

**DENSITY-DEPENDENT HABITAT SELECTION BY PLAINS BISON IN  
GRASSLANDS NATIONAL PARK**

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By

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## ABSTRACT

Habitat selection models are commonly used to inform species conservation and management decisions; however, such models are context dependent, and results may vary depending on how close a population is to the carrying capacity. Despite acknowledgment that habitat selection is density dependent, relatively few researchers account in their analyses for changes in population density over time. Using a long-term dataset (11 years) for GPS-tracked Plains Bison (*Bison bison*) at Grasslands National Park, Saskatchewan, Canada ( $n = 22$ ), I examined seasonal habitat selection during a period of natural population growth following reintroduction and a period of population size manipulations. I used resource selection function (RSF) and latent selection difference function (LSD) analyses to model interactions between selection for vegetation productivity and distance from roads and population density. Bison showed decreased avoidance of roads as density increased and increased avoidance of roads following reductions in population density at most spatio-temporal scales examined. The relationship between selection for vegetation productivity and density was highly seasonally variable: bison selected for abundant forage when density was low and became less selective at high density during and immediately after calving. Consistent with predictions of density-dependent habitat selection, bison were free to select for abundant forage in areas far from human activity when density was low and were required to become less selective as density increased during seasons when the herd is most vulnerable and nutritional requirements are high. My study highlights the importance of considering changes in population density when using habitat selection models to inform decisions on wildlife population management.

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# 1 Introduction

## 1.1 Background

### 1.1.1 *Status of Plains Bison in North America*

Prior to European settlement, an estimated 15–100 million Plains Bison (*Bison bison bison*) roamed the Great Plains of North America (Dary 1989, Shaw 1995). By the end of the 1800s, overhunting, regional drought, introduced diseases, and competition with introduced livestock had reduced Plains Bison to fewer than 1000 individuals in privately owned herds scattered across the Great Plains and in a remote valley in what is now Yellowstone National Park (Gates et al. 2010). Since the late 1800s, conservation efforts by private citizens, the US National Park Service, Parks Canada Agency, and non-profit organizations have resulted in the numeric recovery of the species (Freese et al. 2007). More than 500,000 Plains Bison currently exist in North America (Sanderson et al. 2008). Despite the impressive increase in bison numbers over the past hundred years, the species is considered by many to be ecologically extinct across much of its historic range, meaning that even where bison are present, they are no longer fulfilling the ecological roles that they once did in those ecosystems (Freese et al. 2007, Sanderson et al. 2008). Of the 500,000 remaining Plains Bison, only approximately 20,000 exist in conservation herds that are managed in the public interest (Aune et al. 2017). Furthermore, the majority of conservation herds are small (less than 400 individuals) and occur on small ranges (less than 20 km<sup>2</sup>), and few herds are subject to the full suite of natural limiting factors including resource fluctuations, predation, and interspecific interactions (Gates et al. 2010).

Current obstacles facing bison restoration and conservation include lack of large, continuous tracts of suitable habitat, social intolerance of large, unfenced populations, risk of and

perceived risk of transmission of reportable livestock diseases, cattle gene introgression, and loss of genetic diversity (Gates et al. 2010, COSEWIC 2013, Aune et al. 2017). It is estimated that a population of at least 1,000 individuals is required in order to obtain a 90% probability of maintaining genetic heterozygosity over the next 200 years (Gross et al. 2006). Based on this information, a group of bison specialists produced a mission statement for the ecological recovery of the species which states that bison restoration will be achieved: “when multiple large herds move freely across extensive landscapes within all major habitats of their historic range (Sanderson et al. 2008).” Much of the historical range of the bison is currently being used for agriculture, cattle ranching, resource extraction, and urban development which constrains the opportunities for bison reintroductions and expansion of existing herds (Johnson et al. 1994, Boyd 2003).

### *1.1.2 Ecological and cultural significance of bison*

Once the most abundant and widely distributed ungulate in North America, the Plains Bison played an important role in ecosystem functioning on the Great Plains. Bison alter vegetation community composition and structure through selective grazing (Hartnett et al. 1996, Coppedge et al. 1998, Towne et al. 2005, Veen et al. 2008, McMillan 2017), wallowing (McMillan et al. 2011), browsing and physical damage to trees and shrubs (Bork et al. 2013, Beschta et al. 2020), and seed dispersal (Rosas et al. 2008). They aid in nitrogen cycling by converting large amounts of plant biomass to food for large predators (Mead 1899, Smith et al. 2000) and scavengers (Obermueller et al. 2021) as well as fertilizing the soil with their feces, urine, and carcasses (Day and Detling 1990, Frank and David Evans 1997, Knapp et al. 1999, Towne 2000, Augustine and Frank 2001). Through their effects on soil and vegetation bison indirectly influence the

distribution, abundance, diversity and behaviour of several other wildlife taxa including birds (Fuhlendorf et al. 2006, Powell 2006, Sliwinski 2011, Boyce et al. 2021, Fagre et al. 2022), cervids (Boyce et al. 2022), small mammals (Steuter et al. 1995, Matlack et al. 2001, Guiden et al. 2022), and arthropods (Jonas and Joern 2007, Joern and Laws 2013, Moran 2014, Nickell et al. 2018). While bison grazing can improve habitat for other species, intense bison grazing can also lead to the degradation of grassland (Grudzinski et al. 2016) and riparian habitats (Kaplan et al. 2021, Kauffman et al. 2023).

Before the near extinction of bison, the cultures and livelihoods of several Great Plains indigenous groups were tied to the seasonal movements of large bison herds (Haines 1995, Isenberg 2000). In fact, intentional overhunting of bison in the United States was carried out in part as a way of encouraging indigenous groups to move onto reserves (Isenberg 2000, Phippen 2016). Therefore, the return of bison to the landscape carries strong symbolic and cultural significance to many First Nations. As an iconic symbol of the vast open spaces of North America, bison hold a special place in the hearts of many. Bison were the first species to spark a widespread conservation movement in North America (Plumb and Sucec 2006) and today the chance of viewing bison herds in their natural habitats draws visitors to national, state, and provincial parks (Loomis and Caughlan 2004, Kolipinski et al. 2014). A study on the social and ecological impacts of bison reintroduction in northern Colorado found that restoration of the charismatic herbivore resulted in increased emotional attachment of visitors to the landscape (Wilkins et al. 2019).



### *1.1.3 Habitat selection*

Understanding the spatial and temporal patterns of habitat use by animals is one of the fundamental goals of ecology (Krebs 2001) and thus studies assessing the factors that drive species distributions, densities, and fitness are an important first step in habitat conservation and population management. Habitats are composed of different combinations of environmental variables which differentially impact an individual's fitness (Matthiopoulos et al. 2015). Animals do not utilize all habitat types in proportion to their availability (Cherry 1998). According to Ideal Free Distribution theory (IFD; Fretwell & Lucas Jr., 1969), individuals who are aware of and free to exploit all available habitats should favour those that increase their chances of survival and reproduction.

Resource selection functions (RSFs; Manly et al., 2002) are commonly employed animal-distribution models that compare environmental conditions at locations occupied by individuals with those available to them (Boyce and McDonald 1999, Manly et al. 2002). Selection occurs when an animals' use of a resource or habitat is disproportionate to its availability (Manly et al. 2002, Morris 2003). Though the terms are often considered interchangeable, selection does not equate to preference; preference is defined as the likelihood that a component, such as a habitat type or food item, will be chosen given that all options are equally available (Johnson 1980). Preference can only be determined in an experimental setting where the availability of habitat types or food items can be controlled (Lele et al. 2013). Therefore, the results of resource selection functions calculated with use-availability data collected in field studies does not allow for the estimation of preference.

Habitat selection is hierarchical process and may vary depending on spatial and temporal scale of analysis. A common framework for describing the spatial scale of resource selection

studies was proposed by Johnson (1980) and includes four orders of selection. First-order selection refers to the selection of a geographical range of a species. Second-order selection refers to the selection of an individual's home range within the geographical range of the species. The selection of habitat patches within an individuals' home range is considered third-order selection while the selection of specific food items within a habitat patch is fourth-order selection. These orders are a simplification of what is really a continuum of selection decisions made by individuals from coarse to fine scales. At each of these spatial scales of selection, the factors affecting resource selection may differ. Rettie and Messier (2000) proposed a relationship between the scale of selection for a factor and the importance of that factor in limiting the fitness of a population. According to this hypothesis, the factors most limiting to an individual's survival and reproduction are expected to drive habitat selection at the coarse scale, becoming less evident at successively finer scales until the next most important limiting factor takes over. It is generally believed that for prey species, the risk of predation drives selection at coarser scales while food availability is selected for at finer scales (Boyce 2006). However, selection may not differ between spatial scales if potentially limiting resources are abundant and widely distributed (Boyce 2006).

Similarly, factors affecting selection can be expected to vary depending on the temporal scale of analysis. Habitat selection behaviour may vary by time of day (Northrup et al. 2012, Richter et al. 2020), season (McLoughlin et al. 2011, Mao et al. 2018), or year (Raynor et al. 2017b). Factors influencing habitat selection such as forage availability, human disturbance, and inter- and intraspecific population density can also vary temporally. Spatial and temporal scale are connected with selection at coarser spatial scales occurring over longer temporal scales and selection at finer spatial scales taking place over shorter time periods (Gaillard et al. 2010).

Models of habitat or resource selection may not accurately predict a species distribution in contexts other than those for which they were developed (Avgar et al. 2020). The fitness benefit of a given habitat type depends on its availability (Mysterud and Ims 1998, Osko et al. 2004, Aarts et al. 2013) as well as density dependent processes (Rosenzweig 1981, 1991). Due to spatial and temporal variation in both availability of resources and density of consumers habitat selection models developed in one time and place will not accurately predict distribution of the same species in another situation.

#### *1.1.4 Density-dependence in habitat selection*

Resource selection patterns of a species often change with population density (Rosenzweig 1981, 1991, Morris 1987). Increased abundance of conspecifics, or other species with similar requirements, causes increased competition for limited resources which decreases the fitness of individuals in that habitat (Fretwell 1969, Rosenzweig 1981, Morris 2003). If a species follows the Ideal Free Distribution model (IFD; Fretwell & Lucas Jr., 1969) then individuals should respond to this change in relative fitness between habitat types by decreasing selection for higher quality habitats and increasing use of lower quality habitats. In other words, individuals are expected to become less selective as exploitative competition increases. Evidence for density-dependent resource selection is abundant in the ecological literature and has been demonstrated in observational studies involving populations over periods of population increase and decline (Pérez-Barbería et al. 2013, van Beest et al. 2014a, b, Merrill et al. 2020) as well as in experimental studies using population manipulations (Morris 1989, Mobæk et al. 2009, Morris and MacEachern 2010). For example, Pérez-Barbería (2013) found that the habitat niche breadth

of red deer in Scotland expanded to include lower quality habitat types when and where population density was high.

Animals may exhibit a trade-off between selection for habitats offering high quality food sources and avoidance of habitats with higher perceived or actual risk. The extent to which individuals trade off resource acquisition for safety can also vary with population density. For example, elk in the eastern Rocky Mountains decreased selection for high forage biomass and increased selection for areas with higher risk of wolf predation as population size increased (Merrill et al. 2020). Similarly, elk and moose in Manitoba decreased selection for habitats which provided both abundant forage and cover as population densities increased (van Beest et al. 2014a). Smith et al. (2022) found that elk in Yellowstone National Park switched from habitat selection driven by predation risk at low population density to selection driven primarily by forage availability at high density.

According to density dependant habitat selection theory, RSFs should produce different results depending on how close a population was to carrying capacity at the time of data collection (Matthiopoulos et al. 2015). At low population density, individuals are expected to spend the majority of their time in the highest-quality habitats. In an RSF conducted using GPS collar data, this would be reflected as a high proportion of used points in high-quality habitat. As population size increases individuals are no longer able to be as selective of the habitats in which they forage due to increased competition. At sufficiently high population densities this increased generalization in selectivity may be reflected in an RSF as use of habitats proportional to their availability. Therefore, predictions of habitat use based on RSFs that do not account for density-dependence can lead to misguided management decisions (McLoughlin et al. 2010). Despite the popularity of RSFs in habitat selection research and the knowledge that density may alter the

results of RSF analysis and interpretation (McLoughlin et al. 2010, Matthiopoulos et al. 2015) relatively few such studies have accounted for population density.

Spatial variation in population density, either as a result of natural variation or experimental manipulations has been included in RSF models to test for density dependent habitat selection in wolves (O'Neil et al. 2019), feral horses (Rozen-Rechels et al. 2015, McLoughlin et al. 2016), skunks and racoons (Tardy et al. 2014), and domestic sheep (Mobæk et al. 2009). Where population density varies over time instead of in space the inclusion of density as a variable in RSFs is less simple. RSFs are spatial distribution models and as such non-spatial variables cannot be included as additive terms (Northrup et al. 2022). Studies that have incorporated temporal changes in density into RSFs have done so in two ways; by including density as an interaction term or by creating separate models including the variables of interest for each level of density and then modelling the resulting coefficients as a function of density. For example, van Beest et al. (2014b) included an annual estimate of population density of feral horses on Sable Island, Nova Scotia as an interaction term with vegetation association to test whether density influenced fine scale selection of forage quality. Robson and van Aarde (2018) included the interaction between annual population density of elephants and vegetation type and distance to water sources in Kruger National Park, South Africa to test their prediction that cessation of the elephant cull had led to a generalization in habitat selection. Merrill et al. (2020) on the other hand, separately modelled selection for forage quality and predation risk for individual elk in Alberta and then modelled the resulting selection coefficients as a function of population density to determine whether changes in density would affect the habitat selection of resident and migrant elk differently.

Not all studies that have tested for density-dependence in habitat selection have found support for the theory. For example, selection for forage availability and protective cover and avoidance of human development by moose in northern Norway were not found to be related to local density (Herfindal et al. 2009). The authors of this study suggested that the conditions on the island were favourable and therefore the moose were not yet experiencing the effects of density. Golden-mantled ground squirrels in Colorado were not found to alter their habitat use despite a more than five-fold increase in population density which led to decreased survival rates (Aliperti et al. 2022). In this example, although increased population density appeared to be having a negative effect on individual fitness the benefits of switching to lower quality habitat types may not have outweighed the cost of moving. Additionally, changes in habitat selection may not be immediate if there is a lag in perception of increased density or it takes individuals time to discover new, unoccupied habitats (Kawaguchi and Desrochers 2018).

#### *1.1.5 Habitat selection by bison*

Availability of herbaceous forage biomass appears to be the most important factor influencing foraging distribution of bison (Wallace et al. 1995, Van Vuren 2001, Doan 2019). Bison diet is flexible and varies both seasonally and across the North American range of the species (Bergmann et al. 2015, Hecker et al. 2020, Craine 2021). Bison are bulk feeders, meaning that they are able to process large amounts of fibrous forage (Hudson and Frank 1987). In general, graminoids are the dominant component of most bison diets with forbs and browse making up smaller components (Plumb and Dodd 1993, Steuter et al. 1995, Hecker et al. 2020).

Bison are time-minimizers as opposed to energy maximizers (Bergman et al. 2001) and tend to select for habitats that maximize instantaneous intake of digestible energy (Babin et al.

2011). Whereas energy maximizers maximize the long-term rate of energy intake by consuming intermediate biomass vegetation, time minimizers maximize short-term energy gain by consuming higher biomass vegetation, leaving more time for other fitness-maximizing activities (Hixon 1982, Stephens and Krebs 1986). Several studies have documented strong selection for habitat types with intermediate to high forage biomass and productivity and avoidance of habitat types with limited herbaceous forage. In arid to semi-arid regions of the United States bison have been found to select for areas of high herbaceous vegetation productivity (Van Vuren 2001, Schoenecker et al. 2015, Ritson Jr. 2019). Bison at the American Prairie Reserve in Montana and nearby Grasslands National Park, Saskatchewan exhibited selection for intermediate to high forage biomass (Kohl et al. 2013, Doan 2019). Bison tend to avoid tree and shrub dominated areas and other habitat types with little available herbaceous forage (Allred et al. 2011, Schoenecker et al. 2015). An exception to this pattern of selection for abundant forage exists in tall grass prairie systems where regular patch burning is practiced. Where patch burning is present, bison select for recently burned areas with low to intermediate forage biomass, likely to maximize protein intake which decreases with increasing time since fire (Allred et al. 2011, Raynor et al. 2016a, 2017a).

In areas where predators exist, bison display a trade-off between selection for abundant forage and safety from predation. For example, in Prince Albert National Park, Saskatchewan, avoidance of wolf predation has been found to be a strong driver of habitat selection (Fortin et al. 2009). Selection for food items that maximized energy intake has been shown to decrease as risk of predation by wolves increases (Fortin and Fortin 2009). Many plains bison populations today exist in areas where large predators have been extirpated and where hunting is not permitted. Since antipredator behaviour comes at a cost to other activities such as foraging, resting, mating,

and parental care (White et al. 1999, Duchesne et al. 2000, Steidl and Anthony 2000) antipredator behaviour may be lost in the absence of predation and/or hunting (Lahti et al. 2009). In many ungulate populations under relaxed selection pressure from predators habitat selection is driven solely by forage availability. For example, in a largely predator-free environment in Svalbard habitat selection of calving reindeer was driven by the availability of spatially and temporally variable food (Garfelt-Paulsen et al. 2021). Similar results have also been found for Sitka deer (Bonnot et al. 2016) and white-tailed deer (Massé and Côté 2009) in areas without predation pressure. Conversely, anti-predator behaviour has been found to shape habitat selection of certain ungulates even where predators have been absent for long periods of time (Byers 1997). For example, Moose in Norway were found to select for habitats that maximized protective cover and distance from humans while still providing abundant forage despite living on an island free of predators and outside of the hunting season (Herfindal et al. 2009). Remnant anti-predator behaviour, including habitat selection, in the absence of predation has also been observed in alpine ibex (Grignolio et al. 2007), mouflon (Ciuti et al. 2008), and Japanese serow (Takada 2020). Prey species may also respond to non-lethal human disturbance in the same way as they would to a predator especially if the species has historically been hunted by humans (Frid and Dill 2002). Plains bison evolved on the Great Plains in the presence of large predators including wolves and grizzly bears as well as hunting by indigenous peoples (Clawson et al. 2013). Therefore, bison may avoid areas of high human presence. Evidence for whether or not bison view humans as a risk is mixed. Fortin & Andruskiw (2003) found that the presence of hikers and vehicles increased the daily movements of female bison but did not result in significant changes in resource selection. Similarly, other studies have found that areas of concentrated human activity such as roads, trails, and fences were not an important factor in



space use by bison (Demars et al. 2020, Brockman et al. 2022, Foca and Boyce 2022). In other studies bison appear to select for areas farther from roads and other anthropogenic features (Babin et al. 2011, Ranglack and Du Toit 2015, Sallee et al. 2023). One study comparing habitat selection of free-ranging and captive herds in the United States found that free-ranging bison selected for areas far from human activity while captive herds did not (Ritson Jr. 2019). Female bison are known to select for areas farther away from roads, trails and man-made structures when calving (Kaze et al. 2016).

Topographic variables known to influence space use by bison include elevation, slope, distance to water and distance to roads (Steenweg et al. 2016). Bison consistently select for areas of higher elevation (Kohl et al. 2013, Raynor et al. 2017*b*, Ritson Jr. 2019) and avoid steep slopes (Allred et al. 2011, Steenweg et al. 2016, Ritson Jr. 2019). The influence of distribution of water sources is more variable between studies with some reporting strong selection for areas near permanent water sources (Kohl et al. 2013) and others finding only weak selection (Allred et al. 2011) or no influence at all (Van Vuren 2001, Babin et al. 2011).

Habitat selection varies seasonally and between sexes. Bison form sexually segregated groups most of the year but come together in large, mixed sex groups in the late summer or early fall to mate (Ranglack and Du Toit 2015, Jung 2020). Sexual segregation is thought to be due to differences in nutritional requirements between the females and males. Juveniles and females have been found to consume higher quality diets while adult males require more abundant forage and consume a greater diversity of food items (Mooring et al. 2005, Berini and Badgley 2017). In addition to differences in diet, male and female groups may differ in the degree to which risk avoidance factors into habitat selection.

Few studies have examined the effect of population density on habitat selection in Plains Bison. Free-roaming bison herds have been found to expand their home ranges to include lower quality habitats in response to population growth (Singer and Norland 1994, Plumb et al. 2009, Merkle et al. 2015). Furthermore, a negative relationship has been observed between population density and recruitment (Koons et al. 2012) and population growth rates (Fuller et al. 2007). Given the impact that bison herds have on the ecosystem and other species as well as the growing interest in increasing population sizes, filling the knowledge gaps on how habitat use responds to changes in population density is an important step in both bison conservation and ecosystem management.

#### *1.1.6 Relevance of study area*

The mixed-grass prairie has suffered a high rate of habitat loss and alteration leaving limited opportunities for the reintroduction of fully free-roaming bison herds in this ecoregion.

Grasslands National Park (GNP) represents one of the largest remaining continuous tracts of native mixed-grass prairie in Canada. GNP is home to a number of federally listed species at risk, with 29 listed as of 2019, and approximately 96% of the park is considered critical habitat for species at risk (GNP 2020).

Plains bison are not listed on Schedule 1 of the Species at Risk Act; however, the subspecies is currently under consideration for listing as Threatened. Under the National Parks Act Plains Bison and their habitat is protected within National Parks (Canada National Parks Act 2000). There are currently 4 National Parks with free-roaming or semi-free-roaming herds: Banff, Elk Island, Grasslands, and Prince Albert. Together these herds total between 1000 and

1200 individuals inhabiting 8,348 km<sup>2</sup> of land. Increasing herd size and expanding the herd's range in GNP has the potential to significantly contribute to bison conservation in Canada.

In December 2005, a herd of 71 bison was introduced to a portion of the park. For the next 8 years, the herd was allowed to grow until it neared the estimated carrying capacity of the enclosure. For the purposes of bison management in GNP, carrying capacity was defined as the number of individuals that the bison containment area is able to sustain under the lowest possible biomass production scenario and assuming that 50% of the land will be grazed annually (Parks Canada 2017). In 2013, a biennial surplus event was initiated in which a portion of the herd is removed to maintain the population within the carrying capacity, resulting in a population that fluctuates between approximately 300 and 550 individuals. The surplus is conducted in such a way as to mimic natural processes. GNP follows the IUCN guidelines for management of bison conservations herds which includes maintaining a slightly female biased sex ratio, limiting removal of individuals to 30 – 40% of the population every 2 years, removing juveniles (<2 years) and old (>10 years) individuals at a higher rate, and avoiding removal of individuals based on human selection (Gates et al. 2010, Parks Canada 2017). These guidelines are intended to both retain genetic diversity and emulate mortality patterns observed in wild herds. The period of natural population growth followed by repeated population density manipulations has created a unique opportunity to test density-dependent habitat selection in bison.

## 1.2 Objectives & thesis structure

The objective of my thesis is to examine the effects of population density on habitat selection of Plains Bison. To achieve this, I first examined selection for habitat productivity and distance to roads during a period of natural population increase following the reintroduction of a bison herd

in GNP. I then examined selection within biologically relevant seasons and at two spatial scales: at the level of home range selection (second order) and within-home range selection (third order) using RSFs. Next, I compared habitat selection of the bison herd in years before and after population density reductions during a period when 30—40% of the population was removed on a biennial basis. For the latter, I directly compared selection in high density years (i.e., years before surplus events) with selection in low density years (i.e., years following surplus events) using latent selection difference functions (LSDs; Mueller et al. 2004, Fischer and Gates 2005, Czetwertynski 2008, Latham et al. 2011) a type of modified RSF in which used locations of one group of interest are directly compared to used locations of another group.

At low population density, I expected bison to select for areas of abundant forage (i.e., high vegetation productivity) as well as areas farther from perceived risk. In places where predators and bison coexist, habitat selection of bison has been found to be primarily driven by avoidance of predation risk (Fortin et al. 2009). Little to no predation risk exists in GNP and hunting is not permitted. However, prey species, particularly those with a history of predation by humans, can perceive areas of high human activity (i.e., areas near roads) as risky even in the absence of lethal interactions (Frid and Dill 2002). When a perceived risk is predictable in space and time, as is human presence in GNP, animals are able to incorporate this information into their habitat selection at the landscape level (Kittle et al. 2008). Alternatively, in the absence of lethal interactions with humans, bison may become habituated to human presence (Foca and Boyce 2022).

I hypothesize, because of constraints on movements and habitat use due to intraspecific competition, that habitat selection of bison will be density dependent. If habitat selection patterns in bison are density-dependent, then increased population size will lead to increased exploitative

competition for high quality habitat, thereby reducing the fitness reward of a habitat relative to that of lower-quality habitat types. Individuals are expected to respond to this change in relative fitness conferred by different habitat types by showing increased generalization in resource selection. The predation-sensitive food hypothesis states that both food and predation limit prey populations; as density and therefore competition increase selection for food should increase while selection for safety should decrease (Sinclair and Arcese 1995). I predicted that selection for areas of high vegetation productivity would be high at low population density and that selection would generalize at higher densities. With increased population density inside of the bison containment area forage in areas far from roads will become depleted more rapidly forcing the cow-calf herd to shift towards areas closer to human activity where forage is still abundant. Therefore, I also predicted that selection for areas farther from roads would be high at low population density and would generalize at higher densities.

I expected density dependence to be evident at both spatial scales examined, however, I expected selection for areas of lower perceived risk to be more important at the home-range scale and areas of high vegetation productivity to be more important at the within home-range scale. Due to seasonal differences in nutritional demands, behaviour, and group size, I expected the strength of selection for vegetation productivity and distance from roads to vary seasonally. I expected strong selection for distance from road during calving and immediately post-calving when the cow-calf herd is most vulnerable and human presence in the park is high. I expected weaker selection for distance from roads during the rut when bulls join the cow-calf herd and group size is large as larger groups are known to occupy riskier habitats (Fortin et al. 2009).

If the population density of bison within the GNP bison enclosure is sufficiently high, so as to result in exploitation competition, then reductions in population size should result in a

release from density-dependent selection pressures. I predicted that bison would increase selection for high vegetation productivity and areas farther from roads in years following the removal of individuals from the bison enclosure. Alternatively, bison may respond to decreased density by increasing selection for known areas. A study on habitat selection of Plains Bison in Prince Albert National Park found that home range size increased to include lower quality habitat as the population grew but a subsequent decrease in population size did not result in contraction of home ranges due to strong site fidelity (Merkle et al. 2015). I expected the response of bison to decreases in population density caused by removal of individuals from the bison enclosure to be consistent with the response to population growth (i.e., the results of the LSD analyses will be consistent with the results of the RSFs).

## 2 Methods

### 2.1 Study area

Grasslands National Park (GNP) is a 907 km<sup>2</sup> area located in south-western Saskatchewan along the Canada-US border (Figure 1). GNP was established in 1981 to protect a large intact area of native mixed-grass prairie, an increasingly rare ecosystem in Canada. Gently rolling upland grasslands are dominated by needle grasses (*Stipa* sp., *Hesperostipa* sp.), wheat grasses (*Pascopyrum smithii*, *Elymus* sp.) and blue grama grass (*Bouteloua gracilis*). Dispersed throughout the grassland are patches of low shrubs including western snowberry (*Symphoricarpos occidentalis*) and wild rose (*Rosa* sp.). Steep hillsides are eroded with exposed bear paw shale and creeping juniper (*Juniperus horizontalis*). Lowlands are dominated by sagebrush (*Artemisia cana*) and greasewood (*Sarcobatus vermiculatus*) flats, prairie-dog colonies with short, cropped vegetation and lots of bare ground, and smooth brome (*Bromus inermis*) monoculture and riparian shrub (*Salix* sp., *Shepherdia argentea*) communities along the Frenchman River. The west block of GNP is home to several herbivores including bison, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), pronghorn antelope (*Antilocapra americana*), and black-tailed prairie dogs (*Cynomys ludovicianus*). Elevation within the bison containment unit ranges from 762 to 924 m. GNP has a continental climate with short warm summers and long cold winters. Average annual precipitation in GNP from 2009 to 2020 was 336 mm with the majority of precipitation falling as rain between April and September. Mean monthly temperature ranged from 29.6°C in July to -11.2°C in December.

Following establishment, the Park was left ungrazed for 24 years. In May of 2006, 71 Plains Bison were reintroduced into a 180 km<sup>2</sup> portion of the west block (Figure 1). The remainder of the Park's land is leased to local cattle ranchers. The bison population was allowed to increase naturally until 2013 when a biennial surplus event was initiated in order to maintain the population within the estimated carrying capacity of 397 - 511 individuals within the bison enclosure (Parks Canada 2017). The main predators of bison, wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*), are extirpated from the area. Coyotes are abundant and may occasionally prey on juveniles. Though humans were historically a major predator of bison, hunting is currently prohibited within the national park.



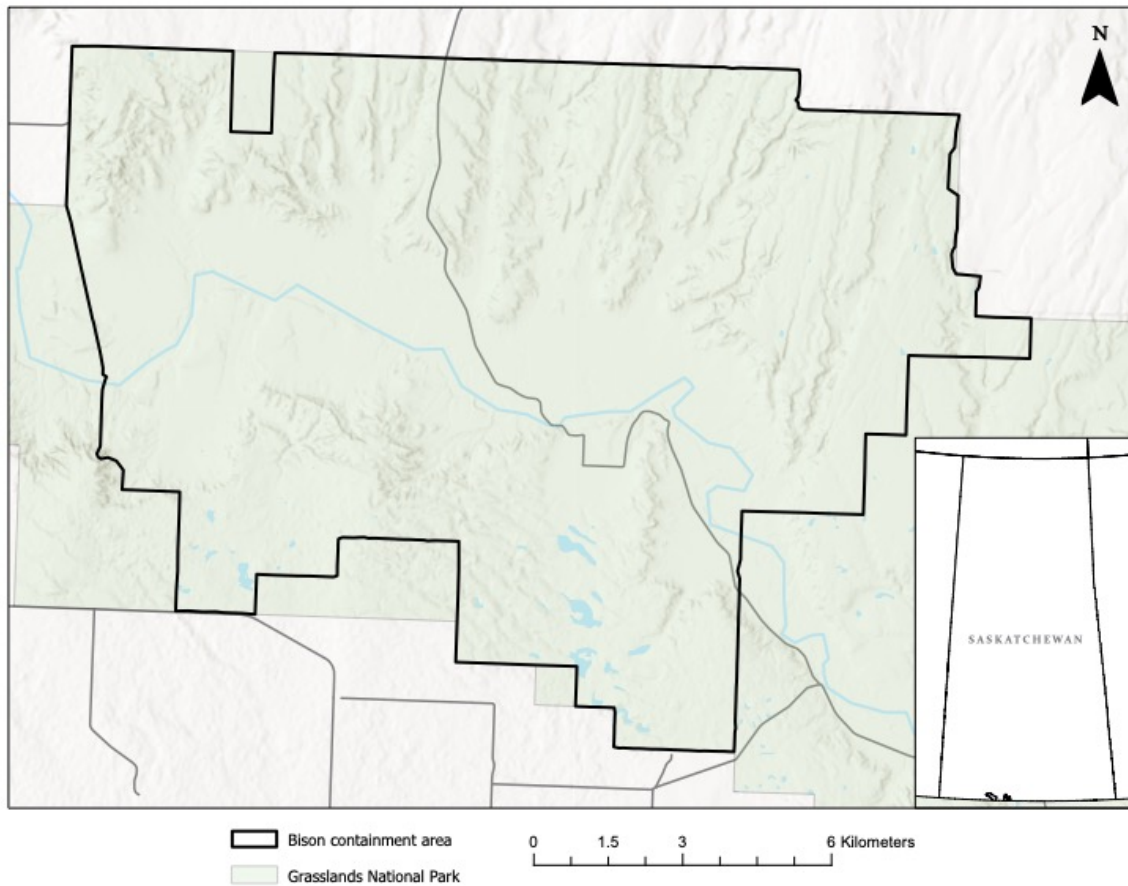


Figure 1. Location of Grasslands National Park in southwestern Saskatchewan, Canada, and the bison containment area where bison were collared from 2006 to 2020.

## 2.2 Data

### 2.2.1 *Bison and telemetry*

The number of collared individuals and the number of relocations per individual required to consistently estimate resource selection using RSFs decrease with increased strength of selection for a given variable, decreased individual variation in selection, and increased landscape

heterogeneity (Street et al. 2021). Based on past RSF studies of bison in GNP (e.g., Babin et al. 2011, Kohl et al. 2013), I expect the strength of selection/avoidance for NDVI and distance from roads to be high. Bison can also be expected to have low individual variation in selection behaviour due to their gregarious nature (Babin et al. 2011). Furthermore, the bison containment area in GNP contains a heterogeneous landscape of habitat types with variable forage availability and proximities to human activity. For these reasons, though the GPS collar data available for this study was limited I believe that it was sufficient to reliably estimate resource selection.

Bison location data was provided by GNP. Between 2006 and 2020, 27 bison were equipped with GPS collars. Collar deployments lasted between 13 and 1029 days and location sampling intervals ranged from 1 to 6 hours. For much of the year, bison form sexually segregated groups (Mooring et al. 2005) due to differences in nutritional requirements (Engle et al. 2005, Berini and Badgley 2017). To eliminate possible variation due to sex or life stage, I only retained location data from adult females for analysis. I removed relocations outside of the bison enclosure as bison do not have access to this area and escapes from the enclosure are rare. I screened relocations for periods when collars clearly malfunctioned (e.g., temporary changes to the sampling schedule) or were released from the animals (i.e., stationary for a long period of time), and removed these locations. I screened the remaining locations for outliers based on the speed of movement and distance between successive locations using the `outlie` function from the `ctmm` package (Fleming and Calabrese 2022). Finally, I removed relocations with a dilution of precision (DOP) greater than 10 (Adams et al. 2013). After data cleaning, 119,240 locations from 22 adult females remained between 2009 and 2020. Due to the gregarious nature of bison, I believe these 22 individuals to be representative of a much larger proportion of the population.

Bison collaring was conducted under protocol number PCA-WHAM-2016-01 which was reviewed by the Parks Canada Animal Care Committee.

### 2.2.2 Population density

I obtained bison population size estimates from an existing database provided by GNP. I calculated population density as the number of individual bison divided by the area within the bison enclosure (180 km<sup>2</sup>). Population density is measured as the number of individuals per kilometre squared.

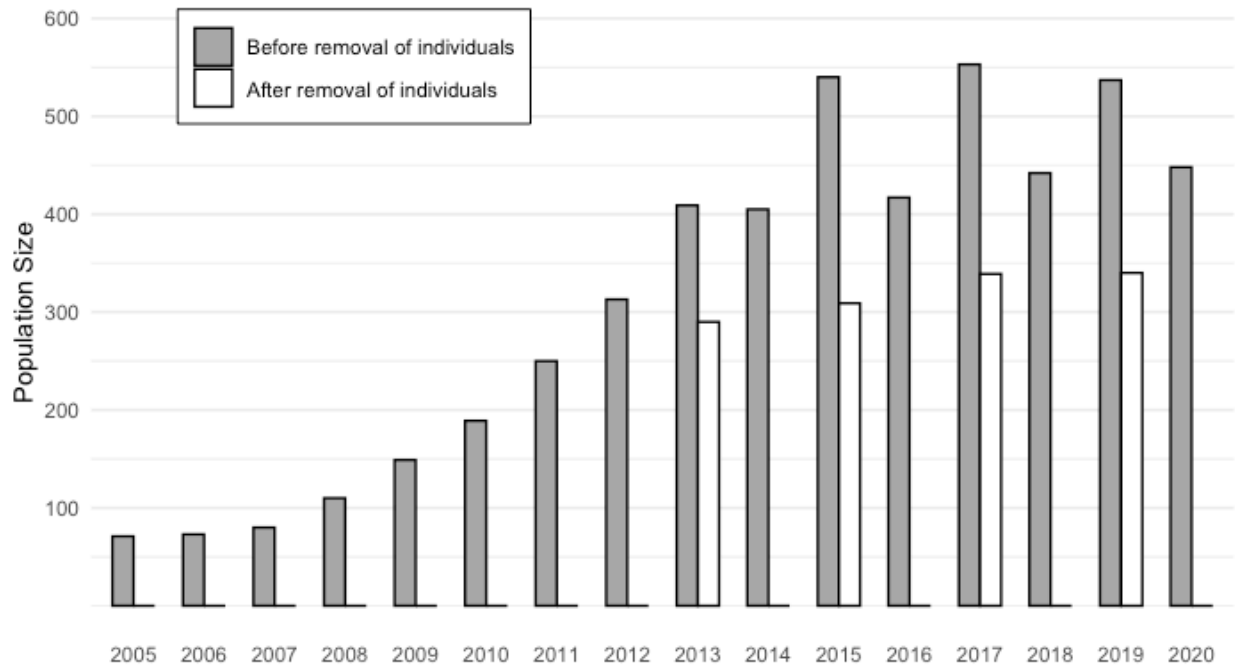


Figure 2. The population size of bison herd in Grasslands National Park, Saskatchewan, Canada. Dark grey bars represent the number of individuals before the surplus event, light grey bars represent the number of individuals after the surplus event for years in which the population was reduced.

### 2.2.3 *Environmental covariates*

I used normalized difference vegetation index (NDVI) as a proxy for vegetation productivity. NDVI is a satellite-derived measure of photosynthetically active vegetation. NDVI has been found to be correlated with green biomass (Zhang and Guo 2008, Grant et al. 2013) and total biomass (Hebblewhite and Merrill 2008, Grant et al. 2013) in the mixed grass prairie region.

I searched USGA Earth Explorer to find a minimum of one image for each month of the study period that covered the entire bison enclosure and was relatively cloud-free. I downloaded pre-processed NDVI data calculated from Landsat 7 and 8 imagery from USGA at 30×30 m resolution. Using the Quality Assessment band, I created a cloud mask for each NDVI layer and applied the cloud masks to the NDVI layers to remove any potentially unreliable pixels that may bias the results of the analysis. I created seasonal mean NDVI layers by averaging the values of all NDVI layers for a given season. Since NDVI is a measure of photosynthetically active vegetation, it is not informative for seasons when vegetation is hidden under snow. Therefore, seasonal NDVI layers could only be created for April through October.

Vegetation productivity in southwestern Saskatchewan varies greatly from year to year due to highly variable annual precipitation. Large grazers such as bison can also alter productivity of vegetation over time. Low to intermediate levels of bison grazing can lead to increased productivity while overgrazing can lead to decreased productivity (Frank et al. 2016, Geremia et al. 2019). Other natural processes such as fires can also have immediate and long-term effects on forage availability. A large wildfire in 2013 burned a substantial portion of the bison enclosure while several smaller prescribed fires occurred during the study period. NDVI was found to be higher in the area burned by the 2013 wildfire than in similar non-burned areas

for 4 years following the fire (Li and Guo 2018). Thus, seasonal NDVI layers take into account these inter- and intra-annual changes in productivity.

NDVI values varied between years as well as between seasons. Mean NDVI within the bison enclosure during the post-calving season – which coincides with peak biomass production in GNP – was 0.48 (0.12 – 0.91) in 2016, the year with the highest annual precipitation (516.7 mm). In 2018, the second year of a drought with annual precipitation of 195.8 mm, NDVI during the post calving season averaged 0.32 (0.11 – 0.85). NDVI values were generally lowest during the spring and highest during the post-calving season. For example, in 2011 (annual precipitation = 397 mm) mean NDVI was 0.19 (-0.06 – 0.43) in the spring and 0.47 (0.13 – 0.87) in the post-calving season.

Natural predators of bison are no longer present in GNP, but human presence is high. In addition to park staff and local residents the park receives tens of thousands of visitors per year. Human presence within the park is mainly associated with the main roads through and around the bison enclosure. One gravel road (Ecotour Road) runs approximately 15 km north-south through the bison enclosure (Figure 1). This road provides park visitors access to the majority of the hiking trails within the bison enclosure, day use areas, and the only campground in the West Block. There are two other gravel grid roads that are directly outside of the bison enclosure and provide entry points to the area: one near the north-west and one at the south-west corner of the enclosure (Figure 1). Though vehicle and human traffic on the roads varies seasonally and has changed over the years as visitation to the park increased, data on timing and volume of traffic was not available for the entire study period. Therefore, I employed a static measurement of distance from roads as a proxy for perceived risk. I calculated distance from roads from a shapefile of roads in and around the bison enclosure provided by GNP. I first filtered road type to

include only regularly driven gravel and dirt roads and highways and exclude truck trails that are only rarely used by park staff. I then created a distance from road raster at 30×30 m resolution using the Euclidean Distance tool in ArcGIS Pro.

## 2.3 Statistical analysis

### 2.3.1 *Defining biologically relevant seasons*

For species whose movement rate changes non-linearly over time biologically relevant seasons can be defined based on movement data of tracked individuals as opposed to defining seasons arbitrarily based on calendar date or based on plant phenology (Vander Wal and Rodgers 2009, van Beest et al. 2013). To define seasons experienced by the GNP bison herd I modelled the movement rate of all collared individuals with at least one year of location data and a minimum of 6 relocations per day with Generalized Additive Mixed Model (GAMM). For individuals with more than 1 complete year of relocations, I considered each year as a separate sample to increase the sample size, resulting in 19 individual-years. Using the R library *mgcv*, I modelled log transformed daily movement rate (m/h/day) as the response variable and day of year as the smoothing function. I used a cyclic cubic regression spline, with the optimal curve estimated by restricted maximum likelihood (Wood 2006). Individual-year was included as a random intercept and slope to account for repeated measures from the same individuals. To account for any temporal dependence between locations I included an autocorrelation structure. I chose a rational quadratic correlation structure (*corRatio*) because it resulted in the best fit based on Akaike's information criterion (AIC). I plotted the model predictions of the GAMM and delineated seasonal boundaries by peaks and troughs of the curve.

It was not possible to identify a distinct calving season for bison using the above-described method. Compared to other ungulate species for which this method has been employed (elk & white-tailed deer - van Beest et al. 2013), bison calves are highly precocious. Bison calves are able to stand and suckle almost immediately following birth and begin following their mothers or the herd shortly thereafter (Rutberg 1984, Lott and Galland 1985, Gates et al. 2010). To identify a calving season, I examined gestation data collected during the 2019 bison surplus event. Using ultrasound technology, 166 females were examined to determine pregnancy status and stage (in number of weeks). Using this information along with the average length of gestation I estimated bison calving dates for the 122 females expected to give birth in 2020. I then defined the calving season as the period which encompassed 95% of the estimated calving dates. Seasons were further constrained by the availability of NDVI data (see section 2.2.3).

### *2.3.2 Home range estimation*

I defined individual home ranges using the 95% autocorrelated kernel density estimation (AKDE) in the package *ctmm*. This method of home range estimation accounts for autocorrelation in tracking data by first fitting an autocorrelated movement model to the data and then using estimates from this model to optimize the smoothing bandwidth for the home kernel density estimation (Fleming and Calabrese 2017). I included the bison enclosure fence as a hard boundary to ensure that home ranges did not extend into areas inaccessible to bison.

### *2.3.3 Resource selection during a period of natural population growth*

Resource selection functions (RSF) are functions that are proportional to the probability of use of a resource unit (Manly et al. 2002). RSFs are estimated using the exponential equation:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \dots \dots \dots (2.1)$$

Where  $w(x)$  is the relative probability of selection given a particular combination of resources, represented by  $x_i$ . The coefficients, represented by  $\beta_i$ , estimate how much the probability of selection changes with every unit increase in the corresponding covariate.

For each season, I modelled RSFs with generalized linear mixed effects models (GLMMs) to compare environmental covariates at used and available locations (Manly et al. 2002) at two spatial scales. I modelled GLMMs using the package `glmmTMB` (Brooks et al. 2017). The estimation of RSF coefficients can be affected by the ratio of used to available points. Coefficient estimates become increasingly stable as the number of available points increases and the RSF converges to an inhomogeneous Poisson point process (IPP) (Warton and Shepherd 2010), however, this stability comes at the cost of high computation times (Northrup et al. 2013). To determine the number of available points per used location at which the RSF coefficients stabilized, I conducted a sensitivity analysis for each season and population density level. I ran 20 repetitions each of the full RSF models with 1, 5, 10, 20 and 50 available locations for every used location and visually determined the point at which the RSF coefficient estimates stabilized (Fieberg et al. 2021). RSF coefficient estimates appeared to stabilize at a ratio of 10:1 available to used locations (Figure 10). At the home-range scale, I generated random points within the bison enclosure. At the within-home-range scale, I generated random points within the individual 95% AKDE home ranges. I assigned a weight of 5000 to available locations and 1 to used locations to further ensure that the RSF converged to an IPP (Warton and Shepherd 2010, Fieberg et al. 2021).

For the RSF analyses, I partitioned the data from years 2009 to 2013. During these years the population was growing naturally without any management intervention or population size



manipulation. This resulted in a dataset of 36,872 locations from 10 individuals. Prior to model fitting, I checked predictor variables for collinearity using variance inflation factors (VIFs). All VIFs were  $<3$  (Zuur et al. 2010), therefore I was able to include all combinations of predictor variables in the same models. To avoid convergence issues, I scaled and centred continuous variables. For each season at each scale, I fit 5 candidate models. Candidate models included different combinations of the distance to road, NDVI and interactions between distance to road, NDVI, and population density. RSFs approximate an inhomogeneous Poisson point process (IPP), which is a spatial model. As such, non-spatial covariates (i.e., population density) cannot be modelled as an additive effect and can only be included as interactions with spatial covariates of interest (Northrup et al. 2022). I did not include other potentially influential environmental variables (e.g., slope, distance to water) because the goal of the analysis was to examine the effect of changing population density on selection for vegetation productivity and avoidance of human disturbance rather than to produce the best predictive model. To account for differences in selection between individuals and unbalanced sampling design I included a random intercept and random slopes for individual (Gillies et al. 2006). To avoid shrinkage of the individual intercepts toward the mean I assigned a large, fixed variance to the intercept (Muff et al. 2020).

I compared models using Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002) and selected the top model based on the lowest  $AIC_c$ . I checked that the top model for each season met the assumptions of logistic regression models using the R package DHARMA (Hartig 2022). I did not consider non-linear effects because the model diagnostics did not indicate any non-linear relationships. To assess the predictive ability of the top models I performed 5-fold cross-validation blocked by population density (Boyce et al. 2002, Roberts et al. 2017). I calculated the Spearman rank correlation ( $R_S$ ) between RSF score

divided into 10 bins and area adjusted frequency (Boyce et al. 2002). The  $R_S$  values represent the ability of the models to predict selection of the population at a population density other than that at which the training data was collected.  $R_S$  values range from negative 1 to positive 1; a model with good predictive ability will result in an  $R_S$  close to positive 1.

#### *2.3.4 Comparison of selection during a period of population size manipulation*

To compare habitat selection between the bison herd in years preceding the population size reductions and years following the reductions (referred to hereafter as high- and low-density years, respectively), I used logistic regression to estimate coefficients for latent selection difference (LSD) functions. To account for seasonal differences in selection I separately modelled LSDs for each biologically relevant season identified in section 2.3.1. LSD models are a type of modified RSF that allow for direct comparison between two groups of interest. The equation for LSD is that same as that of an RSF (Equation 2.1). Rather than comparing used locations with those assumed to be available however, the used locations of one group (coded as 1) are compared to those of another (coded as 0). The resulting selection coefficients are interpreted as the probability of selection by one group relative to a second group as opposed to the selection for a resource unit as it is in RSFs (Czertwytynski 2008, Latham et al. 2011). Random terms cannot be included in an LSD, therefore variation in selection between individuals and unbalanced sampling design cannot be accounted for.

For the LSD analysis I subset the data from years 2014 to 2020. During this period the population sizes of the herd in the high- and low-density years were fairly consistent and non-overlapping. I excluded data from 2013 because the population size in this “high-density” year (409 individuals) was very similar to the population size in the following “low-density” year (405 individuals). This resulted in a dataset of 82,368 locations from 14 individuals. To ensure

that the population density within the bison containment area between high- and low-density years was significantly different I compared the median population densities using a Mann-Whitney test. The Mann-Whitney test is an alternative to the t-test that can be used when it is uncertain whether the samples come from a normal distribution. Since I only had annual population counts for 4 high density and 2 low density years, I was not able to make assumptions about the distribution of the data. A key assumption of LSD is that habitat availability does not vary between the two groups being compared (Latham et al. 2011). To ensure that habitat availability between high- and low-density years was similar I visually compared the 100% minimum convex polygons surrounding locations from high- and low-density samples for each season (Figure 11, Figure 12, Figure 13, Figure 14, Figure 15). I fit LSD models for each season including the variables distance to road and NDVI. To avoid convergence issues, I scaled and centered the continuous variables. I checked the variables for multicollinearity using variance inflation factors (VIFs). VIFs for both variables were  $<3$  (Zuur et al. 2010), therefore there was no problem with including the variables in the same models.

I checked that the model for each season met the assumptions of logistic regression models using the R package DHARMA (Hartig 2022). I did not consider non-linear effects because the model diagnostics did not indicate any non-linear relationships. To assess the ability of the models to correctly discriminate between locations from high- and low-density years, I examined the relative operating characteristic curve (ROC) and calculated the area under the curve (AUC). ROC curves plot the sensitivity, or the true positive rate, against the specificity, or the false positive rate, of a model. AUC is calculated as the area under the ROC curve; an AUC of 1 indicates that a model perfectly discriminates between cases and an AUC of 0.5 indicates that the model has no ability to discriminate between cases.



### 3 Results

#### 3.1 Biologically relevant seasons

The movement rate of female bison varied non-linearly over time, allowing for the identification of biologically relevant seasons. Using this method 4 seasons were identified (Figure 3).

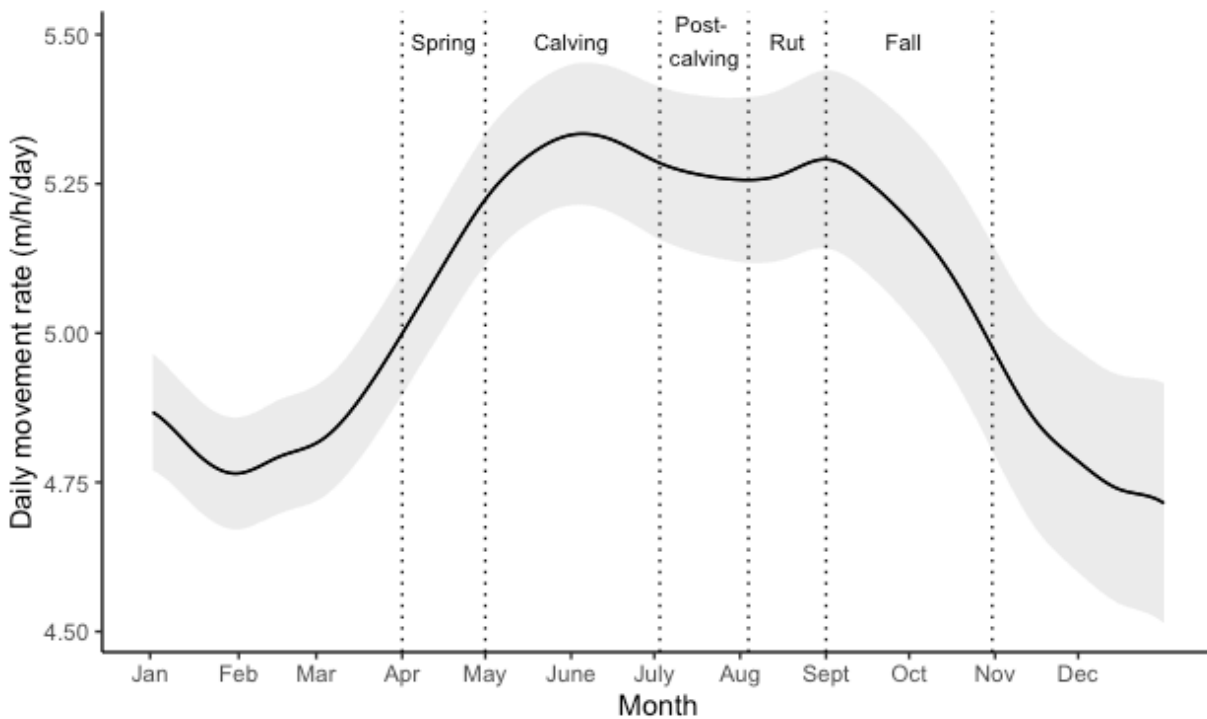


Figure 3. Results of the generalized additive mixed model analysis showing predicted daily movement rate of adult female bison in Grasslands National Park, Saskatchewan, Canada over a year. The solid line is the predicted daily movement rate and the grey ribbons on either side of the line are the confidence intervals (2 times the standard error). The dotted vertical lines indicate the inflection points that delineate seasons.

The estimated calving dates calculated from the 2019 gestation data ranged from April 21 to August 1. The distribution of calving dates was highly right skewed with 95% of calving dates falling between May 1 and July 2 and only one occurring before May 1 and a handful occurring after July 2 (Figure 9). Using this information to refine the seasons identified using the movement rate model resulted in 5 seasons: spring/late winter from February 1 to May 1, calving from May 1 to July 2, post-calving from July 3 to August 3, rut from August 4 to 31, and fall/winter from Sept 1 to January 31.

The spring/late winter season was truncated to April 1 due to the lack of vegetation productivity data prior to April and is hereafter referred to as spring. Similarly, the fall/winter season was truncated to September 1 to October 31 and is hereafter called fall. Thus, habitat selection during winter, November 1 to March 31, was not examined.

### 3.2 Resource selection during a period of natural population growth

From 2009 to 2013, the population density within the bison enclosure increased from 0.83 to 2.27 individuals/km<sup>2</sup>, an increase of 174%. During that time 10 individual adult female bison were collared. The number of relocations varied between individuals and seasons. Six individuals with a total of 3502 GPS points were included in the spring RSFs; each individual contributed an average of 443 locations (25 – 1366). Eight individuals with a total of 5477 GPS points were included in the RSFs for the calving season. Individuals in the calving season RSFs contributed on average 685 GPS points (95 – 1513). Seven individuals with a total of 3340 GPS points were included in the RSFs for the post-calving season. Individuals in the post-calving season RSFs contributed on average 477 GPS points (371 - 700). The rut season RSF analyses included 3026 GPS points from 7 individuals (204 – 655 GPS points per individual, average

432). Six individuals with a total of 5760 locations were included in the fall RSFs; each individual contributed an average of 960 GPS points (731-1376).

At the home-range scale, the full model was the top model for the spring, calving, and fall seasons, the top model for the post-calving season did not include the interaction between NDVI and population density, and the top rut model did not include the interaction between distance from road and density (Table 1). At the within-home-range scale the full model was the top model for the post-calving and fall seasons, the top models for the spring and calving seasons did not include the interaction between NDVI and population density, and the top model for the rut did not include the interaction between distance from road and density (Table 2).

Table 1. Comparison of resource selection function models at the home-range scale for bison in Grasslands National Park, Saskatchewan, Canada from 2009 - 2013. All models include random intercept and random slopes for individual ID. Models are ranked based on Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ).  $N$  is the number of bison and  $n$  the number of GPS locations used for each model.

<b>Season</b>	<b>Model</b>	<b><math>K</math></b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>	
<b>Spring</b>	road + ndvi + density + road:density + ndvi:density	8	41841.5	0.0	
	$N = 6$	road + ndvi + density + road:density	7	41844.8	3.30
	$n = 3502$	road + ndvi	5	41855.1	13.61
	road + ndvi + density + ndvi:density	7	41855.2	13.70	
	Null model	3	41859.8	17.81	
<b>Calving</b>	road + ndvi + density + road:density + ndvi:density	8	114819.5	0.0	
	$N = 8$	road + ndvi + density + road:density	7	114826.8	7.28
	$n = 5477$	road + ndvi + density + ndvi:density	7	114874.1	54.58
	road + ndvi	5	114885.0	65.49	
	Null model	3	114888.4	68.96	
<b>Post-calving</b>	road + ndvi + density + road:density	7	70236.9	0.0	
	$N = 7$	road + ndvi + density + road:density + ndvi:density	8	70237.4	0.45
	$n = 3340$	road + ndvi + density + ndvi:density	7	70498.6	261.66
	road + ndvi	5	70508.5	271.56	
	Null model	3	70512.1	275.12	
<b>Rut</b>	road + ndvi + density + ndvi:density	7	60548.5	0.0	
	$N = 7$	road + ndvi	5	60548.8	0.28



$n = 3026$	road + ndvi + density + road:density + ndvi:density	8	60549.7	1.17
	road + ndvi + density + road:density	7	60551.7	3.18
	Null model	3	60554.6	6.05
<b>Fall</b>	road + ndvi + density + road:density + ndvi:density	8	123744.7	0.0
$N = 6$	road + ndvi + density + road:density	7	123748.4	3.66
$n = 5760$	road + ndvi + density + ndvi:density	7	123786.2	41.47
	road + ndvi	5	123798.2	53.54
	Null model	3	123799.6	54.95

Table 2. Comparison of resource selection function models at the within home-range scale for bison in Grasslands National Park, Saskatchewan, Canada from 2009 - 2013. All models include random intercept and random slopes for individual ID. Models are ranked based on Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ).  $N$  is the number of bison and  $n$  the number of GPS locations used for each model.

<b>Season</b>	<b>Model</b>	<b><math>K</math></b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>
<b>Spring</b>	road + ndvi + density + road:density	7	41954.1	0.00
$N = 6$	road + ndvi + density + road:density + ndvi:density	8	41955.7	1.67
$n = 3502$	road + ndvi	3	41960.0	5.99
	Null model	5	41960.2	6.14
	road + ndvi + density + ndvi:density	7	41963.8	9.70
<b>Calving</b>	road + ndvi + density + road:density	7	116936.4	0.00
$N = 8$	road + ndvi + density + road:density + ndvi:density	8	116936.9	0.51

<i>n</i> = 5477	road + ndvi	5	116992.6	56.19
	Null model	3	116994.4	58.02
	road + ndvi + density + ndvi:density	7	116994.8	58.35
<b>Post-calving</b>	road + ndvi + density + road:density + ndvi:density	8	70998.8	0.00
<i>N</i> = 7	road + ndvi + density + road:density	7	71000.0	1.23
<i>n</i> = 3340	road + ndvi + density + ndvi:density	7	71218.6	219.8
	road + ndvi	5	71237.1	238.3
	Null model	3	71237.4	238.6
<b>Rut</b>	road + ndvi + density + ndvi:density	7	62142.4	0.00
<i>N</i> = 7	road + ndvi + density + road:density + ndvi:density	8	62143.0	0.60
<i>n</i> = 3026	road + ndvi	5	62145.2	2.78
	road + ndvi + density + road:density	7	62145.3	2.94
	Null model	3	62148.0	5.63
<b>Fall</b>	road + ndvi + density + road:density + ndvi:density	8	124672.1	0.0
<i>N</i> = 6	road + ndvi + density + road:density	7	124681.5	9.41
<i>n</i> = 5760	road + ndvi + density + ndvi:density	7	124709.1	37.0
	Null model	3	124737.1	65.04
	road + ndvi	5	124738.2	66.08

Habitat selection in the GNP bison herd was density dependent at both spatial scales examined. Resource selection patterns were fairly consistent between the spatial scales examined but varied greatly between seasons.

Patterns of selection for distance from road as population density increased were fairly consistent across spatial scales and seasons. Bison selected for areas farther from roads when population density was low and decreased selection for areas farther from roads as density increased in all seasons except for the rut (Figure 4, Figure 5). The effect of density on selection for distance from roads was less pronounced in the calving season at the home-range scale than it was at the other spatio-temporal scales. In the calving season selection for home ranges far from roads did decrease slightly with increasing population density but remained high when compared to the other seasons.

At the home-range scale selection for NDVI was density dependent in all seasons except for the post-calving season (Figure 4). The direction of the interaction between NDVI and density varied by season. Bison selected for home ranges with low NDVI values at low population density and increased selection for areas of high NDVI as density increased in both the spring and rut seasons, though this interaction was not significant for the rut (Figure 4). During the calving and fall seasons on the other hand, bison selected for home ranges with high NDVI values when population density was low and increased selection for areas of low NDVI as density increased (Figure 4).

At the within-home-range scale selection for NDVI was density dependent only in the post-calving, rut, and fall seasons (Figure 5). As it did at the home-range scale, the direction of the interaction between NDVI and population density varied by season. During the post-calving and fall seasons bison selected for habitat within their home ranges with high NDVI values when

population density was low and increased selection for areas of low NDVI as density increased (Figure 5). During the rut the pattern reversed, and bison selected for areas of low NDVI when population density was low and increased selection for areas of high NDVI as density increased (Figure 5). The predictive ability of the RSF models for all spatio-temporal scales was poor with Spearman-rank correlations ranging from -0.616 to 0.643 (Table 3).

Table 3. Spearman-rank correlation between ten resource selection function bins and area-adjusted frequencies for the individually blocked five-fold cross validation for models of density-dependent habitat selection of bison in Grasslands National Park, Saskatchewan, Canada from 2009 - 2013. F1, F2, F3, F4, and F5 represent the predictive ability of each fold and mean is the average Spearman-rank correlation of the folds.

Scale	Season	F1	F2	F3	F4	F5	Mean
Home range	Spring	0.939	0.146	0.049	-	-0.673	0.192
	Calving	0.200	0.479	0.176	0.997	-0.939	0.182
	Post-calving	0.382	-0.770	-0.711	-0.985	-0.997	-0.616
	Rut	0.997	0.997	0.976	-0.571	0.818	0.643
	Fall	0.891	0.952	0.967	-0.333	-0.370	0.421
Within home range	Spring	0.224	-0.036	0.321	-	-0.139	0.092
	Calving	-0.370	0.018	-0.042	-0.952	-0.915	-0.452
	Post-calving	0.224	-0.273	-0.721	-0.802	-0.973	-0.509
	Rut	1.00	0.964	0.994	-0.636	0.675	0.599
	Fall	0.988	0.988	0.855	-0.721	0.541	0.530

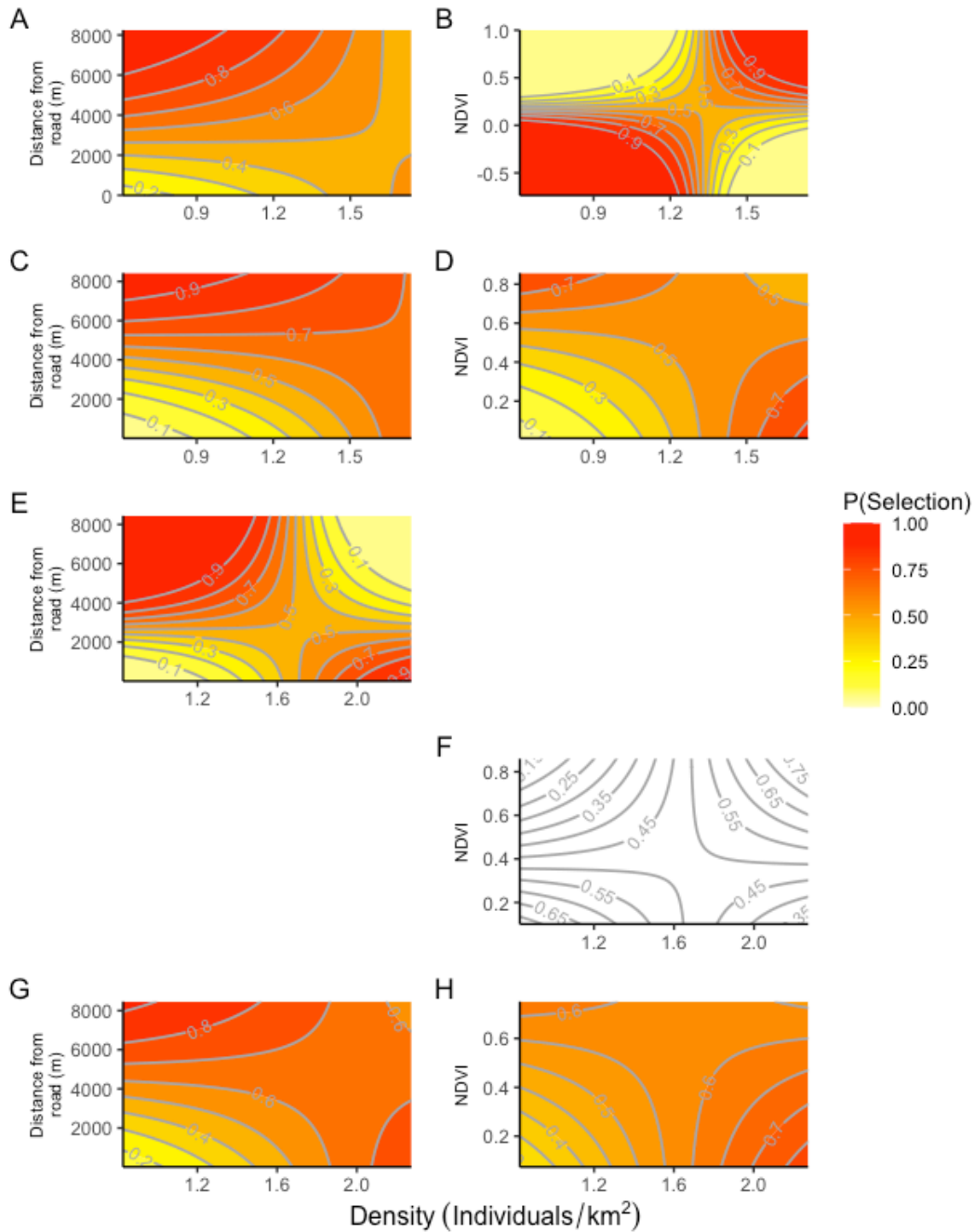


Figure 4. Surface plots showing the mean RSF estimates of Plains Bison selection for distance from roads and NDVI as a function of population density in Grasslands National Park, Saskatchewan, Canada from 2009 to 2013 at the home-range scale. Blank panels indicate that the variable was not included in the top model based on  $AIC_c$  for that season and panels without filled contours represent non-significant ( $p > 0.05$ ) interactions.

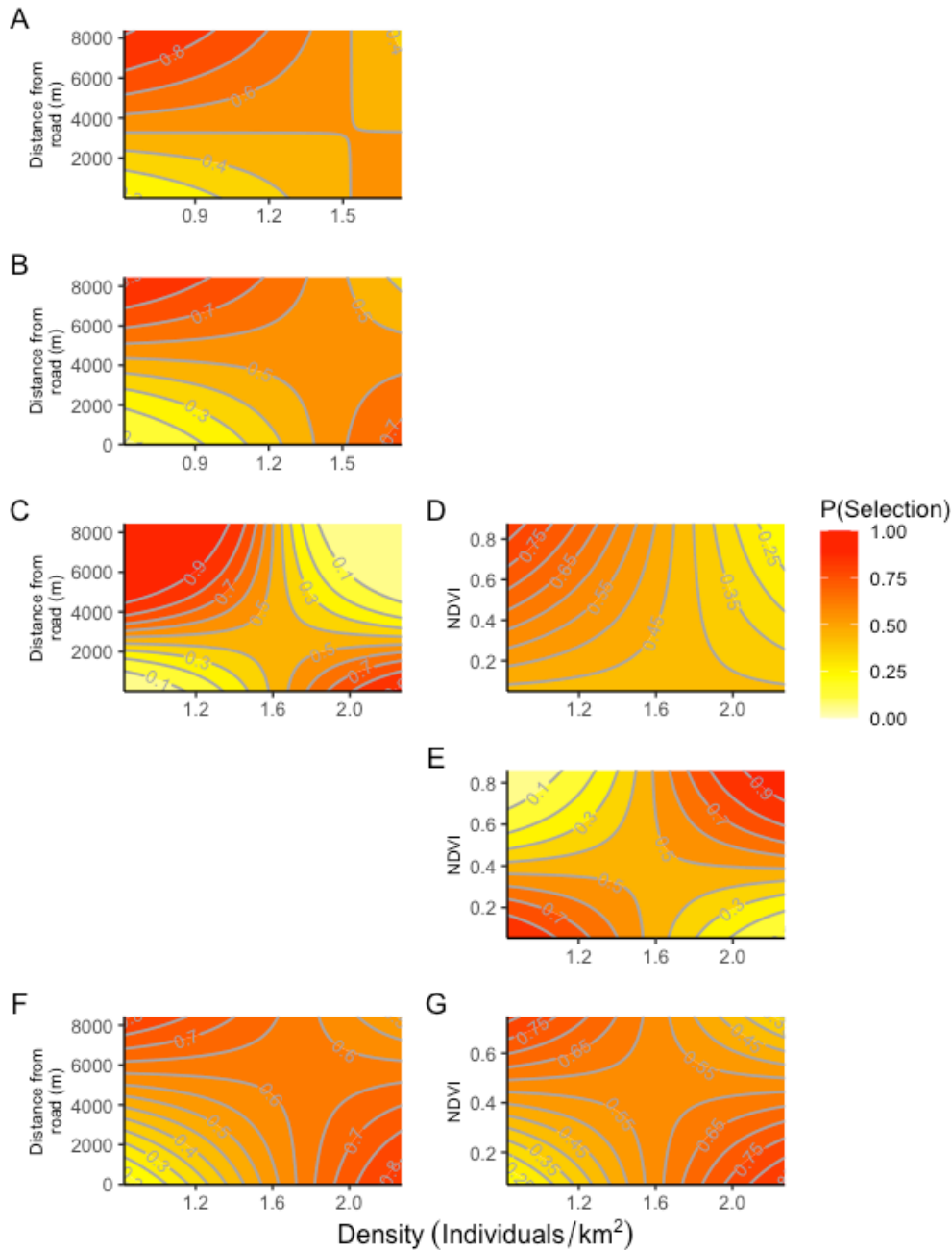


Figure 5. Surface plots showing the mean RSF estimates of Plains Bison selection for distance from roads and NDVI as a function of population density in Grasslands National Park, Saskatchewan, Canada from 2009 to 2013 at the within home-range scale. Blank panels indicate that the variable was not included in the top model based on  $AIC_c$  for that season and panels without filled contours represent non-significant ( $p > 0.05$ ) interactions.

### 3.3 Comparison of selection during a period of population size manipulation

From 2014 to 2020, 14 adult female bison were collared. I used 14,163 locations for the spring LSD with each individual contributing an average of 1,012 GPS points (260 – 780). For the pre-rut LSD all 14 individuals with a total of 11,560 locations were used; individuals contributed an average of 826 GPS points (47 – 708). Thirteen individuals with a total of 5463 locations were used for the rut LSD; individuals contributed an average of 420 GPS points (111 – 336). For the fall LSD 13 individuals and a total of 11,025 locations were used; individuals contributed an average of 848 GPS points (79 – 732).

Population density was significantly different in years of high density before the surplus events and years of relatively low density following the surplus events (Mann-Whitney,  $U = 836456324$ ,  $n_{high\ density} = 4$ ,  $n_{low\ density} = 2$ ,  $p < 0.001$ ). However, due to the low sample size the results of this test must be interpreted with caution. The mean population density in years before and after the surplus events was 2.6 individuals/km<sup>2</sup> and 2.0 individuals/km<sup>2</sup>.

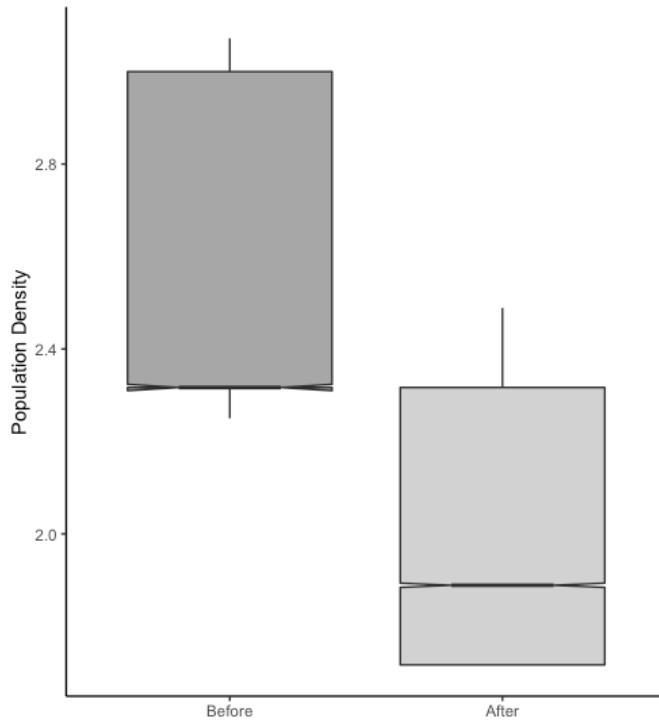


Figure 6. Population density of bison in Grasslands National Park, Saskatchewan, Canada in years of high density before the surplus events and years of relatively low density following the surplus events from 2014 - 2020. The line within the box represents the median density in high- and low-density years and the whiskers indicate the minimum and maximum population densities.

Selection for distance from road and NDVI were significantly different in alternating years of high- and low density but as with the RSFs the results varied by season. In the spring, calving and post-calving seasons, decreased population density led to increased selection for areas farther from roads (Table 4, Figure 7). The increased selection for distance from road was much more pronounced during the post-calving season (Figure 7). In the fall, decreased



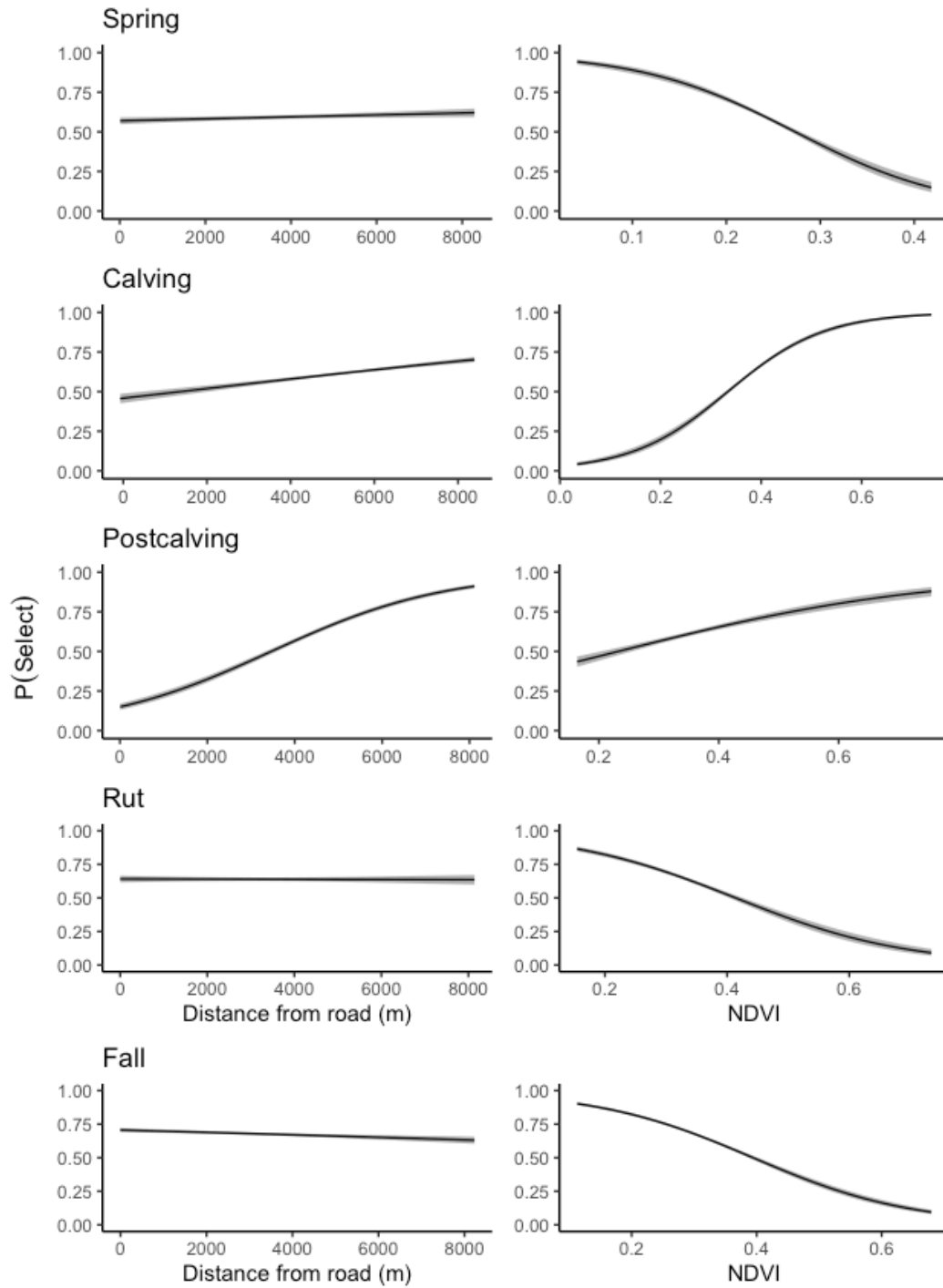


Figure 7. Plots of the predicted probability of selection ( $P(\text{Select})$ ) of a resource unit by bison in Grasslands National Park, Saskatchewan, Canada in low-density years following population size reductions compared to high-density years preceding population size reductions between 2014 and 2020 for each season as a function of distance from roads and NDVI.

population density led to decreased selection for distance from roads. Selection for distance from roads did not vary significantly between years of high- and low-density for the rut season (Table 4). Decreased population density led to increased selection for areas of high NDVI in the calving and post-calving seasons only (Table 4, Figure 7). In the spring, rut, and fall seasons decreased population density led to decreased selection for areas of high NDVI. Apart from the fall season, the results of the LSD analysis agreed with those of the home range and within-home range RSFs.

Table 4. Summary of beta coefficients, standard errors, and *p* for latent selection difference functions comparing resource selection of the bison population in years of reduced density after the population size reductions with the same population in years of high density preceding the reductions in Grasslands National Park, Saskatchewan, Canada from 2014 - 2020.

Season	<i>n</i>	<i>N</i>	Variable	Estimate	SE	<i>p</i>
Spring	6888	14	road	0.059	0.025	0.02*
			ndvi	-0.441	0.027	< 0.001*
Calving	12779	14	road	0.202	0.019	<0.001*
			ndvi	0.514	0.021	<0.001*
Post-calving	6056	13	road	0.968	0.034	<0.001*
			ndvi	0.381	0.033	<0.001*
Rut	5463	13	road	-0.005	0.029	0.852
			ndvi	-0.585	0.031	< 0.001*
Fall	11097	13	road	-0.082	0.021	< 0.001*
			ndvi	-0.669	0.022	< 0.001*

The ability of the LSD models to correctly discriminate between locations from high- and low-density years was good for the post-calving season but the AUC values fell slightly short of good for all other seasons (Figure 8). AUC values between 0.7 and 0.9 indicate good model accuracy, AUC values below 0.7 indicate poor model accuracy. The post-calving model had the highest AUC at 0.78, followed by the fall, rut and calving models with AUC values of 0.69, 0.68 and 0.68 respectively. The spring model had the lowest AUC at 0.61.

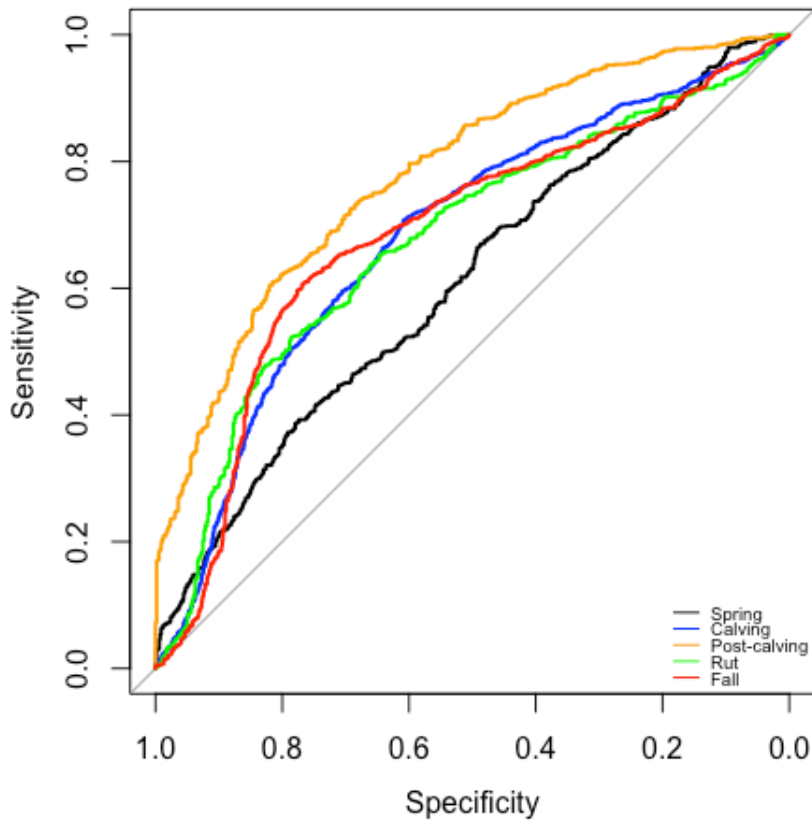


Figure 8. Relative operating characteristic curve (ROC) for seasonal latent selection difference functions comparing habitat selection of bison in Grasslands National Park, Saskatchewan, Canada in high- and low-density years between 2014 and 2020. The straight diagonal line represents and area under the curve (AUC) of 0.5 which indicates that a model has no ability to distinguish between outcomes.

## 4 Discussion & Conclusions

### 4.1 Discussion

My results support the hypothesis that second and third order habitat selection of adult female bison in Grasslands National Park, Canada, is density dependent. While density-dependent effects on habitat selection are expected to be evident in any population experiencing changes in population density (McLoughlin et al. 2010, Avgar et al. 2020), my study is the first to provide evidence that both the direction and magnitude of those changes can vary seasonally.

Consistent with my predictions that bison would avoid areas of higher perceived risk when population density was low and increase use of areas closer to perceived risk as density increased, density-dependence in selection for distance from roads was evident in all seasons and at both spatial scales examined except for the rut. Bison consistently selected for areas farther from roads when population density was low and increased use of areas closer to roads as density increased. Similarly, selection for areas farther from roads increased in the years following population reductions compared to years of relatively high density preceding the reductions.

The above suggests that while bison are not subject to predation or hunting in GNP, humans and vehicles may still be perceived as a potential risk by bison. Foca and Boyce (2022) showed that the density of linear features did not impact habitat selection of bison in any season in Elk Island National Park (EINP), Alberta, Canada (Foca and Boyce 2022). However, these authors suggested that this was because bison in EINP have become habituated to human presence. Similarly, a study conducted on bison at Nachusa Grasslands, a fenced preserve in Illinois, USA, found that bison did not avoid areas of concentrated human activity (Brockman et al. 2022). EINP has much less open habitat – which is preferred by bison – than GNP with more

than 60% of the park being dominated by aspen forest (Foca and Boyce 2022) and receives much higher visitation (Government of Canada 2022). Although Nachusa Grasslands is predominantly open habitat, the pasture available to the bison is much smaller than the bison containment area in GNP. Ritson (2019) found that the Henry Mountains bison herd in Utah, a free roaming herd, selected for home ranges farther from roads than did captive herds and suggested that bison will select for areas farther from human activity when able to do so. Another free roaming bison herd, the Book Cliffs herd, has also been found to avoid anthropogenic features (Sallee et al. 2023). Animals may not respond to a perceived risk by altering habitat use if the benefit of shifting to alternative habitats does not outweigh the cost of remaining in the disturbed habitat, for example if the alternative habitats are too far away or of too low quality (Gill et al. 2001). It is possible that the bison herds at EINP and Nachusa Grasslands are not able to avoid areas of human activity while meeting their nutritional demands due to limited open grassland habitat and small enclosure size. Indeed, ungulates in areas with higher exposure to encounters with humans tend to have reduced flight responses compared with those that infrequently interact with humans (Stankowich 2008). Bison at GNP appear to be able to meet their nutritional demands while still avoiding areas of human activity and appear to have remained wary of humans despite the absence of hunting since the reintroduction of the herd.

Inconsistent with my findings, Fortin and Andruskiw (2003) found that while female bison in Prince Albert National Park (PANP), Saskatchewan, Canada increased their daily radius of movement in response to human disturbance, this increased movement did not result in changes to habitat selection. Like EINP, the area inhabited by the bison herd in PANP consists of patches of open habitat in a predominantly forested landscape. In landscapes like that of GNP with very few trees or tall shrubs, perceived risks are likely to be detected at a greater distance

than in forested landscapes. Ungulates in open areas may be more affected by human recreation than areas where animals are shielded from recreation by vegetation (Taylor and Knight 2003). Additionally, animals have been found to respond differently to risks that are predictable in space and time than risks that are unpredictable. When spatio-temporal predictability of perceived risks is high animals can incorporate this information into habitat selection at the landscape scale by selecting for home ranges farther from the risk (Kittle et al. 2008). When a risk is unpredictable in space and/or time and cannot be effectively avoided it is not possible to incorporate into space use decisions (Kittle et al. 2008, Dupke et al. 2017). In GNP, the majority of human activity is concentrated on or very near the main park roads and human activity in the park follows a predictable annual cycle. This cycle consists of vehicle and human traffic increasing in the spring, peaking in July and August, and decreasing through the fall, and being almost exclusively restricted to park staff and local ranchers in the winter.

Bison did not avoid roads during the rutting season despite the fact that the rut coincides with peak park visitation (Parks Canada 2015) and therefore traffic, within the bison enclosure. During the rut, males that spend most of the year alone or in bachelor groups join the mixed herd. Male ungulates are less wary of human disturbance than females, especially during the breeding season (Stankowich 2008). Rutting behaviour takes a lot of time and energy, leaving less energy for other behaviours such as foraging and predator avoidance (Lima and Dill 1990). This finding is consistent with studies of other ungulates that have found reduced sensitivity to human disturbance during the rut (Reimers et al. 2006, Ciuti et al. 2008). Flight distances of mouflon in Sardinia were shorter during the rut than all other seasons, likely because less energy was available for anti-predator behaviour when the animals were preoccupied with mating. Reindeer in Norway had the lowest flight initiation distance to researchers on foot during the

rutting season even though the rut coincided with hunting season (Reimers et al. 2006). Bison may employ different anti-predator strategies during the rut. In addition to altering habitat selection, animals may avoid perceived risks by changing timing of activity, increasing group size, and/or increasing vigilance (Lima and Dill 1990). For example, elk in Waterton Lakes National Park were found not to avoid roads when they were open to vehicle traffic during the rut but instead increased the time spent vigilant at the cost of decreased courtship and rutting behaviour (St. Clair and Forrest 2009).

The cow-calf herd selected for areas of higher vegetation productivity, as measured by NDVI, when population density was low and increased selection for lower productivity areas as density increased. Similarly, selection for areas of higher vegetation productivity increased when the herd underwent biennial reductions in population size. This pattern is consistent with my predictions that bison would select for high quality habitat when population density was low, and that selection would generalize with increased density. However, this pattern only held true for the calving and post-calving seasons. Calving and lactation are the most nutritionally demanding time of the year for female ungulates (Oftedal 1985, Clutton-Brock et al. 1989). Due to the increased nutritional demands during this time, female ungulates tend to select for habitat with high forage abundance and quality (Barten et al. 2001, Poole et al. 2007, Rearden et al. 2011, Heffelfinger et al. 2020). Bison calves may nurse for more than a year but typically begin to spend more time grazing and less time suckling between 3 to 5 months of age (Green 1990, 1992).

The results for the spring and rut seasons were not consistent with the prediction that bison would select for areas of high vegetation productivity, as measured by NDVI, when population density was low, and that selection would decrease as density increased. In fact, the

exact opposite pattern was observed during these seasons. Similarly, during the spring and rut, bison decreased selection for areas of high productivity when population density was reduced. This suggests that bison are not selecting for vegetation productivity across all seasons examined. Bison may be switching between areas of abundant forage and areas of less abundant but higher quality forage to meet energetic requirements throughout the year. Bison, in particular lactating female bison, have been found to switch between feeding sites with high forage biomass of lower quality and sites with low biomass of higher quality throughout the growing season (Raynor et al. 2016b, 2017a, Shamon et al. 2022). Grazing in areas of high forage biomass results in faster satiation which leaves more time for other activities such as vigilance, reproduction or social interaction. Female bison may forage on high quantity/low quality patches when fast satiation is important, such as when provisioning young, and switch to higher quality forage to replenish depleted energy stores. Furthermore, Raynor et al. (2015) suggested that bison may compensate for low quality forage by consuming more food during times of the year when forage quality is naturally low such as during the early spring or late summer. A combination of foraging strategies in which herbivores make use of both high quantity/low quality and low quantity/high quality grasslands has been found to result in greater intake and growth than the utilization of either strategy exclusively (Prins and Beekman 1989, Owen-Smith 2002). Most studies examining seasonal habitat selection of bison have done so by dividing the year based on arbitrary calendar dates or plant phenology (i.e., growing vs dormant seasons). Examination of selection at coarser temporal scales may result in cases of switching between selection for high quantity/low quality and low quantity/high quality forage habitat being missed.

NDVI is a measure of greenness and is often used as a proxy for vegetation productivity in habitat selection studies. Productivity is defined as the rate at which solar energy is



transformed into resources that can be consumed by animals (Wright 1983). NDVI is not an exact measure of either forage biomass or forage quality. Indeed, remotely sensed NDVI has been found to be more closely correlated with forage abundance than forage quality, as measured by nitrogen content or crude protein in some grassland types (Thoma et al. 2002, Garrouette et al. 2016). While NDVI has been found to be an important factor influencing habitat selection (Merkle et al. 2016, Heffelfinger et al. 2020, Hughey et al. 2021), body condition (Hurley et al. 2014), and the probability of successful reproduction (Hurley et al. 2014, Heffelfinger et al. 2020) in ungulates, more detailed measures of both forage abundance and quality may be required to tease apart the effect of density on selection of foraging habitat in bison.

The patterns observed during the period of population size fluctuations were consistent with those observed during the period of natural population growth. This finding is consistent with studies conducted on other ungulate populations during periods of population declines. Merrill et al. (2020) found that elk increased selection for areas of high forage biomass and reduced selection for areas of high predation risk when the population decreased by 70% over 14 years. Similarly, van Beest et al. (2014a) found that both elk and moose increased selection for higher quality habitats as the population densities of both species decreased. In contrast with my findings, bison in PANP were found to increase their home ranges to include lower productivity habitats but were not found to decrease their use of those lower productivity habitats when population density subsequently decreased, suggesting that site fidelity was a more important driver of habitat selection than energy maximization during periods of population decline (Merkle et al. 2015). Site fidelity can benefit ungulates by increasing movement efficiency, decreasing predation risk, and allowing for more efficient exploitation of food sources (Morrison et al. 2021). It is possible that the benefits of site fidelity are outweighed by the benefits of

selecting for higher quality habitat with decreases in population density in GNP. In GNP movement is not impeded by forests or rugged terrain and the risk of predation is low if not completely absent. It is also possible that site fidelity and selection of vegetation productivity are not mutually exclusive in this system.

A release from density dependence was evident when 30 – 40% of the population was removed, even though the population was still below the carrying capacity of the bison enclosure. The mean exponential rate of increase ( $r = \ln(\lambda)$ ) for the GNP bison herd between reintroduction in 2005 and 2013 when population size manipulations began was 0.22. During the period of population-size fluctuations, the mean exponential rate of increase ( $r$ ) was 0.28. Thus, the annual rate of increase of the GNP bison herd from 2014 to 2020 exceeds the highest rate of increase observed for a bison population under natural conditions, which was 0.21 (Gates et al. 2010). The fact that the average annual rate of increase of the GNP herd is still so high despite a large proportion of the population being removed biennially suggests that the population is not yet near the ecological carrying capacity of the enclosure. Spatial distribution models are expected to return different results depending on how close a population is to its carrying capacity (Matthiopoulos et al. 2015). The difference in selection between years of high density before the removal of individuals and low density following the population reductions would likely be greater if the population were at carrying capacity.

The results of habitat selection models are context dependent and cannot reliably predict selection behaviour in other contexts if population density or resource availability is variable in either space or time (Boyce and McDonald 1999, McLoughlin et al. 2010, Avgar et al. 2020). While the ability of spatial distribution models to make predictions for spatially distinct populations has been tested and found to be poor (Torres et al. 2015), the ability of such models

to predict the distribution or habitat selection of the same population with varying population densities has never been directly tested. Boyce et al. (2002) found that a pooled resource selection probability function (RSPF) created using multiple years of data for boreal songbird species were not good predictors of annual selection and suggested that this may be due to changes in abundance. However, data on population abundance is usually not available for long term datasets of species occurrence, making it difficult to test for density dependence in habitat selection. The long-term monitoring of the bison herd at GNP combined with collar data collected at a variety of population densities allowed for the incorporation of density into seasonal RSF models. These RSF models had poor ability, regardless of season or spatial scale, to predict selection at different population densities. The results of my study further reinforce the already known fact that RSFs that do not take into account population density provide only a snapshot of selection and may lead to misguided management decisions if the results are extrapolated outside of the context of the study.

## 4.2 Limitations

The results of the RSF analysis presented here should be interpreted with caution. Since population size was measured annually and increased each year following reintroduction of the herd in 2005 until 2013, population density and year are strongly correlated. It is difficult to say with certainty that the changes in habitat selection observed were solely due to changes in conspecific density. Forage availability can also change dramatically between years in the study area due to variation in annual rainfall, temperatures, and growing season length. Forage availability can also change throughout the growing season because of grazing patterns of bison and other herbivores, and other natural processes such as fire. By using annual and seasonal

NDVI as a measure of vegetation productivity I attempted to control for the effect of temporal variation in forage availability on selection patterns. NDVI is sensitive to changes in vegetation productivity caused by grazing and fire (Li and Guo 2018, Geremia et al. 2019). Additionally, increased utilization of habitats near the main road through the park over time could represent gradual habituation of the herd to humans. This is not expected to be the case in GNP as the cow-calf and mixed groups are still very skittish, especially during the calving and post-calving seasons. Furthermore, the fact that the patterns observed during the period of population growth were reversed following population size reductions suggests that the changes in habitat selection were at least in part caused by changes in population density.

It is also important to note that only female bison were included in this study and thus the habitat selection patterns discussed may not represent the entire population. Mature males are segregated from the mixed herd for most of the year, remaining solitary or forming smaller bachelor groups. In GNP, mature males make up approximately 30% of the population. Male bison are much larger than females; following the Jarman-Bell principle larger ungulates are able to consume forage of lower quality than smaller ungulates (Sensening et al. 2010). Male bison have been found to select for habitat with more abundant but less nutritious forage than females (Mooring et al. 2005, Berini and Badgley 2017). In bison, as in other ungulates, males are less likely than females, particularly those with young, to avoid human disturbance (Cameron et al. 1979, McLaren and Green 1985, Fortin and Andruskiw 2003, Haidt et al. 2018). Therefore, space use and habitat selection of solitary males and bachelor groups can be expected to differ from that of the mixed herd. Not only can habitat selection vary between the sexes but the effect of density on habitat selection of large herbivores can also vary between males and females (Fortin et al. 2022). Male and female elephants in a fully fenced nature preserve in Kenya frequented

areas near human infrastructure as population size increased but the rate of increase in selection was much greater for males than females (Fortin et al. 2022). Most habitat selection studies using radio telemetry conducted on bison only include females (but see Nekorchuk et al. 2019), due to the difficulties of collaring large males and the lower success rate of GPS collars on males compared to females (Jung and Kuba 2015). Further research is required to determine how population density impacts habitat selection of male bison.

### 4.3 Management Implications

This study highlights the importance of considering population density in habitat selection analyses. The GNP bison herd is currently maintained at approximately 400 to 500 individuals; increasing the size of the bison herd would be a significant contribution to the conservation of the species in Canada. Should the Park choose to increase the size of the bison population within the current bison containment area, habitat selection patterns should be regularly reassessed in order to understand the effect that increasing population density is having on bison space use. Selection of forage availability and avoidance of perceived risk in the GNP bison herd were influenced by population density though not always in predictable ways. In general, bison selected for areas farther from roads when population density was low and increased use of areas near roads when density was high. Further increases in population density may increase the probability of human-bison conflict as the bison herd is forced to use areas of the enclosure where human activity is concentrated. The magnitude and direction of the interaction between selection for vegetation productivity and population density varied by season and spatial scale of analysis. While NDVI is a useful proxy for vegetation productivity, it may not fully represent forage quality. For future studies of bison habitat selection in Grasslands National Park, I

recommend the collection of more detailed measures of seasonal forage abundance and quality. This will aid not only in refining models for density-dependent habitat selection within the current bison containment area but also provide information for the development of a habitat suitability index to inform future expansion of the bison containment area.

The consideration of density dependent effects on habitat selection is especially important for populations of large ungulates that are fully fenced, as bison often are, and therefore may not be able to migrate to follow seasonal forage availability or disperse to new ranges with increasing population density. In such situations understanding how space use may change with fluctuations in population density, either natural or as the result of population management, is key in predicting the effect that bison grazing may have on the ecosystem and other species.

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## 6 Appendix A

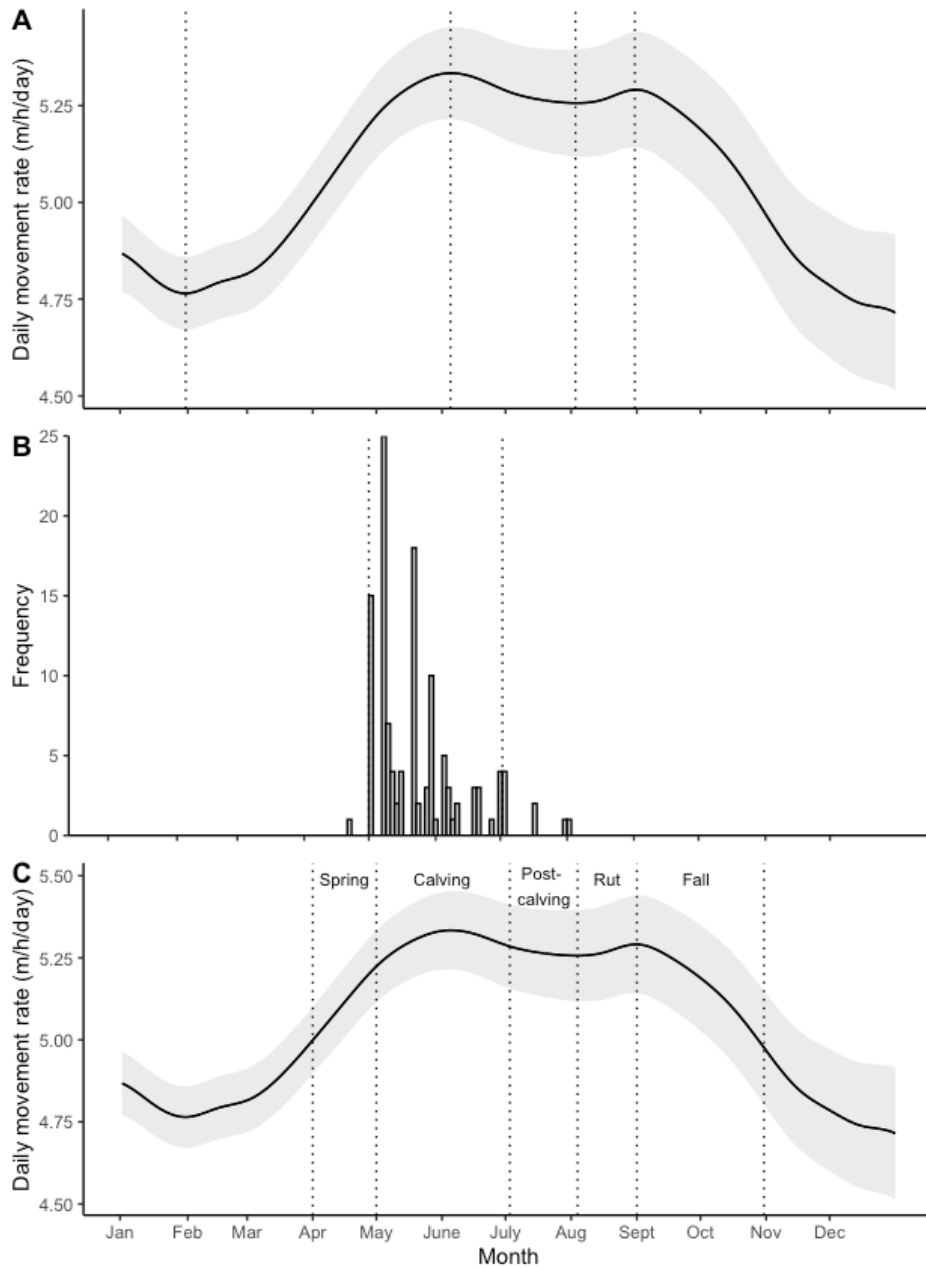


Figure 9. A) Estimated biologically relevant seasons based solely on changes in daily movement rate. Dotted lines indicate peaks and troughs in curve used to delineate seasonal boundaries. B) Frequency of estimated calving dates of pregnant bison in 2020. Dotted lines indicate the window within which 95% of calving dates occurred. C) Biologically relevant seasons refined using calving data and NDVI data availability.



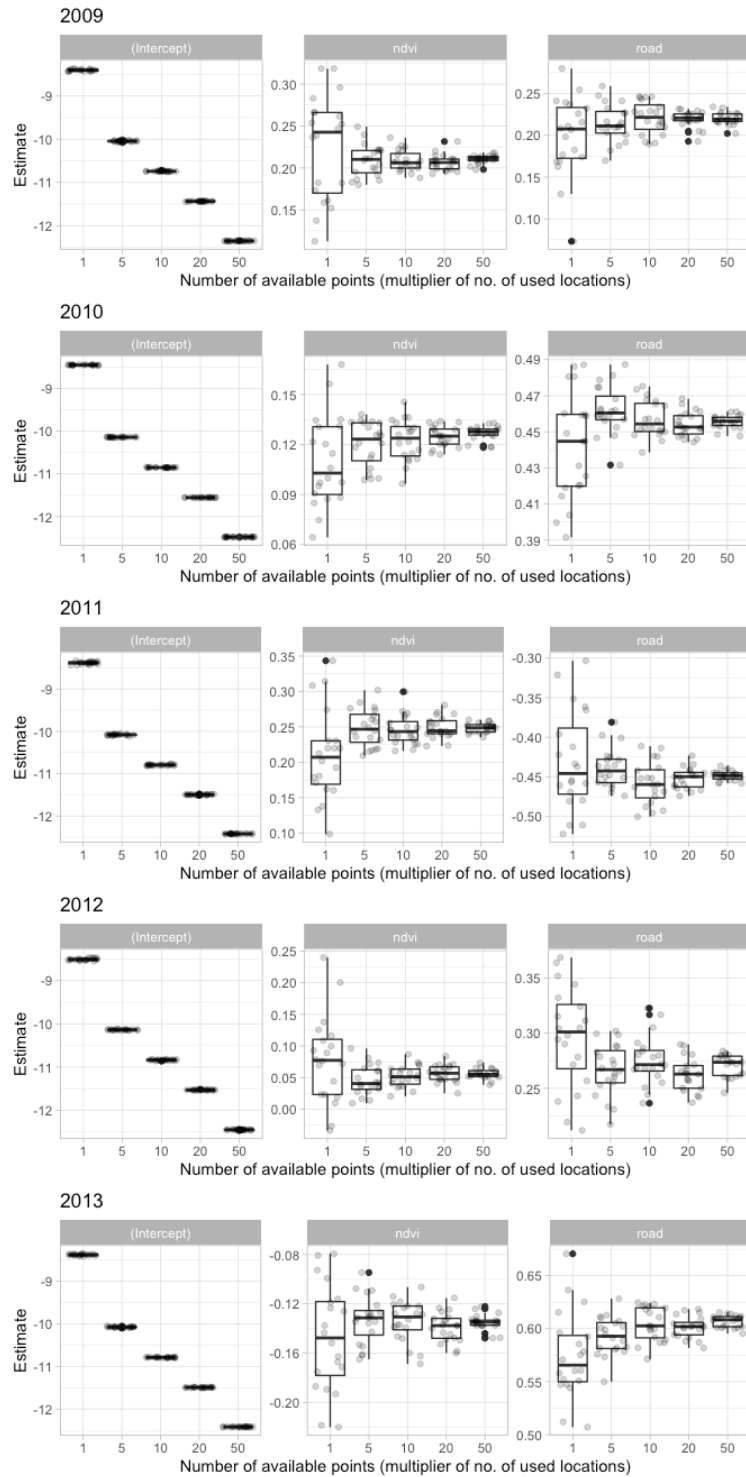


Figure 10. Output plots from the sensitivity analysis used to determine the appropriate number of available locations per used location for the resource selection function for the post-calving season at the home-range scale.

Table 5. Summary of beta coefficients ( $\beta$ ), standard errors (SE), and  $p$  for the seasonal RSFs at the home-range scale for the Grasslands National Park bison. Significant  $p$ -values are bolded.

<i>Predictors</i>	<b>Spring</b>			<b>Calving</b>			<b>Post-calving</b>			<b>Rut</b>			<b>Fall</b>		
	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>
(Intercept)	-0.00	408.25	1.000	-0.00	353.39	1.000	-0.00	378.00	1.000	-0.00	378.01	1.000	-0.00	408.23	1.000
Road	0.48	0.19	<b>0.011</b>	0.59	0.35	0.094	1.00	0.86	0.243	1.00	0.23	<b>&lt;0.001</b>	0.54	0.11	<b>&lt;0.001</b>
NDVI	-0.14	0.30	0.651	0.06	0.09	0.497	-0.00	0.11	0.987	-0.17	0.16	0.302	0.07	0.04	0.121
Density	-0.04	0.16	0.820	0.77	0.12	<b>&lt;0.001</b>	-0.10	0.14	0.483	-0.05	0.12	0.650	0.45	0.08	<b>&lt;0.001</b>
Road*Density	-0.50	0.16	<b>0.002</b>	-0.57	0.08	<b>&lt;0.001</b>	-1.77	0.12	<b>&lt;0.001</b>				-0.37	0.06	<b>&lt;0.001</b>
NDVI*Density	0.52	0.19	<b>0.005</b>	-0.23	0.10	<b>0.018</b>				0.26	0.18	0.152	-0.09	0.04	<b>0.027</b>

Table 6. Summary of beta coefficients ( $\beta$ ), standard errors (SE), and  $p$  for the seasonal RSFs at the within home-range scale for the Grasslands National Park bison. Significant  $p$ -values are bolded.

<i>Predictors</i>	<b>Spring</b>			<b>Calving</b>			<b>Post-calving</b>			<b>Rut</b>			<b>Fall</b>		
	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>	<i>Estimate</i>	<i>SE</i>	<i>p</i>
(Intercept)	-0.00	408.25	1.000	-0.00	353.63	1.000	-0.00	378.00	1.000	-0.00	378.00	1.000	-0.00	408.13	1.000
Road	0.31	0.18	0.078	0.26	0.35	0.460	0.74	0.82	0.367	0.76	0.23	<b>0.001</b>	0.36	0.11	<b>0.001</b>
NDVI	-0.03	0.07	0.678	0.11	0.06	0.056	0.11	0.09	0.224	-0.23	0.29	0.428	0.13	0.06	<b>0.035</b>
Density	0.00	0.14	0.978	0.44	0.11	<b>&lt;0.001</b>	-0.49	0.14	<b>0.001</b>	-0.20	0.12	0.107	0.49	0.08	<b>&lt;0.001</b>
Road*Density	-0.44	0.18	<b>0.015</b>	-0.62	0.08	<b>&lt;0.001</b>	-1.71	0.12	<b>&lt;0.001</b>				-0.36	0.06	<b>&lt;0.001</b>
NDVI*Density							-0.16	0.07	<b>0.037</b>	0.53	0.21	<b>0.012</b>	-0.20	0.05	<b>&lt;0.001</b>

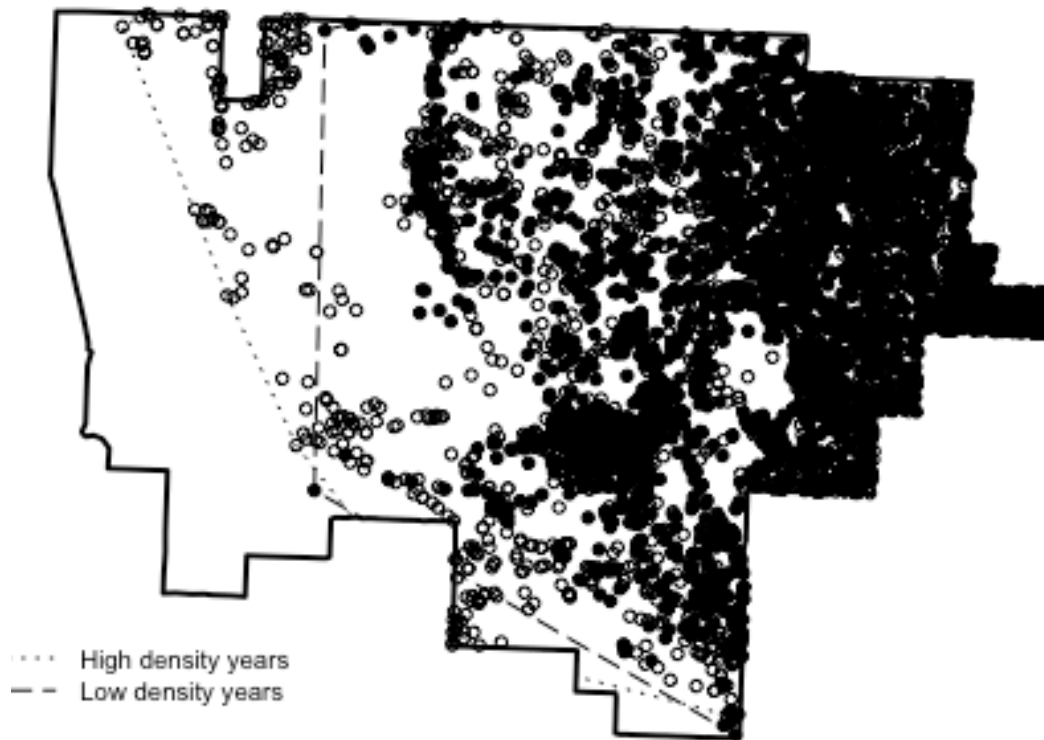


Figure 11. Spatial distribution of the GPS locations for the bison herd within the Grasslands National Park bison enclosure in high-density years preceding population size reductions (empty circles) and low-density years following reductions (filled circles) for the spring season. Dashed line represents the 100% minimum convex polygon (MCP) surrounding the locations from high-density years and dotted line represents the 100% MCP surrounding the locations from low-density years.

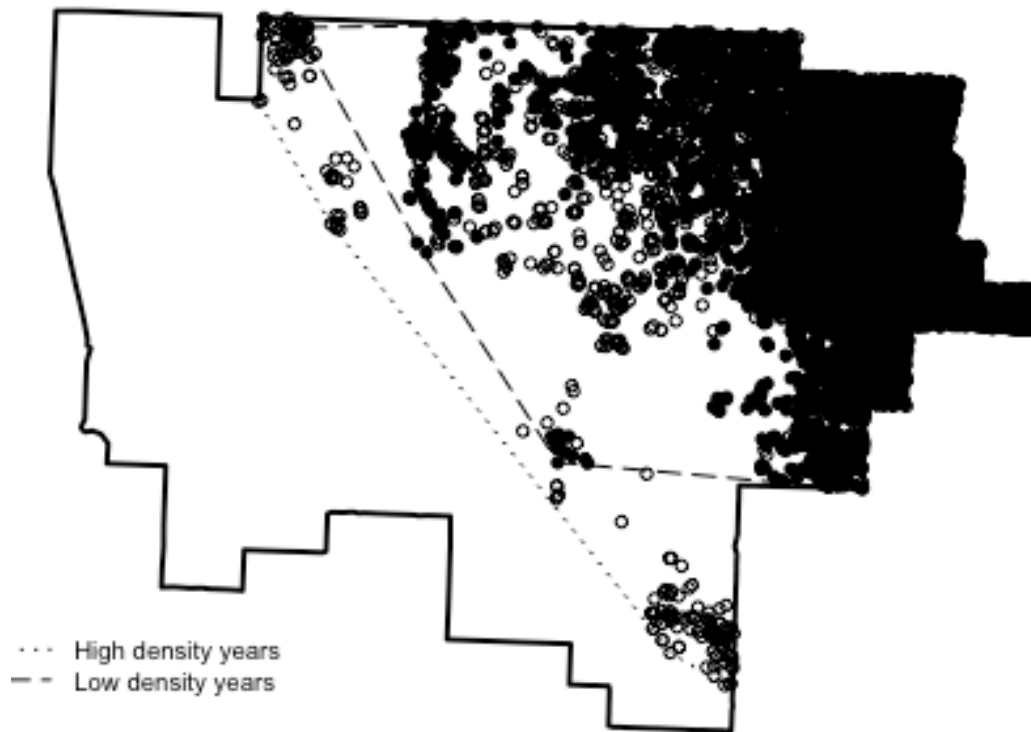


Figure 12. Spatial distribution of the GPS locations for the bison herd within the Grasslands National Park bison enclosure in high-density years preceding population size reductions (empty circles) and low-density years following reductions (filled circles) for the calving season. Dashed line represents the 100% minimum convex polygon (MCP) surrounding the locations from high-density years and dotted line represents the 100% MCP surrounding the locations from low-density years.

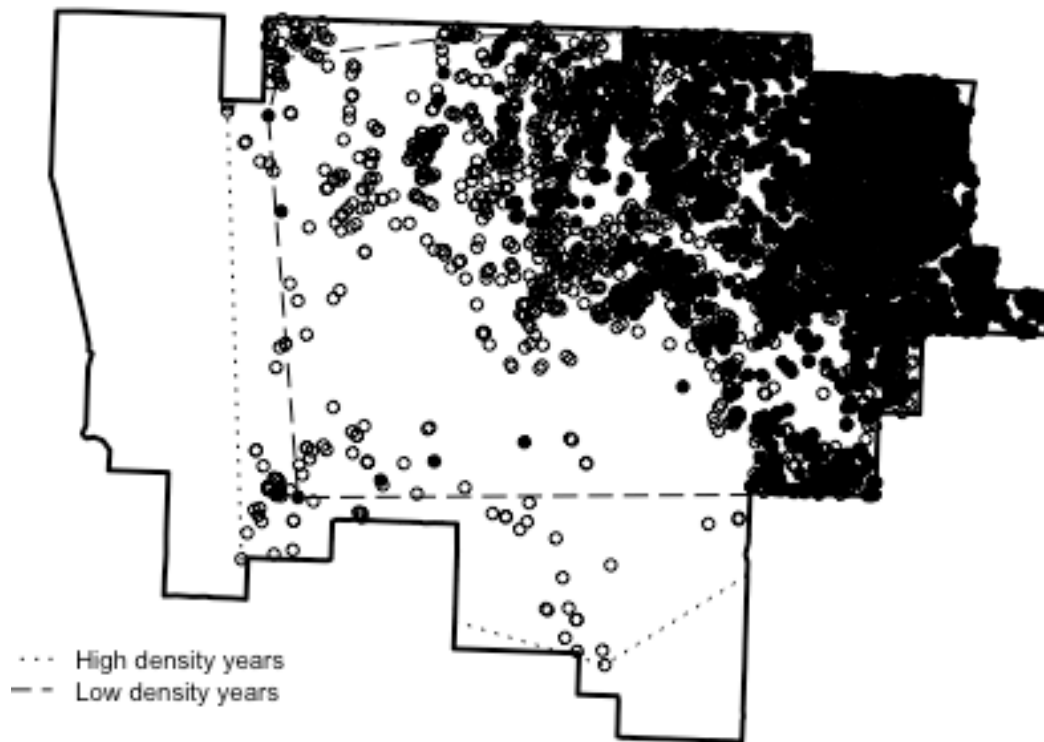


Figure 13. Spatial distribution of the GPS locations for the bison herd within the Grasslands National Park bison enclosure in high-density years preceding population size reductions (empty circles) and low-density years following reductions (filled circles) for the post-calving season. Dashed line represents the 100% minimum convex polygon (MCP) surrounding the locations from high-density years and dotted line represents the 100% MCP surrounding the locations from low-density years.

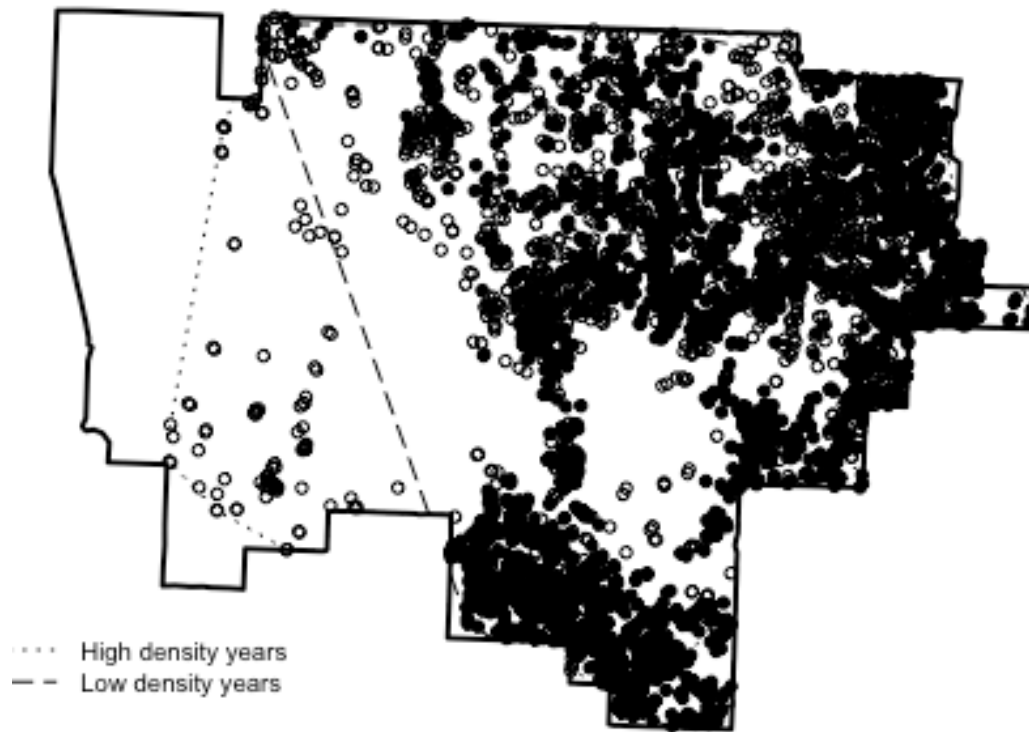


Figure 14. Spatial distribution of the GPS locations for the bison herd within the Grasslands National Park bison enclosure in high-density years preceding population size reductions (empty circles) and low-density years following reductions (filled circles) for the rut season. Dashed line represents the 100% minimum convex polygon (MCP) surrounding the locations from high-density years and dotted line represents the 100% MCP surrounding the locations from low-density years.

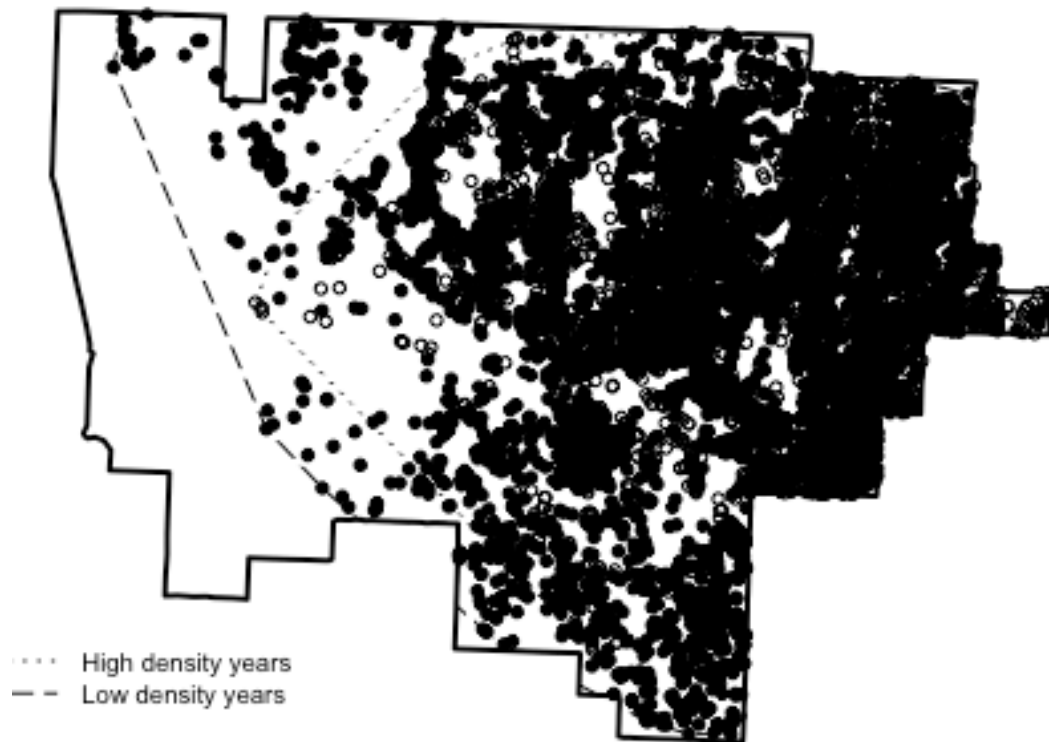


Figure 15. Spatial distribution of the GPS locations for the bison herd within the Grasslands National Park bison enclosure in high-density years preceding population size reductions (empty circles) and low-density years following reductions (filled circles) for the fall season. Dashed line represents the 100% minimum convex polygon (MCP) surrounding the locations from high-density years and dotted line represents the 100% MCP surrounding the locations from low-density years.