a species' diet that allows for population persistence (Coogan et al. 2018a). Thus, the multidimensional nutritional niche is important for understanding ecological relationships between diet and nutrition, with practical implications for species conservation and management (Coogan et al. 2018b, Panthi et al. 2019).

Species that are dispersed across a geographically wide and ecologically diverse range may have diverse diets, especially in terms of the food items consumed between geographically distinct populations (Senior et al. 2016). However, geographically-driven diversity in food items consumed between populations does not necessarily correspond to dietary differences in macronutrient composition (i.e., realized macronutrient niches). For example, in herbivorous mountain gorillas (*Gorilla beringei*) two geographically disjunct populations foraged on different plant species, but acquired a consistent composition of macronutrients (Rothman et al. 2011). These results suggest a degree of generalization in types of foods consumed, yet specialization in the preferred proportion of dietary macronutrients consumed. The opposite pattern was observed in invasive, omnivorous wild boars (*Sus scrofa*), which showed high plasticity in the macronutrient composition of the types of foods consumed, the macronutrient composition of those foods, and the macronutrient balance of their diets, both geographically and seasonally (Senior et al. 2016). Thus, wild boars were considered to have relatively wide food exploitation, food composition, and fundamental macronutrient niches. Therefore, understanding an animal's feeding strategies depends on the breadth of foods available and exploited, and the macronutrients acquired through those foods.

American bison (*Bison bison*) were once nearly ubiquitous across North America, with a range spanning roughly from the Rocky Mountains east to the Appalachians, and from northern Mexico north into the boreal forests of Alaska and the Yukon (Cunfer & Waiser 2016). While their distribution has become more fragmented after near extirpation in the 19th century, bison still occupy a diversity of habitats in North America. Throughout their range, bison have been thought of as obligate grazers (Strong and Gates, 2009). However, there is a growing body of evidence that suggests bison diets include substantial quantities of forbs and shrubs (Bergmann et al. 2015, Craine et al. 2015, Leonard et al. 2017, Jorns et al. 2019). This variation in bison diets is poorly understood. We therefore investigate bison's diet through the lens of multidimensional nutritional niche theory to improve our understanding of bison nutritional ecology.

Here, we review the frequency of different functional forage groups (i.e., graminoid, forb, and browse items) in diets of female bison across North America, and whether or not differences in foods consumed resulted in differences in macronutrient composition. Our objectives are to: 1) examine the food exploitation (differences in consumption of graminoids, forbs, and browse), food composition (estimated macronutrient contents), and realized macronutrient niches (macronutrient composition of subpopulation diets) for bison, thereby providing insight into their fundamental macronutrient niche; 2) assess how these niches change seasonally; 3) investigate how environmental variation in habitat may relate to changes in food or macronutrient consumption; and 4) test differences between the diets of the two subspecies of American bison, plains bison (*B. b. bison*) and wood bison (*B. b. athabascae*). We will accomplish this through a review of studies that quantify the proportions of forage items in bison diets based on fecal analyses and direct observations, and by using literature estimates of the macronutrient compositions of foods consumed. Regarding the food exploitation niche, we predict that female bison diets will be higher in graminoids than forbs or browse as would be expected; however, the degree of variation in the proportions of functional forage groups should differ between subpopulations. As ruminant herbivores, bison digestive systems are adapted to acquire energy from low quality forage items, therefore, we hypothesize that bison will have relatively narrow macronutrient niche breadths, because they subsist by grazing primarily on plant-based foods. However, the variety of macronutrients available in foods consumed by female bison should expand as a wider variety of forage items become available during the growing season (i.e., spring and summer). We predict that there will be differences among the macronutrient proportions of subpopulation diets, due in part to differences in the types of foods ecologically available and dynamic limitations on the amount of food available. However, differences in realized macronutrient niches should be relatively small when compared to omnivorous species. The range of realized niches created from each subpopulation will provide an estimate of the fundamental macronutrient niche for American bison. Furthermore, we investigate how the physical and climatic conditions of the herd's location influenced the items foraged by bison and macronutrients acquired, while controlling for differences in method of diet analysis.

Methods

Literature review and macronutrient estimates

We conducted a review of available literature using the search engines Google Scholar and Web of Science. We used the keyword "bison" with "diet," "diet composition," "microhistology," "faecal analysis," or "faecal composition" to locate peer-reviewed articles that reported results of bison diet composition analyses in terms of relative bulk of forage items in bison diets. When an article was located, we scoured the literature cited for additional peer-reviewed articles. In total, we found 26 published articles, including peer-reviewed articles and book chapters (n = 18), graduate theses (n = 3), government reports (n = 2), and conference proceedings (n = 1) that represented 16 bison subpopulations across North America (Figure 2.1).

When studies differentiated male and female diets, we only used the female diet and consider our results to be estimates of female dietary niches. Given that our study investigates differences in bison diets based on their geographic location, we avoid pseudo-replication by pooling all studies within a herd (Remonti et al. 2015; Table 2.1).

Next, we collected data on the macronutrient content of foods consumed by bison, measured in percent composition of lipids, proteins, and carbohydrates, for each species reported in the female bison's diet, primarily using Duke and Atchley (1986) and Feedipedia.org. For studies that reported percent composition of bison diets in terms of functional forage groups (i.e., graminoids, forbs, and browse), we used mean macronutrient content of dominant species within the study area for each functional forage group. While using macronutrient estimates from the literature may be in some ways a crude approach to estimating macronutrient content of food items, such an approach is useful when making dietary comparisons between groups of animals, and is an informative approach to studying comparative nutritional ecology (Remonti et al. 2016; Senior et al. 2016; Coogan et al. 2017). We then converted macronutrient content of individual foods to metabolizable energy values using appropriate conversion factors: 9 kcal/g for lipids; 4 kcal/g for proteins; and 4 kcal/g for carbohydrates (Merrill & Watt 1973). Metabolizable energy values for each macronutrient in a food were then expressed as a proportion of macronutrient-derived metabolizable energy. We estimated dietary macronutrient proportions by weighting percent metabolizable energy estimates for food items by the frequency of occurrence in the bison's diet (Coogan et al. 2018a). We also examined metabolizable energy values for three functional forage groups for bison: graminoids (loosely defined as all sedges and grasses with both C3 and C4 photosynthetic pathways), forbs, and browse items.

Multidimensional nutritional niche

We used right-angled mixture triangles (RMTs) to graphically visualize patterns in the proportion of macronutrients in foods and diets of bison (RMTs; Raubenheimer 2011). The RMT is a multivariate graphical approach, with an accompanying theoretical framework, that has been implemented to examine nutritional ecology in both natural and experimental settings (Raubenheimer et al. 2015a, Raubenheimer et al. 2015b). In particular, RMTs are useful for visualizing and modelling macronutrients in a three-dimensional simplex. We generated RMTs to evaluate the macronutrient proportions of subpopulation diets (realized macronutrient niches) during the growing season (April – September), non-growing season (January – March), and annual diets of bison. We only found two studies (Larter & Gates 1991; Larter & Allaire 2007) that described bison diets in the fall and early winter, so for consistency we defined our non-growing season as occurring from January through March. For RMTs describing realized macronutrient niches, we generated convex hull polygons around points representing each herd's realized macronutrient niche to provide insight into bison's fundamental macronutrient niche.

We analyzed proportions of macronutrients that account for the greatest variance in bison diets using a principal component analysis (PCA) for compositional data (Filzmoser et al. 2009) as implemented in the package {compositions} (van den Boogaart et al. 2018) in R version 3.6.1. Using biplots we graphically examined the variance between components by looking at the length of each link (i.e., the difference between the ends of each line), which represents the standard deviation of the log-ratio of two components; longer links indicate greater variance accounted for by the ratio of those two components.

Environmental factors affecting realized macronutrient niches

To investigate how the physical and climatic conditions of subpopulation location influences their food exploitation and realized macronutrient niches, we created a series of linear models for annual, growing, and non-growing season diets. Because we used compositional data, we used isometric log-ratios of forage groups and macronutrient compositions as response variables (Aitchison 1982, Coogan et al. 2018) using R package {compositions} (van den Boogaart et al. 2018). For the food exploitation niche, graminoids were used as the denominator in log-ratios, and for the realized macronutrient niche we selected carbohydrates as the denominator in log ratios. We selected three uncorrelated covariates as the predictors for our models: latitude, elevation, and precipitation (seasonality of precipitation for annual diets and the mean value of monthly precipitation during growing and non-growing seasons). Precipitation data were acquired from the WorldClim database (Hijmans et al. 2005). Temperature variables like mean annual temperature were correlated with latitude and performed worse in exploratory models. We therefore excluded temperature variables. Latitude, elevation, and method of diet analysis were acquired from each study. Four models for each season were generated with forbs and browse used as the numerators in the food exploitation niche analyses, and lipids and proteins in the realized macronutrient niche analyses. Method of diet analysis was used as a random effect to control for differences in reported diet composition due to dietary analysis methods. After models were generated, we back-transformed the coefficients for each predictor so that the results can be interpreted as the amount of change in the ratio of forage groups or macronutrient per one unit change in the predictor (Tolosana-Delgado & van der Boogaart 2011).

Lastly, we used simple significance tests (i.e., one-way student's t-tests; Ramsey & Schafer 2002) to assess differences in dietary composition between plains bison and wood bison.

Genetic studies have shown that it is unlikely that “pure” wood bison still exist in the wild as reintroductions of plains bison into what was classically wood bison range have led to genetic introgression (Ball et al. 2016). Therefore, we consider wood bison herds to be those that fall within the historic range of wood bison and plains bison to be herds that are located within the historic range of plains bison (Cunfer & Waiser 2016).

Results

Food exploitation niche

Graminoids were the dominant forage item (mean = 84.8%, SD = 25.2) found in annual female bison diets with forbs items contributing slightly more (8.5%, SD = 14.9) than browse (6.7%, SD = 12.4). During the growing season graminoids were still the dominant forage item (mean = 82.6%, SD = 27.3), with forbs (mean = 8.7%, SD = 17.5) and browse (mean = 8.6%, SD = 14.8) being similar in proportions. In the non-growing season, graminoids were again the dominant forage item (mean = 87.7%, SD = 22.8), followed by forbs (6.3%, SD = 12.2), then browse (mean = 5.9%, SD = 14.3) items. Annually, browse items contributed the largest proportions of lipids to bison diets and forbs contributed the greatest amount of proteins (Figure 2.2).

Food composition and realized macronutrient niches

Overall, items foraged by bison were high in the proportion of metabolizable energy from available carbohydrates, suggesting a relatively narrow food composition niche (Figure 2.3A). There were, however, several foods relatively high in lipid (from approximately 25-35%

metabolizable energy) while no food items exceeded 30% metabolizable energy from protein. Overall, the average proportion of metabolizable energy from macronutrients in annual bison diets was 81.5% (SD = 2.8) carbohydrates, 7.2% (SD = 1.2) lipids, and 11.4% (SD = 1.9) proteins (Figure 2.3B). The coefficient of variation (CV) for each macronutrient was 3.4% for carbohydrates, and 16.7% for both lipids and proteins, demonstrating that carbohydrates varied the least relative to their mean proportions. The realized dietary niches of subpopulations were clustered in the RMT simplex despite variation in the composition of food items, suggesting a relatively narrow fundamental macronutrient niche. The compositional PCA analysis demonstrated that the lowest variation between macronutrient ratios occurred for the protein:lipid ratio (Figure 2.4), while the highest variation in macronutrient ratios was observed between both carbohydrate:lipids and carbohydrate:protein.

Differences between annual and growing season diet composition were nominal, with bison diets composed of 81.4% carbohydrates (SD = 2.8), 7.3% lipids (SD = 1.3), and 11.4% proteins (SD = 1.8) in the growing season. Between the non-growing season and annual diets, differences in macronutrient composition were also nominal with 81.6% of the metabolizable energy coming from carbohydrates (SD = 2.5%), 6.9% from lipids (SD = 1.1%, and 11.5% from proteins (SD = 1.6). Macronutrient niche breadth of bison diets during the growing season was 2.8 times greater than that of the non-growing season, based on differences in the volume of convex hull polygons surrounding diet estimates (Figure 2.5).

Environmental factors affecting niches

Visual examinations of the effect of method of diet analysis on the composition of forage groups in bison diets and macronutrients showed differences in forage groups identified among methods, yet the estimated macronutrient proportions of bison diets remained relatively constant despite this (Figure 2.6). Including the method of diet analysis as a random effect did not improve the fit of linear regression models, except for models of forage group ratios during the growing season. Therefore, we used linear regressions for all other models. The percent browse:graminoid model revealed a significant positive relationship with latitude, with a 1.23% increase per 1˚ increase in latitude (Table 2.2; Figure 2.7). Additionally, the percent lipid:carbohydrate had a significant increase in bison diets of 1.02% per 1˚ of latitude in annual bison diets. Similarly, there was a significant increase of 1.02% per 1˚ of latitude for lipid:carbohydrate in growing season diets. Non-growing season diets a marginally significant increase of 1.17% in the browse:graminoid with a 1˚ increase in latitude.

Wood bison versus plains bison

We found significant differences in diets between plains and wood bison subspecies. Plains bison consumed significantly less browse items (t = -3.070, p = 0.003, α = 0.05), significantly less lipids (t = -2.748, p = 0.007, α = 0.05), and significantly less proteins (t = -1.831, p = 0.041, α = 0.05) in their diets. We did not find any significant difference in the consumption of graminoids, forbs, or carbohydrates between plains and wood bison diets.

Discussion

We used a multidimensional nutritional niche framework to examine the nutritional ecology of female American bison. Regarding the food exploitation niche, large herbivorous bison are limited in the varieties and types of foods consumed in comparison to, for example, omnivorous mammals that consume a variety of animal prey items and vegetative foods. Greater dietary variety also results in omnivores having wider food composition niches. For example, brown bear (*Ursus arctos*) can consume a variety of high-protein and high-lipid animal-based foods, in combination with high-carbohydrate foods, resulting in wide food composition niches, and can also tolerate a relatively wide range of realized diet niches (Coogan et al. 2017). Obligate carnivores, such as feral cats (*Felis silvestris*), consume primarily animal prey, and have been shown to self-select diets that are primarily composed of protein (52% of daily energy intake) and lipid (46%), with only minimal amounts of carbohydrate (2%; Plantinga et al. 2011). In contrast, bison, as other ungulates, are generally restricted to browse, forb, and graminoid-based diets. However, bison show flexibility in the proportions of each type of functional forage group consumed dependent on the ecosystem they are in. Furthermore, diets of bison were relatively high in the proportion of available carbohydrate consumed, which reflects the range of dietary food items they have evolved to forage on.

Bison's realized diet niches occupied a restricted space of the RMT simplex relative to the macronutrient breadth of food items, suggesting that, like many other animals, bison homeostatically regulate their intake of food items to consume a preferred proportion of dietary macronutrients (Simpson et al. 2004). However, we did not examine the availability of food items to establish whether animals were selecting food items disproportionately to availability. Yet, given that macronutrient balancing through differential consumption of food items is a well-established biological phenomenon, such speculation is not unfounded (Simpson & Raubenheimer 2012). Furthermore, diets that contain macronutrients in proportion to the available food items do not necessarily suggest that an animal does not selectively forage. Animals may follow rules of compromise which guide their foraging decisions in the face of an unbalanced diet, while some animals may have evolved macronutrient preferences based on the proportional availability of food items. Importantly, the clustering of realized diet niches within the RMT simplex suggests a similarly small range of fundamental macronutrient niches that a bison population could persist on. Thus, while variation exists in the proportion of macronutrients in bison diets, the source of which we are unable to definitively determine. We also acknowledge that our study focused female bison, which generally have higher quality diets (in terms of stable nitrogen isotopes in fecal samples) males, our macronutrient estimates would probably have included greater amounts of carbohydrates resulting in a more narrow dietary niche if males were included (Berini & Badgley 2017).

As the largest extant terrestrial herbivore in the Americas, bison are well adapted to have diets dominated by low quality graminoids (Mooring et al. 2005). The extended rumination time of their large body allows bison to get the most of these food items (Barboza & Bowyer 2000). The high-carbohydrate diet of bison is similar to that examined for other large herbivores. For example, blue sheep (*Psuedois nayaur*) in Nepal also had a diet dominated by graminoids and corresponding high levels of carbohydrates (Aryal et al. 2015). In our study, we found that diets of North American bison increased in lipids and proteins as the proportions of browse and forb items increased in the diet. In the river flood plains of Alaska, which are dominated by shrubs, particularly willows (*Salix* spp.), over 90% of bison diets were composed of browse items (Waggoner and Hinkes 1986). European bison (*Bison bonasus*; the closest living relative to American bison), which are considered a refugee species with distributions limited to protected forested areas, also have growing season diets dominated by forbs and browse items (Kowalczyk et al. 2011). Having a greater amount of protein and moisture may make forbs and browse more readily digestible and palatable for bison (Craine 2009). Aryal et al. (2015) examined the balance of fiber in the diets of blue sheep, and found that they tended to forage on plants higher in hemicellulose which is likely more readily digestible by them. Therefore, examining the fiber-derived energy in bison diets may yield additional insight into their nutritional ecology. It should also be noted that there are many other aspects to a plant's ecology that influence a herbivore's foraging such as concentrations of secondary compounds and grazing/fire regimes, which require further consideration (Hudson & White 1985). However, macronutrients have been shown to drive the foraging behavior of several species, and are generally correlated with fiber and other micronutrients (Raubenheimer and Simpson 2012).

The over two-fold increase in macronutrient dietary breadth in growing season diets compared to non-growing season diets is consistent with the greater variety of foods available to bison during the growing season. Though not directly addressed in this study, evidence that suggests that during the growing season the more nutritious and digestible young forbs and leaves of shrubs form a substantial part of bison diets (Bergmann et al. 2015, Craine et al. 2015; Leonard et al. 2017). Our results that the winter realized macronutrient niches were more constrained relative to summer diets is not surprising, because throughout North America, bison are limited to consuming standing dead vegetation during the non-growing season, primarily in the form of graminoids. We limited our winter investigation to January – March because data for bison diets in late –fall/early-winter is limited. However, we suggest that further consideration should be taken into account when determining the early winter diets of bison as the few studies that do report bison diets in October - December describe higher levels of consumption of unique forage items, such as lichens and horsetails (*Equisetum spp.;* Larter & Gates 1991, Larter & Allaire 2007). Bison could be foraging more intensively on these items in order to build reserves of particular minerals and micronutrients. For example, *Equisetum* spp. are known to have high levels of cations which are vital for metabolic processes such as active movement of molecules across tissue membranes (van Soest 1982).

Interestingly, we found that bison diets significantly increased in the proportion of lipids relative to carbohydrates as latitude increased. A study of European omnivores suggested that carnivory (and by extension the proportions of lipids and protein in the diet) increases with latitude (Vulla et al. 2009). However, other studies have suggested that spatially explicit environmental factors better explain dietary patterns (Gaston et al. 2008). It is possible that the higher consumption of lipids found within bison diets at higher latitudes could be a mechanism contributing to the pattern described by Bergmann's rule; body size tends to increase with latitude and/or lower temperatures (Bergmann, 1847; Mayr, 1956). For example, studies on endotherms across a variety of taxa show that 70% of these animals follow Bergmann's rule, but the mechanisms that drive this trend are still poorly understood (Millien et al. 2006, Ho et al. 2010). A higher proportion of dietary lipids is likely to be of benefit to animals inhabiting cold climates, because lipids are a greater contributor to stored energy and building of fat reserves than both carbohydrates and protein (van Soest 1982). We found that browse items were the greatest contributor of lipids in bison diets. With the increased intake of browse, there is a corresponding increase in lipid consumption, which may lead to greater fat reserves and overall mass, both of which are necessary for survival in the boreal and north; however, we note that our study specifically examines the proportions of macronutrients in bison diets, and that the amount of food consumed is also a critical aspect of building fat reserves. During the growing season in particular the fat demands of bison are great. Parturition occurs early in the growing season and lactation results in the highest fat demands for bison throughout the year (Hudson & White 1985). Further, bison enter a slump in body weight during winter due to reduced availability or forage and lower metabolic rates making survival dependent on bison's ability to put on adequate mass during the growing season (Parker et al. 2009, Huntington et al. 2019). During breeding in the July or August, females have their highest fat content and spend their time foraging on high quality items, whereas males spend less time foraging and more time tending to females (Cunfer & Waiser 2016). Protein is also an important factor for lean mass deposition and skeletal growth (Solon-Biet et al. 2014), which did increase with latitude in our study (Frandsen et al. 1954), but not significantly. The higher proportions of protein and lipid found in more northerly bison diets may be a reason that some have suggested that bison diets are of higher quality in cooler and wetter regions (Jorns et al. 2019). While we did not explicitly test for differences in available forage, the higher proportion of browse in boreal forests compared to the great plains is likely contributing to observed differences in browse and macronutrient content in bison diets. We would like to encourage those studying animal diets to report the availability of food items if possible, as only three out of the 26 studies we reviewed reported data on forage availability. Recent diet studies in the bison literature have documented a difference between functional forage groups identified in the diet dependent on the method of diet analysis used (e.g., Craine et al. 2015). DNA barcoding of diet suggests that bison consume more forbs than commonly identified among other studies, because DNA barcoding is considered to be unbiased towards less digestible plant materials (e.g., graminoids) compared to more traditional methods, such as microhistology (Varva & Holechek 1980, Garnick et al. 2018). Interestingly, there appears to be no difference in the proportion of macronutrient in diets estimated using different methods (Figure 2.6). This could mean that, assuming the diets have been accurately estimated for each different method, bison regulate their diet towards a preferred dietary intake of macronutrients despite differences in the types of forage groups consumed. Where there are true differences in the proportion of food group estimates within diets between methods of analysis, the consistent proportion of estimated macronutrients found across methods suggests that such analytical differences may have little or no effect on the nutritional estimates of bison diets.

Wood bison and plains bison have long been unique subspecies of the American bison, although genetic evidence suggests all extant wood bison herds share a genetic association with both subspecies (Ball et al. 2016). Size, hump position, and fur coloration are the primary characteristics used to distinguish the two species (Van Zyll de Jong et al. 1995). We suggest that this observed difference in size is a result of wood bison consuming higher proportions of browse and acquiring significantly higher proportions of lipids and proteins in the process. Thus, further emphasizing the latitudinal differences in bison diets. We posit that this information is important for researchers and managers considering translocation or reintroduction of bison in the north. Future research should investigate which shrub and tree species bison are selecting and what macronutrient content these forage items offer to further inform managers on bison’s dietary preferences.

Tables

Table 2.1: A summary of the female bison subpopulations used for dietary niche analyses including the location of the subpopulation, citations for the studies of where diet information was acquired, and the seasons covered in those studies. Studies that reported growing and non-growing season dietary compositions were used in analysis of annual diets. Subpopulations are listed in order of their latitudinal location (most northern to most southern) and the codes listed in the leftmost column will be used to identify each herd in all figures moving forward.

Code	Location	Seasons	Subspecies	Literature
1	Farewell Lake, Alaska, USA	Growing Non-growing	*B. b. athabascae*	Campbell & Hinkes 1983, Waggoner & Hinkes 1986
2	Aishihik Lake, Yukon, Canada	Growing Non-growing	*B. b. athabascae*	Fischer & Gates 2005, Jung 2015, Jung et al. 2015
3	Slave River Lowlands, Northwest Territories, Canada	Growing Non-growing	*B. b. athabascae*	Reynolds et al. 1978
4	Prince Albert National Park, Saskatchewan, Canada	Growing Non-growing	*B. b. bison*	Fortin et al. 2002
5	Elk Island National Park, Alberta, Canada	Growing Non-growing	*B. b. bison*	Holsworth 1960, Telfer & Cairns 1979
6	Pine River Ranch, Manitoba, Canada	Growing	*B. b. bison*	Leonard et al. 2017
7	National Bison Range, Montana, USA	Growing	*B. b. bison*	Mooring et al. 2005
8	Samuel H. Ordway Jr. Memorial Prairie, South Dakota, USA	Growing	*B. b. bison*	Plumb & Dodd 1993
9	Yellowstone National Park, Wyoming, USA	Growing Non-growing	*B. b. bison*	Meagher 1973, Delguidice et al. 1988
10	Wind Cave National Monument, South Dakota, USA	Growing Non-growing	*B. b. bison*	Popp 1981, Krueger 1986
11	Custer State Park, South Dakota, USA	Growing	*B. b. bison*	Keller 2011
12	Neal Smith National Wildlife Refuge, Iowa, USA	Growing	*B. b. bison*	Kagima & Fairbanks 2013
13	Pawnee National Grassland, Colorado, USA	Growing Non-growing	*B. b. bison*	Peden et al. 1974, Peden 1976, Kautz & van Dyne 1978, Schwartz & Ellis 1981
14	Konza Prairie Preserve, Kansas, USA	Growing	*B. b. bison*	Bergmann et al. 2015
15	Henry Mountains, Utah, USA	Growing	*B. b. bison*	van Vuren & Bray 1983, van Vuren 1984
16	Tallgrass Prairie Preserve,	Growing	*B. b. bison*	Coppedge et al. 1998

	Oklahoma, USA	Non-growing		

Table 2.2: Summary of compositional linear models used to investigate the environmental and climactic factors influencing North America bison's (*Bison bison*) food exploitation and realized macronutrient niches. The models were generated using isometric log-ratios of the percentage of forage groups and macronutrients in each herd's diet as the response variables. We have back-transformed the coefficients calculated in the compositional linear models so that the coefficients reported here can be interpreted as the amount of change in the ratio of the forage groups or macronutrient per one unit change in the predictor variable. Compositional linear models were analyzed for annual and seasonal (i.e., growing and non-growing season seasons) diets. Note that for annual and growing season diets a quadratic term was used for latitude in the percent forb:graminoid models due to the spread of the data. For brevity, we abbreviated graminoids (G), browse (B), forbs (F), carbohydrates (C), proteins (P), and lipids (L).

Annual				*Growing*				*Non-growing season*		
B:G	Estimate	*p*		B:G	Estimate	*p*		B:G	Estimate	*p*
Latitude	1.23	0.006		Latitude	1.07	0.481		Latitude	1.17	0.051
Elevation	1.00	0.141		Elevation	1.00	0.756		Elevation	1.00	0.346
Precipitation	1.06	0.231		Precipitation	1.01	0.817		Precipitation	0.97	0.436
F:G	Estimate	*p*		F:G	Estimate	*p*		F:G	Estimate	*p*
Latitude^2	1.01	0.269		Latitude^2	0.94	0.299		Latitude	0.81	0.803
Elevation	1.00	0.277		Elevation	1.00	0.276		Elevation	1.00	0.286
Precipitation	1.03	0.338		Precipitation	1.03	0.641		Precipitation	0.90	0.233
P:C	Estimate	*p*		P:C	Estimate	*p*		P:C	Estimate	*p*
Latitude	1.01	0.456		Latitude	1.02	0.811		Latitude	1.02	0.973
Elevation	1.00	0.197		Elevation	1.00	0.466		Elevation	1.00	0.740
Precipitation	1.00	0.187		Precipitation	1.00	0.977		Precipitation	1.00	0.924
L:C	Estimate	*p*		L:C	Estimate	*p*		L:C	Estimate	*P*
Latitude	1.02	0.016		Latitude	1.02	0.003		Latitude	1.02	0.066
Elevation	1.00	0.838		Elevation	1.00	0.237		Elevation	1.00	0.781
Precipitation	1.00	0.981		Precipitation	1.00	0.284		Precipitation	1.00	0.906

Figures

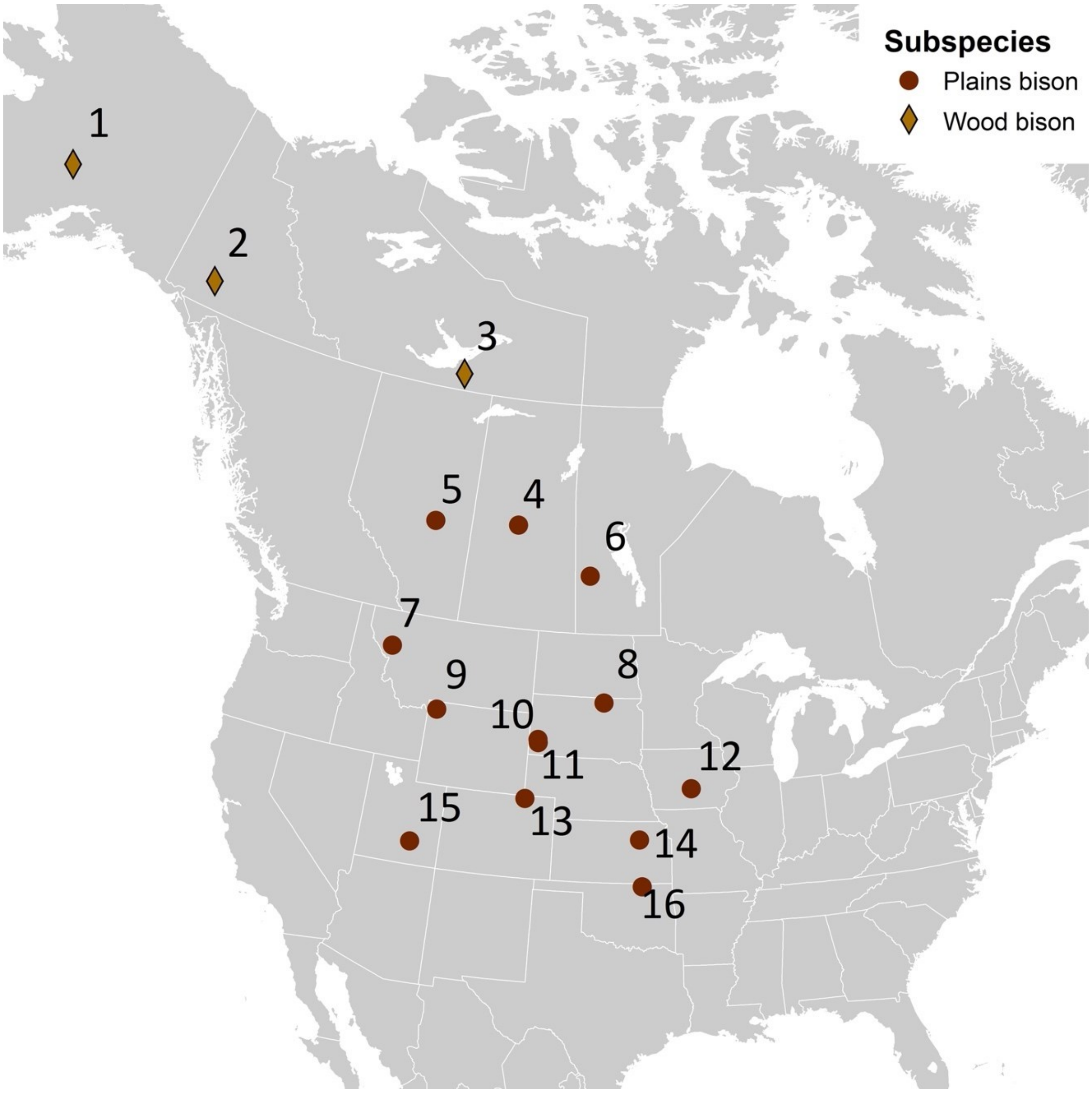

Figure 2.1: Distribution of the 16 American bison (Bison bison) herds used in this review of bison diets. Point symbols indicate herds located in the historic range of plains bison (B. b. bison), while diamond symbols represent herds in the historic range of wood bison (B. b. athabascae). Numbers correspond to the herd codes listed in Table 2.1.

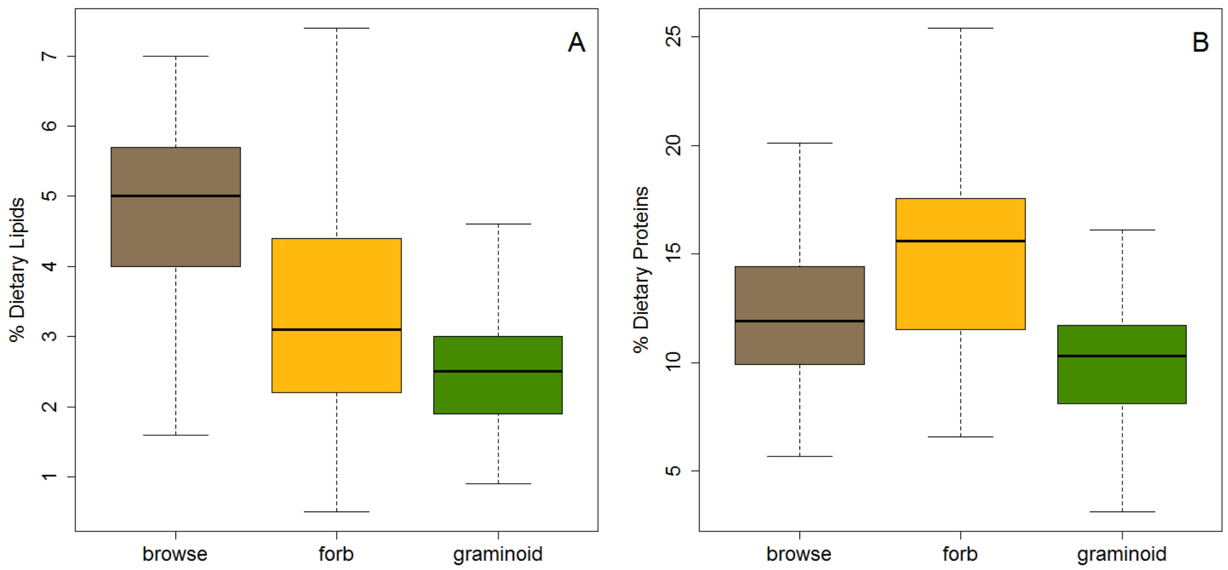

Figure 2.2: Boxplots of the functional forage groups and their relative annual contribution of (A) percent lipids and (B) percent proteins to female bison diets.

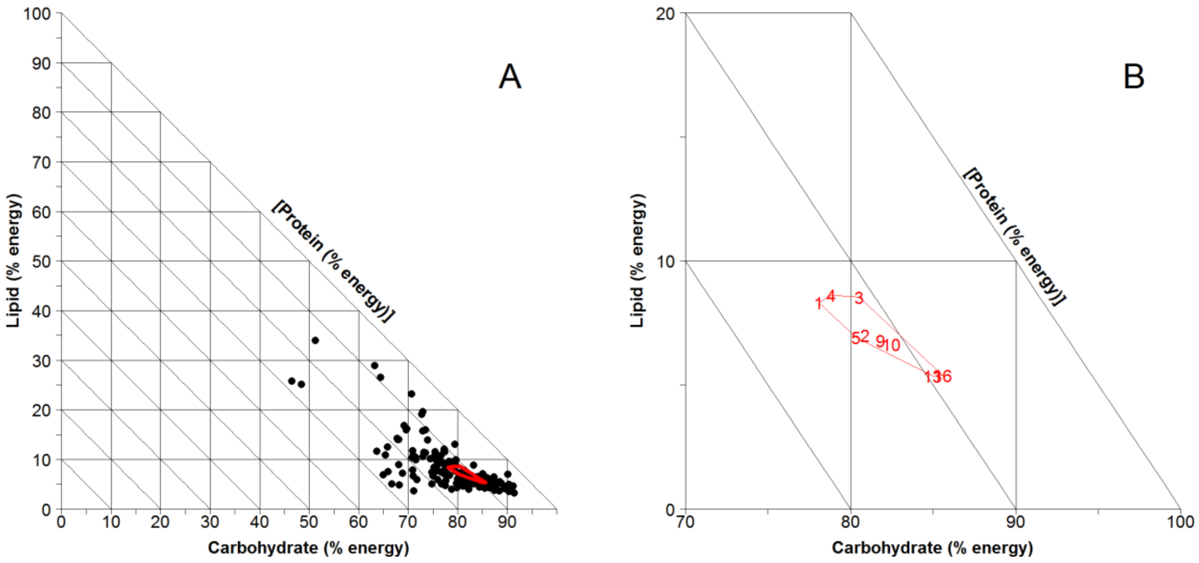

Figure 2.3: (A) Right-angled mixture triangle (RMT) depicting the macronutrient compositions of forage items (food composition niche or macronutrient niche breadth) identified in female bison diets across North America (*n* = 192 unique species) expressed as a percent of metabolizable energy. The red convex polygon shows the region of the simplex outlining each herd's realized macronutrient niches, thereby providing insight into the breadth of bison's fundamental macronutrient niche relative to the range of macronutrient compositions in foods consumed. (B) A close-up of the realized macronutrient niches of each bison herd throughout North America. Numbers refer to specific diet studies labelled in Table 2.1.

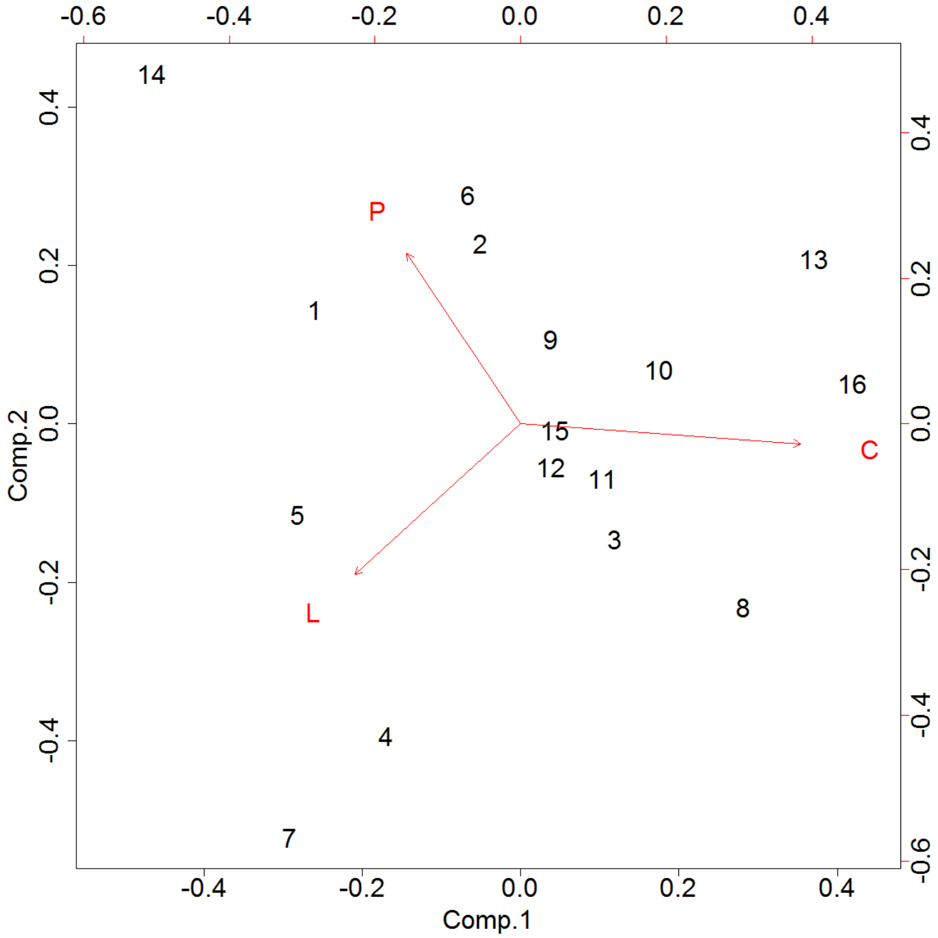

Figure 2.4: Biplot visualizing a compositional principal component analysis of the proportion of metabolizable energy from macronutrients in American bison (*Bison bison*) diets. The length of each link (i.e., the difference between the ends of each line) signifies the standard deviation of the log-ratios between two components. Therefore, the length of each link represents the variation between two components. Numbers refer to each unique bison herd (Table 2.1). P = protein; L = lipid; C = carbohydrate.

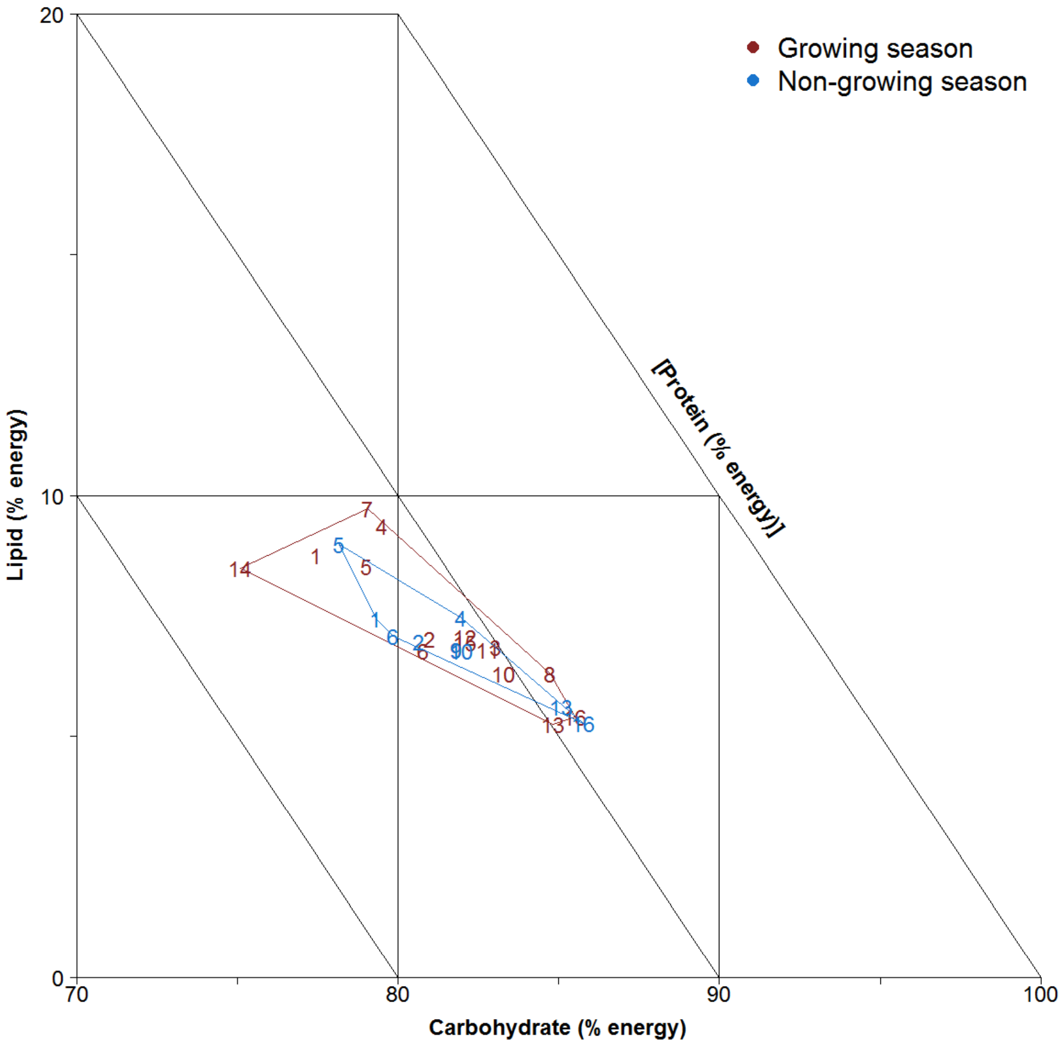

Figure 2.5: Right-angle mixture triangle showing a close up of the seasonal proportions of dietary macronutrients (realized macronutrient niches) for female American bison (*Bison bison*) herds for the growing season (red) and non-growing season (blue). Numbers correspond to herd labels in Table 2.1.

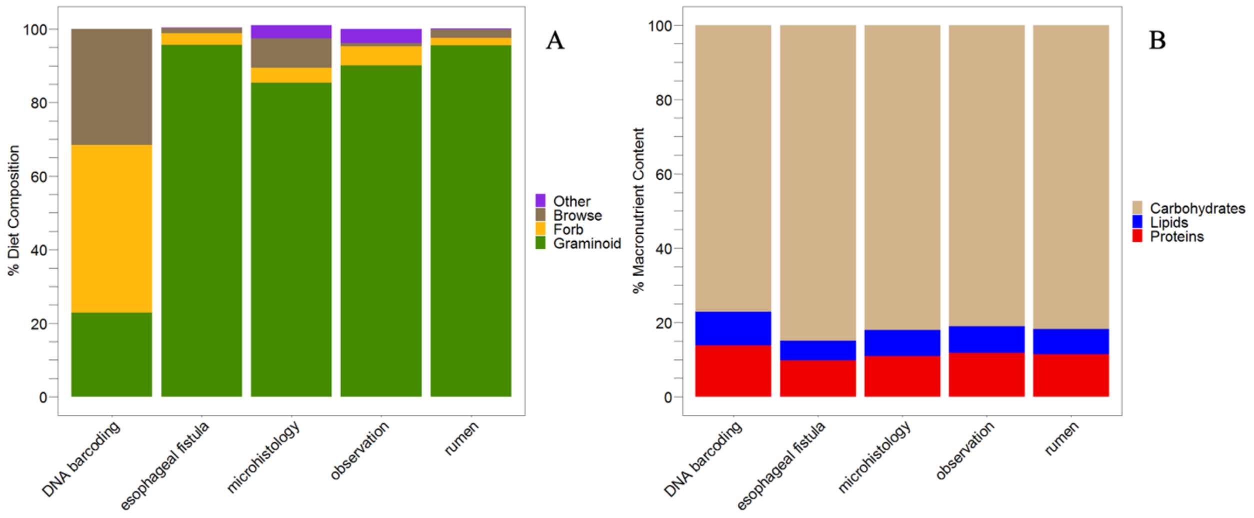

Figure 2.6: Bar-plots showing the (A) functional forage group, and (B) the proportion of metabolizable energy derived from macronutrients in American bison (*Bison bison*) diets based on the method used to analyze the diet.

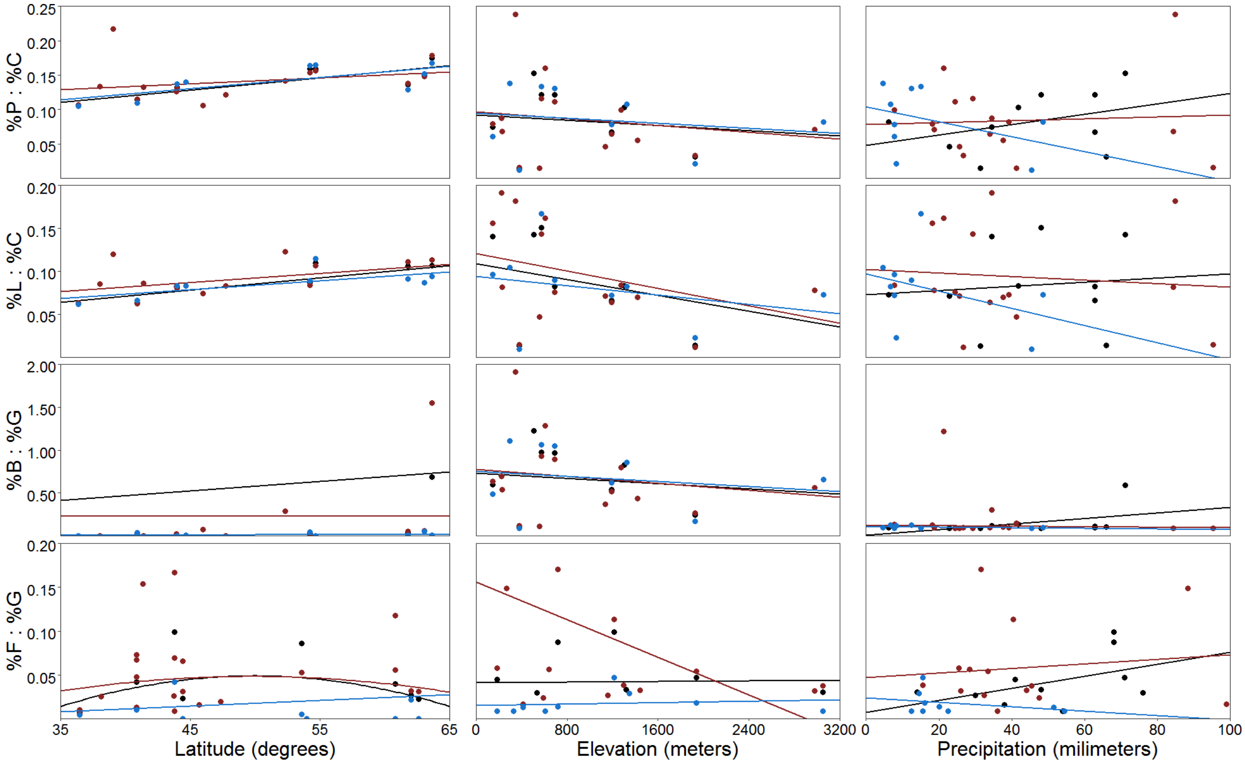

Figure 2.7: Linear and quadratic relationships between ratios of proteins (P) to carbohydrates (C), lipids (L) to carbohydrates, browse (B) to graminoids (G), and forbs (F) to graminoids and the predictors (i.e., latitude, elevation, and precipitation) used in regression models. Points represent individual herds with black points and lines representing annual diets, red points and lines representing growing season diets, and blue points and lines representing non-growing season diets. Note that for annual and growing season diets a quadratic term was used for latitude in the percent forb:graminoid models due to the spread of the data.

Chapter 3: Assessing nutritional consequences of switching foraging behavior in wood bison

Abstract

Diet is one of the most common traits used to organize species of animals into niches. For ruminant herbivores, the breadth and uniqueness of their dietary niche is placed on a spectrum from browsers that consume woody (i.e., browse) and herbaceous (i.e., forbs) plants, to grazers with graminoid-rich diets. However, seasonal changes in plant availability and quality can lead to switching of their dietary niche, even within species. In this study, we examined whether a population of wood bison (*Bison bison athabascae*) in northeast Alberta, Canada seasonally switched their foraging behavior, and if so, whether this was associated with changes in nutrient acquisition. We hypothesized that bison should switch foraging behaviors from grazing in the winter when standing, dead graminoids are the only foliar plants readily available to browsing during spring and summer as nutritious and digestible foliar parts of browse and forbs become available. If bison are switching foraging strategy to maximize protein consumption, then there should be a corresponding shift in the nutritional niche. Alternatively, if bison are eating different plants, but consuming similar amounts of nutrients, then bison are switching their dietary niche to maintain a particular nutrient composition. We found wood bison were grazers in the winter and spring, but switch to a browsing during summer. However, only winter nutrient consumption of consumed plants differed significantly among seasons. Between spring and summer, bison maintained a specific nutritional composition in their diet despite compositional differences in the consumed plants. Our evidence suggests bison are selecting plants to maintain a target macronutrient composition. We posit that herbivore’s can and will switch their dietary niche to maintain a target nutrient composition.

Introduction

Foraging decisions made by herbivores are motivated by the quantity and quality of available vegetation (Fryxell 1991). How the dietary niches of herbivores respond to changes in available vegetation has been the subject of extensive research (e.g., Bailey et al. 1996, Illius and O'Connor 2000, Codron et al. 2007, Spitzer et al. 2020). At high latitudes, seasonal fluctuations in environmental conditions influence both the quantity and quality of vegetation for herbivores (Ungerfeld et al. 2018). Functional groups (growth forms) of vegetation, such as graminoids (i.e., grasses, sedges, and other grass-like plants), browse (i.e., woody plants), and forbs (i.e., herbaceous plants), have different nutrient compositions and their availability, quantity, and quality changes seasonally (Codron et al. 2007, Safari et al. 2011). Selection of different dietary niches should therefore correspond to consumption of different concentrations of nutrients (i.e., different nutritional niches).

Much has been done to place herbivore species along a spectrum of dietary niches based on their consumption of different functional groups of plants (e.g., Kartzinel et al. 2015, Leonard et al. 2017). Grazers have a diet dominated by graminoids and browsers primarily consume forbs and/or browse (Hoffman 1989, Clauss et al. 2010). Intermediate feeders have a flexible dietary niche based on resource availability, consuming intermediate levels of graminoids, forbs, and browse (Hoffman 1989). Despite having unique dietary niches, grazers and browsers tend to have dietary niches with similar breadths (in terms of the diversity of plants consumed) that are narrower than intermediate feeders (Jung et al. 2015). The grazer/browser framework has been used to explain the coexistence or potential coexistence of multiple ruminants in a community (Fischer and Gates 2005, Jung et al. 2015, Abarutov et al. 2016). However, many species classically defined as browsers or grazers will switch between the two foraging behaviors in response to changes in local availability and seasonal quality of vegetation. For example, two distinct populations of Sanga cattle (*Bos taurus africanus*), a quintessential grazer, had unique dietary niches with a population in a forested range browsing, while a population in grasslands was grazing (Radloff et al. 2013). Additionally, browsing elephants (*Loxodonta africana*) switch to a diet dominated by grasses and raid crops in response to new-growth triggered by the onset of the wet season (Ruggerio et al. 1992, Vogel et al. 2020). This dietary plasticity within species and populations warrants investigation into the potential nutritional consequences of switching. Herbivore nutritional quality is typically defined in terms of energy, concentration of limited nutrients (i.e., protein), and limiting factors such as digestibility (i.e., structural carbohydrates concentration), all of which influence herbivore fitness (van Soest 1994, Plumb et al. 2009, Hamel et al. 2012). Forbs and browse tend to have greater quantities of limited nutrients than graminoids and graminoids have more structural carbohydrates, regardless of season (Craine et al. 2013, Hecker et al. 2020). The nutritional niche of herbivores has been estimated using a multidimensional approach known as nutritional geometry (Machovsky-Capuska et al. 2016). Nutritional geometry emphasizes the importance of nutrient balancing as a mechanism influencing foraging behavior across a range of taxa and foraging strategies (Simpson et al. 2004, Simpson and Raubenheimer 2012, Rothman et al. 2012, Erlenbach et al. 2014). For example, disjunct populations of herbivorous mountain gorillas (*Gorilla beringei*) had different available plants, but maintained the same nutrient compositions suggesting regulation for that nutrient niche (Rothman et al. 2007). Ungulate herbivores, such as wild water buffalo (*Bubalus arnee*) and blue sheep (*Psuedois nayaur*), have a realized nutrient niche that contains high levels metabolizable energy from carbohydrates and more proteins than lipids (Aryal et al. 2015, Shrestha et al. 2020). However, the seasonal changes in the nutritional niche of herbivores and how they are influenced by corresponding changes in the dietary niche (especially in highly seasonal environments) has received little attention.

We explored how seasonal switching of herbivory behaviors relates to the composition of nutrients consumed. Specifically, we studied diets of females in a population of wood bison (*Bison bison athabascae*) herd in northern Alberta, Canada. We chose bison because they have been described as obligate grazers and have the morpho-physiology of a grazer (Hoffman 1989, Stong and Gates 2009). Though recently, forbs and browse have been found to contribute significant proportions to some bison diets, especially during summer (Bergmann et al. 2015, Craine et al. 2015, Leonard et al. 2017, Hecker et al. 2021). We elected to examine the diets of females because female bison are known to have higher quality diets that are more diverse in composition than males (Popp et al. 1981, Mooring et al. 2005, Jung 2015). These differences likely arise from the additional pressures of pregnancy, parturition, and lactation that influence female diets seasonally (Berger and Cunningham 1994, Mooring et al. 2005). We predicted that the population would have a dietary niche typical of grazers in the winter and spring when the quality of graminoids was comparable to that of forbs and browse. However, as graminoids lignify in summer, becoming less digestible, bison should select forbs and browse with higher concentrations of limited nutrients thereby switching to an intermediate or browsing dietary niche. Specifically, we consider two competing hypotheses related to switching foraging strategies: 1) Switching from grazing to browsing is a behavioral mechanism used to maximize consumption of limited nutrients as would be evidenced by a corresponding change in the nutritional niche to include more protein; or, 2) Switching from grazing to browsing is a behavioral mechanism used to maintain a particular nutrient composition as would be evidenced by a consistent nutritional niche despite changes in the plants consumed.

Methods

Study system

We studied females in a small population (~186 animals; Ball et al. 2016) wood bison near Ronald Lake, Alberta. The population is of significant conservation value as it has less genetic introgression with the other American bison (*Bison bison*) subspecies, plains bison (*B. b. bison*), than any other wood bison herd on record (Ball et al. 2016). Additionally, the population is free of bovine tuberculosis and brucellosis that are prevalent in nearby Wood Buffalo National Park (WBNP) populations to the north (Shury et al 2015). The population's range extends from the southeastern corner of WBNP into Alberta's oil-sands region to the south, and bordered to the east by the Athabasca River and to the west by the Birch Mountains (Figure 3.1, DeMars et al. 2020). The range is located in the Hay/Slave River Lowlands of the boreal forest ecoregion (Omernik and Griffith, 2014) and is composed of approximately 4% graminoid-dominated wetlands (e.g., marshes and graminoid fens), 37% upland deciduous, 14% upland pine, 9% upland conifer, 38% peatlands and swamps (e.g., shrubby fens, bogs, swamps), and 4% open water (Figure 3.1, Ducks Unlimited Canada, 2016). The dominant tree species in upland habitats are quaking aspen (*Populus tremuloides*) in deciduous forests, jack pine (*Pinus banksiana*) in dry sandy sites, and white spruce (*Picea glauca*) in conifer forests (DeMars et al. 2020). Other ungulates within the range of the bison include white-tailed deer (*Odocoileus virginianus*), moose (*Alces americanus*), and occasionally woodland caribou (*Rangifer* *tarandus*). Between 2013 and 2018, the government of Alberta fitted 58 females with GPS radio-collars (38 Lotek Iridium Track, LOTEK wireless Inc., Newmarket, Canada; 10 Vectronics GPX Vertex Plus, Vectronics Aerospace GmbH, Berlin, Germany; and 10 Tellus GPS, FollowIT AB, Lindenberg, Sweden) with locations acquired every 90 minutes.

Diet content

During winter (January–March), spring (May–June), and summer (July–August) of 2018 and 2019 we visited female bison locations within 10 days of their presence to collect fecal samples that were <15-m of the GPS-collar location. Samples were stored at -20 °C until all samples were collected (one to eight months). To avoid over representing an individual location, date, or bison, we only collected one sample per bison location in the field. Then in the lab, we randomly selected three to five fecal samples per season and extracted 5-ml of fecal matter from the center of each sample and combined these to create a composite sample. We repeated the procedure 10 times per season without replacement of fecal samples. Composite samples were then shipped to Jonah Ventures (Boulder, USA) for diet content analysis using DNA metabarcoding.

Composites were analyzed for plant DNA through sequencing of the *trnL* chloroplast introns (Crain et al. 2015). The *trnL* sequences identify plants to the species, genus, or family level. Therefore, operational taxonomic units (hereafter referred to as "taxonomic units") are used to group sequences with 99% similarity to represent each taxonomic unit (King and Schoenecker, 2019). We used the Basic Local Assignment Search Tool (BLAST) from the National Center for Biotechnology Information to select taxonomic units by running *trnL* sequences through BLAST and selecting the taxonomic unit that had the highest percent match and was known to occur within the study area (NCBI, 2018). DNA metabarcoding reports the number of times a *trnL* sequence is read (i.e., read count) within a sample. We then calculated the relative read abundance (RRA) as the read count of a particular taxonomic unit divided by the total number of reads across all taxonomic units, which is considered a reliable proxy for diet composition (Craine et al. 2015, Deagle et al. 2019). The RRAs can overestimate plants consumed in small quantities (Deagle et al. 2019). Therefore, we used a number of selection criteria to refine out final taxonomic units: if more than one species had the same percent match with the *trnL* sequence, then we used the genera or family as the taxonomic unit; we excluded all sequences that did not occur within the study area; for the final diet content estimates, we only included taxonomic units that accounted for at least 1% of the seasonal diet. To ensure that composites were mixed evenly, we split each composite in half, analyzed each separately, and used non-parametric Mann-Whitney-Wilcoxon tests to look for differences in RRA estimates within composite samples (Ramsey and Schafer, 2002).

Forage quality analysis

We collected plant samples for taxonomic units that accounted for at least one-percent of the RRAs within each season. To account for potential errors associated with reducing species to taxonomic units, we collected all species that were foraged at recent bison locations. For example, the *Carex* genus was the finest taxonomic unit identified for sedges, so we collected the following three sedge species consistently foraged by bison: wheat sedge (*Carex atherodes*), beaked sedge (*C. utriculata*), and water sedge (*C. aquatilis*). At these sites we observed how the plants had been foraged by bison and clipped the species in a similar manor (i.e., same height and same parts of the plants; Shrestha et al. 2020). Clipped samples were dried at 60 °C for 24 hours, then at least 26-g of each sample was cut into <5-cm pieces. Dried vegetation was shipped to Nutrilytical (Calgary, Canada) for chemical analysis of macronutrient and fiber components.

Proximate analyses were conducted on foraged plants for the macronutrient content. Standard methods from the Association of Official Agricultural Chemists were used to measure ash, moisture, crude protein, lignin, acid detergent fiber (ADF), and neutral detergent fiber (NDF), and American Oil Chemists' Society ether extract methods were used to calculate crude fat (AOCS 1998; AOAC 2006). We then determined non-fiber carbohydrates and individual fiber components (i.e., hemicellulose and cellulose) through difference (Aryal et al. 2015, Shrestha et al. 2020):

Equation 1: Non-fiber carbohydrates = 100 – (crude fat + crude protein + ash + moisture + NDF)
Equation 2: Hemicellulose = NDF – ADF
Equation 3: Cellulose = ADF – (Lignin + Ash)

Next, we converted the percent macronutrient content to metabolizable energy values using the 4-kcal/g for carbohydrates and proteins, and 9-kcal/g for fat (Merrill and Watt 1973). These metabolizable energy values represent the percentage of the total metabolizable energy derived from a particular macronutrient without the assistance of microbial fermentation.

Multidimensional nutritional niche

We evaluated changes in the seasonal diet composition of bison using nutritional geometry; a multidimensional method of assessing an animal's dietary nutrition in the context of ecological niche theory (Machovsky-Capuska et al. 2016). We assessed the bison's dietary, macronutrient, and fiber niches. These niche estimates quantified the macronutrient compositions of plants seasonally foraged by bison thus accounting for limitations of availability (Coogan et al. 2018a). We plotted diet, macronutrient, and fiber content on right-angled mixture triangles (RMTs); a three-dimensional simplex, that uses the implicit z-axis to geometrically display the space (i.e., niche) of three components of an animal's diet (Raubenheimer 2011). For diet composition RMTs, we used percent content of browse (x-axis), forbs (y-axis), and graminoids (z-axis) in the diet (Spitzer et al. 2020). In these RMTs, niches closer to the origin represent grazing behavior and niches at the z-axis represent browsing. We used percent metabolizable energy for carbohydrates (x-axis), lipids (y-axis), and protein (z-axis) to create macronutrient RMTs (Machovsky-Capuska et al. 2016). For fiber RMTs, we used percent content of lignin (x-axis), hemicellulose (y-axis), and cellulose (z-axis) (Aryal et al. 2015). To determine if changes in macronutrient composition were significant between seasons, we calculated the mean percent metabolizable energy of all plants consumed within each season and generated a 95% confidence ellipse around the mean (Monette 1990). If the 95% confidence ellipse from one season encapsulated the mean of another season, then those two seasons did not significantly differ (Monette 1990, Fox 2016). We calculated confidence intervals around the means for macronutrient, fiber, and diet components to represent the nutritional components within each plant each season. We then calculated weighted means (using the RRA as the weighting factor) to represent how the components were consumed (i.e., realized niches). Finally, we calculated niche breadth and overlap for seasonal realized diet (at the taxonomic unit and forage group levels), macronutrient, and fiber niches. Niche breadths were calculated as the diversity of taxonomic units, macronutrient concentrations, and fiber concentrations while accounting for the relatedness of taxonomic units using R package *indicspecies* (De Cáceres et al. 2011, R Core

Team 2017) and compared them using Mann-Whitney-Wilcoxon tests (Ramsey and Schafer 2002). We assessed differences in individual macronutrients and fiber components in bison diets using one-way ANOVAs. Then, we used *post-hoc* Tukey's HSD tests for the three seasons and four functional forage groups (Ramsey and Schafer 2002).

Results

Seasonal diets

We collected 129 fecal samples: 46 in winter, 38 in spring, and 45 in summer. DNA metabarcoding found 5,322 unique *trnL* sequences in the female's fecal samples across all seasons, which we reduced to 119 identifiable taxonomic units accounting for 95% of the herds cumulative read count. Winter fecal samples contained 58 taxonomic units, spring samples had 66 taxonomic units, and summer samples had 57 taxonomic units. Mean read count within composite sample pairs did not differ significantly ($p = 0.41$). Therefore, we used the mean of the read count between pairs of composite samples to calculate RRAs.

Seasonal selection for different forage groups was apparent (Figure 3.2; Appendix A). Winter composites had 49.5% of the taxonomic units from browse, 44.4% from graminoids, 3.8% from forbs, and 1.9% from the miscellaneous plants (e.g., mosses, lichens), hereafter referred to as "other." Two taxonomic units associated with wetland graminoids, *Sparganium eurycarpum* and *Carex* spp., had the highest RRAs of 20.6 and 19.1, respectively, followed by two browse items: *Viburnum edule* (RRA = 17.2) and *Cornus sircea* (RRA = 12.7). Spring composites contained 32.4% browse, 25.0% graminoids, 17.9% other, and 12.6% forbs. *Carex* spp. had the highest RRA (19.0) followed by *Sphagnum* spp. (RRA = 11.4), *Salix* spp. (RRA =

9.9), and *Rosa acicularis* (RRA = 9.0) in spring. Summer composites contained 51.6% browse, 44.7% forbs, 1.5% other, and 0.5% graminoids. *Rosa acicularis* was the most frequent (RRA = 37.1) followed by *Chamaenerion angustifolium* (RRA = 29.1), *Ribes* spp. (RRA = 6.3) and *Salix* spp. (RRA = 4.6).

Foraging behavior and dietary niches

The foraging behavior during winter and spring is typical of a grazer/intermediate feeder, but in summer the herd switched to a browsing behavior (Figure 3.3). At the taxonomic level, we found spring dietary niche breadth was significantly greater than summer (W = 75, p = 0.03) and winter (W = 74, p = 0.04; Table 3.1), but similar between summer and winter (W = 54, p = 0.40). The overlap in seasonal dietary niches at the taxonomic unit level was also significantly greater between winter/spring than summer/winter (W = 100, p < 0.01) and spring/summer overlap was significantly greater than summer/winter (W = 80, p = 0.01). The spring/summer and winter/spring overlap did not differ (W = 48, p = 0.57). At the level of forage groups, there was significantly greater niche breadth during spring than summer (W = 100, p < 0.01) and winter (W = 100, p < 0.01), but summer and winter niche breadths were similar (W = 63, p = 0.18; Table 3.1). Dietary niche overlap of forage groups was significantly greater between winter/spring than summer/winter (p = 0.01), but overlap between summer/winter and spring/summer (p = 0.43), and between spring/summer and winter/spring (p = 0.96) did not differ.

Seasonal patterns in nutritional composition

We observed changes in nutrient compositions between some seasons, but we did not observe changes in fiber content (Figure 3.3; Appendix A). The digestible energy in winter diets came from 82.5% (SD = 5.6) carbohydrates, 9.0% (SD = 5.2) lipids, and 8.4% (SD = 3.0) proteins, while fiber consisted of lignin was 26.9% (SD = 12.9), hemicellulose 49.9% (SD = 5.8), and cellulose at 23.3% (SD = 12.2). The energy from macronutrients in spring diets was derived from 70.3% (SD = 6.8) carbohydrates, 11.4% (SD = 4.9%) lipids, and 18.3% (SD = 4.1) proteins, while fiber was 29.7% (SD = 17.0) lignin, 46.8% (SD = 8.9) hemicellulose, and 23.5% (SD = 14.9) cellulose. Digestible energy in macronutrients in the summer diets came from 71.6% (SD = 5.7) carbohydrates, 12.7% (SD = 5.0) lipids, and 15.7% (SD = 2.6) proteins, while summer fiber was 26.4% (SD = 14.6) lignin, 48.6% (SD = 10.0) hemicellulose, and 13.4% (SD = 5.4) cellulose. The nutritional niches of winter significantly differed from spring and summer, primarily through higher carbohydrate consumption in the realized niche compared to if plants were consumed in equal proportions. However, spring and summer realized macronutrient niches did not differ despite the nutritional niches of the consumed plants being significantly different (Figure 3.3). Fiber components were centered around 48.2% (SD = 8.6) cellulose regardless of season and showed no differences between seasons of the consumed plants' niches and the realized niches (Figure 3.4). Macronutrient and fiber compositions of forage groups differed significantly within forage groups between seasons and between forage groups within each season except for browse and forbs in spring (Appendix B).

Analysis of the consumed plants' nutrient and fiber content showed significant changes between seasons and forage groups in the most frequently foraged plants (Table 3.2, Appendix B). Crude protein differed significantly between seasons with spring foods containing the most protein followed by summer, and then winter. Additionally, non-fiber carbohydrates and ash were significantly higher in winter than summer. Between forage groups, lipids were significantly different with browse having the most lipids, followed by forbs, then graminoids and other plants. Non-fiber carbohydrates were significantly greater in graminoids than all other groups. Browse and forbs had significantly higher moisture content than graminoids. Forbs and other items had significantly higher ash than browse. In terms of fiber, winter plants had significantly more lignin than summer foods and significantly more cellulose than spring and summer foods. Graminoids had significantly more hemicellulose content than all other functional forage groups and had significantly more dry matter than forbs or other items. Graminoids and other items contained significantly more cellulose. Lignin content was significantly higher in browse than graminoids.

Discussion

We show that the foraging behavior of females in the Ronald Lake wood bison population changes seasonally, but bison maintained a similar macronutrient composition when possible. Niche overlap was significantly greater in the winter/spring and spring/summer than summer/winter demonstrating a gradual shift in foraging from intermediate-grazing to browsing occurring from winter to spring and spring to summer. Spring diets of female wood bison also had a wider niche breadth compared to the narrow (i.e., specialized) niche breadth of browsing and grazing that occurred in summer and winter, respectively. Our results contribute to a growing body of evidence that suggests bison are browsers during the summer (Waggoner and Hinkes 1983, Bergmann et al. 2015, Leonard et al. 2017). Increased forb and browse content in bison diets in spring and summer is well documented across North America (e.g., Schwarts and Ellis 1981, Larter and Gates 1991, Jung et al. 2015). European bison (*B. bonasus*), the closest extant relative of American bison, are also strict browsers in temperate forests, especially in the summer (Kowalczyk et al. 2011, Zielke et al. 2017, Cromsigt et al. 2018). DNA metabarcoding reflects where the bison acquired their protein, not biomass intake (Craine et al. 2015), and therefore is likely biased toward foods with more protein. However, studies comparing DNA metabarcoding to methods that reflect dry matter intake (i.e., microhistology) report agreement between methods (King and Schoenecker 2019). Therefore, similar to Leonard et al. (2017), we suggest that wood bison are more of an intermediate feeder than previously thought as they exhibit a flexible foraging strategy based on availability and quality of foods. However, we caution against applying these labels to entire species, ignoring the herbivore community structure populations exist in, as the grazer/browser spectrum should only be applied within specific herbivore communities (Rothman et al. 2007, Clauss et al. 2010).

The seasonal switching of foraging behavior correlates with seasonal changes in habitat selection and annual life history events of bison. The Ronald Lake bison exhibit strong selection for graminoid-rich wetlands in the spring and winter, but switch to more use of upland habitats during the summer (DeMars et al. 2020). The increased lignification and decreased protein content of graminoids between spring and summer could be a mechanism driving this switch in habitat. Additionally, in the summer graminoid-rich wetlands have more biting insects and less stable footing than other habitats in the herds range, which could contribute to selection of upland habitats (Belanger et al. 2020). For female bison, spring is the season when fat reserves are lowest as a result of a winter diet with low lipid content and catabolism of fat reserves. Spring is also the seasonal of nutritional stress is highest due to the high energetic demands of parturition and lactation (Hudson and White 1985, Cunfer and Waiser 2016). We found that crude protein was in greater concentrations in consumed plants and dietary niche breadth was the greatest in spring. This suggests that bison are able to meet their nutritional targets while also consuming graminoids that contain more digestible fiber components (i.e., hemicellulose) and therefore more energy (Codron et al. 2007). During summer, female bison are putting on mass in preparation for rut, pregnancy, and winter survival. We show that they switch to a browsing strategy at this time and consume items with more non-digestible fiber components (i.e., lignin) but also more lipids. Lastly, in winter less protein is abundant in consumed plants. At this time, we observed a switch back to more grazing with supplemental browse consumption suggesting selection for energy-rich foods. Interestingly, despite the switching in foraging behavior, potentially in response to seasonal energetic demands, bison were able to maintain a similar nutritional composition. Unfortunately, we were unable to obtain fecal samples during autumn and early winter (September – December). We encourage future investigations into bison diets to target this time period for dietary and nutritional ecology studies as it is poorly represented in the literature and foraging decisions during this time may influence winter survival especially at northern latitudes.

Our investigation into the female Ronald Lake bison's seasonal macronutrient composition provides insight into herbivore nutrient availability and regulation. As herbivores, bison are restricted to a relatively narrow macronutrient niche when compared to omnivores (e.g., Senior et al. 2016) or carnivores (e.g., Tait et al. 2014). Our realized macronutrient and fiber niche measures are similar to other herbivores whose niches have been quantified, such as blue sheep (Aryal et al. 2015) and wild water buffalo (Shrestha et al. 2020). We found that the macronutrient composition of the plants most frequently foraged between spring and summer differed, but bison consumed them at frequencies that kept the macronutrient composition consistent. This suggests that bison are selecting seasonal diets for a particular macronutrient composition within the nutrient space available to them. Homeostatic regulation of macronutrient composition through consumption of different food items has been suggested as a mechanism influencing diet selection (Simpson et al. 2004). In this study, bison consumed more lipids in the spring to maintain a macronutrient composition similar to their summer diets. The winter macronutrient niche of consumed plants did not overlap with spring or summer containing less protein and more carbohydrates. Thus, bison may not have access to enough protein to maintain their nutritional niche resulting in the realized macronutrient niche being different than spring or summer. Alternatively, targeting graminoids and carbohydrates during winter may be an adaptation to maximize short-term energy gains in the winter when homeostatic temperature regulation put greater energetic demands on bison than other seasons (Fortin et al. 2003). Despite this difference, females had the least variation along the protein (z-axis) in all three seasons suggesting that they regulated for relative protein concentration. This is not surprising as protein is more limiting to herbivores than energy (Craine et al. 2013).

Our results support our hypothesis that bison are balancing nutrients rather than maximizing a particular nutrient through their dietary switching. In a study that applied nutritional geometry to winter moose diets in Sweden, Felton et al. (2021) also showed moose maintained a particular protein to energy ratio rather than maximize consumption of either. Utilizing this multidimensional approach provides insight into how these covarying nutritional components interact and the foraging decisions animals make based on these interactions.

Additionally, we used these techniques to quantify and compare multiple levels of the bison's seasonal dietary and nutritional niches: the food exploitation niche (i.e., the range of foods consumed), the food composition niche (i.e., the range of nutritional components in the foods consumed), and the realized nutritional niche (i.e., the range of nutritional components consumed; Coogan et al. 2018a). It is important to note that we quantified the proportionate contribution each individual plants makes to the bison's energy supply, not the energy from fermentation and protein synthesis in the microbes. As ruminants that use foregut fermentation by the microbial community up to 80% of the total absorbable protein in the small intestine comes from microbial protein synthesis in the rumen (Storm and Ørskov 1983, Varel and Dehority 1989). However, these microbes require readily available carbohydrates (i.e., non-structural carbohydrates) and nitrogen is required by microbes for fiber fermentation (van Soest 1994). Since fiber and protein are negatively correlated, the balancing of nutrients by bison may readily be interpreted as nutrient balancing to the microbes' nutritional targets. Further, the diet switching behavior likely helps to maintain this nutritional composition as we have shown.

There is little doubt that bison have the morpho-physiological features of a grazer (Hoffmann 1989). However, the results presented here for a population of bison inhabiting the boreal forest where forage diversity is high suggests that the cumulative macronutrient composition of the plants consumed has greater regulatory influence on bison diet selection than phenotypic traits. We did not explore other factors known to regulate herbivore foraging behavior, such as minerals (Wam et al. 2017), or plant secondary defense compounds like tannins (Windels and Hewitt, 2011). However, we do note differences in ash contents of plants between season and forage group which represents the inorganic mineral elements in plants (Hoffman and Taysom 2005). Future investigations into the macronutrient niches of herbivores should consider the potential for macronutrient or fiber niche differences in herbivore communities classically scaled on a grazer to browser spectrum. Our work sheds light on the importance of macronutrient regulation in herbivore diet selection and we propose that this be taken into consideration when considering population viability and carry capacity analyses of herbivores.

Tables

Table 3.1: Seasonal breadth and overlap of dietary (at levels of the taxonomic unit and four functional forage groups), nutritional, and fiber niches. A larger metric of niche breadth indicates greater diversity (i.e., wider niche). Similarly, a larger metric of niche overlap indicated greater overlap between the two niches in question. The taxonomic unit and forage group describe the dietary niches at the levels of the operational taxonomic units as identified by DNA metabarcoding of wood bison (*Bison bison athabascae*) fecal samples and the four functional forage groups (browse, forbs, graminoids, and other). The macronutrient and fiber niches are composed of carbohydrates, lipids, and proteins, and lignin hemicellulose and cellulose respectively.

	Breadth			Overlap		
	Winter	Spring	Summer	Winter Spring	Spring Summer	Summer Winter
Taxonomic unit	0.369	0.412	0.392	0.332	0.323	0.045
Forage group	0.205	0.329	0.251	0.773	0.613	0.549
Macronutrient	0.135	0.202	0.229	0.990	0.997	0.987
Fiber	0.309	0.319	0.315	0.995	0.976	0.981

Table 3.2: Means and standard deviations (in parentheses) of percent content for nutritional components of plants most frequently consumed by the Ronald Lake wood bison (*Bison bison athabascae*). Results of one-way ANOVA test for differences between three seasons and four functional forage groups are reported as p-values. Bold numbers are those that are significantly different and the symbol indicates the direction of the relationship. The "Carbohydrates" row refers to the non-structural carbohydrates defined in Equation 1. All nutritional component concentrations were based on plant dry matter.

	Season			
	Winter	Spring	Summer	p-value
Ash	**1.64—** **(0.33)**	1.93 (0.37)	**2.11†** **(0.37)**	<0.01
Carbohydrates	**74.50†** **(5.40)**	**62.10—** **(5.15)**	**62.64—** **(5.18)**	< 0.01
Crude Protein	**7.55—** **(2.51)**	**16.17†** **(3.77)**	**13.72*** **(2.33)**	< 0.01
Lipid	3.68 (2.23)	4.57 (2.20)	4.96 (2.09)	0.10
Cellulose	49.85 (5.76)	46.82 (8.92)	48.60 (9.97)	0.59
Hemicellulose	23.96 (12.19)	23.49 (14.94)	24.95 (13.37)	0.92
Lignin	26.89 (12.86)	29.69 (17.03)	26.69 (14.61)	0.77

	Forage Group				
	Browse	Forb	Graminoid	Other	p-value
Ash	**1.74—** **(0.43)**	**2.08†** **(0.20)**	1.91 (0.129)	**2.42†** **(0.70)**	<0.01
Carbohydrates	**64.76—** **(8.57)**	**62.18—** **(3.75)**	**70.97†** **(5.12)**	**61.45—** **(7.29)**	<0.01
Crude Protein	13.12 (5.45)	14.98 (3.22)	11.69 (4.13)	11.45 (2.08)	0.25
Lipid	**1.73†** **(0.37)**	1.43 (0.19)	**0.81—** **(0.39)**	1.15 (0.26)	<0.01
Cellulose	**42.97—** **(8.00)**	**54.88†** **(6.92)**	48.63 (2.06)	**55.51†** **(11.98)**	<0.01
Hemicellulose	**17.50—** **(7.41)**	**16.54—** **(10.91)**	**42.40†** **(4.64)**	**20.54—** **(8.98)**	<0.01
Lignin	**39.54†** **(9.32)**	**28.59*** **(8.26)**	**8.97—** **(3.28)**	**23.95*** **(16.77)**	<0.01

† significantly greater than the other seasons or forage groups

— significantly less than the other seasons or forage groups

* significantly different at an intermediate level (i.e., between the greater and lesser groups)

Figures

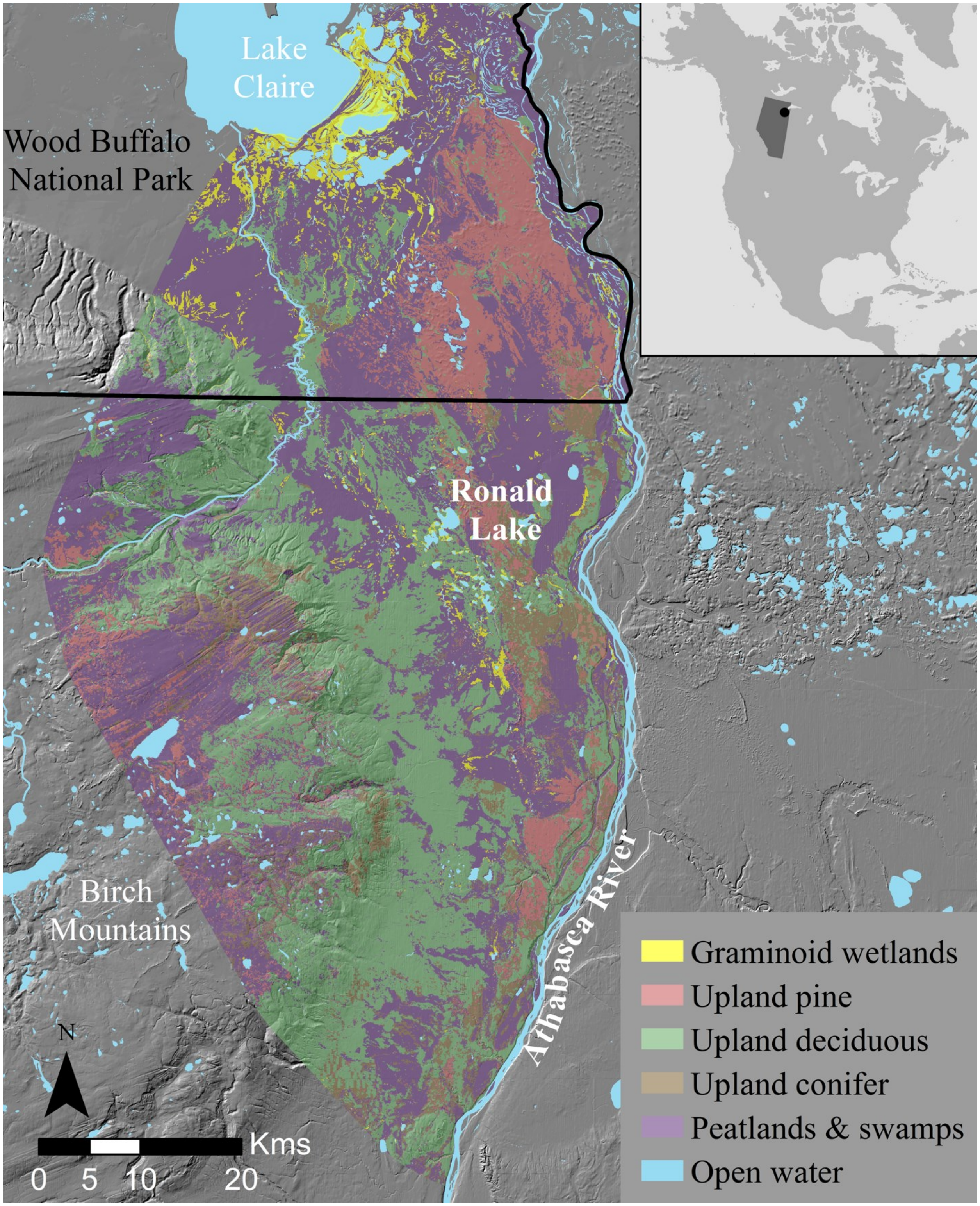
Lake Claire
Wood Buffalo National Park
Ronald Lake
Birch Mountains
Athabasca River
Graminoid wetlands
Upland pine
Upland deciduous
Upland conifer
Peatlands & swamps
Open water
N
Kms
0
5
10
20

Figure 3.1: The Ronald Lake wood bison's (*Bison bison athabascae*) home range (100% minimum convex polygon) with a 15-km buffer, cropped to the west side of the Athabasca River (DeMars et al. 2020). The coloured (non-grey) regions represent the home range and each color represent a unique landcover type. The inset map shows the study area location in Alberta, Canada.

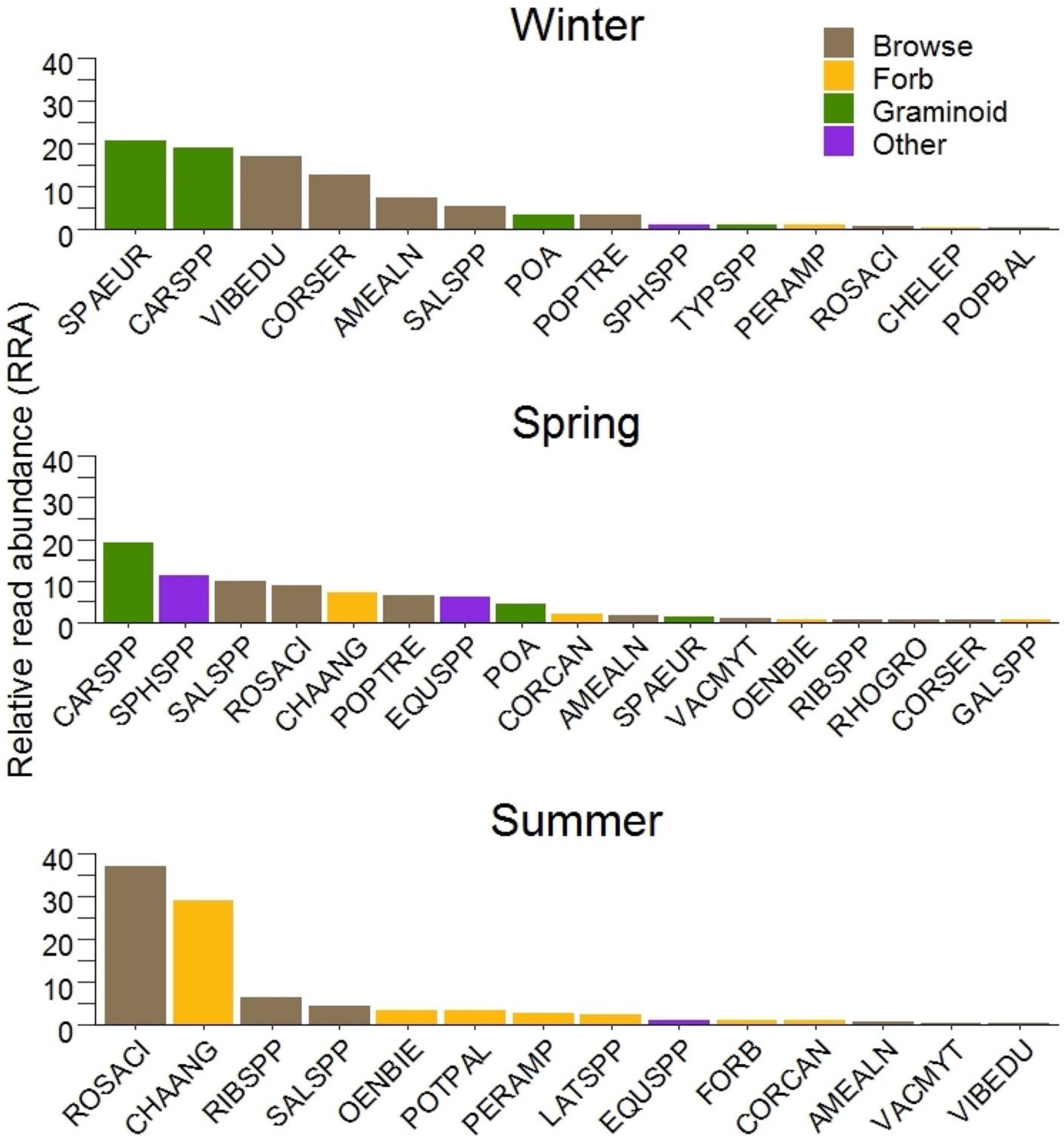
Winter
Browse
Forb
Graminoid
Other
Relative read abundance (RRA)
40
30
20
10
0
SPAEUR
CARSPP
VIBEDU
CORSER
AMEALN
SALSPP
POA
POPTRE
SPHSPP
TYPSPP
PERAMP
ROSACI
CHELEP
POPBAL
Spring
40
30
20
10
0
CARSPP
SPHSPP
SALSPP
ROSACI
CHAANG
POPTRE
EQUSPP
POA
CORCAN
AMEALN
SPAEUR
VACMYT
OENBIE
RIBSPP
RHOGRO
CORSER
GALSPP
Summer
40
30
20
10
0
ROSACI
CHAANG
RIBSPP
SALSPP
OENBIE
POTPAL
PERAMP
LATSPP
EQUSPP
FORB
CORCAN
AMEALN
VACMYT
VIBEDU

Figure 3.2: The diet composition of Ronald Lake wood bison (*Bison bison athabascae*) reported as relative read abundances (RAAs; the number of times a unique DNA sequence was found in a fecal sample divided by the total number of DNA sequences multiplied by 100) of fecal samples for three distinct seasons: spring, summer, and winter. 25 operational taxonomic units were identified overall: *Amelanchier alnifolia* (AMEALN), *Carex* spp. (CARSPP), *Chamaenerion angustifolium* (CHAANG), *Chenopodium leptophyllum* (CHELEP), *Cornus canadensis* (CORCAN), *C. sericea* (CORSER), *Equisetem* spp. (EQUSPP), unknown forb (FORB), *Galium* spp. (GALSPP), *Lathyrus* spp. (LATSPP), *Oenothera biennis* (OENBIE), *Persicaria amphibia* (PERAMP), Poaceae (POA), *Populus balsamifera* (POPBAL), *P. tremuloides* (POPTRE), *Potentilla palustris* (POTPAL), *Rhododendron groenlandicum* (RHOGRO), *Ribes* spp. (RIBSPP), *Rosa acicularis* (ROSACI), *Salix* spp. (SALSPP), *Sparganium eurycarpum* (SPAEUR), *Sphagnum* spp. (SPHSPP), *Typha* spp. (TYPSPP), *Vaccinium mytrilloides* (VACMYT), and *Viburnum edule* (VIBEDU).

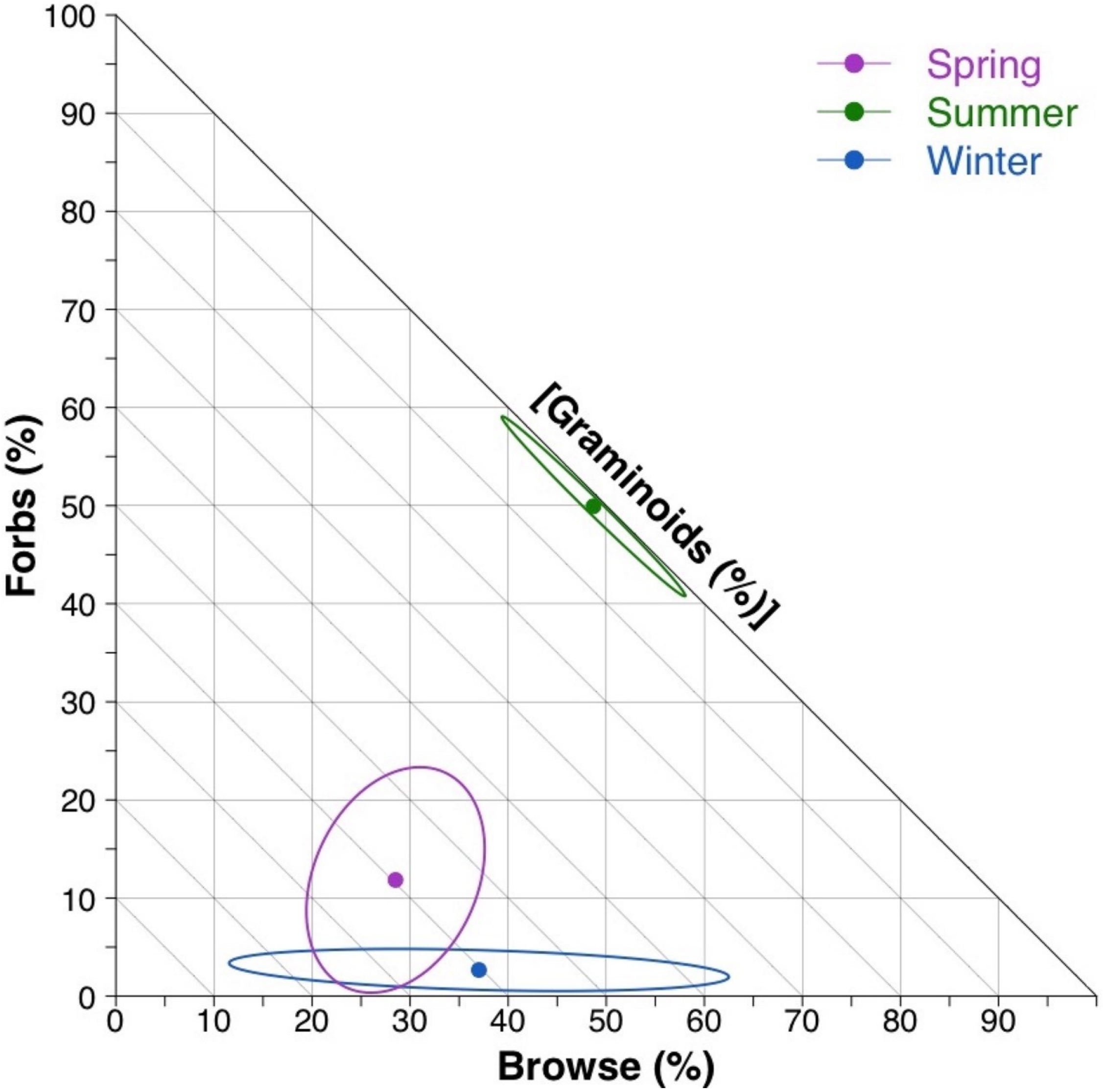

Figure 3.3: Right-angled mixture triangle of the Ronald Lake wood bison (*Bison bison athabascae*) diet in terms of three functional forage groups: browse (woody plants), forbs (herbaceous plants), and graminoids (grass-like plants). Each point represents the mean content of all three forage groups within each season (spring as purple, summer as green, and winter as blue) and the surrounding confidence ellipses the 95% confidence intervals. Grazers will have diets closer to the plot origin (lower left) and browsers will be closer to the z-axis (right). Miscellaneous forage items such as mosses and horsetails (*Equisetem* spp.), are not considered in this plot. All other taxonomic units present in bison fecal samples are considered when calculating means and confidence ellipses.

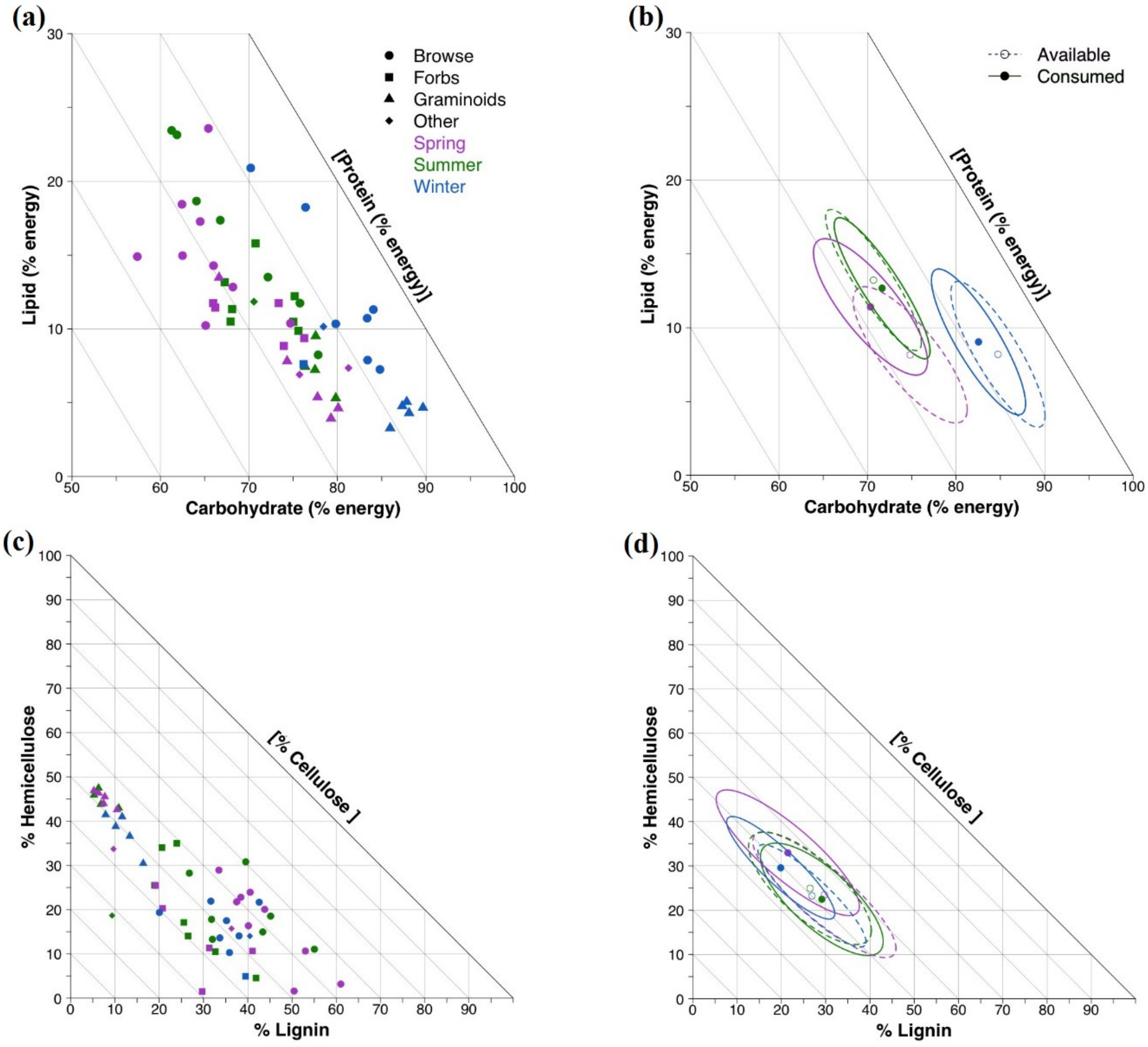
(a)
(b)
(c)
(d)
● Browse
■ Forbs
▲ Graminoids
◆ Other
Spring
Summer
Winter
Available
Consumed
Lipid (% energy)
Carbohydrate (% energy)
[Protein (% energy)]
% Hemicellulose
% Lignin
[% Cellulose]
0
10
20
30
50
60
70
80
90
100

Figure 3.4: (A) Right-angle mixture triangle (RMT) displaying the macronutrient composition of wood bison (*Bison bison athabascae*) diet during three seasons: spring (May – June), summer (July – August), and winter (January – March). Symbols represent the 26 most frequently foraged plants and the functional forage group that each belongs to. (B) RMT showing the seasonal mean macronutrient composition of wood bison. The axes of these RMTs are reported as percent energy because macronutrient concentrations were converted to metabolizable energy provided by each macronutrient as described in the methods. Each point represents the mean macronutrient composition for a given season and the ellipses show the 95% confidence ellipse around that mean. Solid points and lines represent the mean macronutrient composition of the plants consumed each season weighted by their relative read abundance. Dashed lines and hollow points signify the mean macronutrient composition in the same plants if they were consumed in equal proportions. (C) RMT presenting the fiber composition of foods foraged by wood bison during the three seasons. (D) RMT depicting the 95% confidence ellipses around the mean macronutrients weighted (solid dots and lines) by the relative read abundance of each plant and the mean macronutrient content in those forages if they were consumed in equal proportions (hollow points and dashed lines).

Chapter 4: Behavioral habitat selection of wood bison (*Bison bison athabascae*) in Boreal forests.

Abstract

Understanding habitat selection in animals is critical to informing their management and conservation. However, different animal behaviors require utilization of different components of habitat. Not considering different behavioral states in habitat selection analyses can lead one to ignore factors influencing selection, misinterpret the direction of selection, or misjudge the strength of selection. We investigated how behavioral states influence habitat selection in wood bison (*Bison bison athabascae*). Our study focused on female selection during the growing season (May – August) in 2018 – 2020. We visited locations of collared females and random, available locations, to quantify the structural forest and nutritional components of the bison's habitat. Each bison location was labeled in the field as either a foraging, traveling, or bedding site based on signs of these behaviors. We then used resource selection functions to assess habitat selection for each behavioral state and for all bison locations pooled. We used the same seven predictor variables in each model: percent canopy cover, percent soil moisture, coarse (>2.5-cm) woody debris density, sapling density, percent crude protein, percent digestible energy, and foliar biomass. Our models did show significant differences in selection between behavioral states and the pooled model. All behaviors indicated selection for open habitats. Traveling and bedding sites selected for drier soils (i.e., upland habitats), while foraging sites selected for wetter soils (i.e., wetlands). Foraging sites were selected that had plants with more crude protein and digestible energy. Interestingly, traveling sites also had vegetation with significantly more crude protein than random locations. Our results highlight the importance of upland habitats for wood bison in the boreal for particular behaviors and nutrition, which are not

traditionally considered critical habitats for bison. Additionally, our results contribute to the growing body of evidence suggesting that behavioral state should be considered in habitat selection analyses.

Introduction

Habitat selection is a mechanistic process that is influenced by the quality and quantity of forage (i.e., bottom-up effects), predation pressure (i.e., top-down effects), and competition between and within species (Nielsen et al. 2010). These mechanisms are often at odds with each other forcing animals to make compromises in their decision making when selecting habitats. For instance, high quality foraging habitat may have a higher concentration of conspecifics (i.e., competition) and/or higher predation risk (Fortin et al. 2004, Nielsen et al. 2006). As a result, habitat selection is not stagnant for individuals or populations. Further, resources are typically disjunct in both space and time resulting in temporal variation in patterns of selection to optimize the use of clustered resources (Mobaek et al. 2009, Gaillard et al. 2010). Understanding which mechanisms (bottom-up, top-down, or competition) have the greatest influence on habitat selection and how animals balance the competing demands that these mechanisms put on them is the objective of habitat selection studies.

The behavior an animal exhibits at any particular time has the potential to influence how they balance the competing demands and thus drive differences in habitat selection. Different behaviors often require different habitat attributes, which are frequently spatially segregated, especially when the animal occupies a heterogenous range (Roever et al. 2014). For example, when foraging habitats are isolated, travel between patches of foraging habitat and foraging itself occur separately (Owen-Smith et al. 2010). Therefore, habitat selection studies should consider the consequences of the contrasting demands of different behavioral states. Roever et al. (2014) identified three potential drawbacks to pooling location data across behavioral states: 1) failing to detect selection especially when variables are not critical for all behavioral states, 2) underestimating the strength of selection, and 3) misidentifying the direction of selection. The growing use of telemetry data from animals fitted with satellite collars has contributed to the excessive use of pooled habitat selection models as not all collars are not typically capable recording behavioral state (Beyer et al. 2010). Development of state-space models that consider step-length, movement rate, and turn angles has allowed researchers to assign a behavioral state to a given location from collared animals (Morales et al. 2004, Beyer er al. 2013). However, when applied to animal movement these models are species- and potentially site-specific requiring local knowledge of the species' behavior. Often when behavioral differences are considered it is classified into active and inactive states. These broad behavioral states force researchers to group individual behavioral states together or use vague terminology that makes the animals actual behavior unclear. For example, in a study of black-tailed deer (*Odocoileus hemionus*) researchers grouped foraging and traveling which implicitly includes mastication and potentially digestion, then compared those sites to resting or inactive sites (Bose et al. 2018). State-space models were also used to label locations of African savanna elephants (*Loxodonta africana*) as either encamped or exploratory (Roever et al. 2014). While these labels may be appropriate for a specific species or study, they are far from universal.

Here we analyzed habitat selection of wood bison (*Bison bison athabascae*) divided into behavioral states based on observations in the field where behaviors are clearer than can be interpreted from satellite data alone. Wood bison are the larger, darker, and hairier subspecies of American bison (*B. bison*) that occupy the boreal forests and parklands of western Canada and

Alaska. Studies exploring bison habitat selection in the boreal have identified a strong selection for sedge-dominated wetlands in the winter (Larter and Gates 1991, DeMars et al. 2020, Thomas et al. 2021). These habitats offer the only high foliar biomass available in the herd's range during winter. However, as the vegetation emergences and matures during the growing season, patterns of habitat selection and forage use become more variable. Bison still use sedge-wetlands, but the magnitude of selection diminishes greatly (DeMars et al. 2020). During the growing season, some populations selected more opened treed areas, while others selected fluvial habitats or upland forests (Larter and Gates 1991, DeMars et al. 2020, Thomas et al. 2021). In regions where availability of preferred forages (i.e., graminoids) is low, bison will select roadsides and other anthropogenic clearings during summer to supplement their diets (Fortin et al. 2009, Thomas et al. 2021). Generally, bison select forage sites with intermediate levels of biomass and consume forage in a time minimizing fashion, potentially an adaptation to minimize predation risk (Bergman et al. 2001). Group size and individual sex both influence habitat selection in bison. Males tend to roam individually or in relatively small bachelor herds and occupy habitats with lower quality forage (Ranglack and du Toit 2015). Females mostly travel in mixed herds, including calves and immature males and females, occupying habitats with higher quality forage, but the strength of selection is dependent on herd size (Fortin et al. 2009, Ranglack and du Toit 2015). Variation in selection patterns among individuals does occur, but is not as strong during the growing season (Thomas et al. 2021). Despite this wealth of knowledge on habitat preferences in bison, especially while foraging, research on the differences between behavioral states that bison exhibit daily is lacking.

We assessed habitat selection of three distinct behavioral states that bison exhibit on a daily basis: foraging, traveling, and bedding/ruminating/wallowing (hereafter referred to as "bedding"). We used bison locations provided by collared females during the growing season to generate mixed-effects resources selection functions (RSFs) to assess selection of various habitat components within their range (Johnson 1980, Manly 2002). Our initial analysis assessed the importance of various structural forest components of their habitat. We then added nutritional components (i.e., crude protein and digestible energy) of forages and forage biomass to explore bottom-up effects influencing selection. We compared patterns of selection among behavior states and against all bison locations (i.e., not subset by behavior state). We predicted that variables within each behavioral state RSF would change both in their significance and direction of selection. In particular, variables representing structural forest elements of the habitat to be particularly important during travel and bedding as traveling will likely take the path of least resistance and bedding will require particular substrate conditions. Additionally, we predicted that nutritional components of the habitat would only be relevant in our foraging RSFs with bison selecting sites with foliar biomass particularly of plants that have higher concentrations of limiting nutrients (i.e., proteins) and offer more digestible energy. Our results will provide insight to consideration of behavioral state while modeling habitat selection and improve our knowledge of how bison use their range in boreal ecosystems.

Methods

Study system

Ronald Lake is at the center of the Ronald Lake wood bison herd's range. Natural geographic barriers border the herd's range to the east, west, and north; the Athabasca river to the east, the Birch mountains to the west, and Lake Claire and Lake Welstead to the north

(Figure 4.1). The herd's range extends from Wood Buffalo National Park through the most northern extent of land leased by the Canadian government to energy companies. Ground access to the study area is limited to the southeastern and central portions of the herd's ranges. The ground-accessible study area contains a representation of all landcover types described by Ducks Unlimited Enhanced Wetland Classification therefore building upon previous research examining selection of these landcover types by adding an on-the-ground microhabitat perspective while still representing all landcover types available to the herd (Ducks Unlimited Canada 2016). The most recent population estimates the Ronald lake herd to include 272 individuals (pers. comms. AEP 2021). This herd has been of particular conservation interest because it was determined that these bison are genetically distinct among Alberta bison (Ball et al. 2016) and are absent of diseases (i.e., bovine tuberculosis and brucellosis) that are present in nearby herds in Wood Buffalo National Park (Shury et al. 2016). In 2013, Alberta Environment and Parks began deploying GPS-collars on female bison within the Ronald Lake herd (Lotek Newmarket, Canada; Vectronics Berlin, Germany; Tellus Lindenberg, Sweden). To date, 69 female bison have been collared. These collars provide location data every 1.5-hours. We used location data between May and August (i.e., growing season) from 2018 – 2020 during the period that overlapped with field visits of bison locations. Locations were screened by first eliminating all locations with a dilution of precision greater than five (Lewis et al. 2007) and then removing locations outside the feasible range of bison movement within a 90-min interval (>10-km; Bjørneraas et al. 2010, DeMars et al. 2020).

Field data collection

We visited bison (i.e., use) locations that were randomly selected from a subset of locations within the area ranging from Ronald Lake in the north to southern extent of their spring/summer range where bison activity was high and the study area more accessible by ground travel. Available locations were randomly generated in ArcGIS 10.3.1 (ESRI 2015) in the same area as where bison locations before entering the field. A smaller sample ($n = 18$) of more remote bison locations were visited using helicopter travel for one day in the summer of 2019. At each site we collected measurements of the structural forest environment, samples of potential forage, and at bison locations signs of behavior. After arriving at the coordinate provided by the GPS-collar we would search the area for signs of bison presence (i.e., fur, tracks, feces, wallows). We began our sampling at the sign of bison presence nearest to the provided coordinate to account for spatial errors associated with GPS-collars. At each site we took a new waypoint using waypoint averaging of a handheld GPS (Garmin, GPSmap 64s) with at least 100 waypoints taken at the location. Bison locations were visited between five and ten days after bison presence to minimize disturbance to bison (<5 days), yet still ensure accurate interpretation of behavior and similar forage conditions.

At every bison and available location, we established a 30-m x 2-m belt transect centered on the location and three 0.25-m^2 quadrats every 10-m along the belt transect. Along the belt transect we counted the number of trees (>2.5-cm DBH), saplings (≤ 2.5-cm DBH), and coarse (>2.5-cm) woody debris (CWD) to measure the density of the physical obstructions at the location. The three quadrats were placed at the 5-m, 15-m (i.e., bison/available location), and 25-m points along the transect. Within each quadrat, we visually estimated the percent cover of each plant species from ground level to 2-m above ground level to the nearest 10% cover unless the species accounted for less than 10% in which case it was estimated to the nearest 1% (Gautam et al. 2017). After making visual estimates, the foliar portions all of plant species within the quadrat were clipped to be dried and weighed in lab to quantify dry biomass. We shipped the most frequently foraged species (Hecker et al 2021b) to Nutrilytical (Calgary, Canada) for chemical analysis of nutritional content. Crude protein was calculated for each foraged species using methods standardized by the Association of Official Agricultural Chemists (AOCS 1998), and digestible energy (measured as total digestible nutrients) was calculated following the procedures of the National Research Council (NRC 2001). Additionally, at the center of each quadrat we measured canopy cover, slope, aspect, soil moisture, and recorded the dominant substrate type. Using ArcGIS 10.3.1 (ESRI 2015), we calculated Euclidean distance to the nearest body of water, seismic line (a narrow linear disturbance used for oil sands exploration), and wetland classified as either a "marsh meadow," "emergent marsh," or "graminoid-rich fen" (hereafter referred to as graminoid-dominated wetlands) by Ducks Unlimited enhanced wetland classification (Ducks Unlimited Canada 2016). These landcover types were shown to be regularly selected by females in the Ronald Lake throughout the year (DeMars et al. 2020)

Additionally, at each bison location we surveyed the immediate area (within a 15-m radius of the location) for signs of three different behaviors: foraging, traveling, and bedding. Foraging sites had at least 50% of the individual plants showing signs of being recently consumed. Traveling sites contained game trails and/or tracks and may contain individual plants that show signs of foraging, but less than 50%. Bedding/wallowing sites contained areas of depressed vegetation (ideally with fur sheds) or exposed soils with that were recently disturbed and may contain individual plants that show signs of foraging but less than 50%. We did not sample any site that had sign of moose or deer (tracks, fur, or feces) to avoid attributing the behaviors of other ungulates to bison (n = 11). These three behaviors would be used to subset the bison data for analyses of behavior-based habitat selection.

Statistical modeling

We used resource selection functions (RSFs) to assess the bottom-up influences on female habitat selection of bison across behavioral states during the growing season. These functions use logistic regression to compare locations used by bison (1) to random, available locations (0) within the herds range (Johnson 1980, Manly et al. 2002). Exploratory models were created to determine which structural forest features had the greatest relationship to habitat selection regardless of behavior state. In these models, we tested for multicollinearity amongst predictors, removing the least ecologically significant predictors when variance inflation factors (VIF) were ≥3 (Zuur et al. 2010). This resulted in a base model that included six structural forest predictors: percent soil moisture, CWD density, sapling density, and percent canopy cover.

Next, we added forage quality and quantity. Our clipped, dried, and weighed vegetation samples were used to quantify site biomass. To quantify site-level crude protein and digestible energy, we first calculated the percent biomass each species consumed by bison contributed to the total biomass at the site. Then, we multiplied the percent biomass by the percent crude protein and digestible energy values for the species. Finally, we calculated the sum of all these weighted crude protein and digestible energy values and used these as predictors in our RSFs.

To quantify habitat selection by states, we subset our bison location data by our three behavior states for modeling and created an RSF with all the bison locations (“All”). We used the same seven variables in each of these four RSFs: percent soil moisture, percent canopy cover, CWD density, sapling density, foliar biomass, percent crude protein, and percent digestible energy. To assess model fit, we used variance explained by using McFadden's R^2 (McFadden 1987), although for binary data lower fit values are typical. We reported beta coefficients, standard errors, and effect sizes for each predictor and compared these statistics between behavior states.

Finally, we ran one-way ANOVAs on each of our seven variables on just the bison locations to test for significant differences in the variables between behavioral states (Ramsey and Schafer 2002). We then conducted *post-hoc* Tukey's honestly significant difference (HSD) tests to determine which behavioral states were significantly different from one another (Tukey 1949). All analyses were conducted in R version 3.6.1 (R Core Team 2019).

Results

We visited 480 bison and available locations. Of these, 251 were available locations and 229 were recent bison locations. Of the bison locations, 52 were foraging sites (23%), 132 were traveling sites (58%), and 45 were bedding sites (20%). The same random locations were used in all four of the models.

The behavioral habitat selection models revealed differences in nutritional and structural forest characteristics of the habitats wood bison use. When not subset by behavior, bison avoided habitats with more CWD, saplings, and foliar biomass of all plants and wetter soils (Table 4.1). For example, a 1% increase in canopy cover or soil moisture resulted in a 1% decrease in the probability of a bison selecting that habitat, while every additional piece of CWD and sapling caused an 8% and 1% decrease in selection, respectively (Figure 4.2). While forage biomass was found to be significantly avoided but, the effect size was negligible (<1%). Neither crude protein or digestible energy content of the vegetation was found to have a significant effect on selection.

At foraging sites, bison selected habitats with significantly less CWD and saplings, and vegetation with significantly more crude protein. We also found more digestible energy had a marginally significant effect on habitat selection (Table 4.1). Again, every additional piece of CWD reduced probability of selection by 8% and every additional sapling reduced selection by 1%. However, a 1% increase in crude protein content resulted in a 3% increase in selection and a 1% increase in digestible energy caused a 1% increase in selection (Figure 4.2). Percent canopy cover, soil moisture, and total biomass did not significantly affect the selection of foraging sites.

While traveling, bison selected habitats with significantly less canopy cover, drier soils, less CWD and saplings, and vegetation with more crude protein but less digestible energy. Foliar biomass of foraged plants was not found to have a significant effect on habitat selection while traveling (Table 4.1). Increasing canopy cover by 1% reduced selection by 1% and increasing soil moisture by 1% reduced selection by 3%. Further, each additional piece of CWD reduced selection by 3% and each additional sapling reduced selection probability by 1%. Crude protein and digestible energy content in vegetation were significant for traveling locations, but their effect sizes were <1% (Figure 4.2).

And finally, at bedding sites we found selection for sites with significantly less soil moisture, CWD, and saplings. Increases in all foliar biomass caused marginally significant decreases in habitat selection. Canopy cover, crude protein, and digestible energy content in vegetation did not significantly affect bedding site selection (Table 4.1). A 1% increase in soil moisture corresponded with a 2% decrease in selection. The addition of a single piece of CWD caused an 11% decrease in selection, while every additional sapling resulted in a 1% decrease in selection. Foliar biomass of all plants had a marginally significant negative effect on habitat selection, but the effect size was negligible (Figure 4.2).

Our assessment of differences within the seven variables used in the RSFs between behavior states revealed significant differences in six of the variables (Figure 4.3). Foraging sites had significantly less canopy cover (χ^2 = 33.77, p-value < 0.01), wetter soils (χ^2 = 66.66, p-value < 0.01), and significantly more foliar biomass (χ^2 = 6.78, p-value = 0.03) than traveling or bedding sites. Traveling sites had significantly more CWD than foraging or bedding sites (χ^2 = 22.44, p-value < 0.01) and significantly more saplings (χ^2 = 6.24, p-value = 0.04). The vegetation at bedding locations had significantly less crude protein than foraging or traveling locations (χ^2 = 9.46, p-value = 0.01). Percent digestible energy content in vegetation was the same for all behavioral states (χ^2 = 0.03, p-value = 0.98).

Discussion

We found support for the prediction that behavioral states have different patterns in habitat selection of the Ronald Lake wood bison herd. Therefore, assessing habitat selection by behavioral state provides additional insight into the factors known to influence variation in habitat selection furthering our knowledge of the species preferences. This research contributes to the growing body of evidence that ignoring behavioral state can have significant consequences when attempting to quantify habitat selection (Munro et al. 2006, Roever et al. 2014, Bose et al. 2018). Either the direction of selection or significance for five of our seven variables changed between behavioral states and/or the full model. Our full model did provide insight into the influence of structural forest characteristics on bison habitat selection, but failed to identify nutritional components known to influence habitat selection in bison. This is perhaps not unsurprising given that use of all telemetry locations that include movement and bedding is going to attenuate forage-base relationships to habitat selection that may be considered more insightful for understanding resource limitation since opportunities for bedding and movement are often less limiting (Nielsen et al. 2010). These outcomes also exemplify fine-scale trade-offs between nutritional requirements and energy expenditure made by ungulates living on heterogeneous landscapes (Fortin et al. 2003). These results therefore provide additional support for behavioral state applications of RSFs, but also important knowledge on the ecology of bison in boreal forests.

Understanding that behavioral state influences environmental variable selection is important to consider in studies of habitat selection, but understanding how these variables change is also vital to wood bison ecology, management, and conservation. The only variables that remained constant across all behavior states and the full model of all behaviors were the density of CWD and saplings where bison always showed avoidance of these structural forest variables and thus selecting for more open habitats and forest understory. There are advantages of open habitats for all three behaviors we explored. First, sedges including *Carex atherodes*, *C. utriculate*, and *C. aquatilis* are exclusively found in wetlands such as meadow marshes, emergent marshes, and graminoid rich fens (Strong and Gates 2009). In the early part of the growing season (May and June), these plants dominate the diets of the Ronald Lake herd (Hecker et al. 2021b). The habitats that these plants are found are void of trees as exemplified by foraging sites having lower canopy cover than bedding or travel locations. The lack of trees results in little to no CWD being present. The only saplings present in these habitats are clusters of willows (*Salix* spp.) that tend to be patchily distributed throughout the wetlands. Both of CWD and saplings represent physical obstructions to movement. Additionally, traveling habitats were the only sites that had significantly less canopy cover (i.e., lower tree density). Open habitats can reduce the energetic costs of movement and can increase rate of movement. When moving through logging slash, energetic expenditure of elk (*Cervus canadensis*) and mule deer (*O. hemoinus*) increased as a function of obstacle density and height (Parker et al. 194). The Ronald Lake wood bison were shown to increase their movement rates when traveling on seismic lines (i.e., linear openings through the landscape created during oil exploration), which initially remove all physical obstructions and remain relatively open for potentially decades (Lee and Boutin 2006, DeMars et al. 2020). One factor that correlated with higher densities of CWD and saplings in boreal forests is forest fires (Filicetti et al. 2021). In 2011, the Richardson fire burned over 1.5 million acres including roughly 400,000-acres along the eastern edge of the Ronald Lake herd's range increasing understory structure with pine regeneration (Filicetti & Nielsen, 2018). Therefore, our results could be interpreted as the bison avoiding habitats burned during this fire. This relationship is in stark contrast to plains bison in grasslands which are commonly observed selecting recently burned patches for intensive grazing, particularly within two years of the fire (Biondini et al. 1998, Wallace and Crosthwaite 2005, Schuler et al. 2006, Allred et al., 2011). The increased costs of mobility due to high CWD and sapling densities in burned boreal forests likely outweigh the benefits provided by the high-quality forage post-burn. Additionally, open habitats provide greater visibility of potential predators such as wolves (*Canis lupus*) and black bears (*Ursus americanus*). Early predator detection is critical for establishing defensive behaviors during all three behaviors, but in particular while foraging and ruminating (Carbyn and Trottier 1988). When foraging bison in wetlands used by wolves they sacrifice consuming more high-quality vegetation to be more vigilant (Harvey and Fortin 2013). While ruminating, most individuals will be lying down reducing their ability to be vigilant, which emphasizes the need to occupy habitats that are open during this behavior. Further, large open habitats allow many bison to bed and ruminate in close proximity to each other providing a passive defense against predators. Our results support this idea as there were significantly less saplings and CWD at bedding sites than travel locations. In addition to predator detection, bison need open locations at bedding to create wallows. Plains bison also select less vegetated habitats for wallowing in tallgrass prairies (McMillan et al. 2011). An alternative to bison selecting open habitats is that intensive and repeated foraging by bison on shrubs and saplings could be reducing their density creating open habitats. Shrub biomass has been shown to be reduced after bison reintroduction (Wilkins et al. 2019). However, this alternative hypothesis would not explain the avoidance of CWD.

We found that soil moisture had a significant effect on habitat selection for all behaviors, but the direction of that selection was behavior dependent. While traveling and bedding bison avoided wetter soils, but while foraging they selected habitats with wetter soils. These results support the work of Belanger et al. (2020) who used structural equation models to show wood bison select foraging habitats with more sedges, but worse footing and more biting insects. To access the sedges, wood bison enter wetlands thus sacrificing footing (i.e., wetter soils) for access to forages high in digestible energy (Fortin 2002, Belanger et al. 2020). Likewise, we found foraging sites had significantly higher soil moisture than traveling or bedding sites. Wetter soils increase the energetic costs of movement in mammals (Karasov 1992). Therefore, the wood bison selected upland habitats while traveling. A quintessential example of this is the repeated use of a large esker (an elevated ridge created by deposits from meltwater of retreating glaciers) as a travel corridor in the middle of the herd’s range south of Ronald Lake. Bedding and wallowing sites were located in drier soils likely for a few reasons. These upland habitats tend to have lower densities of biting insects (Belanger et al. 2020). By selecting these habitats, bison are reducing the level of insect harassment they experience, a behavior that has been observed in other northern ungulates such as caribou (*Rangifer tarandus*) and moose (*Alces Alces*) (Renecker and Hudson 1990, Skarin et al. 2004, Benedict and Barboza 2022). Drier soils tend to be correlated with sandier soils, which have been shown to be selected by bison for wallows (Polley and Collins 1984). These coarse, dry soils would also increase abrasiveness making them more efficient at reducing skin irritation and help shed fur, which is thought to be the main functions of wallowing behavior, although other reasons such as improved digestion are also potential motivators for wallowing (Coppedge and Shaw 2000).

The quality of vegetation had an impact on habitat selection when bison were foraging and traveling and the quantity of vegetation influenced bedding site selection. These results confirm our hypothesis that nutritional variables should have a positive impact of habitat selection. Sites with plants that had greater amounts of crude protein and digestible were selected for foraging. There was also significantly more foliar biomass at foraging sites than traveling or bedding sites. The primary source of energy for bison in the boreal are wetland sedges and bison are known to forage in a time minimizing fashion while in these wetlands (Bergman et al. 2001). These sedges grow in dense patches in habitats, which explains the greater amount of foliar biomass at foraging sites. Sedges contain high levels of digestible fiber components like hemicellulose providing more energy to the consumer (Codron et al. 2007, Hecker et al. 2021b). We build upon this knowledge by showing that bison select specific wetlands with sedges that contain more crude protein and digestible energy. Protein is a limiting nutrient in the diet of ungulates and these sedges have less protein available in them than forbs or woody plants (Craine et al. 2015, Hecker et al. 2021a). Therefore, we interpret our result showing that traveling sites had more crude protein as bison supplement their graminoid- and carbohydrate-dominated diet. We observed signs of foraging on shrubs and forbs at 95 of our 134 (71%)

traveling locations. These results suggest that while bison intensively forage in sedge dominated wetlands, they also forage on the relatively protein-dense and easily digestible leaves of shrubs and forbs. While the break-down of the thick cell walls of graminoids requires long rumination periods (Plumb and Dodd 1993), these plants can be consumed while traveling in smaller amounts without requiring the individual to stop to ruminate. Further, shrubs such as prickly rose (*Rosa acicularis*) and currants (*Ribes* spp.), and forbs like fireweed (*Chamaenerion angustifolium*), make significant contributions to the diet of the Ronald Lake bison (Hecker et al. 2021b). These plants occur in the upland habitats we have shown the bison use for travelling and are likely driving the selection of crude protein during travel. The act of foraging initiates plant regeneration and fresh plant material has higher concentrations of crude protein (Bergmann et al. 2015; Geremia et al. 2019). Therefore, vegetation with more crude protein at traveling sites could reflect this regeneration after bison foraging. We attempted to control for this by only clipping vegetation that did not show signs of foraging. During bedding we also showed selection for upland habitats, but in this case, bison avoided vegetation all together. Again, these results suggest that bison are selecting open habitats for the reasons previously discussed.

We acknowledge that behavioral state is not the only factor that influences an animal's habitat selection and subsequent resources use. Temporal variation in habitat selection occurs over years as population demographics and climatic conditions change, seasonally in accordance with changing environmental conditions, or within a single day based on the animals circadian rhythms (Monteith et al. 2001, Fryxell et al. 2008, McMillan et al. 2021). The physiological state (e.g., pregnant vs not or diseased vs healthy), age, and sex can all have a significantly influence on habitat selection (Keech et al. 2000, Robertson and Hamilton 2012, Rossman et al. 2015, Ranglack and du Toit 2015). We controlled for these confounding factors by examining habitat selection during the growing season and only using location data from mature females in mixed (including calves, juveniles cows and bulls, and both lactating and non-lactating cows) herds. We also did not consider top-down mechanisms influencing habitat selection. Wolves and black bears pose as potential predators to the Ronald Lake wood bison. However, the only recorded successful predation events in the study area occurred in late winter (March) by wolves. During the growing season the wolves switch to a diet of smaller game primarily beavers (*Castor canadensis*) and waterfowl (Rawleigh et al. 2021).

Studies of animal habitat selection typically aim to quantify the influence of bottom-up and top-down mechanisms or predict changes in habitat use as a result of upcoming phenomena (e.g., climate change), landscape disturbances, management techniques, or changing or novel distributions. However, failing to incorporate behavioral states leads to conclusions that describe common patterns, but overlook important differences in the factors influencing habitat selection that are behaviorally driven. Further, our field-based approach allows for finer sub-setting of behavioral states that is unattainable using methods based on telemetry data. By incorporating behavioral state into our habitat selection study, we were able to highlight the importance of both structural forbs and nutritional aspects of the habitat to selection by bison. We also were able to show how these habitat components changed in their influence based on the animal's behavioral state. We encourage the incorporation of behavioral states into habitat selection studies. This consideration will be particularly important for studies related to conservation planning for species to ensure that managers have the more robust understanding of the species habitat use as possible.

Tables

Table 4.1: Results of the resource selection functions for each behavioral state and all bison locations pooled together. Here, we coefficients (ß), standard errors (SE), and p-values for each variable in each model, and pseudo R^2 values for each model. The same seven variables were used in each model: percent canopy cover, percent soil moisture, coarse (>2.5-cm) woody debris density, sapling density, percent crude protein (CP), percent digestible energy (DE), and foliar biomass of plants within the 30x30-m plot. Variables with an * next to their p-value are considered significant within the model and those with a ^ are considered marginally significant.

Behavior state	Variable	ß	SE	p-value	Pseudo R^2
Full	% canopy cover	-0.012	0.005	0.010*	0.15
	% soil moisture	-0.014	0.004	<0.001*	
	CWD density	-0.089	0.012	<0.001*	
	Sapling density	-0.009	0.002	<0.001*	
	% CP	0.076	0.071	0.285	
	% DE	0.003	0.020	0.872	
	Foliar biomass (kg)	-0.001	0.001	0.016*	
Foraging	% canopy cover	-0.012	0.012	0.285	0.17
	% soil moisture	-0.006	0.006	0.294	
	CWD density	-0.087	0.036	0.016*	
	Sapling density	-0.006	0.004	0.114	
	% CP	0.279	0.127	0.028*	
	% DE	0.052	0.030	0.090^	
	Foliar biomass (kg)	-0.001	0.001	0.417	
Traveling	% canopy cover	-0.012	0.005	0.010*	0.15
	% soil moisture	-0.005	0.005	<0.001*	
	CWD density	-0.012	0.012	0.030*	
	Sapling density	-0.008	0.003	0.004*	
	% CP	0.003	0.001	0.001*	
	% DE	-0.001	0.001	0.001*	
	Foliar biomass (kg)	-0.001	0.001	0.108	
Bedding	% canopy cover	-0.003	0.008	0.712	0.22
	% soil moisture	-0.029	0.007	0.001*	
	CWD density	-0.118	0.034	<0.001*	
	Sapling density	-0.012	0.005	0.013*	
	% CP	0.001	0.001	0.299	
	% DE	-0.001	0.001	0.395	
	Foliar biomass (kg)	-0.001	0.001	0.084^	

Figures

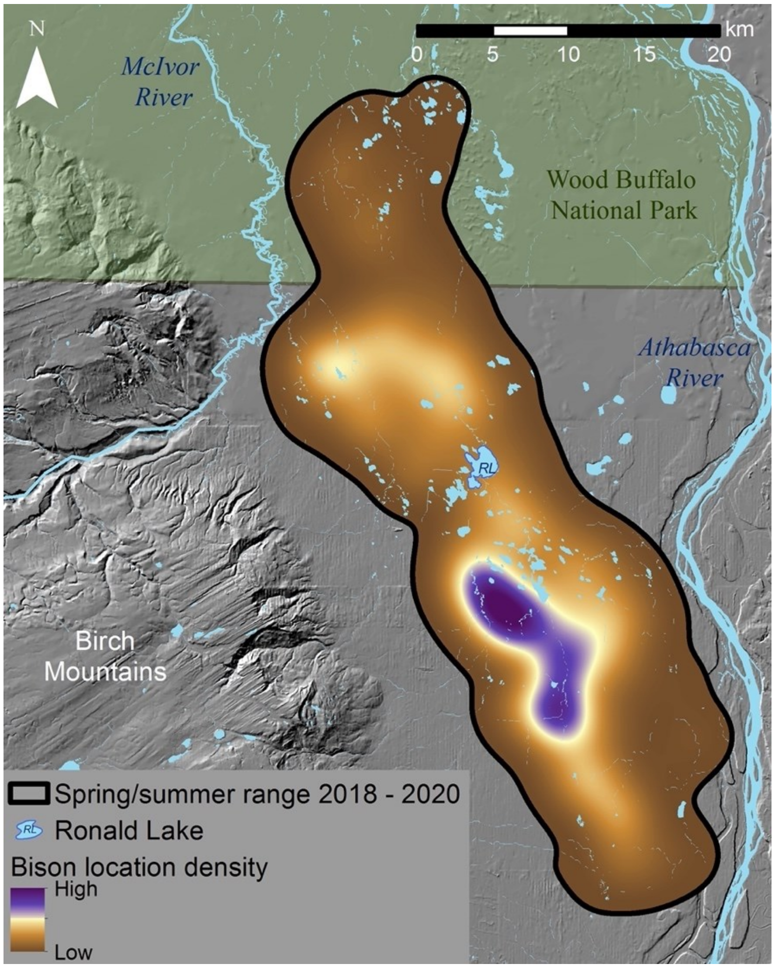

Figure 4.1: The home range of the Ronald Lake wood bison (*Bison bison athabascae*) calculated as a 99% utilization distribution using all available bison locations. The portion of that range that is accessible via a series of seismic lines and trapper's trails is outlines in white.

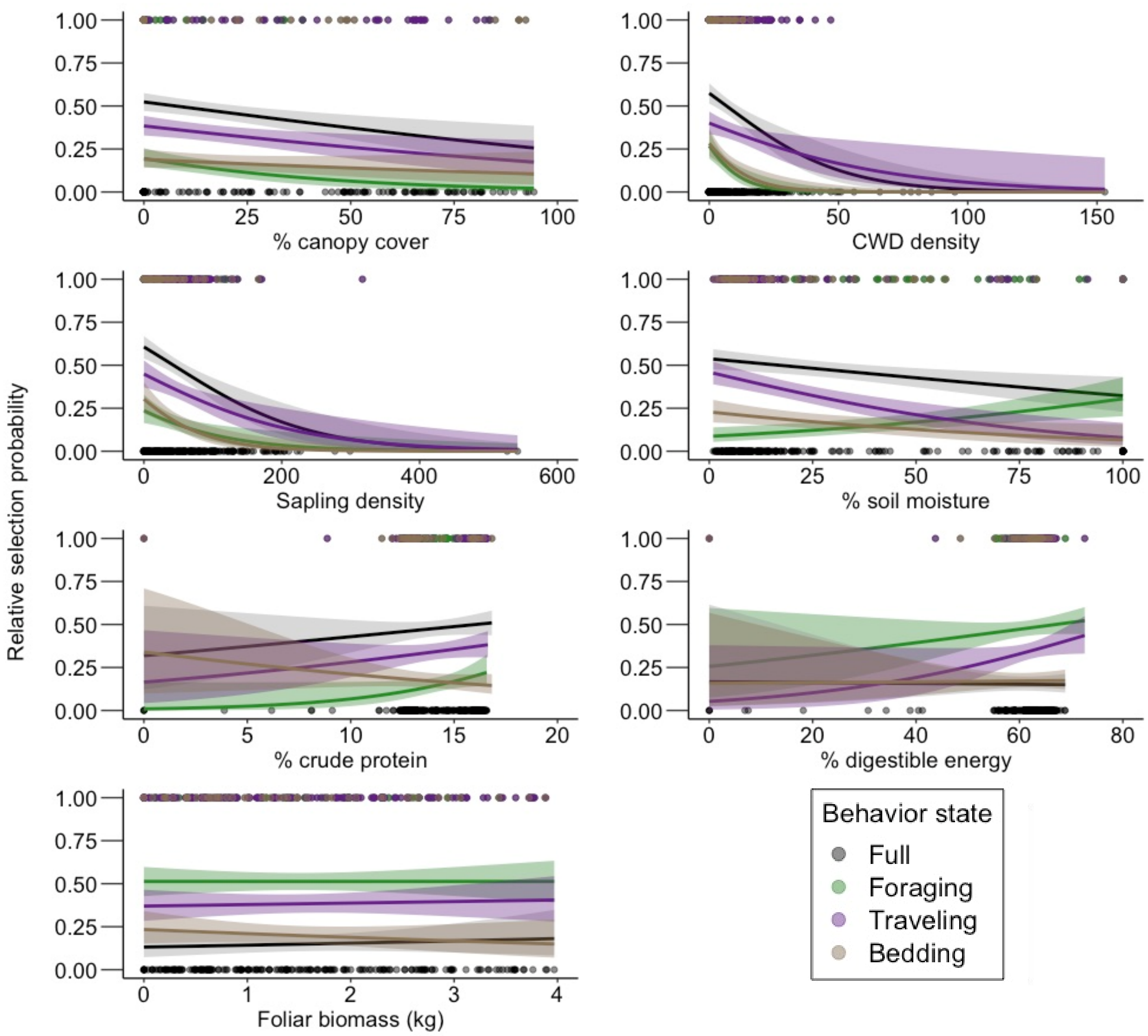

Figure 4.2: Response curves for each predictor used in the resource selection functions. The color of each line or point denotes the behavior state. Coarse (>2.5cm diameter) woody debris (CWD) and sapling densities are counts of those features along a 2x30-m belt transect centered on the bison or random location.

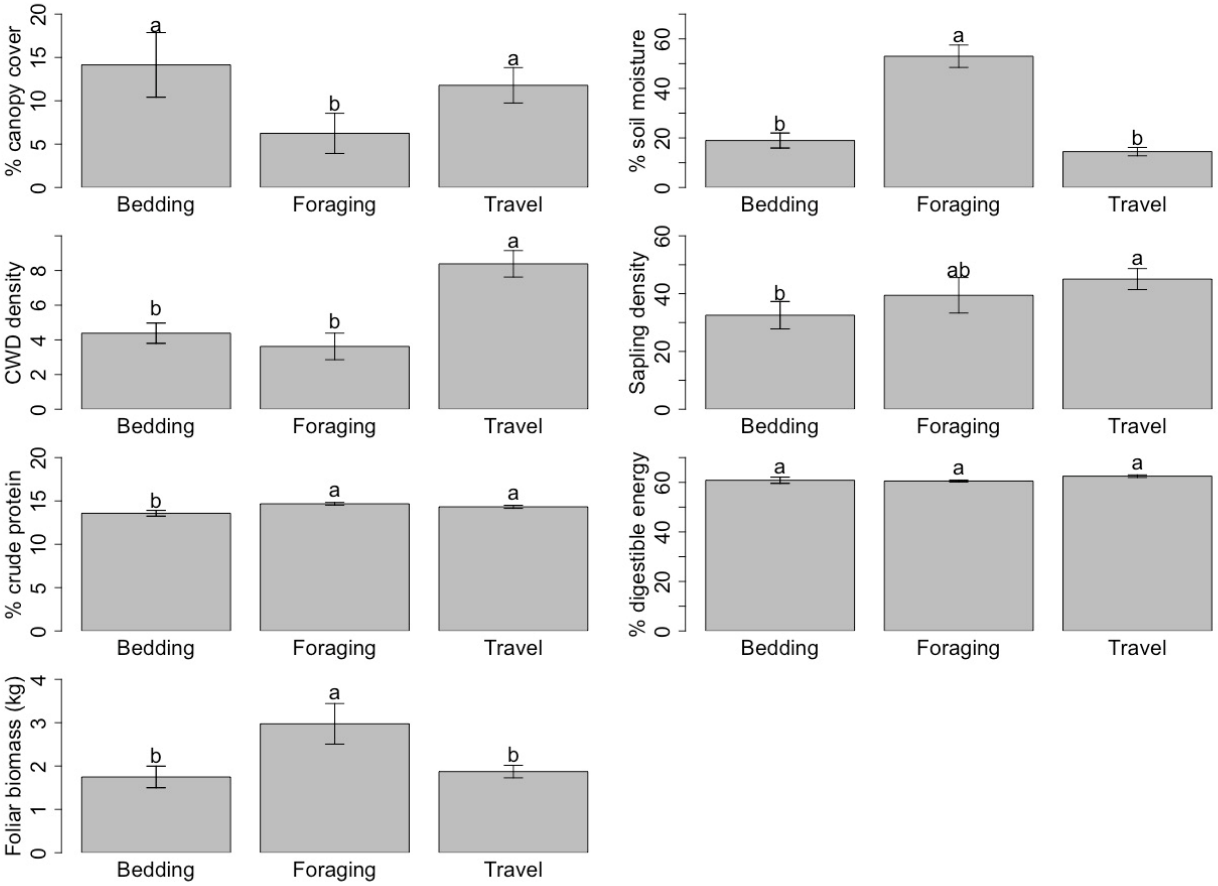

Figure 4.3: Results of post-hoc Tukey's honestly significant difference (HSD) test for the seven predictors used in resource selection functions for each behavior state. These tests were used on data from bison locations only. The letters above each bar denote significant differences between behavior states. Bars labeled with different letters indicate significant differences between behavioral states.

Chapter 5: Migration leads to nursery herd formation in a wild wood bison (*Bison bison athabascae*) population

Abstract

Migration is an evolutionarily stable adaptation when the costs of movement are outweighed by fitness gains. Migration is defined as the predictable movement between seasonal ranges in response to differential resource availability. However, migrations to locate suitable mates, calving or nursery grounds are also common across taxa. For ungulates, the growth of new vegetation has been identified as a key mechanism influencing migration between seasonal ranges. We investigated how the green-wave influenced migration to calving/nursery sites in a wood bison (*Bison bison athabascae*) population in northern Alberta, Canada, while also considering risk of calf predation by wolves (*Canis lupus*). Each year, all females of the herd migrated an average of 28-kilometers over 6-days to a region at the western edge of their annual range between late-May and early-June individually. By late-June they migrated back to their core range as a large group, averaging a 40-kilometer migration distance over 10-days. We found that the green-wave influenced both the timing of migration and selection of habitats during migration. Risk of predation did not influence selection during migration. However, the herd congregating and leaving their spring range as a group suggests risk of predation may be an evolutionary mechanism contributing to this migratory behavior. Our research demonstrates an annual migration in the boreal forest by wood bison to nursery sites that is closely tied to the green-wave. We provide a framework to assess interrelated mechanisms influencing migration, the understanding of which is critical to those studying, managing, and/or conserving migratory ungulates.

Introduction

Migration is the predictable, seasonal movement of individuals or populations between distinct ranges often in response to changes in environmental conditions (Hansson and Åkesson, 2014). This behavior is evolutionarily adaptive when the seasonal occupation of a different ranges provides fitness benefits that outweigh the costs of movement (Alerstam et al., 2003, Avgar et al., 2014). Potential fitness benefits include acquisition of higher quality food (Middleton et al., 2018), predator and parasite avoidance (Hebblewhite and Merri,ll 2007; Mysterud et al., 2016), and access to mates (Wallace and Diller, 2001). Within species and populations, migration strategies of individuals vary with corresponding fitness consequences (Bêty et al., 2004; Bunnefeld et al., 2011; Bischof et al., 2012). For example, migratory red deer (*Cervus elaphus*) in Norway had lower parasite (i.e., tick) loads than resident (i.e., non-migratory) individuals (Mysterud et al., 2016). Similarly, migratory elk (*Cervus canadensis*) in Alberta, Canada had lower probability of wolf (*Canis lupus*) predation than resident individuals (Hebblewhite and Merrill, 2007). Mule deer (*Odocoileus hemionus*) in Wyoming, USA tracked the green-up of vegetation (i.e., green-wave) along an altitudinal gradient giving them access to better quality forage (Aikens et al., 2017). Understanding the factors governing migration behavior in individuals and populations is important for the management and conservation of wildlife. This knowledge is especially important now as urbanization and natural resource extraction fragment migration corridors and alter habitat within migratory ranges (Gaillard et al., 2000; Kauffman et al., 2021).

Advancements in GPS-tracking and remote sensing technologies provide unobtrusive tools to explore mechanisms motivating migration behavior. For herbivores, emphasis has been placed on the green-wave and forage-maturation hypotheses, which state animals should select habitats at the peak green-up of vegetation in spring as these plants are at an ideal (i.e., lots of digestible energy and protein without too much undigestible fiber), intermediate phenological state (Fryxell, 1991; van der Graaf et al. 2006). The integration of these two hypotheses has been used to explain the timing of and habitat selection during migration for terrestrial ungulates (Bischof et al. 2012; Merkle et al., 2016; Aikens et al. 2017), birds (Bêty et al., 2004; van der Graaf et al. 2006), and marine fauna (Lok et al., 2012; Abrahms et al., 2019). In some cases, animals "surf" the peak of the green-wave while migrating (Merkle et al., 2016; Middleton et al., 2018), while in other instances individuals jump ahead of the green-wave (Bischof et al., 2012). Evidence from ungulates translocated to novel ranges suggests that surfing the green-wave is a learned process. Translocated moose (*Alces alces*) and bighorn sheep (*Ovis canadensis*) populations improved their ability to track the green-wave over time suggesting that social learning through the inter-generational, cultural transmission of knowledge may be taking place (Jesmer et al., 2018). Correlations between resource quality and migration offer valuable insight to the migration decisions of ungulates, but do not address other ecological mechanisms potentially influencing migration.

For many ungulate species, migrations terminate at calving grounds (Estes, 1976; Schaller et al., 2006; Kerby et al., 2013; Cameron et al., 2020). At high latitudes, calving is often synchronized within populations (Post et al., 2001). Synchronized births typically occur when local vegetation is greening-up in spring, and migrations to calving sites with higher quality vegetation are common (Post et al., 2001; English et al., 2012). Female ungulates will isolate themselves for hours, days or weeks around the time of parturition (Rearden et al., 2011, Kelley et al., 2015, Karsh et al., 2016). After parturition, females rejoin conspecifics often forming nursery herds with other females and their neonates. Because of these behaviors, methods traditionally used to identify calving sites actually identify nursey grounds due to biases in observations (Karsh et al., 2016). Given that annual calf survival rate is among the most important statistics for evaluating population sustainability, knowledge of the mechanisms that regulate habitat selection during calving and migration to and from calving sites is a priority for those managing migratory ungulates (Haddad et al., 2015). Hunting, natural resource extraction and exploration, and agricultural lands have all been shown to influence the habitat selection of ungulates during migration and use of calving sites (Singh et al., 2010; Fullman et al., 2017; Paton et al., 2017). Movement rates are at their lowest during and immediately following parturition, then remaining lower than pre-parturition rates for weeks following (Rutberg, 1984; DeMars et al., 2013; Cameron et al., 2020; Walker et al., 2021). Ungulates are expected to select habitats with less predator activity and with higher quality forage after parturition (Carbyn and Trottier, 1987; Cameron et al., 2020).

We investigated the migratory behavior of a wood bison (*Bison bison athabascae*) population to assess the relationship between reproductive behavior, migration, and habitat selection. American bison (*B. bison*), of which wood bison are the northern subspecies (the southern being plains bison; *B. b. bison*) are well documented migrators according to both written and oral history (Cunfer and Waiser, 2016). Modern bison populations respond differently with respect to tracking the green-wave during migration; some do not track the green-wave, some surf the peak of the green-wave (Merkle et al., 2016), and some forage so intensively along their migration corridors that they manipulate how the green-wave propagates across the landscape (Geremia et al., 2019). Birth synchrony and congregation on calving grounds have also been described in bison, particularly in northern populations (Rutberg, 1984; Carbyn and Trottier, 1987; Gogan et al., 2005; Kaze et al., 2016). Parturition is typically synchronized during a 3–4 week period between April and June, but early and late births have been documented (Berger and Cunningham, 1994; Jung et al., 2018). Parturition sites are selected to provide concealment as an anti-predatory defense (Rutberg, 1984). On open ranges, females congregate and conspecifics provide concealment, whereas in forested habitats individuals will break off from herds giving birth in dense shrub cover (Lott and Galland 1985). While migrations are likely to occur in wood bison, as it is a strategy utilized by both plains bison and extinct bison species (Plumb et al., 2009; Funck, 2020), studies explicitly investigating the mechanisms influencing migration for wood bison are lacking.

The Ronald Lake wood bison population of northern Alberta is known through oral history and data provided by GPS-collars to undergo a unique migration. Each spring, every female in population migrates from across their annual range and congregate in a distinct region at the western edge of their annual range. The migration in unique in that, the bison remain there for a few weeks before migrating out of this region and dispersing across their annual range. It is believed that this behavior is a migration to a calving range. Here we seek to understand if the same mechanisms that govern migrations between summer and winter ranges apply to migrations that terminate in what are believed to be calving or nursery sites. First, we mapped the population's migration. Then, we used migrations metrics (distance traveled, travel speed, and duration of migration) and observations of bison traveling along migration corridors to determine if this migration terminated at calving or nursery grounds. Next, we tested the green-wave hypothesis by investigating how the timing of migration and the habitat selection during migration related to the phenology of the plants during the green-wave. Finally, we also tested the alternative, non-mutually exclusive hypothesis that predation pressure influences migration

(Table 1). Our results will provide insight into the migratory behavior of ungulates as it relates to changing environmental conditions, risk of predation, and human disturbance.

Methods

Study area

The Ronald Lake wood bison population consists of approximately 272 individuals in the boreal forests of northeastern Alberta (Alberta Environment and Parks, personal communication). The population is of conservation significance due to its importance to the traditional practices of regional Indigenous communities, their lack of disease (i.e., brucellosis and bovine tuberculosis) that is prevalent in the neighboring Wood Buffalo National Park (WBNP) populations (Shury et al., 2015), and they are genetically differentiated from other Alberta herd's with less plains bison introgression (Ball et al., 2016). Their range stretches from the southeast corner of WBNP into the northern fringes of Alberta's oil-sands region with the Birch Mountains and Athabasca River forming the western and eastern boarders, respectively (Figure 1). The herd's range is relatively flat with elevation varying from 240-m to 300-m. Upland habitats in the range are primarily deciduous forests dominated by quaking aspen (*Populus tremuloides*) intermixed with coniferous stands of primarily jack pine (*Pinus banksiana*). Intermixed with uplands stands is a mosaic of bogs, swamps, fens, and marshes with bison showing a strong preferences for sedge-dominated rich-fens and marshes (Duck's Unlimited Canada, 2016; DeMars et al., 2020). Anthropogenic disturbances from oil-exploration including well-pads and seismic lines, which are clear-cut corridors used for mapping underground petroleum reserves, are prevalent throughout the herd's range (DeMars et al., 2020).

Between 2013 and 2019, 58 females were fitted with Global Positioning System (GPS) collars by Alberta Environment and Parks at a 1.5-hr fix-rate for various lengths of time (n = 38 Lotek Newmarket, Canada; 10 Vectronics Berlin, Germany; 10 Tellus Lindenberg, Sweden). We observed an annual spring migration by all females (i.e., complete migration; Avgar et al., 2014) in May or early-June to a distinct region near where the McIvor River exits the Birch Mountains (hereafter referred to as the "spring range"; Figure 1). The spring range is primarily composed of deciduous forests, but also contains a large upland meadow complex approximately 2.0-km by 0.5-km and some bald slopes of the Birch Mountains. The upland meadow is composed of dense shrub cover, primarily wild rose (*Rosa acicularis*) and raspberry (*Rubus occidentalis*) with patches of grasses scattered throughout. The upland meadow is a unique feature in the herd's range as all other forest openings observed are wetlands. We estimated the spring range by generating a 99% utilization distribution (UD) using a subset of individual locations starting when they first arrive at the upland meadow and concluding when they begin their migration east (Figure 1). We used the "adehabitatHR" package in program R to estimate 99% UDs using a bivariate normal kernel (Benhamou and Cornélis, 2010; R Core Team, 2019).

Migration metrics and corridors

We excluded locations from first two-weeks after collaring to avoid the effects of capture-related behavioral alterations (Morellet et al., 2007) and those with low accuracy (dilution of precision > 5; Lewis et al., 2007; Bjørneraas et al., 2010). We then subset the dataset to only include locations from 1 April to 31 July each year to focus on spring locations and to provide enough of a temporal buffer to account for migration periods. For each individual, we determined the ingress (i.e., migration into the spring range) and egress (i.e., migration out of the spring range) periods by calculating net-squared displacement (NSD; Bennefeld et al., 2011). We added a location at the center of the spring range the beginning of each set of bison locations so that NSD would be calculated from that point. We then defined the ingress period as the set of bison location starting with the first location in a continuous set of locations that had reducing NSD values and ending with the first location of a continuous set of locations with NSD values <100-m^2 (i.e., within 100-m^2 of the centroid of the spring range). Similarly, egress was defined as the first location in a set of continuous locations with NSD values >100-m^2 and the end as the first locations of a set that had decreasing NSD values (i.e., when the bison has stopped moving away from the spring range). We calculated three standard statistics of migration for each migration period: (1) total distance, (2) total duration, and (3) mean speed (Bunnefeld et al., 2011). We tested for differences in migration metrics between ingress and egress using Mann-Whitney-Wilcoxon tests (Ramsey and Schafer, 2002). Calculations of NSD and significance tests were conducted in R version 3.5.3 (R Core Team, 2019).

To map the migration and identify potential migration corridors, we calculated kernel densities using dynamic Brownian bridge movement models (dBBMM) using R package 'move' (Horne et al., 2007; Kranstauber et al., 2012; R Core Team, 2019). We defined each migration event as an individual's ingress or egress within a year and modeled all events separately (e.g., bison 1, egress, 2015). Then, we created a mean ingress and mean egress dBBMMs by taking the mean density for each 30×30-m cell of all migration events.

Timing and spatial assessment of migration

We investigated the ecological factors and timing influencing migration using a three-pronged approach. First, we calculated instantaneous rate of green-up (IRG) as the first derivative of the positive slope of the normalized difference vegetation index (NDVI; MOD9Q1 product from MODIS terra satellite) curve for a given 250×250-m cell (Pettorelli et al., 2005; Bischof et al., 2012; Merkle et al., 2019). Higher IRG values reflect vegetation that is at a more intermediate phenophase and is therefore more nutritious and palatable for herbivores (Aikens et al., 2017). To assess the timing of bison arrival in the spring range relative to forage quality, we calculated the mean start, peak, and end date for all cells within the spring range (Berman et al., 2020). Then, we calculated the absolute difference between the Julian date of the start, peak, and end of green-up (i.e., spring), and the Julian date of the start and end of egress and ingress. We then calculated the repeatability (R) of these differences to determine how consistent timing is for individuals and the population over the years (Lessells and Boag, 1987).

Second, to determine if individuals were surfing or tracking the green-wave more than random or not at all, we regressed the date of peak spring against the date of bison occupancy of a particular cell (Aikens et al. 2017; Geremia et al. 2019). Green-wave surfers would have 95% confidence intervals (CI) around a slope included one and 95% CIs around the intercept which included zero. Bison tracking the green-wave more than random had a positive slope with a 95% CI that did not include zero. Bison that did not track the green-wave had negative slopes or a slope with a 95% CI that included zero (Aikens et al. 2017). We generated linear models separately for each migration event.

Lastly, we used step selection functions to assess the influence of forage quality on the herd's habitat selection while migrating (Fortin et al., 2005; Merkle et al., 2016). We identified each step as the consecutive locations for an individual (2-hour interval). We compared habitat characteristics of bison (i.e., source) locations and 25 randomly placed available (i.e., target) locations within the one standard deviation above the mean step-length (2250-m) for all bison locations during migratory periods (Merkle et al., 2016). All random locations were generated within this buffer of the source location for each step to provide a suite of potential target locations and were compared to the next bison location in the sequence (Fortin et al., 2005). We then created base models that included all explanatory variables known to influence bison movements: distance between source and target locations, landcover type (Ducks Unlimited Enhanced Wetland Classification, 2016), ground-wetness (estimated using the compound topographic index [CTI]), normalized difference vegetation index (NDVI), integrated NDVI (iNDVI; the sum of all NDVI values at a location, considered an estimation of biomass), and distance to linear disturbance (Merkle et al., 2016; Aikens et al., 2017; Belanger et al., 2020; DeMars et al., 2020). Note that CTI is a measure of "soil wetness" which correlates negatively with footing stability in large ungulates, but also correlates positively with wetland habitats that may contain preferred forages for bison (Moore et al., 1991, Belanger et al., 2020). Then, we added IRG to base ingress and egress models to determine whether it improved the base model, which would indicate bison are selecting habitats with hire quality forage while migrating (Merkel et al., 2017). We used Akaike information criteria (AIC) to determine if the addition of IRG and/or risk of predation created more parsimonious modes than the base model. Models with lower AIC values and a difference greater than two are considered more parsimonious (Burnham and Anderson, 2002).

We also assessed the influence of predation pressure on the herd's habitat selection during migration for a truncated time period (i.e., just 2019). In 2019, we fitted Vectronics Vertex Lite Global Positioning System (GPS) collars to wolves (n = 4) in two packs within the bison's range. We subset wolf locations to match the date range of bison locations during bison ingress and egress for that year. Then, we calculated dBBMMs for each pack and generated a mean ingress and egress wolf dBBMM from individual events. We analyzed an additional set of models for just 2019, using the same base models and adding the kernel density estimates from the wolf dBBMMs as a proxy for risk of predation, IRG, and both as additional predictors to the base models.

Calf monitoring

In the summer of 2015, we deployed camera traps (Reconyx, Holmen, USA) in the upland meadow. We retrieved images and re-deployed cameras annually until 2018. In 2018, we began deploying camera traps at other centers of bison activity throughout their range and along the identified migration corridors. We noted the date of the first calf observation in the upland meadow. We compared this date to the date of the first observation in the rest of the range (hereafter referred to as "core range"), along migration corridors, and the arrival of collared bison in the spring range. These data provided us with a coarse estimate of the timing of parturition relative to migration.

Results

Migration metrics and corridors

We identified 217 migration events from 2013 to 2019. During ingress, bison moved an average of 28-km during 6-days at 0.33-km/hr, and during egress, bison migrated for an average of 10-days over 40-km at 0.28-km/hr (Figure 2). During ingress the speed of migration was significantly higher than egress ($p < 0.01$). Our dBBMMs show collared females begin their ingress scattered as individuals or in small groups. Then moved along one of two corridors and congregated in the spring range (88.4-km^2, 99% UD) at the western edge of their annual range (Figure 3). The end of ingress and start of egress both appear to occur along legacy (>20 years old) seismic-lines. Camera traps confirm the use of these two lines as migration corridors. Camera traps also confirm the extensive use of the large upland meadow complex.

Timing and spatial assessment of migration

The timing of both start and end of ingress were significantly closer to the peak and end of spring in the spring range than the start of spring (Figure 4). In particular, the difference between the end of ingress and the end of spring in the spring range (mean = 8.9, SD = 7.8) was more consistent on an annual basis than any other migration and spring period. At the population level, timing of all migrations was consistent (i.e., positive R values), but there was no consistency in individual timing of migration since all confidence intervals overlap with zero (Figure 4).

Our linear regressions revealed that none of the migration events surfed tracked the green-wave. During ingress, 51 (52%) bison events aligned with the green-wave more than random and 47 (48%) did not, and during egress, 58 (49%) bison events aligned with the green-wave more than random and 61 (51%) did not (Supplementary information i). We found that locations more frequently used tended to reach peek of spring (i.e., peek IRG) earlier during ingress, but did not necessarily have higher peak greenness (i.e., NDVI) values. Locations more frequently used during egress had a later peek of spring , but also did not necessarily have higher peak greenness values (e.g., Figure 5; for all years see Supplemental Information ii).

Logistic regressions during ingress and egress revealed similar results. During ingress and egress, adding IRG to a base model produced a more parsimonious model (Table 2; see Supplementary Information ii for full list of coefficients for selected models). The most parsimonious model during ingress showed a one unit increase in IRG (ß = 0.308, SE = 0.058) that resulted in 36% increase in habitat preference. The most parsimonious model during egress showed a one unit increase in IRG (ß = 0.761, SE = 0.080) caused a 114% increase in habitat preference.

Spatial assessment of migration including predation

In 2019, the ingress models including IRG, and risk of predation and IRG were comparably parsimonious and more parsimonious than the base model. In the model with IRG and risk of predation a one unit increase in IRG (ß = 1.058, SE = 0.264) caused a 118% increase in habitat preference, and a one unit change in wolf dBBMMs (ß = -33.950, SE = 33.790) resulted in a <0.01% decrease habitat preference. Similarly, the egress 2019 models including IRG, and risk of predation and IRG were comparably parsimonious and more parsimonious than the base model. In the model with IRG and risk of predation we report a one unit increase in IRG (ß = 1.278, SE = 0.398) produced a 260% increase in habitat preference and a one unit change in wolf dBBMMs (ß = -27.93, SE = 17.41) caused a 0.37% decrease in habitat preference. Our base models and models with just risk of predation were equally parsimonious (Table 3; see Supplementary Information ii for full list of coefficients for selected models).

Calf monitoring

Camera trap data indicated that collared-bison and calves appear in the spring range (specifically the upland meadow) within days of each other (Table 4). During the two years we had cameras in the spring range, along migration corridors, and throughout the core range and we observed calves in the herd's core range before entering the spring range. In 2019, calves were observed in the core range on March 30 and during ingress on May 10 before the first collared bison arrived in the spring range on May 19. In 2020, we observed calves in the core range a month before the first bison arrived in the spring range (Table 4).

Discussion

We found that the Ronald Lake wood bison's primary motivation for migration is the formation of nursery herds during peak green-up. Our spatial analyses indicate support for the green-wave hypothesis as a factor encouraging migration and influencing habitat selection during migration. We did not find support for the predation hypothesis as adding risk of predation from wolves alone did not improve the base model. Our results provide insight into the complexity of the factors that influence migration decisions and behavior associated with parturition.

Our maps of migration corridors contribute to the growing knowledge of different migrations by ungulates worldwide and provide novel perspectives on the influence of anthropogenic disturbances on migration. Recently, the importance of mapping and describing the migrations of wild ungulates has been highlighted as a key knowledge gap in their conservation (Kauffman et al., 2021). We addressed this issue by mapping the Ronald Lake herd's migration, which is unique in that calves are present during both migration periods, the migration terminates in the formation of nursery herds, and bison utilize anthropogenic disturbances to reach the spring range. While not one of our specific objections, we found that both migration corridors used by the bison included legacy seismic lines used for mapping sub-surface energy resources. Camera traps on these seismic lines confirmed their use. This finding contradicts the results studies of other ungulates such as mule deer, which found a negative impact of linear disturbances on habitat selection during migration (Lendrum et al., 2012). However, we consider these lines to be abandoned disturbances as most were created 30 years ago and are re-vegetated in the understory but often still lack forest cover. We posit that the forest openings created by these lines reduces the cost of movement for migrating bison encouraging their selection. Female bison in the Ronald Lake herd are known to increase their movement rates on seismic lines (DeMars et al., 2020). Further, grasses and forbs persist on seismic lines in upland deciduous forests for decades (Lee and Boutin, 2006), potentially providing both higher quantities and higher quality forages than in the surrounding forests (van Rensen et al., 2015). By accurately describing the diversity of migration behaviors and factors influencing migration, critical knowledge is accumulated that can inform planners and policy-makers concerned with managing migratory species and their habitats.

We found that the timing of migration and habitat selection during migration were both related to the green-wave. The herd consistently arrived in the spring range close to the end of spring when NDVI values are at their peak and IRG values have tapered off. This result suggests that bison are trailing the green-wave. Similarly, mule deer and bighorn sheep in Wyoming, USA selected habitats at the trialing edge of the green-wave (Merkle et al. 2017). While the herd consistently assembled in the spring range close to the end of spring, the timing of individuals' migrations was variable. Female bison typically give birth two out of three or three out of four consecutive years (Berger and Cunningham, 1994; Sweitzer et al., 2005), so differences in physiological state could be contributing to the inconsistency in individual timing. However, Aikens et al. (2017) did not find a relationship between green-wave surfing and physiological state in mule deer. We also found that half the bison tracked the green-wave more than random and half did not appear to track the green-wave at all. Our results are comparable to migrating red deer in Sweden, of which only 52% surfed the green-wave (Bischof et al., 2012), but differ from migrating mule deer in Wyoming, which mostly tracked the green-wave at least better than random (Aikens et al., 2017). These differences likely arise from a combination of effects including species physiology, migration distance, propagation of the green-wave across each landscape, and the overall productivity of the ecosystem. Larger herbivores are better able to digest lower quality forages and therefore should be less selective of the phenophase of their forages (Müller et al., 2013). Wood bison are the largest extant terrestrial animal in North America with diets dominated by low-quality graminoids, especially during green-up (Hecker et al., 2021a). Mule deer are smaller and stricter browsers than the larger red deer, which are intermediate feeders (Hoffman, 1989; Main and Coblentz, 1996). The mean distance (ingress = 28-km; egress = 40-km) and duration (ingress = 6-days; egress = 10-days) of Ronald Lake herd's migrations was also closer to that of the Swedish red deer (distance = 23-km, duration = 7-days; Bischof et al., 2012) than Wyoming's mule deer (distance = 67-km, duration = 34-days; Aikens et al., 2017). When migrations occur over greater distances, especially along a latitudinal or altitudinal gradient, the green-wave should be more rapid and ordered along migration corridors leading to higher proportions of individuals tracking it (Aikens et al., 2020). The Ronald Lake bison's range is flat (60-m difference between maximum and minimum elevations) and their migrations generally follows an east-west pattern. We found only moderate levels of green-wave tracking likely due to the flatness of the herd's range, short migration distance, and bison's ability to readily digest low-quality forages. Additionally, these bison are known to switch their foraging behavior from a heavily reliant on grazing in the winter to a diet dominated by forbs and woody plants by later summer (Hecker et al., 2021b). These browse items are primarily found in upland habitats and the movement from one landcover type to another may be convoluting the bison's ability to track the green-wave. While these patterns provide some support for the green-wave hypothesis, we do not completely exclude the additionally non-mutually exclusive alternative hypotheses.

The results of our spatial analyses do not support the hypothesis that risk of predation influences habitat selection during migration. However, the grouping behavior after ingress and through egress indicates that at some point in their evolutionary history anti-predatory behavior was critical to population viability. We acknowledge that our single year sample of wolves is limited and conclusions should be interpreted accordingly. Additionally, we had collars on two wolf packs in 2019, but a third pack has been observed with a range that overlaps with the bison. In neighboring WBNP, wolf packs of four to six individuals regularly target bison herds with calves, leading to bison congregating on calving grounds for greater vigilance and more apt defenses (Carbyn and Trottier, 1987; Carbyn and Trottier, 1988). Black bears (*Ursus americanus*) in and around the spring range when the bison are present. Black bears are known to prey on ungulate calves, especially shortly after parturition (Zager and Beecham, 2006), but we are not aware of any instances of bison calf predation here. Black bears may opportunistically prey on calves or scavenge the highly nutritious afterbirth (Horstman and Gunson 1982; Wilton, 1983). We did find that ingress occurred at a significantly faster rate than egress. Additionally, ingress migrations were carried out by individuals or small groups with calves. If parturition is the mechanism initiating ingress, then the faster rate of ingress could be interpreted as an anti-predatory behavior as adults with calves in-tow should quickly seek the safety of larger numbers. Similarly, the correlation of slower movement rates during egress could be a result of the bison maintaining larger groups at this time as an anti-predator behavior. We therefore do not completely dismiss the predation as a mechanism influencing migration and synchronized calving in the Ronald Lake bison. This migration and congregation may be an example of the "ghost of predation past" (Brown and Vincent, 1992) as risk of predation does not appear to currently impact habitat selection but manifests in other aspects of the bison's behavior.

We did not explore other factors that might influence migration including parasite avoidance, limited resource allocation, and social learning. Caribou (*Rangifer tarandus*) in Norway migrated to regions with significantly lower biting insect abundance and red deer migrated to higher elevations to avoid ticks (Folstad et al., 1991; Mysterud et al., 2016). However, ticks are not present in the Ronald Lake herd's range and studies have shown that their preferred forages occur in areas with higher densities of biting insects (Belanger et al., 2020). Mountain goats (*Oreamnos americanus*) are known to migrate to access salt licks in regions where sodium is limited (Butler, 1993). The Ronald Lake wood bison migration may be influenced by the potential presence of salt-licks and other mineral concentrations. A number of minerals (i.e., sodium, calcium, magnesium, sulphate, chloride) are known to fluctuate in concretions between winter and summer in the McIvor River (the northern border of the spring range; Jantzie, 1976). Evidence of social learning was observed in translocated moose and bighorn sheep, which tracked the green-wave better over decades suggesting behaviors learned by one generation were taught to the next (Jesmer et al. 2018). Additionally, given that all females migrated every year, but female bison do not give birth every year. This result provokes questions related to what other social mechanisms, such as kin selection, encourage this migratory behavior. Additionally, it is possible that the bison depleted the available forage during winter in the rest of their range and are migrating to take advantage of a region that was only lightly foraged during the winter. Despite these potential additional effects on migration, our results provide value insight into a unique ungulate migration.

We tested the factors affecting spring migration by wood bison. We observed that bison during ingress were accompanied by calves and during egress bison moved in larger groups indicating that these bison migrate to form nursery herds. During migratory periods bison selected vegetation at an intermediate phenophase and roughly half the migrations tracked the green-wave lending marginal support to the green-wave hypothesis. We did not find support in spatial analyses for risk of predation influencing habitat selection, but observations of defensive behaviors suggest a ghost of previous predation. Our research provides valuable insight into the complexity of interrelated factors influencing migration, especially as it relates to calving behavior in ungulates.

Tables

Table 5.1: Migration hypotheses, metrics used to test hypotheses, and the expected outcomes (predictions).

Hypothesis	Metric	Prediction
Green-wave	Dates of arrival in spring range	Bison will arrive at the spring range closer to the peak of spring green-up than the beginning or end of spring
	Instantaneous rate of green-up (IRG)	While migrating bison will select habitats with higher IRG
Predation	Kernel density estimates of wolf locations	While migrating bison will avoid locations where wolves are likely to occur. This avoidance should be stronger during egress if parturition occurs in the spring range.
Parturition	Camera trapping	If the spring range is strictly a calving site, calves will not be observed during ingress and the first calf of a given year should be observed in the spring range. If the spring range is a nursery site, calves will be observed on migration cameras before bison or calves are observed in the spring range.

Table 5.2: Comparisons of logistic regression models that assess factors that influence the habitat selection of wood bison (*Bison bison athabascae*) while migrating. Models are divided into two periods: ingress (migration into the spring range) and egress (migration out of the spring range). Base models include variables known to influence bison habitat selection: landcover type (landcover), distance to linear disturbance (dist. line), distance to open water, footing (measured using a compound topographic index; CTI), distance to potential target location, landscape greenness (measured as a normalized difference vegetation index; NDVI), and vegetation biomass (integrated NDVI; iNDVI). Green-wave models also include a measure of forage quality (instantaneous rate of green-up; IRG). We compared models using Akaike information criterion (AIC) with models at least 2 AIC values lower (ΔAIC) being more parsimonious.

2013 – 2019 models				
Period	Model	Parameters	AIC	ΔAIC
Ingress	Green-wave	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI + IRG	59820.1	0.0
	Base	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI	59846.6	46.6
Egress	Green-wave	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI + IRG	51744.6	0.0
	Base	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI	51834.4	89.8

Table 5.3: Comparisons of 2019 logistic regression models that assess the mechanisms influencing the habitat selection of wood bison (*Bison bison athabascae*) while migrating. Models are divided into two periods: ingress (migration into the spring range) and egress (migration out of the spring range). Base models include variables known to influence bison habitat selection: landcover type (landcover), distance to linear disturbance (dist. line), distance to open water, footing (measured using a compound topographic index; CTI), distance to potential target location, landscape greenness (measured as a normalized difference vegetation index; NDVI), and vegetation biomass (integrated NDVI; iNDVI). Green-wave models also include a measure of forage quality (instantaneous rate of green-up; IRG) and predation models a measure of wolf (*Canis lupus*) predation risk (kernel density estimates from Brownian bridge movement models; BBMMs). We compared models using Akaike information criterion (AIC) with models at least 2 AIC values lower (ΔAIC) being more parsimonious.

2019 models				
Period	Model	Parameters	AIC	ΔAIC
Ingress	Green-wave	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI + IRG	4791.3	0.0
	Green-wave & predation	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI +IRG + wolf BBMM	4792.2	0.9
	Base	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI	4805.5	14.2
	Predation	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI + wolf BBMM	4807.0	15.7
Egress	Green-wave	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI + IRG	2637.8	0.0
	Green-wave & predation	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI +IRG + wolf BBMM	2638.1	0.3
	Base	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI	2646.4	8.6
	Predation	Landcover + dist. line + dist. water + CTI + dist. target + NDVI + iNDVI + wolf BBMM	2646.5	8.7

Table 5.4: Summary of the dates the first female wood bison (*Bison bison athabascae*) outfitted with a GPS-collar arrived in the spring range (spring range 1st collar), the first calf observed in the spring range (spring range 1st calf), and the first calf observed in the rest of the herd's range including migration corridors (range 1st calf).

Spring range 1st collar	Spring range 1st calf	Range 1st calf
May 21, 2013	NA	NA
June 1, 2014	NA	NA
May 14, 2015	NA	NA
May 3, 2016	May 5, 2016	NA
May 18, 2017	May 10, 2017	NA
May 13, 2018	May 8, 2018	NA
May 19, 2019	May 12, 2019	Mar. 30, 2019 May 10, 2019
June 3, 2020	NA	May 1, 2020

Figures

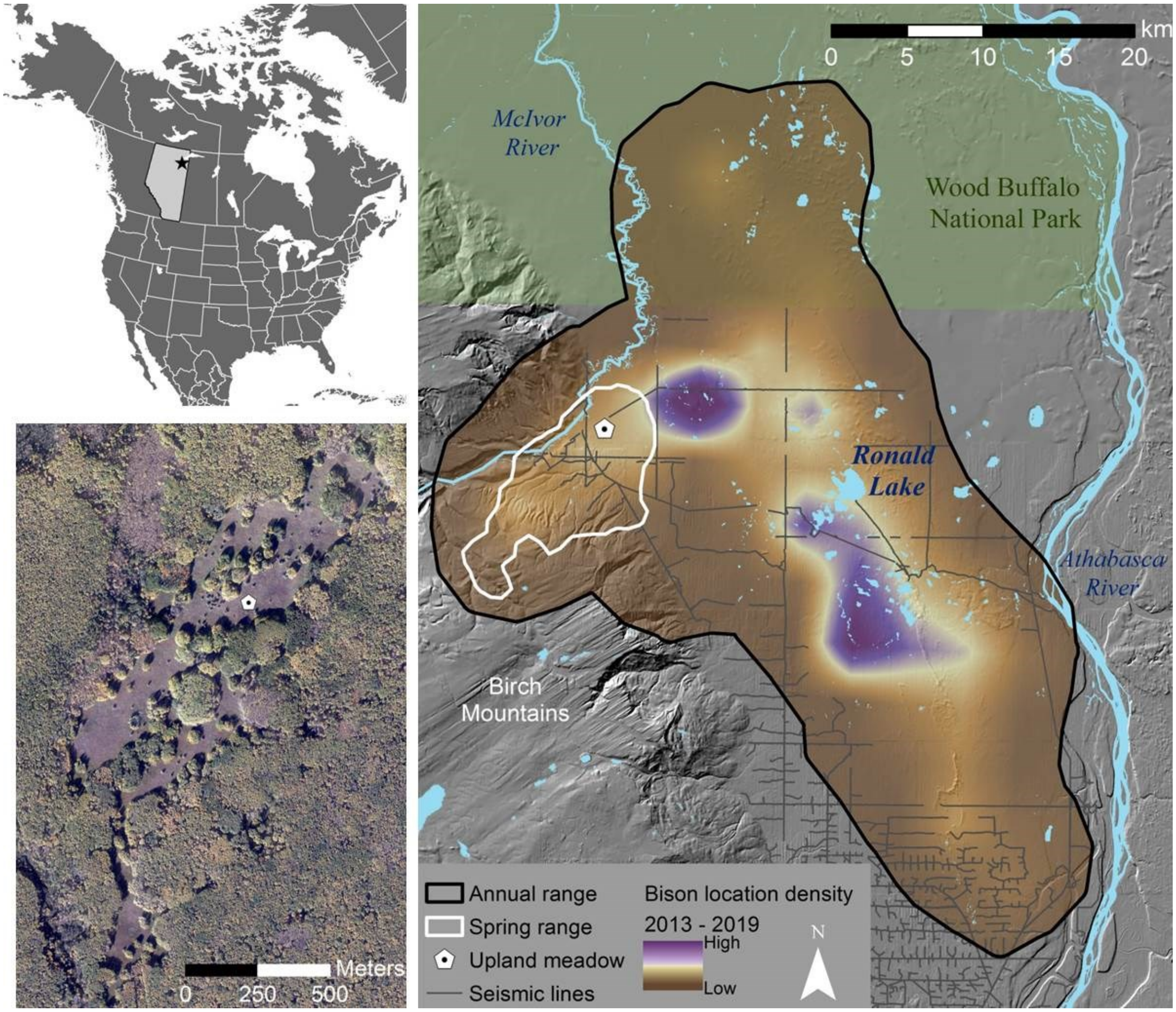

Figure 5.1: The annual and spring ranges of the Ronald Lake wood bison (*Bison bison athabascae*) herd calculated as a 99% utilization distribution (UD) of GPS-collared bison locations from 2013 to 2019. The black outline represents the 99% UD polygon for the annual range and the white polygon is the 99% UD when bison occupy the spring range in the west adjacent to the Birch Mountains. The inset map (top left) provides the location of the study area relative to North America. The aerial image (bottom left) shows the upland meadow that is an epicenter of activity within the spring range.

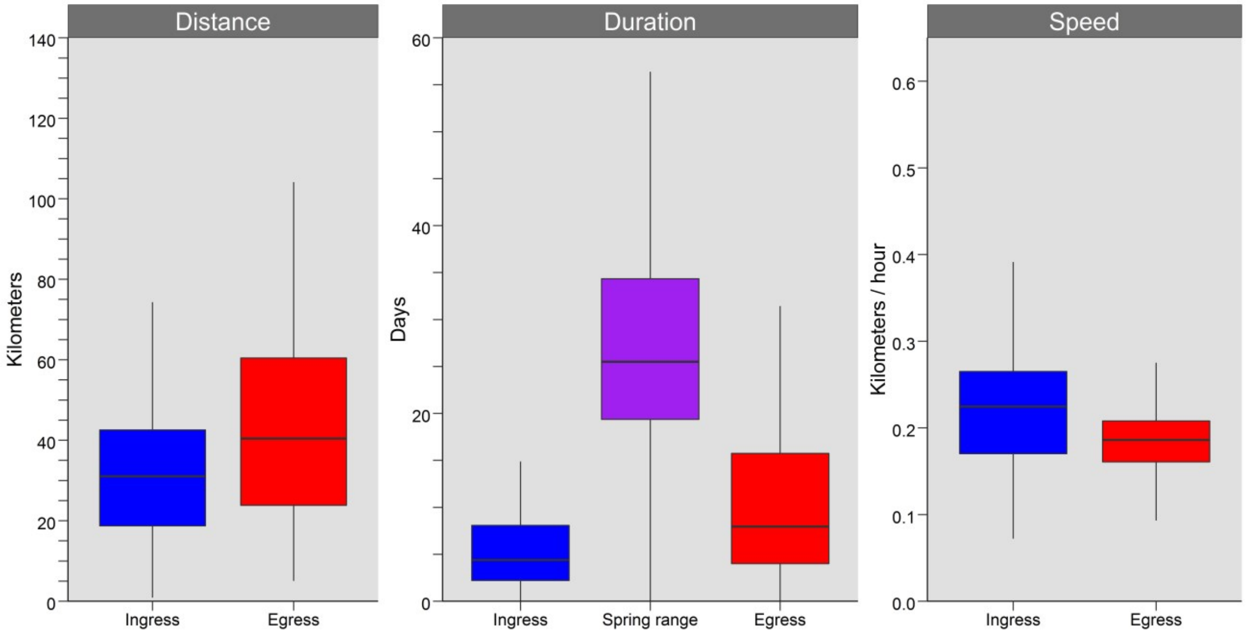

Figure 5.2: A summary of migration metrics (i.e., distance, duration, and speed) for the Ronald Lake wood bison (*Bison bison athabascae*) herd's spring migration. Ingress is the migration into the spring range and egress is the migration out of the spring range.

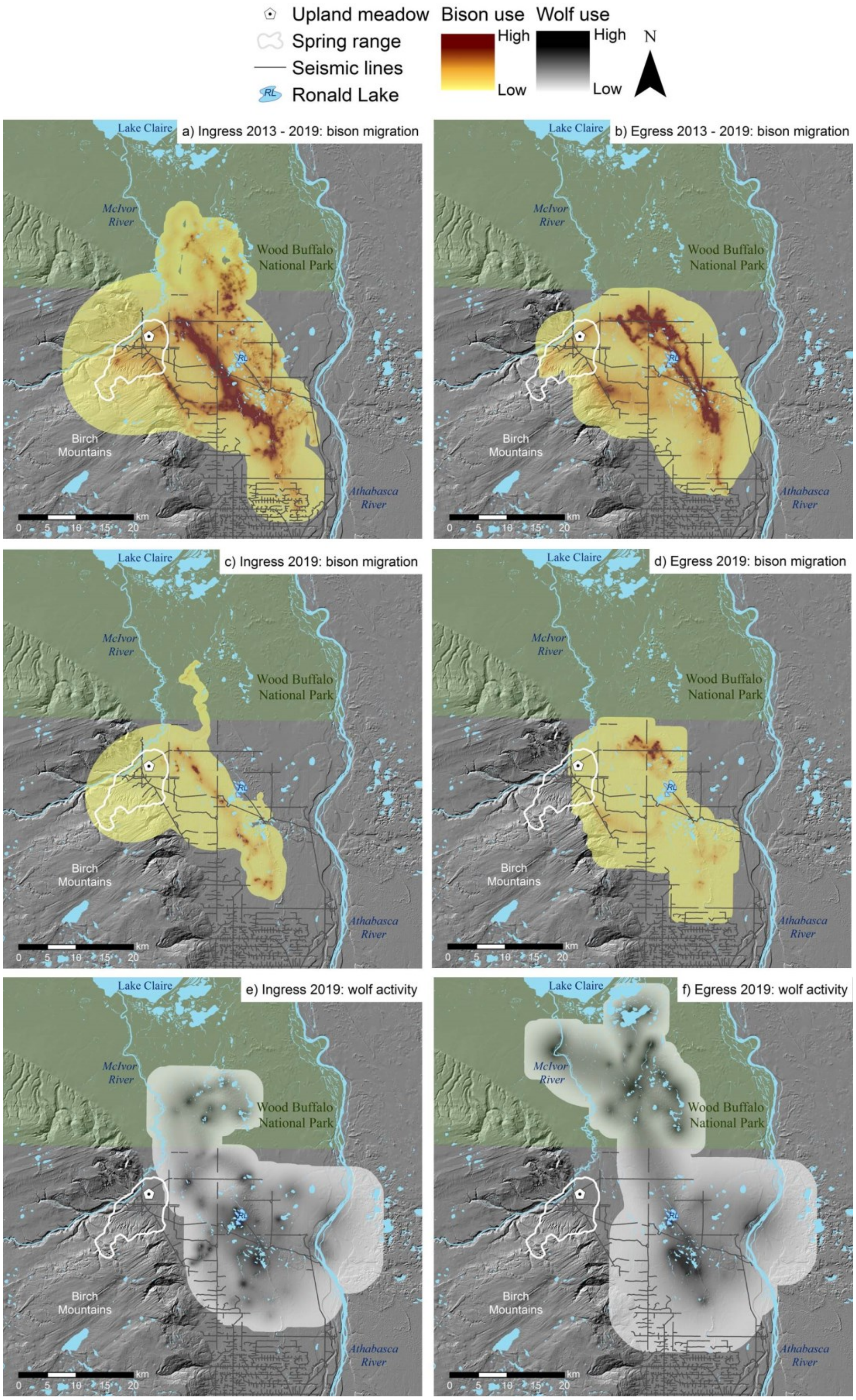
Upland meadow
Spring range
Seismic lines
Ronald Lake
Bison use
High
Low
Wolf use
High
Low
N
a) Ingress 2013 - 2019: bison migration
b) Egress 2013 - 2019: bison migration
c) Ingress 2019: bison migration
d) Egress 2019: bison migration
e) Ingress 2019: wolf activity
f) Egress 2019: wolf activity
Lake Claire
McIvor River
Wood Buffalo National Park
RL
Birch Mountains
Athabasca River
0 5 10 15 20 km

Figure 5.3: a) Brownian bridge movement model (BBMM) for bison ingress (migration into the spring range) locations from 2013 - 2019. b) A BBMM for bison egress (migration out of the calving range) locations 2013 - 2019. c) A BBMM for bison ingress (migration out of the calving range) locations from 2019. d) A BBMM for bison dgress (migration out of the calving range) locations from 2019. e) The combined 2019 BBMM for two wolf packs during the bison’s ingress. f) The combined 2019 BBMM for two wolf packs during the bison’s egress. The legend applies to all panels. Bison and wolf use is measured at the kernel density of bison locations using BBMMs.

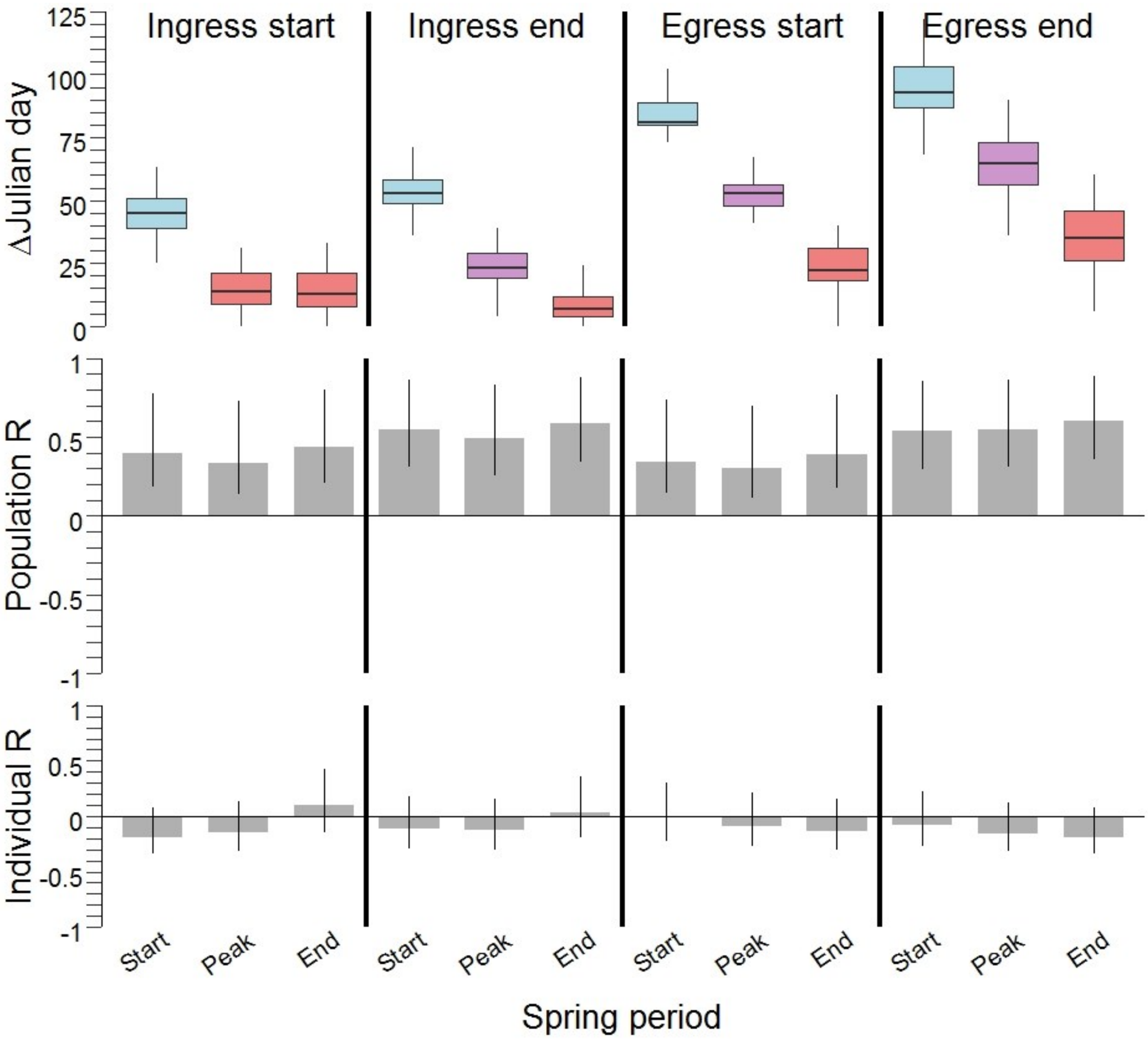

Figure 5.4: Top row shows the absolute value difference between the date of start, peak, and end of spring in the spring range and the fate of start and end of ingress (migration into the calving range) and egress (migration out of the spring range; exact dates are available Appendix C). Colors represent differences between dates that are significantly different with red being less time with red being significantly lower differences, blue being significantly greater differences, and purple were significantly different at a moderate level. The middle and bottom rows report repeatability (R) statistics for the differences in dates. The vertical line represents a 95% confidence region. Positive values indicate repeatability and negative values are events that are not repeated consistently. If the confidence region overlaps with zero then repeatability is inconclusive.

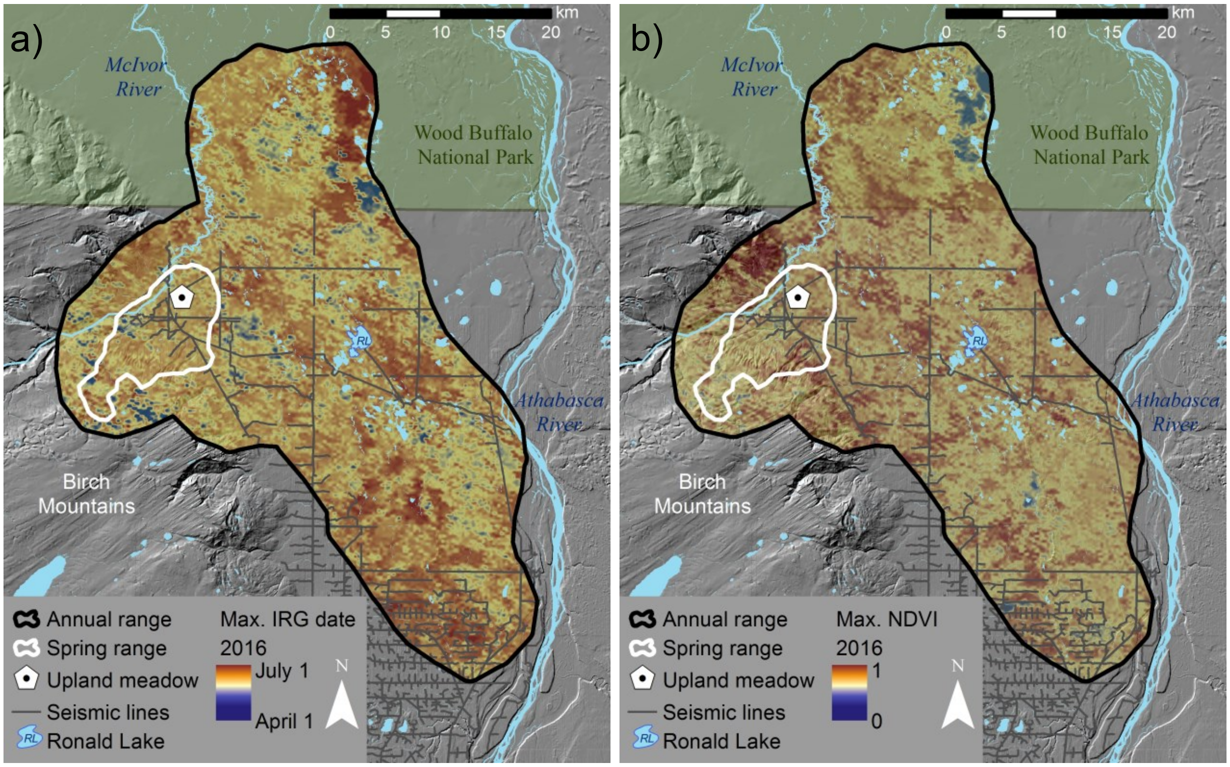

Figure 5.5: Date of maximum (max) instantaneous rate of green-up (IRG) across the herd's range in 2016. Here, we use an example year of 2016 as it was the year when the most bison carried active collars and was not a drought or flooding year.

Chapter 6: Conclusions

At one point American bison nearly rangeed the entire continent of North America occupying a great diversity of habitats. While they no longer range across the continent, they still occupy a variety of habitats (Schoenecker et al. 2015, Jorns et al. 2020, Thomas et al. 2021). This ecological generalism requires us to better understand the reasons and consequences for this plasticity and adaptability. This dissertation contributes towards a better understanding of bison life history by assessing the ecology of a population in an environment unique to the species and by quantifying the plasticity in both their diet and habitat selection. The Ronald Lake bison's range spans across an intersection of Athabasca Plain and Central Mixedwood boreal forests. This area is typified by having a mosaic of upland habitats with soils ranging from sand to loam and pocketed with wetlands of bogs, swamps, fens, and marshes unlike any other bison population's range (Neville et al. 2010). Notably, the portion of Wood Buffalo National Park (WBNP) south of Lake Claire that overlaps with the Ronald Lake herd's range is primarily composed of wetlands avoided by bison (Hecker et al. 2019). The little upland habitat that exists in that region was burned in the 2011 Richardson Fire decreasing the likelihood of their use (Chapter 4). These factors would decrease the probability of interactions between WBNP bison and the Ronald Lake herd, subsequently decreasing the possibility of disease transmission (ECCC 2020). More generally, I have shown that the Ronald Lake bison have adapted to this landscape through plasticity in their behavior (habitat use) and in particular utilize the highest quality forages available to then, when they are present (chapters 3-5). Now, I explore how the information gained from this dissertation can be used to further the management and conservation of the population, and what conclusions can be drawn upon by the broader bison community.

Contributing to the understanding of the Ronald Lake bison's ecology, I have described the seasonal diet composition, nutritional targets, habitat preferences, and provided insight into their unique migratory behavior. My biggest takeaway from these results is that the bison have adapted to the distribution of habitats and forage within landscape. When the results of my analysis of seasonal diet composition are compared to seasonal habitat selection, patterns are clear. In the winter and spring, bison selected graminoid-dominated wetlands, such as marshes and fens, while upland habitats were avoided. The bison were primarily grazers at this time. During summer, the opposite is observed. Bison selected against graminoid-dominated habitats, selected for upland habitats, and exhibited a mixed-browsing foraging strategy (Belanger et al. 2017, DeMars et al. 2020, Hecker et al. 2021b). This juxtaposition is driven by the consequences of living within a heterogenous landscape with strong seasonality. Bison balanced the energetic costs of movement with their nutritional demands.

When we compare patterns in bison diet composition and habitat selection, between winter and the growing season, is when we witness the benefits for bison of utilizing a diversity of habitats. In spring, the Ronald Lake bison began to consume a greater diversity of forage items but relied heavily on graminoids, particularly sedges (Hecker et al. 2021b). They also continued to select graminoid-dominant habitats and avoided upland habitats, but the strength of selection was lower than winter (Belanger et al. 2017, DeMars et al. 2020). It appears the relatively higher digestibility and greater amounts of protein in graminoids outweigh the higher energetic costs of moving through wetlands. However, as these graminoids mature and lignify this benefit diminishes and bison are observed foraging more on forbs and browse. The growing season is the time when bison need to increase their body mass to prepare for winter, the rut, and potential pregnancy (Parker et al. 2009, Middleton et al. 2018). One way bison accomplish this is by green-wave surfing during spring (Chapter 5) and another is by selection of forage higher in protein and fats (Hecker et al. 2021b). In the case of Ronald Lake bison, both of these strategies require a heterogenous landscape. Given the lack of a significant altitudinal or latitudinal gradient within their range, the different vegetative structures provide the only opportunity for the bison to attempt to track the green-wave, which they do to some degree (Chapter 5). The mixture of upland and wetland habitats provide a means for bison to meet their daily energetic requirement through grazing while also having ample access to protein and lipid heavy forbs and woody plants via browsing. The diversity of habitats and the forages associated with them allow the bison to maintain diets that meet their nutritional targets throughout the growing season (Hecker et al 2021b). One potentially important future line of research is to understand the limitations that secondary compounds, such as tannins, found in browse items affect the bison's ability to consume them given that they do not have the physiological traits to mitigate their negative effects (Hofman 1989, Owen-Smith 1993).

If the Frontier Oil Sands Mine Project ends up moving forward, the results of my research will be helpful in informing mitigation and reclamation strategies. First, it will be important to have an accurate estimation of the nutritional carrying capacity of the landscape. This dissertation has provided the dietary information, habitat preferences, and biomass estimates necessary to conduct these calculations. Accurate impact assessments of various mine development stages and potential reclamation strategies will rely on the estimation of the population's ability to find adequate forage that meets their nutritional requirements. Current impact assessments have relied on loss of "preferred foraging habitat" to address this issue. The assessments estimate an 18% loss based of these habitats within a range calculated as a 100% minimum convex polygon (MCP) using locations from 2013 – 2017 and an overall 24% of the total range (ECCC 2020). However, this assessment only considers graminoid-dominated wetlands as foraging habitat and ignores the important forages that upland habitats provide. Further, 100% MCPs simply connect the most extreme animal locations including outlier locations and typically over-estimate the area actually used (Clapp and Beck 2015). Using a 99% utilization distribution for the same time period, I calculated a 1% loss of "preferred foraging habitat" (ECCC 2020) and a 2% loss of total range. To provide an accurate assessment of the mines imminent threat "based on the best information available" (ECCC 2020) would require a range of estimates of habitat loss based on a variety of home range estimates including those based on Indigenous knowledge, shapefiles for which exist but are beyond the scope of this project. The evidence presented in this dissertation suggests that the population is currently below their ranges carrying capacity. However, I did not quantify carrying capacity and recommend future research addresses this question.

When reclamation strategies are discussed, it will be important to note that the heterogeneity of the current range provides important diversity to the bison's diet and their habitat selection. Especially, unique habitats that are vital during times of high stress such as parturition and lactation. Suggestions have been put forward to potentially reclaim the mine in an effort to bolster the population size by creating more marshes (ECCC 2020). I would caution against this reclamation approach and would recommend an effort to reclaim environments that reflect the natural heterogeneity that these bison have adapted to utilize.

The idea that range heterogeneity is something that is critical to bison survival is something that can be applied to all bison conservation and management efforts. American bison are a dynamic species that requires different habitats for different aspects of their life histories and daily behaviors. Bison reintroduction efforts have become a critical tool not only for bison conservation, but also for food sovereignty and the rekindling of cultural traditions for Indigenous communities. In the past decade, reintroductions have been occurring in areas as diverse as arid northern New Mexico, eastern plains of Montana, Canadian Rockies of Alberta, and the confluence of the Innoko and Yukon rivers in Alaska. Understanding the different ways that bison utilize different forages when available to meet nutritional targets, require different habitats for different behaviors, and potentially unique habitats will be invaluable to the success of any of these projects. Management of populations already in existence will also benefit from taking this holistic understanding of the particular populations needs on their range.

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Appendices

Appendix A: Right-angled mixture triangles of realized macronutrient and fiber niches describing differences between and withing forage groups and seasons.

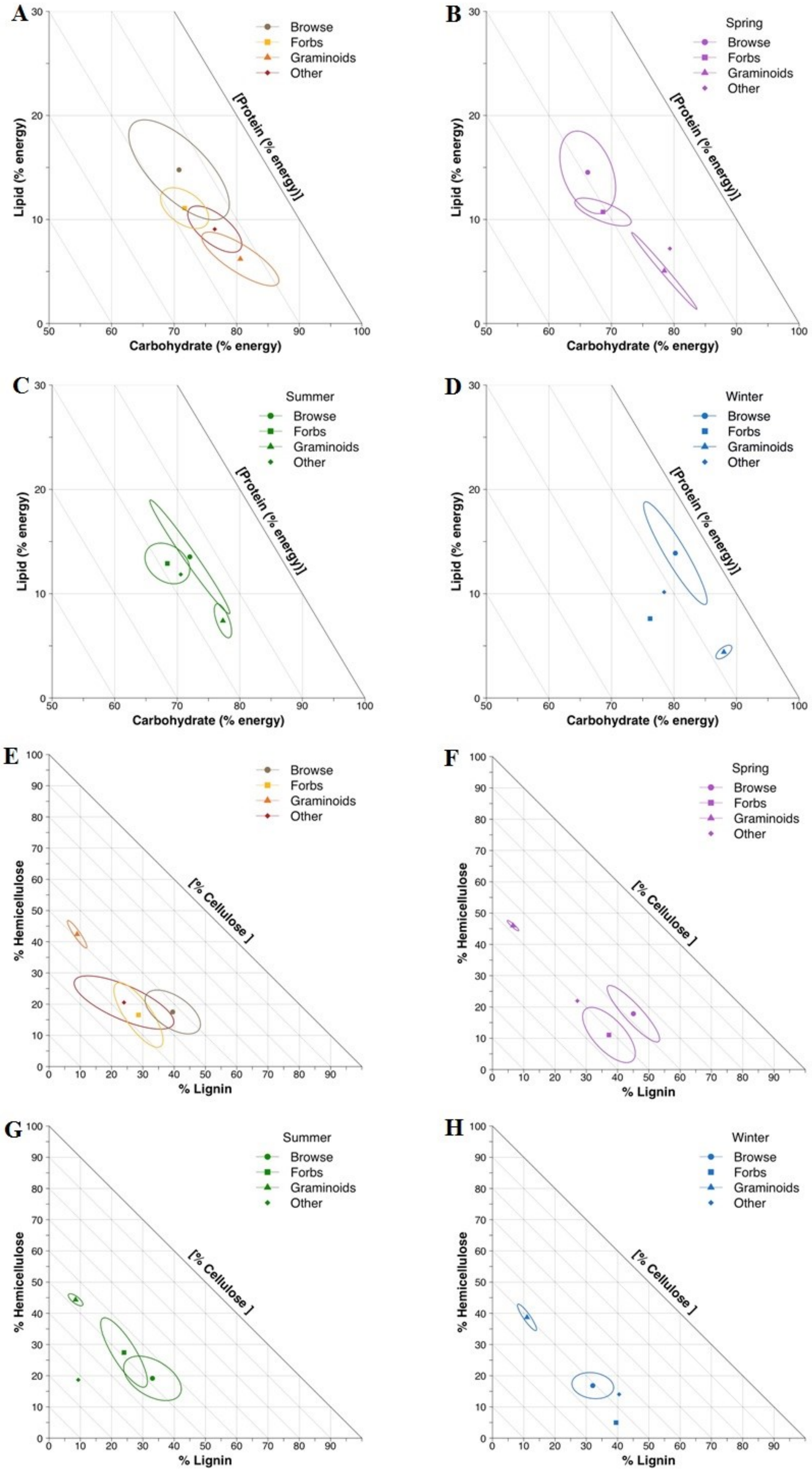

A
Browse
Forbs
Graminoids
Other
Lipid (% energy)
Carbohydrate (% energy)
[Protein (% energy)]
B
Spring
Browse
Forbs
Graminoids
Other
C
Summer
Browse
Forbs
Graminoids
Other
D
Winter
Browse
Forbs
Graminoids
Other
0
10
20
30
50
60
70
80
90
100
E
Browse
Forbs
Graminoids
Other
% Hemicellulose
% Lignin
[% Cellulose]
F
Spring
Browse
Forbs
Graminoids
Other
G
Summer
Browse
Forbs
Graminoids
Other
H
Winter
Browse
Forbs
Graminoids
Other
0
10
20
30
40
50
60
70
80
90
100

Figure A.1: Mean macronutrient and fiber compositions within season. Points that lie within another forage group or season’s 95% confidence ellipse are not significantly different. (A) Annual, mean macronutrient composition of each forage group. (B-D) Mean macronutrient compositions of forage groups (graminoids, forbs, browse, other) within each season. (E) Annual, mean fiber compositions within forage group. (F-H) Shows significant within season differences based on 95% confidence ellipses among of forage groups.

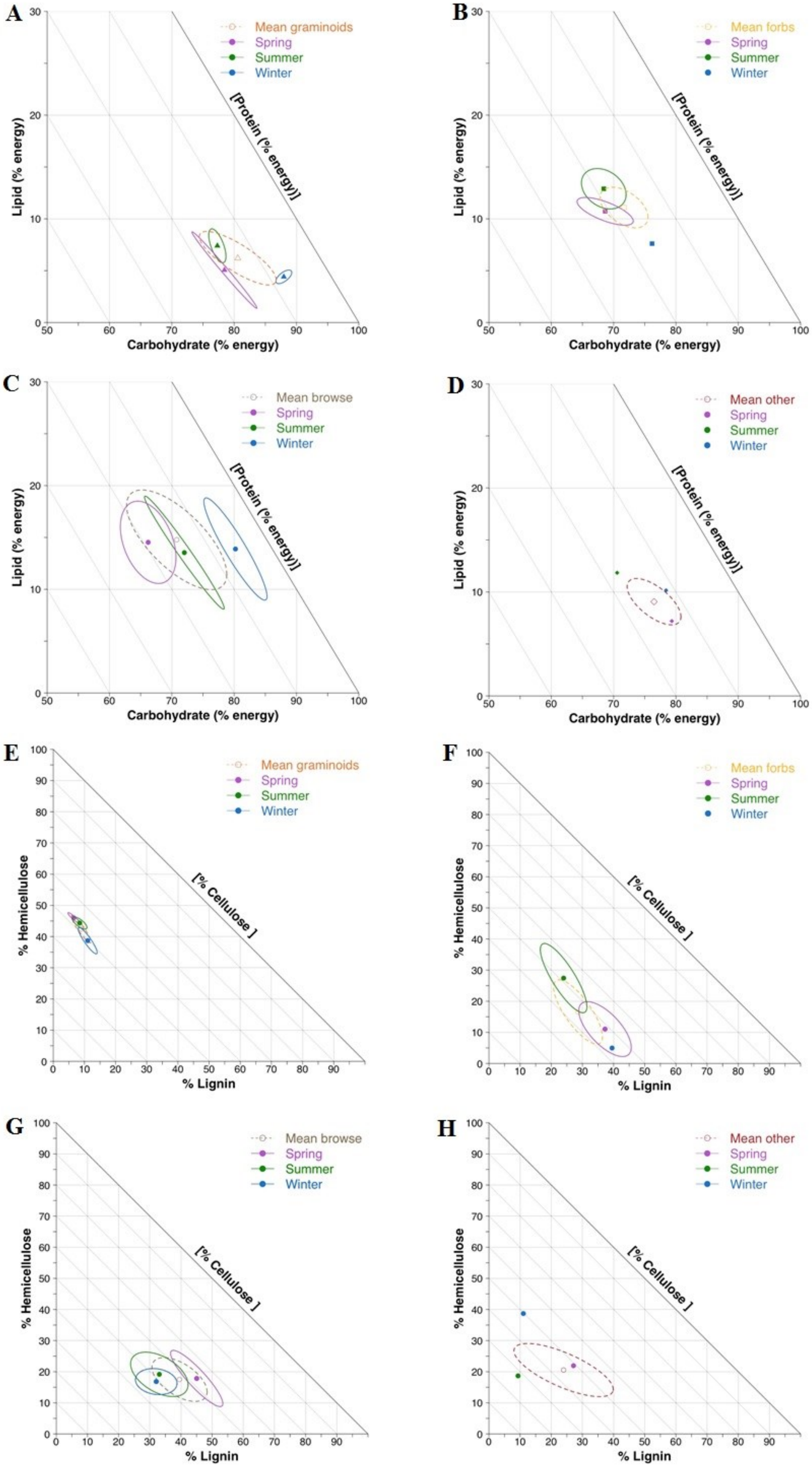

A
Mean graminoids
Spring
Summer
Winter
Lipid (% energy)
[Protein (% energy)]
Carbohydrate (% energy)
0
10
20
30
50
60
70
80
90
100
B
Mean forbs
Spring
Summer
Winter
Lipid (% energy)
[Protein (% energy)]
Carbohydrate (% energy)
C
Mean browse
Spring
Summer
Winter
Lipid (% energy)
[Protein (% energy)]
Carbohydrate (% energy)
D
Mean other
Spring
Summer
Winter
Lipid (% energy)
[Protein (% energy)]
Carbohydrate (% energy)
E
Mean graminoids
Spring
Summer
Winter
% Hemicellulose
[% Cellulose]
% Lignin
0
10
20
30
40
50
60
70
80
90
100
F
Mean forbs
Spring
Summer
Winter
% Hemicellulose
[% Cellulose]
% Lignin
G
Mean browse
Spring
Summer
Winter
% Hemicellulose
[% Cellulose]
% Lignin
H
Mean other
Spring
Summer
Winter
% Hemicellulose
[% Cellulose]
% Lignin

Figure A.2: Mean macronutrient and fiber compositions within forage groups. Points that lie withing another forage group or season's 95% confidence ellipse are not significantly different. (A-D) Mean macronutrient compositions of each season and annual mean within each forage group (graminoids, forbs, browse, other). (E -H) Shows within forage group differences based on 95% confidence ellipses among of seasons and annual means.

Appendix B: Results of proximate and fiber analyses of the forage items with at least 1% relative read abundance (RRA) or that were frequently observed being consumed in the field.

Table B.1: Raw results of macronutrient and fiber analyses from items frequently foraged by the Ronald Lake wood bison herd (RLBH). The table is broken down into three seasons (winter, spring and summer) and within each season the plants are listed in order of highest to lowest relative read abundance (RRA). Proximate analyses were conducted by Nutrilytical and results presented here report moisture (water in the forage), dry matter (DM; air-dried component with all moisture removed), ash (inorganic mineral elements), crude protein (CP; total nitrogen time 6.25), soluble protein (SP; the proportion of crude protein that will be consumed by rumen microbes), and crude fat (Fat; lipids). Fiber analyses include lignin (Lign), acid detergent fiber (ADF) and neutral detergent fiber (NDF). We used results of the proximate to calculate non-fiber carbohydrates (Carbs; Equation 1) and results of fiber analyses to calculate hemicellulose (Hemi; Equation 2) and cellulose (Cell; Equation 3). Note, that three sedge (*Carex*) species each have their own macronutrient values reported, but could not be differentiated to the species level in the DNA barcoding analysis of the RLBH's diet contents. Therefore, their percent seasonal diet is reported only for the first species listed.

Winter raw values														
Species	FG	RRA	DM	Moisture	Ash	CP	SP	Fat	Carbs	Lign	ADF	NDF	Hemi	Cell
Carex aquatilis	Graminoid	-	91.4	8.6	6.7	6.6	29.0	1.7	76.5	7.2	43.4	70.9	27.5	36.2
Carex atherodes	Graminoid	-	91.2	8.8	7.1	4.9	33.0	1.8	77.4	5.7	42.4	72.4	30.0	36.7
Carex utriculata	Graminoid	19.1	91.8	8.2	5.6	7.0	32.0	1.9	77.4	8.5	43.2	73.2	30.0	34.7
Viburnum edule	Browse	17.2	93.9	6.1	5.2	5.3	26.0	8.0	75.4	20.8	47	54.7	7.7	26.2
Cornus sericea	Browse	12.7	93.4	6.6	2.3	4.5	26.0	4.9	81.8	11.8	47.5	58.9	11.4	35.7
Typha	Graminoid	11.0	93.3	6.7	5.8	9.6	28.0	1.3	76.6	11.3	48	69	21.0	36.7

latifolia														
Amelanchier alnifolia	Browse	7.5	93.2	6.8	4.2	5.6	25.0	4.5	78.9	18.8	48.2	55.8	7.6	29.4
Salix spp.	Browse	5.4	92.4	7.6	3.1	7.4	21.0	3.0	78.9	18.2	44.9	57.5	12.6	26.7
Poaceae	Graminoid	3.5	91.3	8.7	6.6	6.2	29.0	2.0	76.5	9.4	44.7	70.5	25.8	35.3
Populus tremuloides	Browse	3.4	87.1	12.9	6.6	8.1	18.0	8.5	63.9	22.4	41.2	52.6	11.4	18.8
Sphagnum spp.	Other	1.3	84.9	15.1	5.7	9.6	26.0	3.8	65.9	32.3	68.6	79.8	11.2	36.3
Persicaria amphibia	Forb	1.1	89.7	10.3	6.4	14.1	25.0	2.9	66.2	17.5	42.1	44.3	2.2	24.6
Rosa acicularis	Browse	0.8	90.1	9.9	4.5	7.8	18.0	3.1	74.7	17.4	43.5	48.5	5.0	26.1
Populus balsamifera	Browse	0.5	92.2	7.8	6.5	9	19.0	4.2	72.9	19.5	45.7	55.4	9.7	26.2
Winter mean (standard deviation)														
	Browse	48.6	91.5 (2.3)	8.5 (2.3)	4.8 (1.6)	7.7 (3.0)	22.3 (3.6)	4.9 (2.2)	74.1 (3.1)	18.3 (2.6)	45.0 (4.9)	53.5 (6.2)	8.5 (3.6)	26.7 (4.7)
	Forb	1.1	89.7 (0)	10.3 (0)	6.4 (0)	14.1 (0)	25.0 (0)	2.9 (0)	66.2 (0)	17.5 (0)	42.1 (0)	44.3 (0)	2.2 (0)	24.6 (0)
	Graminoid	33.6	91.8 (0.9)	8.2 (0.9)	6.3 (0.6)	6.9 (1.7)	30.2 (2.2)	1.7 (0.3)	76.9 (2.1)	8.4 (2.2)	44.3 (1.6)	71.2 (0.5)	26.9 (3.7)	35.9 (0.9)
	Other	1.3	84.9 (0)	15.1 (0)	5.7 (0)	9.6 (0)	26.0 (0)	3.8 (0)	65.9 (0)	32.3 (0)	68.6 (0)	79.8 (0)	11.2 (0)	36.3 (0)
	Total	83.5	91.1 (2.5)	8.9 (2.5)	5.4 (1.4)	7.6 (2.5)	25.4 (4.8)	3.7 (2.2)	74.5 (7.2)	15.8 (6.8)	46.5 (10.7)	61.7 (5.4)	15.2 (9.6)	30.7 (5.9)
Spring raw values														
Species	FG	RRA	DM	Moisture	Ash	CP	SP	Fat	Carbs	Lign	ADF	NDF	Hemi	Cell
Carex aquatilis	Graminoid	19.0	92.7	7.3	6.6	13.5	21.0	1.8	70.8	4.2	35.8	66.7	30.9	31.6
Carex atherodes	Graminoid	19.0	91.4	8.6	8.1	14.3	30.0	1.5	67.5	4.8	34	62.4	28.4	29.2

Carex utriculata	Graminoid	19.0	91.8	8.2	7.3	14.7	34.0	2.1	67.7	3.4	34.6	65.1	30.5	31.2
Sphagnum spp.	Other	11.4	88.4	11.6	6.8	9.7	30.0	2.8	69.1	29.1	67.5	80.1	12.6	38.4
Salix spp.	Browse	9.9	89.7	10.3	5.1	17.3	19.0	5.2	62.2	16.1	30.2	39.7	9.5	14.1
Rosa acicularis	Browse	9.0	89.3	10.7	6.7	17.7	20.0	5.7	59.2	11.3	22.7	29.4	6.7	11.4
Populus tremuloides	Browse	6.6	91.5	8.5	4.7	17.5	19.0	7.4	61.9	19.1	30.3	31.3	1.0	11.2
Equisetum spp.	Other	6.0	91.6	8.4	18.6	13.2	23.0	2.3	57.5	3.5	24	36.2	12.2	20.5
Chamaenerion angustifolium	Forb	5.0	85.3	14.7	6.6	18.8	38.0	4.3	55.7	10.8	23.5	26.3	2.8	12.7
Poaceae	Graminoid	4.5	92.6	7.4	5.9	16.2	41.0	3.2	67.4	4.8	36.2	64.6	28.4	31.4
Cornus canadensis	Forb	2.1	87.7	12.3	9.9	14.1	20.0	3.2	60.5	10.2	28.9	32.6	3.7	18.7
Amelanchier alnifolia	Browse	1.7	89.8	10.2	6.4	20.5	33.0	6.1	56.8	21.9	36.9	41.3	4.4	15.0
Sparganium eurycarpum	Graminoid	1.3	92	8	7.8	18.1	19.0	5.5	60.6	5.5	30.2	52.6	22.4	24.7
Ribes spp.	Browse	0.8	89.3	10.7	8.2	21.2	23.0	3.9	56.0	8.1	16.9	21.6	4.7	8.8
Vaccinium myrtilloides	Browse	0.8	87.8	12.2	3.2	13.4	5.0	4.1	67.0	10.8	22.5	26.9	4.4	11.7
Rhododendron groenlandicum	Browse	0.6	90.5	9.5	3.6	11	11.0	10.5	65.4	14.2	25.9	32.4	6.5	11.7
Cornus sericea	Browse	0.5	89.5	10.5	7.1	24.9	25.0	6.0	51.6	8.1	17.2	24.2	7.0	9.1
Populus balsamifera	Browse	0.3	92	8	6.6	18.2	15.0	7.8	59.4	15.7	30.6	31.1	0.5	14.9
Asteraceae	Forb	0.2	90.7	9.3	11.6	12.6	30.0	4.4	62.1	7.9	26.2	26.6	0.4	18.3
Lathyrus	Forb	0.2	92.2	7.8	7.9	20.1	35.0	4.7	59.5	9.4	36.1	45.3	9.2	26.7

spp.														
Rubus spp.	Forb	0.1	89.1	11	6.6	12.5	9.0	3.6	66.2	6.4	24.9	33.4	8.5	18.5
Spring mean (standard deviation)														
	Browse	30.2	89.9 (1.3)	10.1 (1.3)	5.7 (1.7)	18.0 (4.1)	18.9 (8.1)	6.3 (2.0)	59.9 (4.8)	13.9 (6.7)	25.9 (6.5)	30.9 (4.8)	5.0 (2.9)	12.0 (2.3)
	Forb	7.6	89.0 (2.7)	11.0 (2.7)	8.5 (2.2)	15.6 (3.6)	26.4 (11.9)	4.1 (0.6)	60.8 (1.8)	8.9 (5.0)	27.9 (7.7)	32.8 (3.9)	4.9 (3.8)	19.0 (5.0)
	Graminoid	62.8	92.1 (0.5)	7.9 (0.5)	7.1 (0.9)	15.4 (1.8)	29.0 (9.1)	2.8 (1.6)	66.8 (0.8)	4.5 (2.4)	34.2 (5.6)	62.3 (3.7)	28.1 (3.4)	29.6 (2.9)
	Other	17.4	90.0 (2.3)	10.0 (2.3)	12.7 (8.3)	11.5 (2.5)	26.5 (4.9	2.6 (0.3)	63.3 (18.1)	16.3 (30.8)	45.8 (31.0)	58.2 (8.2)	12.4 (0.3)	29.5 (12.7)
	Total	80.0	90.2 (1.9)	9.8 (1.9)	7.4 (3.2)	16.2 (3.8)	23.8 (9.6)	4.6 (2.2)	62.1 (6.7)	10.7 (10.4)	30.2 (17.0)	41.4 (5.2)	11.2 (10.4)	19.5 (8.8)
Summer raw values														
Rosa acicularis	Browse	37.1	87.3	12.7	7.4	12.4	18.0	5.2	62.4	8.4	21.7	26.4	4.7	13.3
Chamaenerion angustifolium	Forb	20.7	87.1	12.9	7.5	16.8	28.0	5.0	57.7	4.0	12.8	19.4	6.6	8.8
Ribes spp.	Browse	6.3	90.7	9.3	12.0	11.5	14.0	3.0	64.2	9.3	24.9	34.7	9.8	15.6
Salix spp.	Browse	4.6	87.6	12.4	6.8	14.2	9.0	6.9	59.7	17.3	31.2	38.3	7.1	13.9
Potentilla palustris	Forb	3.5	90.0	10.0	8.7	12.0	19.0	6.3	63.1	11.5	31.5	35.2	3.7	20.0
Vaccinium myrtilloides	Browse	3.5	87.6	12.5	3.7	11.2	2.0	4.7	67.9	14.0	24.5	35.4	10.9	10.5
Persicaria amphibia	Forb	2.7	89.1	10.9	6.6	18.9	20.0	4.1	59.5	14.7	33.5	35.1	1.6	18.8
Lathyrus spp.	Forb	2.5	93.0	7.0	8.3	18.6	36.0	4.6	61.6	9.5	37.4	50.2	12.8	27.9
Asteraceae	Forb	1.1	92.3	7.7	7.8	13.0	33.0	3.9	67.6	12.4	40.2	48.5	8.3	27.8
Equisetum	Other	1.1	93.5	6.5	22.9	13.3	24.0	4.0	53.4	3.8	33.1	40.7	7.6	29.3

spp.														
Cornus canadensis	Browse	1.0	87.4	12.6	11.3	10.3	5.0	4.4	61.4	6.3	17.1	26.3	9.2	10.8
Viburnum edule	Browse	1.0	89.3	10.7	11.9	13.6	15.0	9.3	54.5	17.4	34.1	40.1	6.0	16.7
Amelanchier alnifolia	Browse	0.7	90.5	9.5	7.9	14.2	15.0	9.8	58.6	23.4	37.8	42.5	4.7	14.4
Poaceae	Graminoid	0.3	92.5	7.5	5.6	14.7	37.0	3.0	69.2	7.7	40.5	71.0	30.5	32.8
Cornus sericea	Browse	0.2	88.7	11.3	9.8	15.2	21.0	7.3	56.4	6.5	17.6	20.3	2.7	11.1
Carex aquatilis	Graminoid	0.1	91.7	8.3	7.5	12.9	19.0	2.1	69.2	4.3	35.4	63.0	27.6	31.1
Carex atherodes	Graminoid	0.1	91.2	8.8	7.8	13.3	31.0	2.8	67.3	3.1	32.0	59.1	27.1	28.9
Carex utriculata	Graminoid	0.1	91.7	8.3	6.8	11.6	19.0	3.8	69.5	4.1	34.3	65.3	31.0	30.2
Galium spp.	Forb	0.1	91.7	8.3	7.3	13.0	27.0	4.2	67.3	10.0	32.4	37.7	5.3	22.4
				Summer mean (standard deviation)										
	Browse	54.4	88.6 (1.4)	11.4 (1.4)	8.9 (2.9)	12.8 (1.7)	12.4 (6.5)	6.3 (2.4)	12.8 (6.2)	26.1 (7.6)	33.0 (7.8)	60.6 (4.3)	6.9 (2.9)	13.3 (2.3)
	Forb	30.6	90.5 (2.2)	9.5 (2.2)	7.7 (0.7)	15.4 (3.1)	27.2 (6.8)	4.7 (0.9)	10.4 (3.6)	31.3 (9.6)	37.7 (11.1)	62.8 (4.0)	6.4 (3.9)	21.0 (7.1)
	Graminoid	0.6	91.8 (0.5)	8.2 (0.5)	6.9 (1.0)	13.1 (1.3)	26.5 (9.0)	2.9 (0.7)	4.8 (2.0)	35.6 (3.6)	64.6 (5.0)	68.8 (1.0)	29.1 (2.0)	30.8 (1.6)
	Other	1.1	93.5 (0)	6.5 (0)	22.9 (0)	13.3 (0)	24.0 (0)	4.0 (0)	3.8 (0)	33.1 (0)	40.7 (0)	53.4 (0)	7.6 (0)	29.3 (0)
	Total	86.7	90.2 (2.1)	9.9 (2.1)	8.8 (4.0)	13.7 (2.3)	20.6 (9.8)	5.0 (2.1)	9.9 (5.6)	30.1 (8.1)	41.5 (14.8)	62.6 (5.2)	11.4 (9.8)	20.2 (8.2)

Appendix C: Summary of the dates (dd/mm/yyyy) for the start, peak and end of green-up (as measured my instantaneous rate of green-up) within the spring range and the dates of the start and end of ingress and egress for every individual collared wood bison (*Bison bison athabascae*).

Table C.1: Summary of the dates (dd/mm/yyyy) for the start, peak and end of green-up (as measured my instantaneous rate of green-up) within the spring range and the dates of the start and end of ingress and egress for every individual collared wood bison (*Bison bison athabascae*).

Year	**Bison ID**	**Spring start**	**Spring peak**	**Spring end**	**Ingress start**	**Ingress end**	**Egress start**	**Egress end**
2013	33912	05/03/2013	09/04/2013	27/05/2013	19/05/2013	23/05/2013	29/06/2013	03/07/2013
2013	33913	03/05/2013	09/04/2013	27/05/2013	14/05/2013	26/05/2013	29/06/2013	09/07/2013
2013	33914	03/05/2013	09/04/2013	27/05/2013	18/05/2013	27/05/2013	29/06/2013	16/07/2013
2013	33915	03/05/2013	09/04/2013	27/05/2013	18/05/2013	23/05/2013	29/06/2013	16/07/2013
2013	33916	03/05/2013	09/04/2013	27/05/2013	15/05/2013	26/05/2013	29/06/2013	16/07/2013
2013	33917	03/05/2013	09/04/2013	27/05/2013	24/05/2013	28/05/2013	29/06/2013	15/07/2013
2013	33919	03/05/2013	09/04/2013	27/05/2013	14/05/2013	21/05/2013	29/06/2013	09/07/2013
2013	33920	03/05/2013	09/04/2013	27/05/2013	18/05/2013	26/05/2013	28/06/2013	09/07/2013
2013	33921	03/05/2013	09/04/2013	27/05/2013	15/05/2013	21/05/2013	29/06/2013	09/07/2013
2013	33923	03/05/2013	09/04/2013	27/05/2013	02/06/2013	04/06/2013	28/06/2013	16/07/2013
2014	33912	07/05/2014	07/04/2014	06/07/2014	04/06/2014	07/06/2014	26/06/2014	30/06/2014
2014	33913	07/05/2014	07/04/2014	06/07/2014	03/06/2014	07/06/2014	26/06/2014	02/07/2014
2014	33914	07/05/2014	07/04/2014	06/07/2014	29/05/2014	31/05/2014	26/06/2014	02/07/2014
2014	33917	07/05/2014	07/04/2014	06/07/2014	29/05/2014	02/06/2014	26/06/2014	03/07/2014
2014	33919	07/05/2014	07/04/2014	06/07/2014	02/06/2014	06/06/2014	26/06/2014	30/06/2014
2014	33920	07/05/2014	07/04/2014	06/07/2014	22/05/2014	31/05/2014	26/06/2014	30/06/2014
2014	33922	07/05/2014	07/04/2014	06/07/2014	29/05/2014	02/06/2014	25/06/2014	05/07/2014
2014	33923	07/05/2014	07/04/2014	06/07/2014	28/05/2014	07/06/2014	26/06/2014	08/07/2014
2014	35447	07/05/2014	07/04/2014	06/07/2014	28/05/2014	31/05/2014	26/06/2014	03/07/2014
2014	35449	07/05/2014	07/04/2014	06/07/2014	20/05/2014	31/05/2014	26/06/2014	03/07/2014
2014	35450	07/05/2014	07/04/2014	06/07/2014	26/05/2014	03/06/2014	26/06/2014	03/07/2014
2014	35451	07/05/2014	07/04/2014	06/07/2014	27/05/2014	31/05/2014	26/06/2014	02/07/2014
2014	35452	07/05/2014	07/04/2014	06/07/2014	02/06/2014	06/06/2014	26/06/2014	30/06/2014
2014	35453	07/05/2014	07/04/2014	06/07/2014	20/05/2014	31/05/2014	26/06/2014	30/06/2014
2014	35454	07/05/2014	07/04/2014	06/07/2014	20/05/2014	31/05/2014	26/06/2014	03/07/2014
2014	35455	07/05/2014	07/04/2014	06/07/2014	20/05/2014	07/06/2014	26/06/2014	02/07/2014
2014	35456	07/05/2014	07/04/2014	06/07/2014	03/06/2014	07/06/2014	26/06/2014	30/06/2014
2015	33912	29/04/2015	31/03/2015	28/05/2015	29/04/2015	03/05/2015	15/06/2015	05/07/2015
2015	33913	29/04/2015	31/03/2015	28/05/2015	19/05/2015	21/05/2015	16/06/2015	02/07/2015
2015	33914	29/04/2015	31/03/2015	28/05/2015	15/05/2015	23/05/2015	15/06/2015	27/06/2015
2015	33917	29/04/2015	31/03/2015	28/05/2015	16/05/2015	21/05/2015	15/06/2015	05/07/2015
2015	33919	29/04/2015	31/03/2015	28/05/2015	19/05/2015	21/05/2015	15/06/2015	02/07/2015
2015	33922	29/04/2015	31/03/2015	28/05/2015	13/05/2015	15/05/2015	15/06/2015	02/07/2015
2015	33923	29/04/2015	31/03/2015	28/05/2015	28/04/2015	30/04/2015	15/06/2015	05/07/2015
2015	35447	29/04/2015	31/03/2015	28/05/2015	25/04/2015	09/05/2015	15/06/2015	05/07/2015
2015	35448	29/04/2015	31/03/2015	28/05/2015	19/05/2015	23/05/2015	18/07/2015	21/07/2015
2015	35449	29/04/2015	31/03/2015	28/05/2015	23/05/2015	28/05/2015	15/06/2015	05/07/2015
2015	35451	29/04/2015	31/03/2015	28/05/2015	19/05/2015	21/05/2015	23/06/2015	05/07/2015
2015	35452	29/04/2015	31/03/2015	28/05/2015	19/05/2015	21/05/2015	15/06/2015	29/06/2015

2015	35453	29/04/2015	31/03/2015	28/05/2015	28/04/2015	30/04/2015	15/06/2015	24/06/2015
2015	35454	29/04/2015	31/03/2015	28/05/2015	19/05/2015	24/05/2015	18/07/2015	21/07/2015
2015	35454	29/04/2015	31/03/2015	28/05/2015	13/05/2015	20/05/2015	15/06/2015	29/06/2015
2015	35456	29/04/2015	31/03/2015	28/05/2015	19/05/2015	21/05/2015	05/07/2015	09/07/2015
2016	41225	27/04/2016	26/03/2016	29/05/2016	24/04/2016	02/05/2016	06/06/2016	14/06/2016
2016	41226	27/04/2016	26/03/2016	30/05/2016	28/04/2016	03/05/2016	11/06/2016	15/06/2016
2016	41227	27/04/2016	26/03/2016	31/05/2016	30/04/2016	02/05/2016	06/06/2016	11/06/2016
2016	41228	27/04/2016	26/03/2016	01/06/2016	25/04/2016	05/05/2016	11/06/2016	15/06/2016
2016	41229	27/04/2016	26/03/2016	02/06/2016	28/04/2016	03/05/2016	13/06/2016	16/06/2016
2016	41231	27/04/2016	26/03/2016	04/06/2016	25/04/2016	02/05/2016	06/06/2016	14/06/2016
2016	41232	27/04/2016	26/03/2016	05/06/2016	24/04/2016	08/05/2016	11/06/2016	15/06/2016
2016	41234	27/04/2016	26/03/2016	06/06/2016	28/04/2016	02/05/2016	06/06/2016	14/06/2016
2016	41236	27/04/2016	26/03/2016	07/06/2016	25/04/2016	02/05/2016	06/06/2016	14/06/2016
2016	41237	27/04/2016	26/03/2016	08/06/2016	25/04/2016	30/04/2016	06/06/2016	14/06/2016
2016	41238	27/04/2016	26/03/2016	09/06/2016	05/05/2016	10/05/2016	13/06/2016	16/06/2016
2017	23268	28/04/2017	30/03/2017	27/05/2017	19/05/2017	21/05/2017	20/06/2017	12/07/2017
2017	23269	28/04/2017	30/03/2017	27/05/2017	05/05/2017	19/05/2017	18/06/2017	28/06/2017
2017	23270	28/04/2017	30/03/2017	27/05/2017	21/05/2017	03/06/2017	27/06/2017	13/07/2017
2017	23271	28/04/2017	30/03/2017	27/05/2017	21/05/2017	29/05/2017	13/06/2017	12/07/2017
2017	23272	28/04/2017	30/03/2017	27/05/2017	19/05/2017	23/05/2017	20/06/2017	25/06/2017
2017	23274	28/04/2017	30/03/2017	27/05/2017	07/05/2017	18/05/2017	29/06/2017	12/07/2017
2017	23275	28/04/2017	30/03/2017	27/05/2017	19/05/2017	25/05/2017	20/06/2017	13/07/2017
2017	23276	28/04/2017	30/03/2017	27/05/2017	03/05/2017	18/05/2017	28/06/2017	13/07/2017
2017	23277	28/04/2017	30/03/2017	27/05/2017	19/05/2017	23/05/2017	18/06/2017	26/06/2017
2017	41225	28/04/2017	30/03/2017	27/05/2017	21/05/2017	01/06/2017	27/06/2017	12/07/2017
2017	41226	28/04/2017	30/03/2017	27/05/2017	18/05/2017	23/05/2017	17/06/2017	25/06/2017
2017	41228	28/04/2017	30/03/2017	27/05/2017	21/05/2017	01/06/2017	27/06/2017	13/07/2017
2017	41229	28/04/2017	30/03/2017	27/05/2017	18/05/2017	24/05/2017	19/06/2017	29/06/2017
2017	41230	28/04/2017	30/03/2017	27/05/2017	19/05/2017	21/05/2017	23/06/2017	10/07/2017
2017	41231	28/04/2017	30/03/2017	27/05/2017	08/05/2017	19/05/2017	20/06/2017	12/07/2017
2017	41232	28/04/2017	30/03/2017	27/05/2017	18/05/2017	24/05/2017	18/06/2017	14/07/2017
2017	41236	28/04/2017	30/03/2017	27/05/2017	19/05/2017	26/05/2017	19/06/2017	13/07/2017
2017	41237	28/04/2017	30/03/2017	27/05/2017	06/05/2017	18/05/2017	21/06/2017	13/07/2017
2018	6343	24/04/2018	22/03/2018	26/05/2018	09/06/2018	15/06/2018	20/06/2018	02/07/2018
2018	6344	24/04/2018	22/03/2018	26/05/2018	09/06/2018	15/06/2018	20/06/2018	02/07/2018
2018	6345	24/04/2018	22/03/2018	26/05/2018	06/05/2018	24/05/2018	10/06/2018	23/06/2018
2018	6347	24/04/2018	22/03/2018	26/05/2018	20/05/2018	26/05/2018	02/07/2018	06/07/2018
2018	6348	24/04/2018	22/03/2018	26/05/2018	21/05/2018	26/05/2018	18/06/2018	23/06/2018
2018	6350	24/04/2018	22/03/2018	26/05/2018	08/05/2018	28/05/2018	17/06/2018	28/06/2018
2018	6351	24/04/2018	22/03/2018	26/05/2018	06/05/2018	13/05/2018	20/06/2018	01/07/2018
2018	23269	24/04/2018	22/03/2018	26/05/2018	19/05/2018	30/05/2018	16/06/2018	21/06/2018
2018	23270	24/04/2018	22/03/2018	26/05/2018	06/05/2018	14/05/2018	18/06/2018	28/06/2018
2018	23274	24/04/2018	22/03/2018	26/05/2018	06/05/2018	14/05/2018	16/06/2018	21/06/2018
2018	23275	24/04/2018	22/03/2018	26/05/2018	09/06/2018	11/06/2018	19/06/2018	03/07/2018
2018	23277	24/04/2018	22/03/2018	26/05/2018	20/05/2018	27/05/2018	16/06/2018	21/06/2018
2018	41225	24/04/2018	22/03/2018	26/05/2018	21/05/2018	26/05/2018	19/06/2018	19/06/2018
2018	41226	24/04/2018	22/03/2018	26/05/2018	09/06/2018	11/06/2018	20/06/2018	02/07/2018
2018	41228	24/04/2018	22/03/2018	26/05/2018	06/05/2018	14/05/2018	16/06/2018	29/06/2018
2018	41230	24/04/2018	22/03/2018	26/05/2018	08/05/2018	14/05/2018	21/06/2018	03/07/2018
2018	41236	24/04/2018	22/03/2018	26/05/2018	06/05/2018	13/05/2018	16/06/2018	20/06/2018
2018	41237	24/04/2018	22/03/2018	26/05/2018	06/05/2018	25/05/2018	19/06/2018	21/06/2018
2019	6345	01/05/2019	31/03/2019	01/06/2019	09/05/2019	21/05/2019	30/06/2019	29/07/2019
2019	6350	01/05/2019	31/03/2019	01/06/2019	11/05/2019	20/05/2019	05/07/2019	29/07/2019

2019	23275	01/05/2019	31/03/2019	01/06/2019	03/05/2019	19/05/2019	06/07/2019	30/07/2019
2019	23277	01/05/2019	31/03/2019	01/06/2019	09/05/2019	20/05/2019	01/06/2019	07/06/2019
2019	37488	01/05/2019	31/03/2019	01/06/2019	08/05/2019	19/05/2019	11/07/2019	19/07/2019
2019	37489	01/05/2019	31/03/2019	01/06/2019	01/06/2019	10/06/2019	06/07/2019	25/07/2019
2019	37490	01/05/2019	31/03/2019	01/06/2019	16/05/2019	25/05/2019	08/07/2019	16/07/2019
2019	37491	01/05/2019	31/03/2019	01/06/2019	07/05/2019	23/05/2019	03/07/2019	30/07/2019
2019	37492	01/05/2019	31/03/2019	01/06/2019	02/06/2019	08/06/2019	05/07/2019	31/07/2019
2019	37495	01/05/2019	31/03/2019	01/06/2019	09/05/2019	25/05/2019	27/06/2019	29/07/2019
2019	37497	01/05/2019	31/03/2019	01/06/2019	09/05/2019	19/05/2019	06/07/2019	29/07/2019

Appendix D: Coefficients, standard errors, and p-values for the most parsimonious logistic regression models during ingress and egress. These statistics are presented in two tables; one for each migration period. Both tables include statistics for the selected 2013 – 2019 and just 2019 models. Landcover covariates refer to landcover types as defined by Duck's Unlimited's Enhanced Wetland Classification.

Table D.1: Statistics from the most parsimonious logistic regression models during the ingress migration for the entire study period (2013 – 2019) and a single year 2019. Models were separated into these two time frames because wolves were only collared during 2019, which is why the wolf row is black out in the 2013 – 2019 section. The first 27 rows provide selection statistics for landcover types as described by Ducks Unlimited's Enhanced Wetland Classification (Ducks Unlimited Canada, 2016.), and are relative to the most common landcover type in the study area (upland deciduous). Covariate abbreviations are as follows: normalized difference vegetation index (NDVI), integrated NDVI (iNDVI), Brownian bridge movement models (BBMM), instantaneous rate of green-up (IRG), and compound topographic index (CTI).

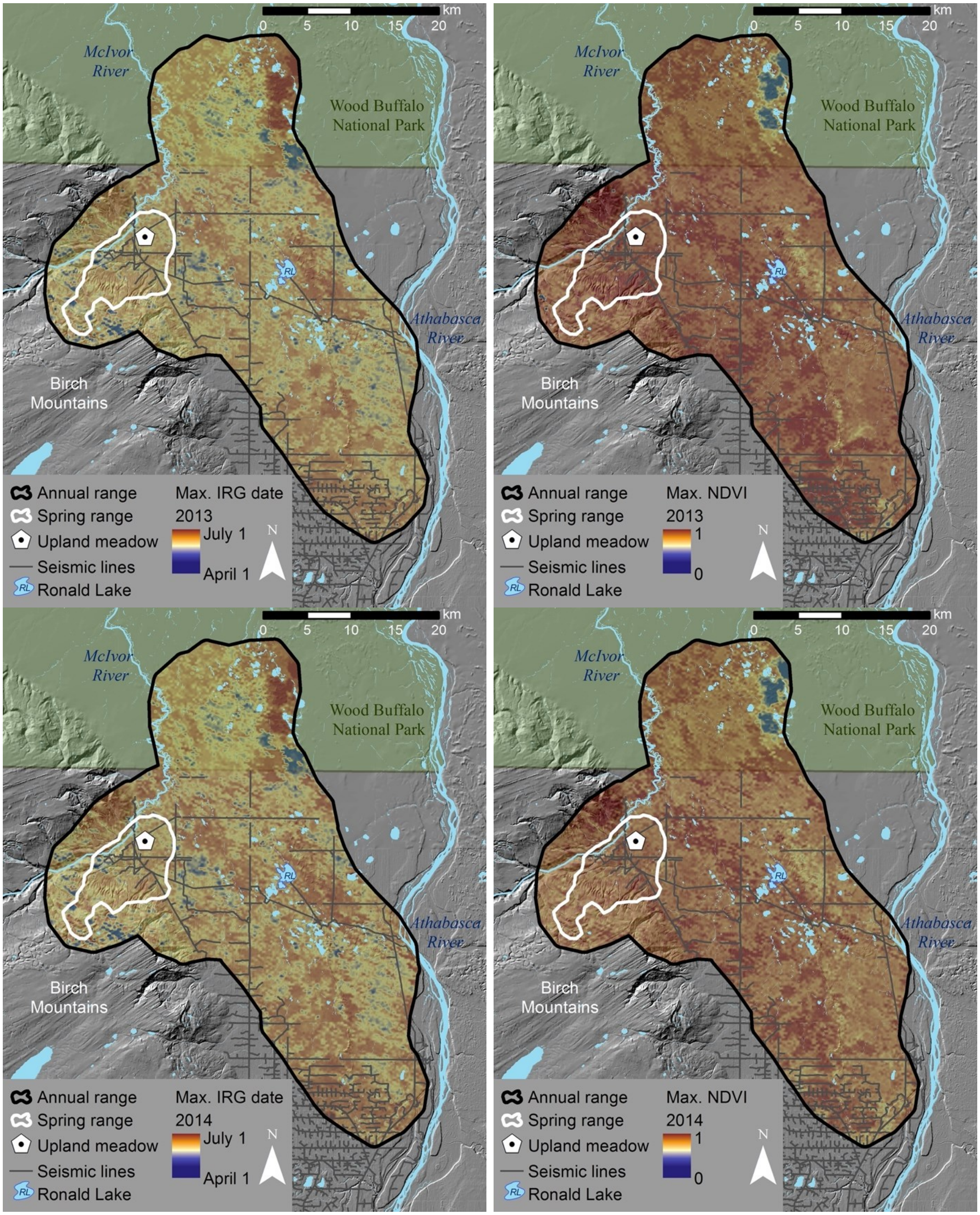
Ingress	**2013 - 2019**			**2019**		
Covariates	**Beta**	**SE**	**p-value**	**Beta**	**SE**	**p-value**
Open Water	-15.000	786.400	0.998	NA	NA	NA
Aquatic Bed	0.113	0.067	0.095	0.562	0.226	0.013
Mudflats	-1.326	0.068	0.069	0.271	1.200	0.821
Emergent Marsh	0.802	0.064	<0.001	1.273	0.203	<0.001
Meadow Marsh	1.299	0.041	<0.001	1.454	0.135	<0.001
Graminoid Rich Fen	0.921	0.063	<0.001	0.885	0.188	<0.001
Graminoid Poor Fen	-0.195	0.081	0.017	-0.716	0.358	0.045
Shrubby Rich Fen	0.186	0.051	<0.001	0.242	0.150	0.108
Shrubby Poor Fen	0.169	0.057	0.003	250.000	0.176	0.154
Treed Rich Fen	0.086	0.042	0.039	0.231	0.144	0.108
Treed Poor Fen	-0.123	0.050	0.014	0.240	0.163	0.141
Open Bog	0.444	0.569	0.436	-13.610	895.200	0.999
Shrubby Bog	-0.340	0.195	0.081	-13.360	111.700	0.990
Treed Bog	0.510	0.092	<0.001	0.855	0.435	0.049
Shrub Swamp	0.306	0.042	<0.001	0.727	0.119	<0.001
Hardwood Swamp	0.071	0.065	0.272	0.516	0.192	0.007
Mixed-wood Swamp	-0.183	0.104	0.080	0.297	0.319	0.352
Tamarack Swamp	-0.400	0.240	0.950	-0.207	0.562	0.713
Conifer Swamp	-0.088	0.050	0.075	0.086	0.209	0.680
Upland Conifer	-0.090	0.058	0.117	-0.234	0.383	0.541
Upland Mixed-wood	0.515	0.335	0.124	-0.211	1.143	0.854
Upland other	-12.740	45.390	0.978	-1.382	154.400	0.999
Cutblock	-1.036	1.045	0.321	NA	NA	NA
Anthropogenic	-12.690	53.840	0.981	-1.328	243.400	0.999
Cloud	-13.290	68.970	0.985	-1.139	712.000	0.999
Cloud Shadow	-12.440	38.520	0.974	-1.267	172.300	0.994

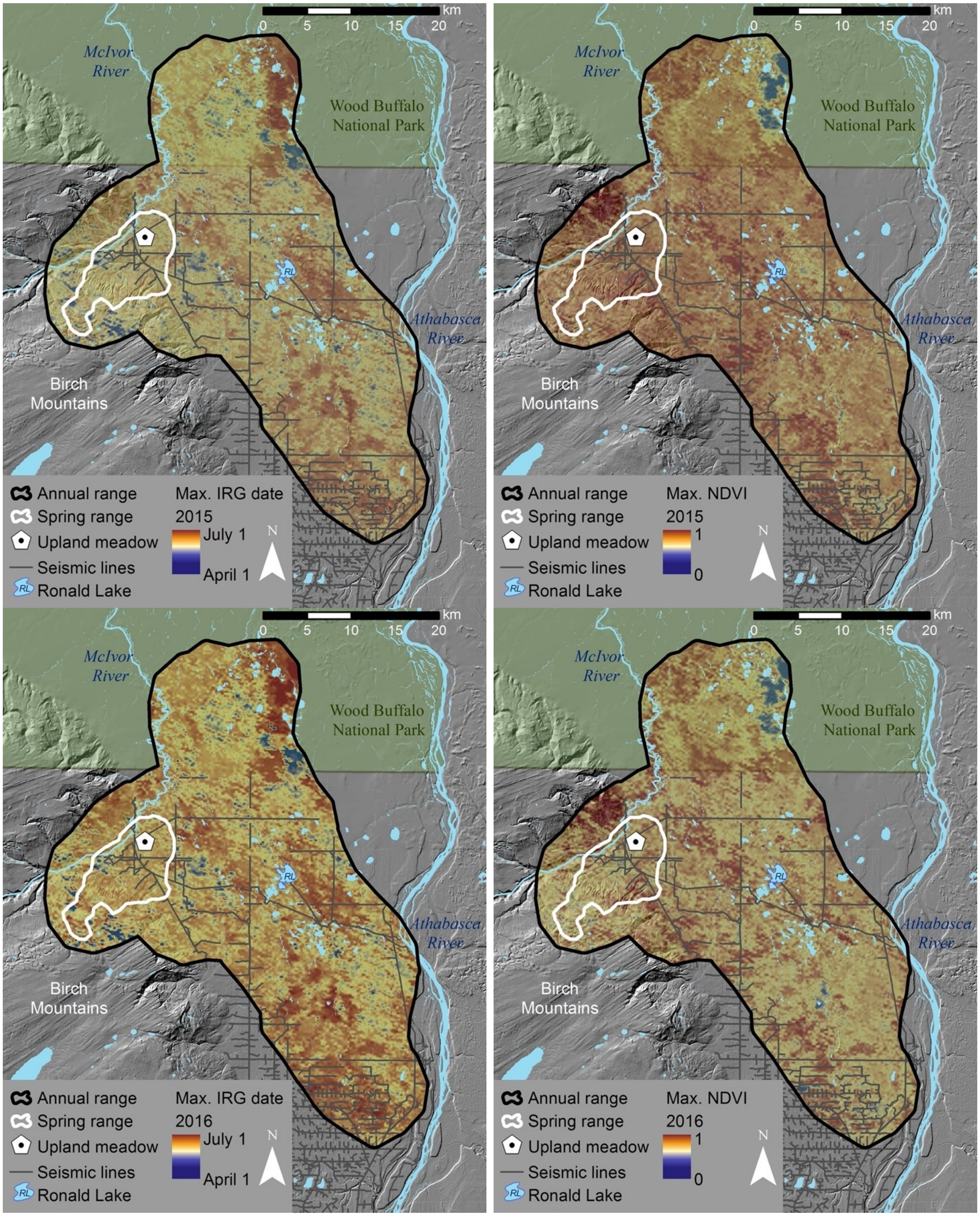
Upland Pine	0.326	0.049	<0.001	0.277	0.263	0.292
NDVI	-1.572	0.017	<0.001	-4.490	0.449	<0.001
iNDVI	0.002	<0.001	0.003	0.008	0.002	<0.001
Wolf BBMM	[redacted]	[redacted]	[redacted]	33.950	33.790	0.315
IRG	0.308	0.058	<0.001	1.058	2.879	<0.001
Distance to water	<0.001	<0.001	<0.001	<0.001	<0.001	0.601
Distance to seismic line	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
CTI	0.015	0.005	0.005	0.005	0.018	0.783
Distance to next location	-0.003	<0.001	<0.001	-0.002	<0.001	<0.001

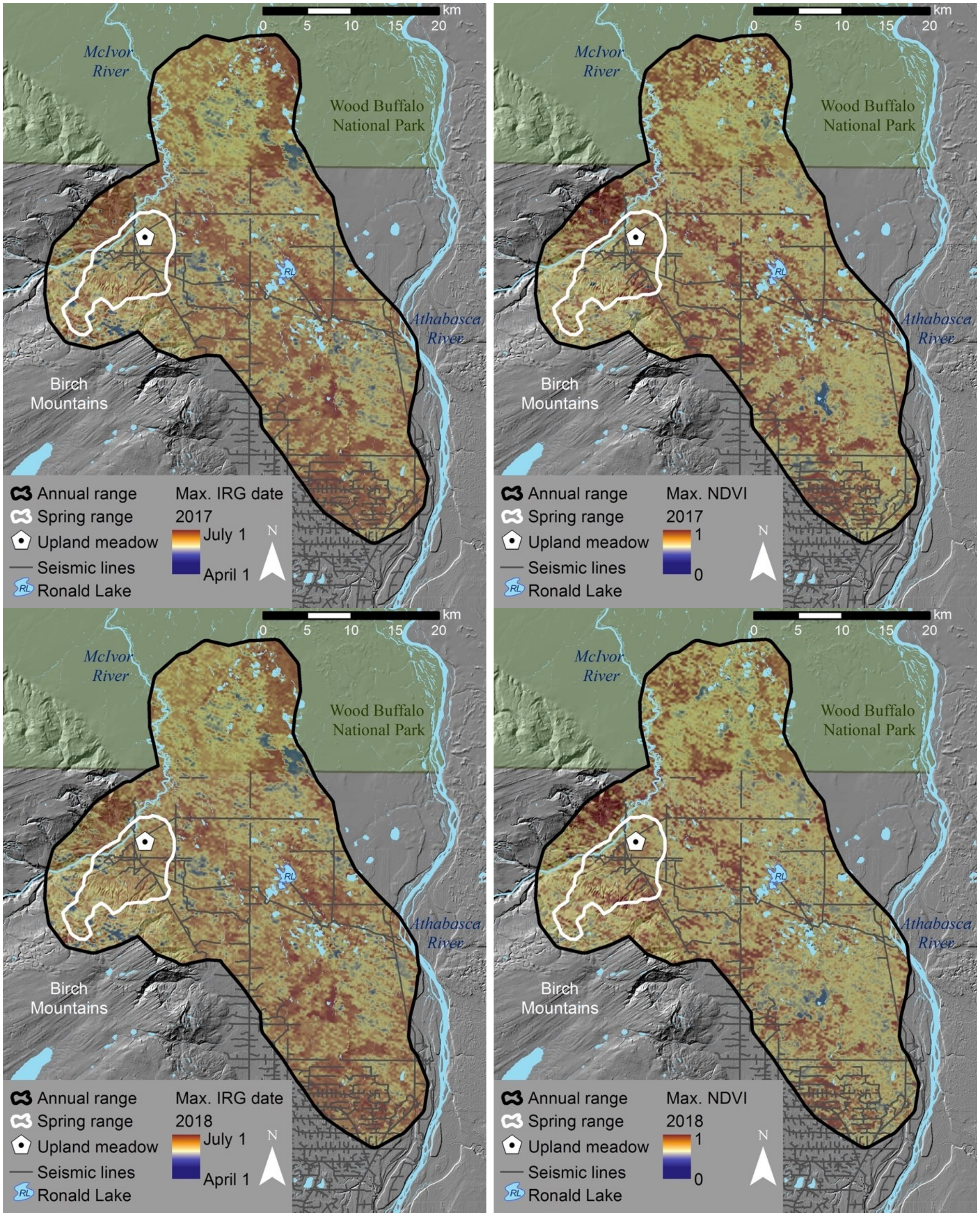
Table D.2: Statistics from the most parsimonious logistic regression models during the egress migration for the entire study period (2013 – 2019) and a single year 2019. Models were separated into these two time frames because wolves were only collared during 2019, which is why the wolf row is blacked out in the 2013 – 2019 section. The first 27 rows provide selection statistics for landcover types as described by Ducks Unlimited's Enhanced Wetland Classification (Ducks Unlimited Canada, 2016.), and are relative to the most common landcover type in the study area (upland deciduous). Covariate abbreviations are as follows: normalized difference vegetation index (NDVI), integrated NDVI (iNDVI), Brownian bridge movement models (BBMM), instantaneous rate of green-up (IRG), and compound topographic index (CTI).

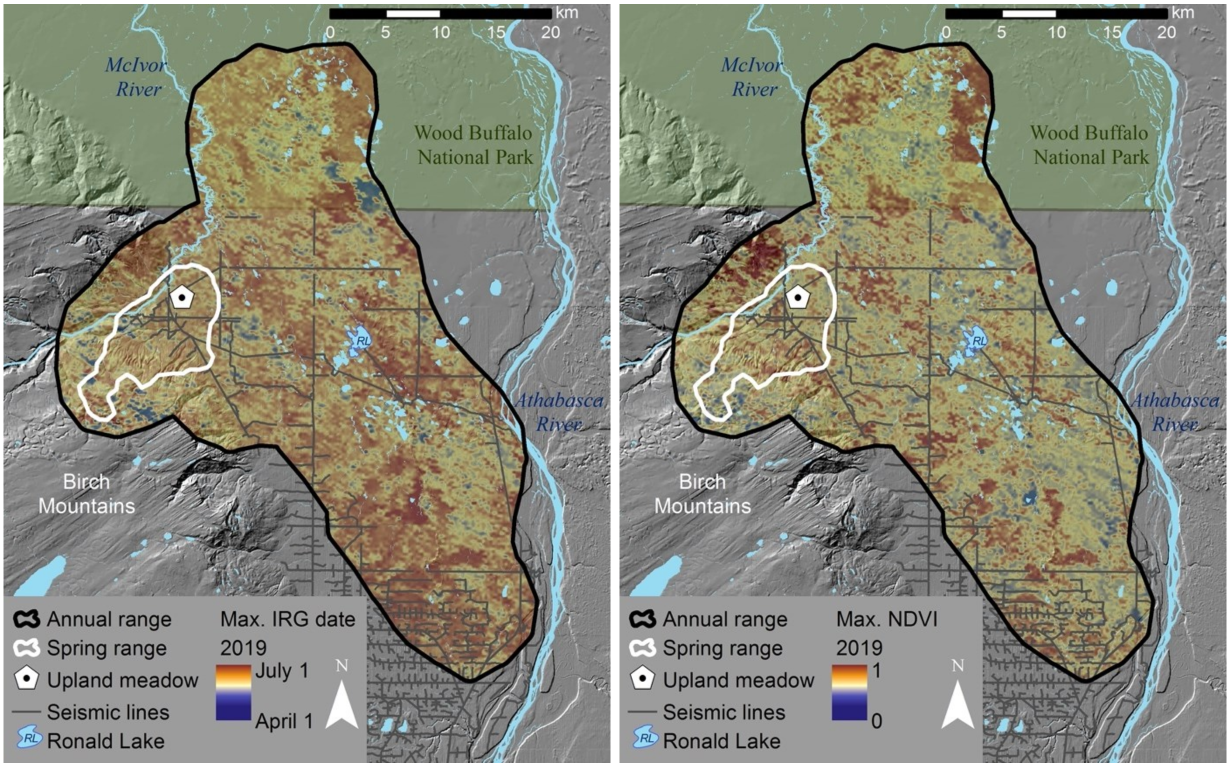
Egress	**2013 - 2019**			**2019**		
Covariates	**Beta**	**SE**	**p-value**	**Beta**	**SE**	**p-value**
Open Water	-13.160	722.500	0.999	NA	NA	NA
Aquatic Bed	-0.923	0.106	<0.001	-0.019	0.489	0.969
Mudflats	-1.782	0.592	0.003	-14.680	325.900	0.996
Emergent Marsh	-0.170	0.112	0.129	0.970	0.485	0.045
Meadow Marsh	0.425	0.062	<0.001	0.569	0.325	0.080
Graminoid Rich Fen	-0.617	0.143	<0.001	-0.127	0.360	0.724
Graminoid Poor Fen	-0.028	0.086	0.747	-0.303	0.373	0.416
Shrubby Rich Fen	0.653	0.088	<0.001	0.161	0.345	0.641
Shrubby Poor Fen	-0.813	0.106	<0.001	-0.520	0.461	0.260
Treed Rich Fen	-0.205	0.042	<0.001	-0.255	0.183	0.164
Treed Poor Fen	-0.261	0.053	<0.001	0.024	0.196	0.904
Open Bog	-12.660	341.700	0.970	-15.000	561.700	0.260
Shrubby Bog	-1.462	0.263	<0.001	-0.844	0.625	0.177
Treed Bog	-0.829	0.275	0.003	-15.700	162.200	0.992
Shrub Swamp	-0.602	0.077	<0.001	-0.080	0.262	0.758
Hardwood Swamp	-0.164	0.090	0.674	-0.053	0.341	0.878
Mixed-wood Swamp	-0.196	0.115	0.089	0.323	0.463	0.485
Tamarack Swamp	-0.338	0.196	0.085	-0.629	0.815	0.440
Conifer Swamp	0.049	0.038	0.197	0.299	0.153	0.052
Upland Conifer	-0.172	0.045	<0.001	-0.373	0.295	0.206
Upland Mixed-wood	-12.110	107.700	0.991	NA	NA	NA
Upland other	-11.910	833.500	0.989	-14.980	263.300	0.999
Cutblock	NA	NA	NA	NA	NA	NA
Anthropogenic	-12.730	119.100	0.991	-13.980	329.300	0.999
Cloud	NA	NA	NA	NA	NA	NA
Cloud Shadow	NA	NA	NA	NA	NA	NA
Upland Pine	0.144	0.048	0.003	-0.297	0.330	0.369
NDVI	5.540	0.346	<0.001	9.775	1.813	<0.001
iNDVI	<0.001	<0.001	<0.001	0.018	0.003	<0.001
Wolf BBMM				23.980	174.100	0.168
IRG	0.761	0.080	<0.001	1.278	0.398	0.001
Distance to water	<0.001	<0.001	0.024	<0.001	<0.001	0.454
Distance to seismic line	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
CTI	0.001	0.006	0.819	0.039	0.026	0.130
Distance to next location	-0.003	<0.001	<0.001	-0.003	<0.001	<0.001

Appendix E: Date of maximum (max) instantaneous rate of green-up (IG) across the Ronald Lake wood bison (*Bison bison athabascae*) herd’s range. Here, we present maps of the max IRG for each year studied.




km
0 5 10 15 20
McIvor River
Wood Buffalo National Park
RL
Athabasca River
Birch Mountains
Annual range
Spring range
Upland meadow
Seismic lines
Ronald Lake
Max. IRG date 2015
July 1
April 1
N
Max. NDVI 2015
1
0
Max. IRG date 2016
Max. NDVI 2016


km
0 5 10 15 20
McIvor River
Wood Buffalo National Park
Athabasca River
Birch Mountains
RL
Annual range
Spring range
Upland meadow
Seismic lines
Ronald Lake
Max. IRG date 2017
July 1
April 1
Max. NDVI 2017
1
0
Max. IRG date 2018
Max. NDVI 2018
N


km
0
5
10
15
20
McIvor River
Wood Buffalo National Park
RL
Athabasca River
Birch Mountains
Annual range
Spring range
Upland meadow
Seismic lines
Ronald Lake
Max. IRG date 2019
July 1
April 1
N
km
0
5
10
15
20
McIvor River
Wood Buffalo National Park
RL
Athabasca River
Birch Mountains
Annual range
Spring range
Upland meadow
Seismic lines
Ronald Lake
Max. NDVI 2019
1
0
N