APPLICATION OF REMOTE SENSING AND GIS IN MODELLING BISON CARRYING CAPACITY IN MIXED-GRASS PRAIRIE

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ABSTRACT

Understanding carrying capacity of plains bison (*B. bison bison*) is critical for protecting this wild species and grassland ecosystem in mixed-grass prairie. The overall goal of this study is to examine plains bison carrying capacity in the mixed-grass prairie. There are four specific objectives: 1) investigate annual space use of plains bison and their seasonal core ranges, 2) assess seasonal Resources Selection Functions (RSFs) of plains bison, 3) estimate vegetation biomass and productivity of mixed-grass prairie, and 4) estimate carrying capacity taking into account RSFs. I used Kernel Density Estimator to address the first objective. Generalized Linear Mixed Effects models were used for the second objective. The last two objectives were completed using Sentinel-2 Multispectral Image (MSI). This study highlights the power of remote sensing and Geographic Information Systems (GIS) techniques in estimating key driver of bison carrying capacity (available forage) and adjusting factor (RSFs). Results show that bison family groups in Grasslands National Park frequent specific areas. They mainly use the northeast corner of the West Block and expand the core range when it comes to dormant season. Vegetation type information and other landscape factors (slope, distance to water, roads, fences, and prairie dog town) are influencing seasonal RSFs of bison family groups. Vegetation productivity is 734 kg ha^{-1} supporting 671 - 959 Bison Unit as the carrying capacity. Our study not only contributes to a better bison management plan for Grasslands National Park, one of seven conservation areas of wild plains bison in Canada, but also assists in understanding the interaction of this wild species with the mixed-grass prairie ecosystem.

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I want to thank Dr. Winston Zeng for giving me chance to have working experiences as a GIS analyst in the Spatial Initiative, Mr. Yunpei Lu for his help with collecting data. I thank my fellow labmates: Tengfei Cui, Xiaolei Yu, Thiago Frank, and Jeff Harder for the stimulating discussions, their enthusiastic help during the field seasons, and for all the fun we have had in the last two years. Many thanks go to Saskatchewan Innovation and Opportunities Scholarship, the Department of Geography and Planning, and the University of Saskatchewan for their financial support.

Finally, I want to deeply express my love and thanks to my family, my parents, my younger sister, and my friends who always support every step of my life journey. This work is dedicated to my parents, my younger sister, and the special one who spent seven years of life to love me indeed.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

IUCN	International Union for Conservation of Nature
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
GIS	Geographic Information System
RSFs	Resources Selection Functions
HSI	Habitat Suitability Index
AVHRR	Advanced Very High-Resolution Radiometer
MODIS	Moderate Resolution Imaging Spectroradiometer
NPP	Net Primary Productivity
Landsat MSS	Landsat Multispectral Scanner
Landsat TM	Landsat Thematic Mapper
Landsat ETM+	Landsat Enhanced Thematic Mapper Plus
Sentinel-2 MSI	Sentinel-2 Multispectral Imagers
DEM	Digital Elevation Model
ρ	Reflectance
VIs	Vegetation Indices
GNP	Grasslands National Park
UG	Upland grassland
SG	Slope grassland
VG	Valley grassland
EC	Eroded community
SC	Shrub community
TC	Tree community
DC	Disturbed community
NDVI	Normalized Difference Vegetation Index
ESA	European Space Agency
SNAP	Sentinel Application Platform
KDE	Kernel Density Estimator
GME	Geospatial Modelling Environment
AICc	Second - order Akaike Information Criterion
MLR	Multiple Linear Regression

r^2	Coefficient of determination
RMSE	Root Mean Square Error
SR	Simple Ratio
EVI	Enhanced Vegetation Index
RCI	Ratio Cover Index
$NDVI_n$	Narrow Normalized Vegetation Index
PVI_n	Narrow Perpendicular Vegetation Index
$GSAVI_n$	Narrow Green Normalized Difference Vegetation Index
$MSAVI_n$	Narrow Modified Soil-adjusted Vegetation Index
$NDVI_{ngreen}$	Narrow Green Normalized Difference Vegetation Index
EVI_n	Narrow Enhanced Vegetation Index
EVI_{2n}	Narrow Enhanced Vegetation Index 2
$MTVI_{1n}$	Narrow Modified Triangular Vegetation Index 1
$NDII_{7n}$	Narrow Normalized Difference Infrared Index 7
$NDVI_{re2n}$	Narrow Normalized Difference Vegetation Index red-edge 2
$NDVI_{re3n}$	Narrow Normalized Difference Vegetation Index red-edge 3

Chapter 1 INTRODUCTION

1.1. General context of plains bison in Northern Great Plains

In North America, the American bison (Bison bison) is the largest terrestrial mammals (Campbell, Campbell, Blyth, & McAndrews, 1994; Hartnett, Hickman, & Walter, 1996; Knapp et al., 1999). Its range was originally distributed across the continent (Freese et al., 2007). Plains bison (B. bison bison), one of the two recognized subspecies of American bison (COSEWIC, 2013), occupy less than 1% of the Northern Great Plains, their historical range (Sanderson et al., 2008). About 20,500 bison were managed as of 2008 for conservation purposes across 62 conservation herds, the majority of which had fewer than 400 animals (Gates, Freese, Gogan, & Kotzman, 2010). In a global context, plains bison is listed as a near-threatened species according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species 2017 (Aune, Jørgensen, & Gates, 2018). Nationally, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designates plains bison as threatened because less than 0.5 % of its former range is being occupied in Canada (COSEWIC, 2013). This threatened species has been recovering since the early 20th century, when it was hunted to near extinction (Arthun & Holechek, 1982; Markewicz, 2018). The fluctuation of plains bison population in North America is shown in Figure 1-1. Yet, the conservation programs remain challenged by the rarity of large wild populations, the need to preserve the bison genome, and the presence of diseases at the wildlife-livestock interface (Gates et al., 2010). In this context, the proper assessment of ecological carrying capacity is critical for habitat management and species restoration.

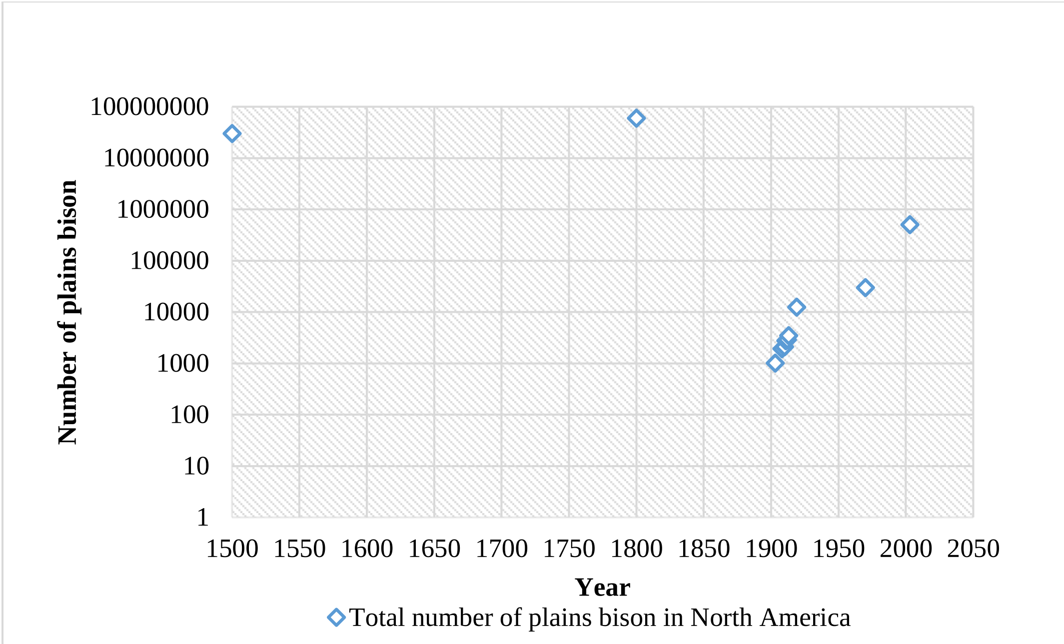

Figure 1-1 Estimated plains bison population in North America from 1500 to 2003 (American Bison Society, 2019; Boyd, 2003; Shaw & Meagher, 2000; US Fish and Wildlife Service, 2014).

1.2. Grasslands ecosystem in Northern Great Plains

Grasslands are highly dynamics ecosystem that covers about one quarter of the Earth's surface (Friedl et al., 2002, 2010; Henwood, 1998). Grasslands occur in the steppes of Eurasia, the prairies of North America, the pampas of South America and the veld of South Africa (Watkinson & Ormerod, 2001). This ecosystem provides numerous goods (fertilizer, fiber, foods, medicines, forage, energy, construction, and craft materials) and services (recreation, erosion control, wildlife habitat, climate regulation, water and nutrient cycling) to serve human needs (White, Murray, & Rohweder, 2000). Despite the multi-functionality of grasslands, this ecosystem is facing numerous challenges. The Northern Great Plains is a typical example.

Broadly defined, the Northern Great Plains includes the southeast part of Alberta, southern Saskatchewan, the southwest corner of Manitoba, and portions of Montana, North and South Dakota, and Wyoming (Coupland, 1961; Hendrickson, Sedivec, Toledo, & Printz, 2019) (Figure 1-2). Major grassland types in this area are tall-grass prairie, mixed-grass prairie, and short-grass prairie (Cooper, 2008; Samson, Knopf, & Ostlie, 2004). Basically, the grassland vegetation is similar over most of Northern Great Plains with three main genera of grass: *Agropyron*, *Stipa*, and *Bouteloua* (Barker & Whitman, 1988). Grasslands in the Northern Great Plains are productive and highly resilient, however they are disappearing because of land use conversion, non-native species invasion, and biodiversity loss (Hendrickson et al., 2019; World Wildlife Fund, 2013). About 42% of the grasslands in the Great Plains have been converted to cropland (World Wildlife Fund, 2018). To sustain healthy grassland ecosystem, ecological disturbances are fundamental and natural components (Li & Guo, 2014).

Along with drought and fire, grazing is major disturbance in grasslands (Anderson, 2006; Li & Guo, 2014) affecting their maintenance, productivity, economic use, and biodiversity management (Watkinson & Ormerod, 2001). First, grazing removes plants' parts, resulting in decreases in photosynthesis, productivity, and vigor of single plants (Doan & Guo, 2019; Knapp et al., 1999). Second, plant removal by grazing may reduce biodiversity, break soil structure, invite invasion of exotic species (Knapp et al., 1999; Li & Guo, 2014). In contrast, grazing can promote the growth of some specific plant species due to the reduced competition and increased sunlight energy and nutrient availability (Frank & Groffman, 1998). Moreover, the proper grazing practices can help manage fire behaviors by reducing flammable material, as well as remove invasive species based on the understanding of herbivores' selectivity in forage consumption (DiTomaso, Brooks, Allen, & Minnichi, 2006; DiTomaso, Masters, & Peterson, 2010; Menke, 1992; Taylor Jr., 2006).

In Northern Great Plains, plains bison were the keystone grazers for thousands of years until their near extirpation in the 18th century (Allred, Fuhlendorf, & Hamilton, 2011; Freese et al., 2007; Knapp et al., 1999; McMillan, Kunkel, Hagan, & Jachowski, 2019). In spite of a noticeable recovery of plains bison, the population bottleneck of this species brings negative impacts to grasslands ecosystem (Cooper, 2008). Hence, reintroducing plains bison is a potential strategy to conserve grasslands ecosystem in the Northern Great Plains for a long-term vision.

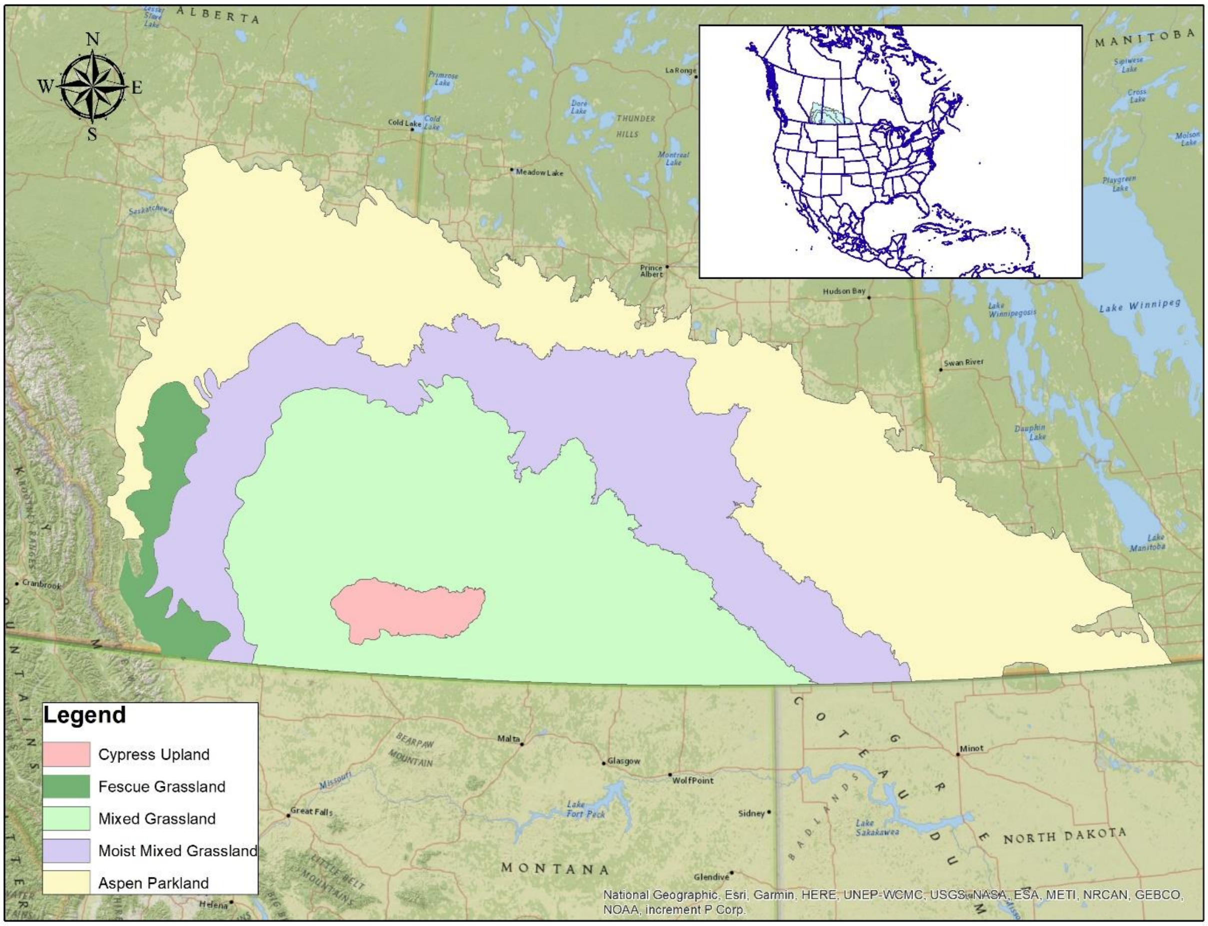

Figure 1-2 Location and ecoregions of the Northern Great Plains in Canada (ecoregion layer is from Government of Canada).

1.3. Plains bison carrying capacity estimation

Carrying capacity estimation is pivotal to sustainable grazing (Beck, Peek, & Strand, 2006; Doan & Guo, 2019; Holechek, Pieper, & Herbel, 1995; Scarnecchia, 1990). Carrying capacity is defined as the ecologically sustainable stocking rate or the number of animals supported in a specific area that ensures both long-term ecosystem health and achievement of grazing objectives (Beck et al., 2006; Doan & Guo, 2019; Holechek, Gomes, Molinar, & Galt, 1998). There are many methods of estimating carrying capacity (Doan & Guo, 2019; McLeod, 1997). These methods highlight that the fundamental drivers for carrying capacity are forage availability and animal consumption requirements (Doan & Guo, 2019; Long, Li, Wei, & Hua-Kun, 2010). Beside these two drivers, carrying capacity needs to take into account habitat/resources selection displayed by herbivores and an appropriate utilization rate to maintain ecological sustainability of grazing areas (e.g., for wildlife, water infiltration, erosion prevention) (Beck et al., 2006; Doan & Guo, 2019; Manly, McDonald, Thomas, McDonald, & Erickson, 2007; Steenweg, Hebblewhite, Gummer, Low, & Hunt, 2016). Herbivores unevenly select spatial patterns of distribution and temporally modify their space use due to their behavioral habitat/resources selection (Ciuti, Pipia, Grignolio, Ghiandai, & Apollonio, 2009; Millspaugh et al., 2006; Pringle & Landsberg, 2004). Thus, Beck et al (2006) considered habitat/resources selection as an adjustment of carrying capacity due to the recognition of over-estimation of carrying capacity in some case studies (i.e. conservative elk-population in North Park, Colorado, USA (Weisberg, Thompson Hobbs, Ellis, & Coughenour, 2002), white-tailed deer population in the eastern United States (DeCalesta & Stout, 1997)). Since then, a number of studies have been published showing the consensus of scholars towards the adjustment of carrying capacity by habitat/resources selection (Doan & Guo, 2019; Long et al., 2010; Reid, Slotow, Howison, & Balfour, 2007; Steenweg et al., 2016; Stephenson, Van Ballenberghe, Peek, & MacCracken, 2006). Resources selection is the process that the animals choose out of what is actually available, and it is a function of resource availability (Johnson, 1980). To understand habitat/resources selection, Resource Selection Functions (RSFs) modeling is widely used (Morris, Proffitt, & Blackburn, 2016) for various animals (Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006; Lemaître & Villard, 2005; McLoughlin, Morris, Fortin, Wal, & Contasti, 2010). Numerous factors are reported to influence plains bison RSFs, including vegetation type, slope, distance to water sources, distance to roads and fences, climatic factors, and competition (Doan & Guo, 2019; Kohl, Krausman, Kunkel, & Williams, 2013; Steenweg et al., 2016). The influence of these factors on bison RSFs varies among bison herds due to ecological variability of sites, forcing conservationists to use adaptive grazing management plans.

1.4. Remote sensing and GIS application in carrying capacity estimation

Remote sensing and Geographic Information Systems (GIS) have been increasingly common in assessing and adjusting the carrying capacity estimates. The usefulness of remote sensing in estimating biomass and productivity in grasslands is well established (Ahamed, Tian, Zhang, & Ting, 2011; Friedl, Schimel, Michaelsen, Davis, & Walker, 1994; Jin et al., 2014; Luo, Li, & Zhu, 2002; Piao, Fang, Zhou, Tan, & Tao, 2007; Prince, 1991; Psomas, Kneubühler, Huber, Itten, & Zimmermann, 2011; Reeves, Winslow, & Running, 2001; Scurlock, Johnson, & Olson, 2002; Todd, Hoffer, & Milchunas, 1998; Yang, Fang, Pan, & Ji, 2009). Hyperspectral data is able to characterize nutritional or species components of vegetation (Adjorlolo, Mutanga, Cho, & Ismail, 2012; Schmidt & Skidmore, 2001; Starks, Coleman, & Phillips, 2004; Yang et al., 2010). Multispectral data, however, is intensively used in carrying capacity studies because it provides data over large areas, especially in remote locations (Doan & Guo, 2019; Kumar & Mutanga, 2017). Furthermore, there is continuous improvement of the associated sensors. GIS tracking data help to analyze RSFs of species that incorporate all relevant variables (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006; Rondinini, Stuart, & Boitani, 2005; Santos et al., 2006; Steenweg et al., 2016). Thus, the integration of multispectral remotely sensed data and GIS is a better solution for carrying capacity studies.

1.5. Overall goals and specific objectives

The overall goal of this study was to examine plains bison carrying capacity in the mixed-grass prairie. The specific objectives were to:

1) Investigate annual space use of plains bison and their seasonal core ranges;
2) Assess seasonal RSFs of plains bison;
3) Estimate vegetation biomass and productivity of the mixed-grass prairie;
4) Estimate bison carrying capacity taking into account RSFs.

Chapter 2 LITERATURE REVIEW

2.1. Preface

The detail of the literature review has been fully published as a review paper:

Doan, T., & Guo, X. (2019). Understanding bison carrying capacity estimation in Northern Great Plains using remote sensing and GIS. *Canadian Journal of Remote Sensing*. DOI: 10.1080/07038992.2019.1608518.

The CJRS is published by Taylor & Francis Group in which the publishing agreement states the right to include the published work to be used as content of a dissertation. This manuscript was completed by Thuy Doan under the supervision of Dr. Xulin Guo, and the manuscript was improved by the valuable comments of Dr. Xulin Guo. The major findings from the literature review of bison carrying capacity estimation in Northern Great Plains from GIS and remote sensing have been reorganized in sections 2.2 and 2.3.

2.2. Past and present carrying capacity studies

Since being expressed in 1922, the term "carrying capacity" has had numerous definitions (Dhondt, 1988; Edwards & Fowle, 2013; McLeod, 1997). Although the term "carrying capacity" has been applied in different fields, this study only limits searching in literature for carrying capacity definitions relating to grazing. In domestic and wildlife grazing practices, the common definition of carrying capacity, stated in Buynooghe and Macdonald (2008, p. 104) is "the measure of a safe utilization level of an ecological site due to average annual forage production and vegetation's tolerance of grazing pressure". It was noted that there is uncertainty in the definitions of stocking rate and carrying capacity. Stocking rate is defined as "the actual number of stock per unit area at a particular time" (Redfearn & Bidwell, 2003). In contrast, carrying capacity is defined as "the average number of animals supporting by a defined area during a time period" (Chapman & Byron, 2018; Meehan, Sedivec, Printz, & Brummer, 2018). Determining carrying capacity for grazing practices is critical to maintaining or improving ecological health (Launchbaugh, 2014). Hence, carrying capacity can be expressed as the "Ecological Sustainable Stocking Rates which considers animal requirement, vegetation production, and the site ecology" (Adams et al., 2009) ('Ecological Sustainable' component signifies consideration of ecological health).

To date, numerous methods have been used to estimate carrying capacity. The common methods are summarized in Table 2-1. McLeod (1997) indicated that the interactive model is potentially applied for long-term grazing studies in frequently and significantly dynamic environments. However, the interactive model removes the 'long-term' component (McLeod, 1997, p.536), resulting in a conflict with the definition of carrying capacity. The table shows that productivity-stocking rate, habitat use/availability, and nutritional approach have been widely applied in recent studies. Researchers have used these models with the introduction of several factors based on understanding of animals' behaviors and ecological sustainability of various vegetation types.

In general, carrying capacity is expressed as a function of certain resources (Monte-Luna, Brook, Zetina-Rejón, & Cruz-Escalona, 2004). An overall look at all existing carrying capacity estimating methods highlights that food availability and animal requirement are always the fundamental drivers. In bison conservation practices, carrying capacity should be estimated from the primary production of vegetation as it is their ultimate source of food (Monte-Luna et al., 2004). Food availability can be evaluated based on species components (grass, forbs, shrubs) (Coppedge, Leslie Jr, & Shaw, 1998; Fortin, Fryxell, O'Brodovich, & Frandsen, 2003; Larter & Gates, 1991; Peden, Van Dyne, Rice, & Hansen, 1974) and nutritional components (Delgiudice, Moen, Singer, & Riggs, 2001; Leslie Jr, Bowyer, & Jenks, 2008). Meanwhile, animal requirement depends on physiological structure of animal population (species, size, physiological and health status) (Allison, 1985). The underlying reason for estimating forage availability from species or nutritional components for grazing practices is the urgent need to understand the availability of nutrients in habitats relating to an animal's specific nutritional requirements (Beck et al., 2006; Peden et al., 1974) and its preference in selecting plant species for consumption (Peden, 1976). Graminoids constitute majority of bison diet (>95%) (Steenweg et al., 2016). Grassland vegetation in North America is a mixture of warm season species (C_4 photosynthesis) and cool season species (C_3 photosynthesis) (Nippert, Fay, & Knapp, 2007; Paruelo & Lauenroth, 1996) differing by their ecological functions to the ecosystem (Still, Berry, Collatz, & DeFries, 2003). Cool season plants start their growth in late spring (Shoko, Mutanga, & Dube, 2016). The phenology variation of cool season and warm season species throughout a year influences availability and quantity of forage biomass (Shoko et al., 2016). Blue gramma (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), two warm season species, are the most abundant plant species in bison diets (Peden, 1976). Another carrying capacity driver is animal requirement. Animal requirement depends on many factors such as animal factors (body size, breed, sex, age, stage of lactation/pregnancy, nutritional status, and diseases), forage factors (chemical composition, palatability, digestibility, and energy concentration), and environmental factors (climatic condition, period of time) (Allison, 1985; Ingvartsen, 1994). Many models have been built to predict the amount of herbivores' forage intake from afore-mentioned factors (Ingvartsen, 1994). Animal factors appear to be the decisive control over the amount of forage intake (Allison, 1985).

Table 2-1 List of carrying capacity estimating methods.

No.	Name of method	Assumptions	Description	Denote	Sources	Criticism
1	Key species	(1) Unlimited food intake (2) No modification of animal's preference in food (3) Equivalent relation between food consumption and animal density	• Total permission use is the sum of 'forage factor' of all key plant species. • Carrying capacity is set up when total intake of animal population equals total permission use.	Forage factor of a key plant species is defined based on levels of its palatability, resilience, nutrition, abundance and productivity (Standing 1938).	(Dasmann, 1945; Smith, 1965)	The model provides a quantitative estimate; however, it is subjective in the step of evaluating forage factor of each key species, the assumption of unlimited food intake is unrealistic, and it is not applicable in a variable environment (McLeod, 1997).
2	Productivity-stocking rate	(1) No need to adjust animal density (2) Independence between stocking rate and forage productivity	• Carrying capacity is determined when at least one of productivity per unit area or productivity per animal is maximized.	Carrying capacity is referred to as the optimum stocking rate (Mott 1960).	(Cowlishaw, 1969; Holechek, 1988; Jones & Sandland, 1974; Mentis, 1977; Mott, 1960; Norton, 1986; Oesterheld, DiBella, & Kerdiles, 1998; Sandland & Jones, 1975;	The model provides a quantitative estimate objectively; however, the productivity-stocking rate relationship is not consistent (linearity, exponent), resulting in over- or under-estimation (McLeod, 1997). In grazing practices, population control is critical (Parks Canada, 2017) to avoid overgrazing, so the assumption of

					Schönbach et al., 2009; Yu, Zhou, Liu, & Zhou, 2010)	non-adjustment to animal density could fail. This model is not applicable in a variable environment (McLeod, 1997).
3	Habitat use/availability	(1) Ideally free grazing (2) Predictable resource availability (3) Inverse relation between individual productivity and population density	• Spatial use patterns of herbivores rely on numerous external factors. • The direct relation between carrying capacity and the habitat use/availability indices is proportional.	External factors from surrounding environment include vegetation communities, topography, and others (Hobbs & Hanley, 1990; McLeod, 1997). Habitat use/availability indices are ratios between radio-derived grazing locations, fecal indices, counted population density, and others (Hobbs & Hanley, 1990).	(Downs, Gates, & Murray, 2008; Fagen, 1988; Hirzel et al., 2006; Jędrzejewski et al., 2008; Steenweg et al., 2016)	Habitat use/availability and carrying capacity can be independent when quality and quantity of habitat resources are not directly associated (Hobbs & Hanley, 1990). Carrying capacity estimation based on habitat use/availability can be applied to evaluate potential of grazing practices in specific areas (Jędrzejewski et al., 2008; Steenweg et al., 2016). Although this model is objective and quantitatively estimates carrying capacity, it is not applicable in a variable environment

						(McLeod, 1997). Also, grazing in confined areas breaks the assumption of ideally free grazing.
4	Nutritional approach	(1) Constant individual’s nutrient intake (2) Balance in plant-herbivore system	• Carrying capacity is estimated based on food, or nutrients requirement of individual animal.	Examples of nutrients are nitrogen, energy, plant dry-matter (McLeod, 1997); crude fat, crude fibre, crude protein (Paton, Nuñez-Trujillo, Díaz, & Muñoz, 1999).	(Coughenour, 2005; DeYoung, Hellgren, Fulbright, Robbins, & Humphreys, 2000; Freeland & Choquenot, 1990; Guthery, 1999; Hanley & Rogers, 1989; Hobbs & Swift, 1985; Hobbs, Baker, Ellis, Swift, & Green, 1982; Kuzyk, 2008; McCall, Brown, & Bender, 1997; Paton et al., 1999; Svejcar &	This method is objective and provides a quantitative estimate, however, it is not applicable in a variable environment (McLeod, 1997). The assumption of constant individual nutrient intake is hardly met because the amount of necessary nutrient may vary depending on body size, physical status, and health condition.

					Vavra, 1985)	
5	Interactive model		• Carrying capacity is estimated based on interactive relation between plant biomass and food intake of herbivores.	Interactive considerations comprise both intrinsicality and extrinsicality of grazing system, such as: plant growth increment responding to environmental variables (rainfall, temperature), herbivores population increment responding to plant biomass, herbivores population increment responding to herbivores density, and food intake rate per animal responding to plant biomass (McLeod, 1997).	(Crête, 1989; McLeod, 1997)	No assumptions are required. This method satisfies the objectiveness and is usable in highly variable environments (McLeod, 1997). However, carrying capacity estimations that apply interactive models are rare to find in literature.

Besides the two key drivers, many factors have been added to the procedure for carrying capacity estimation. These additions are derived from understanding grazing behaviors of herbivores. When herbivores are kept in fenced areas with a choice of grazing locations, they initially select a patch when choosing their grazing bout before searching for desirable forage (Vallentine, 2000). Herbivores select grazing locations using three basic criteria: perception of area, experience with plants, and memory about potential choices (Bruggeman, 2006; Lyons & Machen, 2002). When they are introduced to new ranges with which they are not familiar, they will spend more time grazing but eat less until they learn the environment (Lyons & Machen, 2002). Hence, all available forage within grazing sites are not fully consumed if herbivores first graze in new areas or still have options for preferred grazing locations. Observations and former studies have explored the influences of numerous factors to animals' distribution which subsequently affect carrying capacity. Animal distribution depends temporally on vegetation type, slope, distance to water, distance to roads and fences, climate, and competition. The influence of these factors to grazing behaviors is discussed below.

Vegetation types: Large herbivores are attracted to different vegetation types (Grunow, 1980; Loarie, van Aarde, & Pimm, 2009; Taylor & Walker, 1978). It could be explained by the alteration of forage quality and quantity across vegetation types (Hebblewhite, Merrill, & McDermid, 2008). Steenweg et al. (2016) calculated the Habitat Suitability Index of plains bison for all typical vegetation types in Banff National Park. These vegetation communities are typical for vegetation communities of the Canadian Rocky Mountains, which differ from mixed-grass prairie. To date, there is a lack of studies which provide a comparison of seasonal plains bison's selection among different vegetation types in the mixed-grass prairie.

Slope: Slope steepness is a significant driver of cattle distribution (Mueggler, 1965). It has different effects among animal species (Vallentine, 2000). There have been many studies that quantitatively show topographic selection by North America herbivores (Cook, 1966; Lyons & Machen, 2002; Mueggler, 1965; Steenweg et al., 2016; Vallentine, 2000; Vuren, 2001). Cattle often graze on shallow slopes, less than 10% like valley bottoms and more level land near water before moving into rougher terrain (Cook, 1966; Lyons & Machen, 2002). Mueggler (1965) found a negative exponential relationship between relative use and upslope distance, strongly indicating that cattle only select low slopes to graze on. In contrast to cattle, horse and deer exhibit an avoidance of level to rolling terrain, starting from 30% to 40% steepness (Ganskopp & Vavra, 1987). Ganskopp and Vavra (1987) also reported that grazing activities of bighorn sheep is not influenced by 80% steepness of slope. Unlike cattle, bison prefer higher elevation (Vuren, 2001). Interestingly, although bison tend to move over the moderate sloping terrain (Larson et al., 2013), their preference range of slope steepness changes seasonally. Specifically, bison prioritizes lower than 70% steepness and strongly avoid higher than 84% steepness in summer (Steenweg et al., 2016). Dissimilarly, in winter they only prefer less than 27% steepness and strongly avoid higher than 36% steepness (Steenweg et al., 2016).

Distance to water: One critical factor influencing range forage use of herbivores is distance to water (Adler, Raff, & Lauenroth, 2001; Andrew, 1988; Bruynooghe & Macdonald, 2008; Horn, 2005; Roath & Krueger, 1982; Stumpp, Wesche, Retzer, & Miehe, 2005). Herbivores need a water source to survive, so their physiological performance depend on their proximity to water sources (Pringle & Landsberg, 2004). The location and number of water sources can control the mobility and aggregation of grazing animals (Lyons & Machen, 2002). Forage resources adjacent to water locations are more commonly selected than those farther away (Lyons & Machen, 2002). In winter, snow can be a substitute source of water for herbivores (Vallentine, 2000). The difference between travel distances for water in many types of stock is significant (Lyons & Machen, 2002). Sheep walk from 3 to 5 km for water, but cattle do not travel more than 1.6 km (Bruynooghe & Macdonald, 2008). A quantitative study conducted by Adler and Hall (2005) found that forage consumption of cattle and distance to water has a negative quadratic relationship. This finding is consistent with findings of past studies by Vuren (2001) that indicate a negative exponential relationship between foraging distribution of cattle and bison and adjacency to water points. Understanding plains bison performance in relation to distance to water supports the adjustment of bison population to match with carrying capacity. Bison prefer to graze within 700 m of a water source (Vuren, 2001) but they do not avoid distant grazing from water sources like cattle do (Allred et al., 2011).

Distance to roads and fences: Trombulak and Frissell (2000) stated that roads can modify animal behaviors. Specifically, Babin et al. (2011) added that bison tend to stay away from roads but prefer grazing near fences. Distance to the closest road and fence is one of the physical attributes of grazing locations of bison populations (Babin et al., 2011). Fences as artificial barriers can strongly influence movement patterns of animals within protected reserves (Vanak, Thaker, &

Slotow, 2010). Exploring the control of fencing on bison in Yellowstone National Park, Meagher (1989) reported that bison would sometimes break fences before learning to graze in new blocked areas. Few quantitative studies have been carried out on the influence of distance to roads on bison behavior. For example, Bruggeman (2006) and Bruggeman et al. (2007) pointed out that bison ecology and spatial distribution have been impacted by road grooming in winter for snowmobile and snowcoach facilitation. Moreover, distance to road and probability of bison travel were negatively correlated, and bison did not show a preference in using groomed roads (Bruggeman et al., 2007).

Climatic factors: Snow and droughts are climatic factors that influence herbivores' choice of habitat selection in temperate ecosystems (Bruggeman, 2006; Truett, Phillips, Kunkel, & Miller, 2001). Regarding snow, bison do not move south to get warmer temperature when the winter is coming (World Wildlife Fund, n.d.). Bison often dig into snow layer to access their food (Babin et al., 2011). Generally, bison need more energy when the snow layer is thicker. Based on the previous study of Fortin and Andruskiw (2003), Steenweg et al. (2016) discovered a quadratic relationship between snow depth and habitat selection of bison. From the drawn empirical relationship, bison prefer not to dig into snow layers thicker than 40 cm, and bison tend to avoid grazing in snow layer deeper than 100 cm. Drought is another extreme climatic condition that influences bison grazing. Flores (1991) pointed out that drought is one of the contributing factors to the massive loss of bison population in the 19th century. Woodhouse et al. (2002) believed the movement of bison population is towards moister regions. So far, there have been no attempt to explore the relationship between droughts and bison grazing behaviors. However, the impact of drought on food sources for herbivores was mentioned in Frank and McNaughton (1992). The availability of food sources is important for determining carrying capacity, shown by the analysis of existing methods of carrying capacity estimation.

Competition: Baptestini et al. (2009) reported an interaction between competition and carrying capacity. In general, competition between different species shaped grazing patterns and altered food availability (Maclin, 2018). When reintroducing plains bison into their natural habitat, they compete with other wild animals living within the same area due to overlapping resource use (Fischer & Gates, 2005). Although pronghorn do not have consistent grazing patterns, pronghorn and bison make frequent use of prairie dog towns (Krueger, 1986). However, the reintroduction of bison in the southwestern Yukon revealed no significant overlap between bison and caribou in winter resource selection (Fischer & Gates, 2005). The competition between different species and different individuals of a single species can influence carrying capacity of ecosystems (Monte-Luna et al., 2004). Therefore, competition should be considered when estimating bison carrying capacity. Literature review showed no existing plains bison carrying capacity studies that factored in competition.

After adding the influences of spatio-temporal bison distribution to carrying capacity, sustainable utilization rate should also be recommended to maintain ecological sustainability of grazing sites. Grazing intensity was assessed quantitatively into five categories (light to nonuse, conservative, moderate, heavy, and severe) based on the percentage of utilization of available forage (Holechek & Galt, 2000). Determining sustainable utilization, expressed by conservation grazing intensity, is important to rangeland health (Holechek et al., 1998). Holechek (1988) defined the utilization guidelines of moderate grazing for different range types. Therefore, utilization guidelines of conservation grazing should be the lower thresholds of moderate levels derived from Holechek (1988) for different range types in Table 2-2. Only range types which can be possible habitats of plains bison were selected from the list provided by Holechek (1988). In addition to range type, erosion has been considered to adjust livestock carrying capacity and suitable utilization rate of a site (Yu et al., 2010). Soil, the most important resource for food production, is eroding due to agricultural practices and accumulated impacts of wind, which causes land degradation (Khanif, 2010). One of the main reasons for soil erosion is the loss of vegetation cover (Pimentel et al., 1995). Erosion washes nutrients away from soil and results in infertile farmland (Zhao, Mu, Wen, Wang, & Gao, 2013). According to Arnalds and Barkarson (2003a), erosion is stressful for plants and degrades vegetation production making it unsuitable for grazing systems. Hence, soil erosion is a key consideration in adjusting carrying capacity and figuring out how to better use the land for grazing. In Yu et al. (2010), they suggested that 10% of carrying capacity is reduced in case of light to moderate soil erosion. Soil erosion can be visually evaluated based on suggestion from Adams et al. (2009). Light to moderate soil erosion results in little to no evidence of soil movement, unclear flow patterns, and scouring or hoof sheering (Adams et al., 2009). In contrast, serious or extremely serious soil erosion will result in evident soil movement, deep scouring and hoof sheering, clear flow patterns, no or little deposition and plant pedestalling, and coarse sand or aggregate remnants (Adams et al., 2009).

Table 2-2 Recommended maximum forage utilization for conservation grazing in different range types (Holechek, 1988).

Range types	**Allowable use (%)**
Salt desert shrubland	25
Semidesert grass and shrubland	30
Sagebrush grassland	30
Palouse prairie	30
Shortgrass prairie	40
California annual grassland	50
Mixed prairie	40
Mountain shrubland	30
Tall grass prairie	45

In a nutshell, the overall picture of bison carrying capacity includes forage availability and animal requirement as key drivers, and has several adjusting factors such as spatio-temporal distribution of animals and sustainable consideration (Figure 2-1). In Figure 2-1 , key drivers of carrying capacity are on the left side while adjusting factors are on the right side. After unfolding all independent variables of carrying capacity estimation, the question of how to estimate carrying capacity from remote sensing and GIS perspectives will be answered.

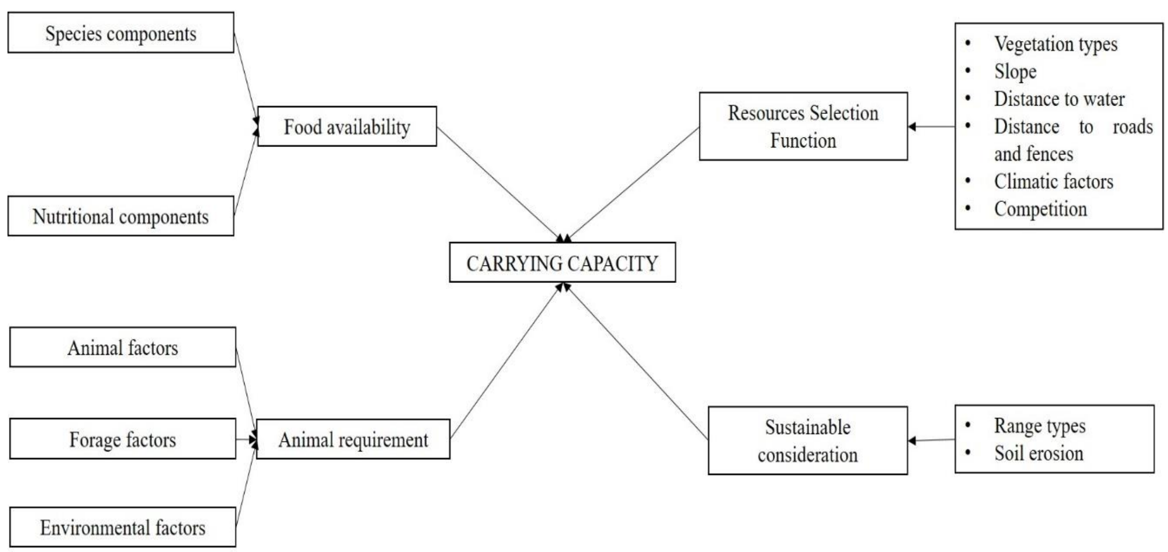

Figure 2-1 Independent variables of carrying capacity estimation. Food availability and animal requirement are carrying capacity's drivers, Resources Selection Function and sustainable consideration are adjusting factors of carrying capacity.

2.3. Remote sensing and GIS application in estimating bison carrying capacity

Numerous earth observation satellites have been launched to provide frequent imagery of its surface (Vrieling, 2006). Information derived from these spaceborne sensors in accordance with GIS technology can provide useful information for carrying capacity estimation, although few studies have actually yet been made pursuing this purpose. As remote sensing and GIS have no power to investigate bison requirement for food, the review will not include this variable. Future carrying capacity studies can adopt the method of Steenweg et al. (2016) to estimate bison requirement. In this section, the capability of remote sensing and GIS integration in carrying capacity studies will be scrutinized, in terms of each variable (forage availability and adjusting factors) of carrying capacity to the overall estimation.

Forage availability

One of the most significant indicators to determine optimum carrying capacity is available forage, measured as total forage biomass (Hunt Jr et al., 2003; Hunt Jr & Miyake, 2006; Yu et al., 2010). It is one of the carrying capacity drivers, in addition to animal requirements. The ability of remote sensing to estimate forage biomass in grasslands has been verified in published studies (Ahamed et al., 2011; Jin et al., 2014; Marsett et al., 2006; Piao et al., 2007; Psomas et al., 2011; Todd et al., 1998; Yang et al., 2009; Yu et al., 2010). Although remote sensing is effective in biomass estimation for feedstock production (Ahamed et al., 2011), there are few studies concerning the relationship between forage biomass and carrying capacity using remote sensing and GIS.

Forage availability can be evaluated based on chemical nutrients of forage (DeYoung et al., 2000; Paton et al., 1999). The literature proved that forage chemical composition can be examined using remote sensing. Nutritional status of *Festuca arundinacea*, a cool season grass species, can be assessed by monitoring photosynthetic pigments derived from hyperspectral data (Yang et al., 2010). Yang et al. (2010) observed a strong correlation between chlorophyll/carotenoid and canopy spectral reflectance using a combination of two wavelength regions: 540-560 nm and 750-950 nm. Earlier, Stark et al. (2004) showed the capability of hyperspectral data for estimating concentrations of forage chemical composition, including nitrogen, neutral detergent fiber, and acid detergent fiber ($R^2 > 0.7$). In short, hyperspectral data is commonly applied to assess nutritional values of forage.

Besides chemical nutrients in forage, estimating carrying capacity based on species components has been applied using the understanding of animals' preferences. From a remote sensing perspective, warm season grass-dominated grasslands have higher reflectance in visible and infrared spectrums with removal of noisy atmospheric water absorption bands (Adjorlolo et al., 2012). To estimate forage biomass from hyperspectral data, there are numerous Vegetation Indices (VIs) being employed (Table 2-3). Use of broadband sensors masks spectral diagnostic features of cool season grass and warm grass species (Adjorlolo, Mutanga, Ismail, & Cho, 2012), resulting in impractical application to discriminate the two groups. Meanwhile, hyperspectral data can provide detailed spectral information to differentiate not only cool and warm groups of species (Adjorlolo et al., 2012) but also to discriminate spectral information of grass species (Schmidt & Skidmore, 2001). However, this remote sensing data has high dimensionality, multicollinearity problems (Adjorlolo et al., 2012), and can't be used for investigating spatial variation due to the narrow field of view.

Table 2-3 Hyperspectral Vegetation Indices used in biomass estimation in grasslands.

Index	Definition	References
Normalized Difference Vegetation Index	$NDVI = \frac{R_{800} - R_{670}}{R_{800} + R_{670}}$	Rouse et al. (1974)
Renormalized Difference Vegetation Index	$RDVI = \frac{R_{800} - R_{670}}{\sqrt{R_{800} + R_{670}}}$	Reujean and Breon (1995)
Perpendicular Vegetation Index	$PVI = \frac{R_{800} - a \times R_{670} - b}{\sqrt{1 + a^2}}$	Richardson and Wiegand (1977)
Soil Adjusted Vegetation Index	$SAVI = (1 + L) \times \frac{(R_{800} - R_{670})}{(R_{800} + R_{670} + L)}$	Huete (1988)
Modified Soil Adjusted Vegetation Index	$MSAVI = \frac{2 \times (R_{800} + 1) - \sqrt{(2R_{800} + 1)^2 - 8 \times (R_{800} - R_{670})}}{2}$	Qi et al. (1994a)
Transformed Soil Adjusted Vegetation Index	$TSAVI = \frac{a \times (R_{800} - aR_{670} - b)}{aR_{800} + R_{670} - ab}$	Baret et al. (1989)
Litter-adjusted Soil Adjusted Vegetation Index	$L - SAVI = \frac{1.5 \times (1 + L \times CAI) \times (R_{NIR} - R_{Red})}{R_{NIR} + R_{Red} + 0.5 + L \times CAI}$ $CAI = 100 \times \left(\frac{R_{2000} + R_{2200}}{2} - R_{2100}\right)$	Ren and Zhou (2014a)
Band depth	$BD = 1 - \frac{R}{R_c}$	Ren and Zhou (2012); Ren and Zhou (2014b)
Band depth ratio	$BDR = \frac{BD}{BD_{max}}$ $BD_{max} = max(BD_{650-740})$	Ren and Zhou (2014b)
Normalized band depth index	$NBDI = \frac{BD - BD_{max}}{BD + BD_{max}}$ $BD_{max} = \max(BD_{650-740})$	Ren and Zhou (2014b)

Band depth normalized to area	$BNA = \frac{BD}{BD_{area}}$ $BD_{area} = \sum_{i=650}^{740}$	Ren and Zhou (2014b)
Litter-corrected Adjusted Transformed Soil-Adjusted Vegetation Index	$L-ATSAVI = \frac{a \times (R_{NIR} - a \times R_{Red} - b)}{a \times R_{NIR} + R_{Red} - a \times b + 0.08 \times (1 + a^2) + 10 \times \left(\frac{R_{2000}}{\right.}}$	He et al. (2006)
Cellulose Absorption Index	$CAI = [0.5 \times (R_{2.0} + R_{2.2}) - R_{2.1}] \times 100$	Daughtry (2001)
Lignocellulose Absorption Depth	$LCD = \max(BD_{2015-2155nm})$	Numata et al. (2008)
Lignocellulose Absorption Area	$LCA = \sum_{i=2015}^{2155} BD_i$	Numata et al. (2008)

R: original reflectance of red absorption region; R_i: reflectance at wavelength I; Rc: reflectance of continuum line at corresponding wavelength; BD_i: band depth at wavelength i; BD_{max}: maximum reflectance at 650-740 nm; R_{NIR}: mean reflectance at 760-900 nm; R_{Red}: mean reflectance at 630-690 nm; R_{2000}: mean reflectance at 2000-2050 nm; R_{2000}: mean reflectance at 2000-2050 nm; R_{2100}: mean reflectance at 2080-2130 nm; R_{2200}: mean reflectance at 2190-2240nm; L: adjustment factor; a: slope of soil line; b: intercept of soil line.

Although hyperspectral data measurement can be used for assessing nutrients and species components of available forage, this approach is not practical for capturing spatio-temporal variation of aboveground biomass. Multispectral imagery has been used intensively because it can provide data over large areas and is able to access distant or inaccessible places (Kumar & Mutanga, 2017). The capability of multispectral satellite sensors for measuring aboveground biomass is discussed here in terms of increasing spatial resolution. Commonly used coarse spatial resolution (greater than 100 m) data are NOAA Advanced Very High-Resolution Radiometer (AVHRR) and Moderate Resolution Imaging Spectroradiometer (MODIS). While the NOAA AVHRR satellite has nearly 4 decades (launched in June 1979) of data with a spectral range covering 0.58-12.5 µm, the MODIS satellite was launched in 1999 with extended spectral range from 0.4 to 14.4 µm. The application of coarse spatial resolution data in measuring aboveground biomass in grasslands can be found in many publications in China. The reason for this focus is that China has the world’s third largest area of grasslands with 42% territory coverage (Bain, 2010). MODIS-Vegetation Indices (VIs) were suggested to be more reliable detectors of forage quantity of grassland steppe areas compared with AVHRR-VIs (Kawamura et al., 2005). Additionally, the arrival of MODIS Net Primary Productivity (NPP) specifically for tracking vegetative production is advantageous for spatio-temporal aboveground biomass estimation in grasslands (Zhao et al., 2014). Piao et al. (2007) used time series-AVHRR-derived Normalized Difference Vegetation Index (NDVI) to investigate the trend of biomass carbon stocks in China's grasslands during a 17-year period (1982-1999). In general, these large-scene size satellite data are often used at national, continental, and global scales (Avitabile, Baccini, Friedl, & Schmullius, 2012; Lu, 2006). A major difficulty of using coarse spatial resolution data is the integration of sample data and remote sensing-derived variables because of differences between pixel size and field-measurement data (Baccini, Friedl, Woodcock, & Zhu, 2007; Lu, 2006). Despite this problem, MODIS data has been used in recent studies on monitoring grassland biomass (Jin et al., 2014; Xia et al., 2014; Zhang et al., 2016; Zhang et al., 2018; Zhao et al., 2014). A common solution for reducing the effects of this issue is to place field plots in homogeneous areas (Eisfelder, Kuenzer, & Dech, 2012). At local and regional scale, recent studies on aboveground biomass of grasslands used medium spatial resolution (10-100 m) data (Marsett et al., 2006; Xie, Sha, Yu, Bai, & Zhang, 2009). Landsat satellite collections, launched in 1972, are the most frequently used medium spatial resolution data in the field of biomass estimation. Landsat collections have three types of sensors: Multispectral Scanner (MSS; 1972-1983), Thematic Mapper (TM; 1984-2013), and Enhanced Thematic Mapper Plus (ETM+; 1999-present). The use of medium remote sensing data overcomes the limitation of coarse spatial resolution data in integrating sample data and remotely sensed information, through it does have a few issues. The Landsat 7 satellite experienced scan line corrector failure on May 31, 2003 resulting in a 22% loss of data per scene (Scaramuzza & Barsi, 2005). Although several methods have been proposed to fill the gaps of Landsat 7 data, these processes are time consuming and produces inconsistencies in historical series of Landsat imagery data. However, Landsat 8 Operational Land Imager was successfully launched soon after Landsat TM was turned off. The development of Operation Land Imager (OLI) on Landsat 8 not only maintains the continuity of long-term annual Landsat data but also opens a new Landsat era of pushbroom sensors (Knight & Kvaran, 2014). In addition, Avitabile et al. (2012) pointed out the challenges of achieving temporally and radiometrically consistent cloud-free Landsat datasets over large areas. According to Lu (2006), identifying suitable image textures is more important than identifying spectral information for aboveground biomass estimation, and poses a problem in areas of complex vegetation stand structures. Unlike these aforementioned remote sensing data, fine spatial-resolution (<10 m) data is the most useful dataset for detailed biomass studies. The fine spatial-resolution data can be obtained from airborne sensors (HyMap and aerial photographs) and spaceborne sensors (e.g. GeoEye, IKONOS, Quickbird, SPOT, WorldView, and KOMPSAT). Hall (2012) showed the capability of Quickbird in supplying fine-scale species diversity in semi-natural grassland sites. Hence, the use of fine spatial resolution data has potential in detecting nutritional or species components of grassland vegetation. However, not only is fine spatial resolution application costly and time consuming (Lu, 2006), it has other issues like cloud cover and limited coverage extents (Oswald & Harris, 2016). In a nutshell, such remote sensing applications have benefits and difficulties in estimating aboveground biomass or forage availability in grasslands.

Spectral vegetation indices (VIs) calculated from remote sensing-derived combinations of radiance values (Kalaitzidis, Heinzel, & Zianis, 2010) are useful for characterizing spatial and temporal aboveground biomass (Anderson, Hanson, & Haas, 1993; Richardson & Everitt, 1992; Silleos, Alexandridis, Gitas, & Perakis, 2006; Todd et al., 1998). The list of developed VIs for multispectral satellite data used in previous studies of biophysical properties (biomass included) of grassland vegetation is shown in Table 2-4. Hence, they are all potential predictors of biomass estimation in grasslands. Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) are commonly used VIs to estimate aboveground biomass. Use of EVI is becoming frequent due to its capability of considering soil background effects (Jiang et al., 2015), removal of atmospheric effects, and improvement of sensitivity in high biomass vegetation (Huete et al., 2002). Besides these, a number of other VIs have been developed to respond to canopy background (e.g. Perpendicular Vegetation Index (PVI), Soil Adjusted Vegetation Index (SAVI)), canopy variation (e.g. Modified Soil Adjusted Vegetation Index (MSAVI)), high coverage of senesced vegetation component (e.g. Normalized Difference Index (NDI)), and so on. Nevertheless, none of the listed VIs in Table 2-4 have been reported to be the optimal predictor in assessing spatio-temporal variation of aboveground biomass in grasslands. Regression models used in estimating AGB in grasslands from remote sensing derived VIs have been listed in Table 2-5. Although linear regression is traditional, it might perform better than other advanced statistical methods in some case studies (Marabel & Alvarez-Taboada, 2013; Otgonbayar, Atzberger, Chambers, & Damdinsuren, 2019).

Table 2-4 List of Vegetation Indices used for characterizing different biophysical properties of grasslands.

Group	Index	Definition	References
Red-NIR VIs	Red Index	$RED = R_{Red}$	Todd et al. (1998)
	Simple Ratio	$SR = \frac{R_{NIR}}{R_{Red}}$	Jordan (1969)
	Normalized Difference Vegetation Index	$NDVI = \frac{R_{NIR} - R_{Red}}{R_{NIR} + R_{Red}}$	Rouse et al. (1974)
	Soil adjusted Vegetation Index	$SAVI = (1 + 0.5)\frac{R_{NIR} - R_{Red}}{R_{NIR} + R_{Red} + 0.5}$	Huete (1988)
	Modified Soil Adjusted Vegetation Index	$MSAVI = 0.5 \times \left((2 \times R_{NIR} + 1) - \sqrt{(2 \times R_{NIR} + 1)^2 - 8 \times (R_{NIR} - R_{Red})}\right)$	Qi et al. (1994)
	Optimized Soil adjusted Vegetation Index	$OSAVI = 1.16 \times \frac{R_{NIR} - R_{Red}}{R_{NIR} + R_{Red} + 0.16}$	Rondeaux et al. (1996)
	Transformed Soil adjusted Vegetation Index	$TSAVI = \frac{a \times (R_{NIR} - a \times R_{Red} - b)}{a \times R_{NIR} + R_{Red} + a \times b}$	Baret et al. (1989)
	Adjusted Transformed Soil adjusted Vegetation Index	$ATSAVI = \frac{a \times (R_{NIR} - a \times R_{Red} - b)}{a \times R_{NIR} + R_{Red} - a \times b + 0.08 \times (1 + a^2)}$	Baret and Guyot (1991)
	Perpendicular Vegetation Index	$PVI = \frac{R_{NIR} - a \times R_{Red} - b}{\sqrt{1 + a^2}}$	Richardson and Wiegand (1977)
Green-NIR-Red VIs	Modified Triangular Vegetation Index 1	$MTVI1 = 1.2 \times [1.2 \times (R_{NIR} - R_{Green}) - 2.5 \times (R_{Red} - R_{Green})]$	Haboudane et al. (2004)
	Plant Senescence Reflectance Index	$PSRI = \frac{R_{Red} - R_{Green}}{R_{NIR}}$	Merzlyak et al. (1999)
Green-NIR VIs	Green Adjusted Vegetation Index	$GSAVI = 1.5 \times \frac{R_{NIR} - R_{Green}}{R_{NIR} + R_{Green} + 0.5}$	Tian et al. (2005)
Blue-NIR-Red VIs	Enhanced Vegetation Index	$EVI = 2.5 \times \frac{R_{NIR} - R_{Red}}{R_{NIR} + 6R_{Red} - 7.5R_{Blue} + 1}$	Justice et al. (1998)
	Canopy Index	$CI = R_{SWIR1} - R_{Green}$	Vescovo and

SWIR1-involved VIs			Gianelle (2008)
	Normalized Canopy Index	$NCI = \frac{R_{SWIR1} - R_{Green}}{R_{SWIR1} + R_{Green}}$	Vescovo and Gianelle (2008)
	Ratio Cover Index	$RCI = \frac{R_{SWIR1}}{R_{Green}}$	Zhang and Guo (2008)
	Normalized Difference Water Index/Normalized Difference Index	$NDWI = NDI = \frac{R_{NIR} - R_{SWIR1}}{R_{NIR} + R_{SWIR1}}$	Gao (1996); Hardisky (1983); McNairn and Protz (1993)
	Normalized Difference Cover Index	$NDCI = \frac{R_{SWIR1} - R_{Red}}{R_{SWIR1} + R_{Red}}$	Zhang and Guo (2008)
	Soil Adjusted Corn Residue Index	$SACRI = a\frac{R_{NIR} - R_{SWIR1} - a}{aR_{NIR} + R_{SWIR1} - ab}$	Biard and Baret (1997)
SWIR2-involved VIs	Seven/Four Ratio	$\frac{R_{SWIR2}}{R_{NIR}}$	Jansen et al. (2016)
	Normalized Difference Infrared Index 7	$NDII7 = \frac{R_{NIR} - R_{SWIR2}}{R_{NIR} + R_{SWIR2}}$	Hardisky et al. (1983)
	Soil Adjusted Total Vegetation Index	$SATVI = \frac{R_{SWIR1} - R_{Red}}{R_{SWIR1} + R_{Red} + 0.5} \times (1 + 0.5)\left(\frac{R_{SWIR2}}{2}\right)$	Marsett et al. (2006)
	Modified Soil Adjusted Corn Residue Index	$MSAVI = 5 \times \frac{a(R_{SWIR1} - a - b)}{aR_{SWIR1} + R_{SWIR2} - ab}$	Bannari et al. (2000)
	Dead Fuel Index	$DFI = 100\left(1 - \frac{R_{SWIR2}}{R_{SWIR1}}\right)\left(\frac{R_{Red}}{R_{NIR}}\right)$	Cao et al. (2010)
Tasselled cap	Brightness Index	$BI = \beta_1 \times R_{Blue} + \beta_2 \times R_{Green} + \beta_3 \times R_{Red} + \beta_4 \times R_{NIR} + \beta_5 \times R_{SWIR1} + \beta_6 \times R_{SWIR2}$	Crist (1985)
	Greenness Index	$GI = \beta_1 \times R_{Blue} - \beta_2 \times R_{Green} - \beta_3 \times R_{Red} + \beta_4 \times R_{NIR} - \beta_5 \times R_{SWIR1} - \beta_6 \times R_{SWIR2}$	Crist (1985)
	Wetness Index	$WI = \beta_1 \times R_{Blue} + \beta_2 \times R_{Green} + \beta_3 \times R_{Red} + \beta_4 \times R_{NIR} - \beta_5 \times R_{SWIR1} - \beta_6 \times R_{SWIR2}$	Crist (1985)

a: slope of soil line; b: intercept of soil line; β_n: coefficients for corresponding reflectance factors (β_n varies depending on sensors)

Table 2-5 List of regression models which have been used in estimating AGB in grasslands using remote sensing data.

Regression model	Studies
Linear regression analysis	Anaya et al. (2009); Chen et al. (2009); Jin et al. (2014); Marabel and Alvarez-Taboada (2013); Otgonbayar et al. (2019); Psomas et al. (2011); Psomas et al. (1998); Xie et al. (2009); Yang et al. (2009)
Nonlinear regression analysis	Lu (2006); Chen et al. (2009); Jin et al. (2014)
Support Vector regression	Marabel and Alvarez-Taboada (2013); Ge et al. (2018)
Artificial neutral networks	Xie et al. (2009); Yang et al. (2018)
Random Forest	Otgonbayar et al. (2019); Anderson et al. (2018)

Resources Selection Functions of plains bison and sustainable consideration

The Global Positioning System (GPS) helps researchers to effectively locate grazing locations, and monitor animal behaviors (Bjørneraas, Moorter, Rolandsen, & Herfindal, 2010; Bruggeman, 2006; Cagnacci, Boitani, Powell, & Boyce, 2010; Handcock et al., 2009; Tomkiewicz, Fuller, Kie, & Bates, 2010; Turner, Udal, Larson, & Shearer, 2000). GPS has a measure of error in locating an animal's true location, depending on the amount of satellite by which the GPS can receive its signal (Bjørneraas et al., 2010). To improve GPS performance, Bjørneraas et al. (2010) recommended screening methods for better analysis of animal distribution. GPS collars can be combined with remote sensing data through communication methods such as wireless sensor networks to monitor animal-environment interaction (Handcock et al., 2009). To understand Resources Selection Functions (RSFs) of bison, Bruggeman (2006) used GPS collars to identify general bison travel paths. Traveling vectors were mapped into Geographic Information Systems (GIS) layers following different temporal patterns for analyzing influences of climate, topography, and habitat features on bison distribution (Bruggeman, 2006). In short, spatial distribution of bison is affected by topographic and habitat attributes; meanwhile, snow and drought influence the number and timing of migrating bison (Bruggeman, 2006). Similar to Bruggeman's method, Coopedge and Shaw (2000) assessed bison habitat use and bison wallow information by digitizing locations of bison group and wallow locations into a GIS.

GIS and remote sensing integration have the capability of monitoring several factors influencing carrying capacity. To date, there are numerous free GIS software packages available to meet people's mapping demand. Many helpful algorithms and toolboxes were developed with these software packages to investigate environmental features of GIS layers. Digital Elevation Model (DEM), for example, provides a digital representation of surface topography (Balasubramanian, 2017; Croneborg, Saito, Matera, McKeown, & van Aardt, 2015). Algorithms have been built to determine various terrain attributes such as slope from DEM (Dozier & Frew, 1990). For instance, Yu et al. (2010) used DEM to determine the slope in estimating livestock carrying capacity in the Golog Tibertan Autonomous Prefecture, Qinghai province, China. Distance from each grazing point to the nearest water sources, fences, and roads can be estimated by using toolsets corresponding to different programs. Impact of competition on carrying capacity depends on circumstances like dissimilar animal population structure and existing fauna in specific areas. Several studies have been carried out using niche-based modeling to analyze animal competition (Anderson, Peterson, & Gómez-Laverde, 2002; Hemami et al., 2018). Applying a *priori* hypothesized models, Bruggeman (2006) not only examined the effect of intraspecific competition but also successfully drew the interaction of bison migration paths with snow and drought. Moreover, we can forecast and assess the risk of extreme climatic events (Belal, El-Ramady, Mohamed, & Saleh, 2014; Che, Li, Jin, Armstrong, & Zhang, 2008; Cline, Bales, & Dozier, 1998; Hall, 2012; Han, Wang, Zhang, & Zhu, 2010; Mishra & Singh, 2011; Valipour, 2012).

In addition to variables influencing spatial distribution of bison, the significance of range types and soil erosion were discussed in estimating carrying capacity. Accelerated soil erosion (Zhao et al., 2013) needs frequently updated assessment to more accurately estimate carrying capacity. GIS and remote sensing have been commonly used in soil erosion assessment (Alexakis, Hadjimitsis, & Agapiou, 2013; Dabral, Baithuri, & Pandey, 2008; Fu et al., 2005; Lu, Li, Valladares, & Batistella, 2004; Pradhan, Chaudhari, Adinarayana, & Buchroithner, 2012; Renschler & Harbor, 2002). Universal Soil Loss Equation (ULSE) and Revised USLE (Foster, McCool, Renard, & Moldenhauer, 1981; Renard, Foster, Weesies, McCool, & Yoder, 1997) are commonly used in studies of soil erosion assessment (Fistikoglu & Harmancioglu, 2002). They are empirical models allowing the estimation of average annual soil loss from erosion risk factors (Meusburger, Konz, Schaub, & Alewell, 2010). While environmental factors (land cover, soil, topography) can be extracted from satellite images, GIS environment helps to calculate the USLE factors (Alexakis et al., 2013) in the form of raster layers (Kouli, Soupios, & Vallianatos, 2009).

For instance, the C factor accounting for vegetation characteristics can be mapped using image classification, NDVI and linear spectral unmixing (Meusburger et al., 2010). The LS (slope length and steepness) factor, described in Desmet and Govers (1996), could be constructed using DEMs following an automatic GIS procedure. The power of remote sensing and GIS techniques for soil erosion assessment has been proven in multiple studies (Chen, Niu, Li, Zhang, & Du, 2011; Dabral et al., 2008; Lu et al., 2004; Meusburger et al., 2010; Pradhan et al., 2012). To improve vegetation input data, high resolution multispectral imagery like Quickbird was recommended (Meusburger et al., 2010). After estimating the amount of soil loss, a fuzzy class membership approach might help in soil loss classification (very slight, slight, moderate, severe, and very severe) (Ahamed, Rao, & Murthy, 2000).

Bison carrying capacity estimation

After investigating each variable of carrying capacity, GIS is able to incorporate these variables into carrying capacity estimation using Habitat Suitability Index (HSI)/Resources Selection Functions (RSFs), which help to determine species niche requirements and predict the spatial distribution of species (Hirzel et al., 2006). Incorporating essential life requirements, these models demonstrate the capability of specific areas for providing the requisites to species, shown by HSI (Donovan, Rabe, & Olson, 1987) or probability maps (Store & Kangas, 2001). Each species has their own specific life requirements, called habitat factors which connect to become the crucial characteristics of the habitat (Store & Kangas, 2001). Developing HSI Models have been applied in conservation programs (Rondinini et al., 2011, 2005; Steenweg et al., 2016), especially in wildlife management (Hirzel et al., 2006; Santos et al., 2006; Steenweg et al., 2016). Hence, incorporating HSI models in estimating plains bison carrying capacity is reasonable and effective. Two common methods for building HSI models are the Presence-Absence model (or Generalized Linear Model) (Brotons, Thuiller, Araújo, & Hirzel, 2004; Hirzel, Helfer, & Metral, 2001; Manel, Williams, & Ormerod, 2001; Royle & Nichols, 2003) and Presence-only model (or Ecological Niche Factor Analysis) (Brotons et al., 2004; Hirzel et al., 2001, 2001; Pearce & Boyce, 2006; Raes & Steege, 2007; Santos et al., 2006; Starks et al., 2004). Because of ambiguous geo-referenced absence data of species, a Presence-only model is favored in recent studies. This model should be based on recorded presence data by GPS collars fitted on bison.

A GIS storing large volumes of map data is useful in building a Habitat Suitability Model (Donovan et al., 1987; Store & Jokimäki, 2003; Store & Kangas, 2001). The ability of GIS to implement ecological modeling techniques has been advancing in recent decades (Santos et al., 2006). Store and Kangas (2001), for example, evaluated GIS-based habitat suitability by integrating spatial multi-criteria evaluation and expert knowledge. Additive techniques (standardizing criterion scores, multiplying each criterion score by corresponding weight factor, adding the results to get total score) were suggested by Store and Kangas (2001) in GIS environment for performing spatial multi-criteria evaluation. GIS-based HSI promises high accuracy. It was used in predicting suitable habitats for loggerhead shrike in Kansas with 82% accuracy (Lauver, Busby, & Whister, 2002).

2.4. Research gaps

Since knowledge of carrying capacity becomes essential for wildlife conservation (Ayllón, Almodóvar, Nicola, Parra, & Elvira, 2012), the need for bison carrying capacity estimation is increasingly in importance. Such knowledge helps to protect this emblematic species of western North America. Remotely sensed data and GIS can be integrated to retrieve bison carrying capacity estimation. However, there are a number of gaps revealed in the literature.

The priority of remote sensing data in carrying capacity estimation is providing a historical track of available forage. As one of two carrying capacity drivers, monitoring spatio-temporal variation of forage will help with understanding short- and long-term ecological effects of grazing practices. In order to investigate chemical-nutritional or species components of available forage, hyperspectral data can be used to distinguish these components due to detailed spectral information. However, hyperspectral data is not applicable in exploring its spatial variation. Conversely, multispectral data application can investigate spatio-temporal variation of available forage but has the issue of masking spectral details of nutritional and species components. Remote sensing cannot provide a perfect database for carrying capacity studies because each operational sensor system has its own advantages and disadvantages. MODIS, the most common remote sensor used for estimating herbivores carrying capacity brings challenges to carrying out field data collection. A major challenge of future carrying capacity studies is data fusion between hyperspectral data and multispectral data to obtain detailed biomass information with spatial and temporal coverage. Moreover, although numerous VIs and regression models have been employed to examine their performance in aboveground biomass estimation in grasslands, the accuracy of this estimation varies from case to case. Hence, there is a need for future carrying capacity studies to examine the capability of VIs derived from finer spatial resolution datasets, including spaceborne sensors and UAV-based sensors.

Other limitations of existing bison ecological studies are related to the adjustment of bison selection on habitat/resource. Initially, the list of adjusting factors to spatio-temporal distribution of carrying capacity as well as their effects are summarized based on previous experimental studies. Suitable selection of adjusting factors depends on circumstances of climatic features, fauna and flora systems, and specific management goals. After selecting variables, the construction of a model describing bison selection on habitat/resources was criticized to easily over- or under-estimate bison distribution. Second, HSI, which illustrates bison selection on habitat/resources, was integrated into plains bison carrying capacity (Steenweg et al., 2016). This index is built based on expert knowledge (Store & Kangas, 2001) instead of empirical data like RSFs (C. J. Johnson et al., 2006). Cumulative Environmental Management Association (CEMA) (2011) revealed that RSF models are more properly validated in contrast with HSI. The reliability can be obtained if GPS collar data are employed to examine the temporal space use and seasonal core range of bison herd followed by RSFs construction (Doan & Guo, 2019). Plains bison carrying capacity in Grasslands National Park was estimated prior to the reintroduction of the species (Parks Canada, 2005). Notwithstanding, habitat use and selection by bison were unknown and not accounted for. In the meantime, GIS environments help to integrate all related variables to build RSFs and finally determine spatio-temporal variation of bison carrying capacity. Therefore, this dissertation fulfils the given research gaps.

Chapter 3 STUDY AREA & RESEARCH METHODOLOGY

3.1. Study area

3.1.1. Physical geography

The study area is in the West block of Grasslands National Park (GNP), located in Southern Saskatchewan, adjacent to the Montana border (49°07'N 107°45'W) (Figure 3-1). The park was established in 1988 and encompasses over 900 km^2 of mixed-grass prairie (Parks Canada Agency, 2018). GNP is characterized by semi-arid continental climate with hot summers, cold winters, and low precipitation (Parks Canada, 2014). Annual precipitation in the growing season (May – September) in this region is about 340 mm, and average temperature throughout the year is 3.4 ˚C (Guo, Wilmshurst, McCanny, Fargey, & Richard, 2004). The lowest temperature in GNP can drop to -50 ˚C and the average January temperature is -22 ˚C (Grasslands National Park, 2005). GNP is occasionally hit by strong snow storm and snow cover is not long existing (Gjetvaj, 2012).

The typical features of semi-arid continental climate result in a unique flora and fauna. According to vegetation inventories of GNP, there are seven vegetation types inside the administrative boundary of the West block: upland grassland (UG), slope grassland (SG), valley grassland (VG), eroded community (EC), shrub community (SC), tree community (TC), and disturbed community (DC) (Michalsky & Ellis, 1994). These types were classified based on topography, soil types, and plants communities (Li & Guo, 2018). UG, SG, and VG are three major vegetation types in the study area, making up almost 70% of GNP West block (Parks Canada, 2017). Upland vegetation communities are dominated by needle and thread (*Stipa comate* Trin. & Rupr.), blue grama (*Bouteloua gracilis* Lag. Ex Steud), and crested wheatgrass (*Agropyron cristatum* L.) (Babin et al., 2011; Li & Guo, 2018). Valley grassland are dominated by silver sagebrush (*Artemisia cana*), needle and thread, and western wheatgrass (*Agropyron smithii* Rydb.) (Babin et al., 2011; Zhang & Guo, 2008). Slope grassland is comprised of the species in both of the afore-mentioned vegetation types (Xu, Guo, Li, Yang, & Yin, 2014).

The grazing community in GNP West block is plentiful and diverse. Black-tailed prairie dogs live in about 25 large colonies in and around the park (Parks Canada, n.d). The prairie dogs colonies have been investigated their temporal extension by the park. Other grazers occupying the West block comprise mule deer, white-tailed deer, and Richardson's ground squirrel. Besides grazing community, the park's wildlife has a number of other animal species such as coyote badgers, shunk, bobcats (Grasslands National Park, 2005), eastern yellow-bellied racer, greater short-horned lizard, mormon metalmark, mountain plover, prairie loggerhead shrike, sprague's pipit, and swift fox (Parks Canada Agency, 2016).

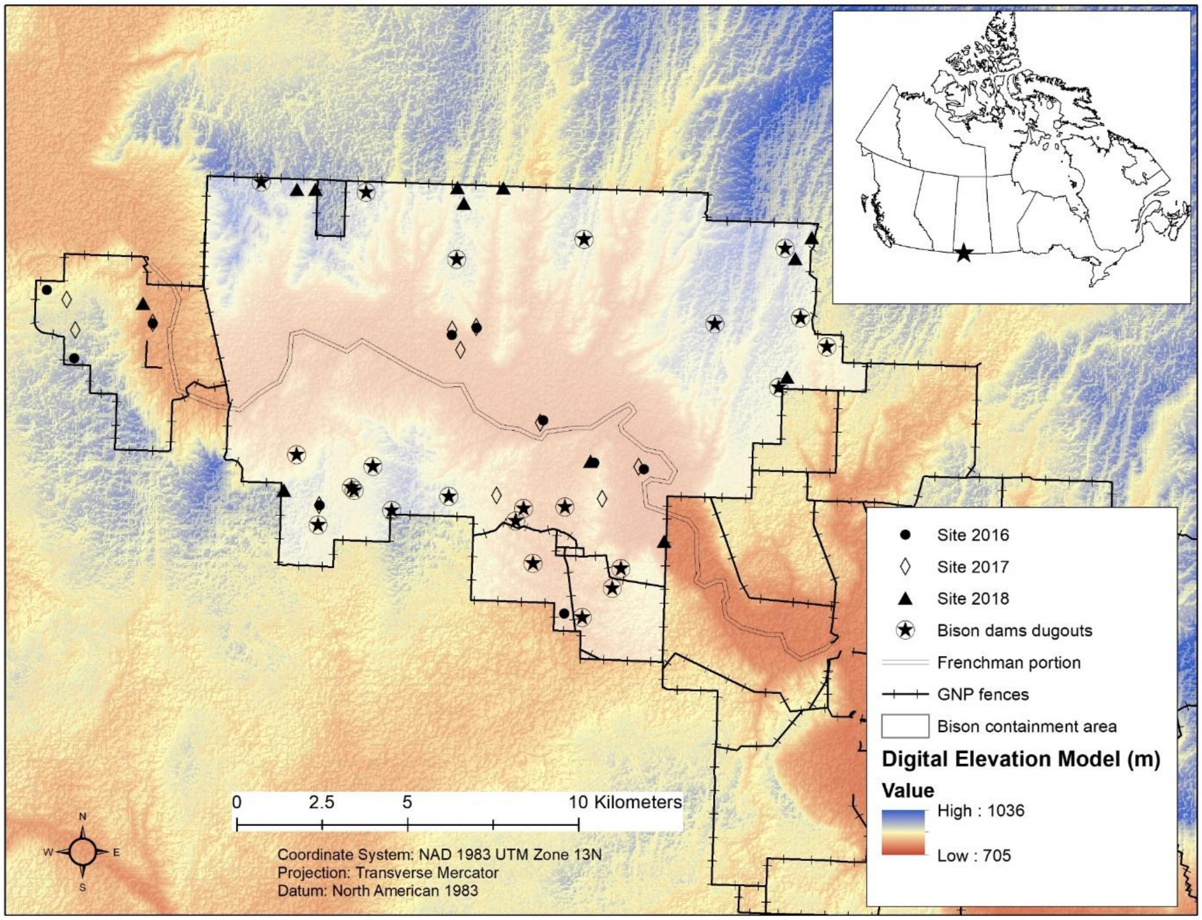

Figure 3-1 Geographic location of Grasslands National Park West block (black star in the index map). Bison herd was kept inside their containment area (white polygon). A total of 33 sampling sites were established in the peak of growing season (June-July) in 2016 (10 sites), 2017 (11 sites), and 2018 (12 sites). Bison dams and dugouts (circled black stars) and Frenchman river portion (double black lines) are available water sources for bison herd.

3.1.2. Situation of plains bison conservation

In December 2005, 71 plains bison were reintroduced from Elk Island National Park to the West Block of GNP, aiming to restore grazing as an ecological process in the park ecosystem (Parks Canada, 2005). The bison population is contained within an entirely fenced area of approximately 180 km^2 (i.e., bison containment area; Figure 3-1, Figure 3-2). Annual bison population data in GNP is provided in Figure 3-3. Average annual growth rate reported for the bison population in 2009-2013 was 28% (Parks Canada, 2017). Since 2013, the bison herd has been managed through biennial surplus to maintain a target population of 400-500 individuals. Since 2017, GNP adheres to IUCN guidelines for bison conservation herds, including maintaining a 50:50 ratio of males to females and maintaining genetic diversity (Parks Canada, 2017).

Figure 3-2 Plains bison family group in Grasslands National Park West block, summer 2018.

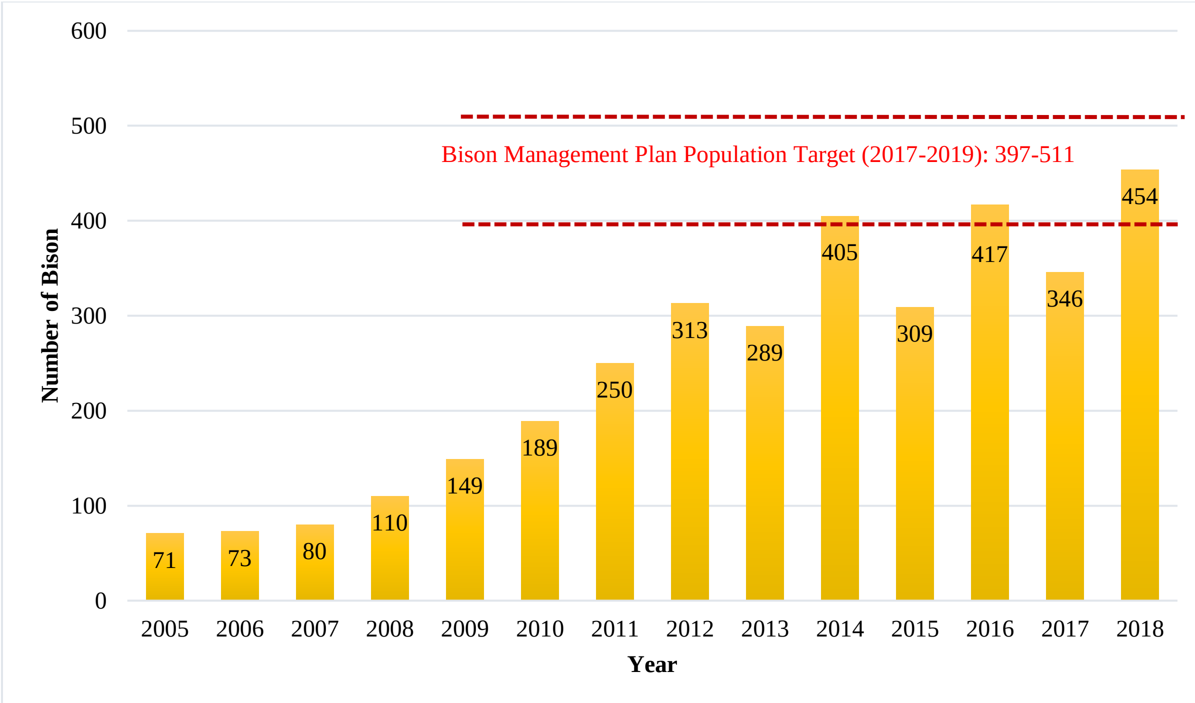

Figure 3-3 Annual bison population size in Grasslands National Park West block during 2005-2018 (data is provided by Grasslands National Park, Parks Canada).

Since bison were reintroduced, Xu and Guo (2015) noticed that there was an alteration of vegetation shown by historical Landsat imagery (Figure 3-4). As can be seen from Figure 3-4, the West block encircled by a yellow boundary was darker than the surrounding area, indicating clear vegetative difference between surrounding crops and conservation grasslands ecosystem. However, this afore-mentioned difference diminished apparently along with bison reintroduction from 2005. Hence, it is critical to assess whether overgrazing or under-grazing is happening for maintaining grasslands ecosystem health as well as achieving conservation goals.

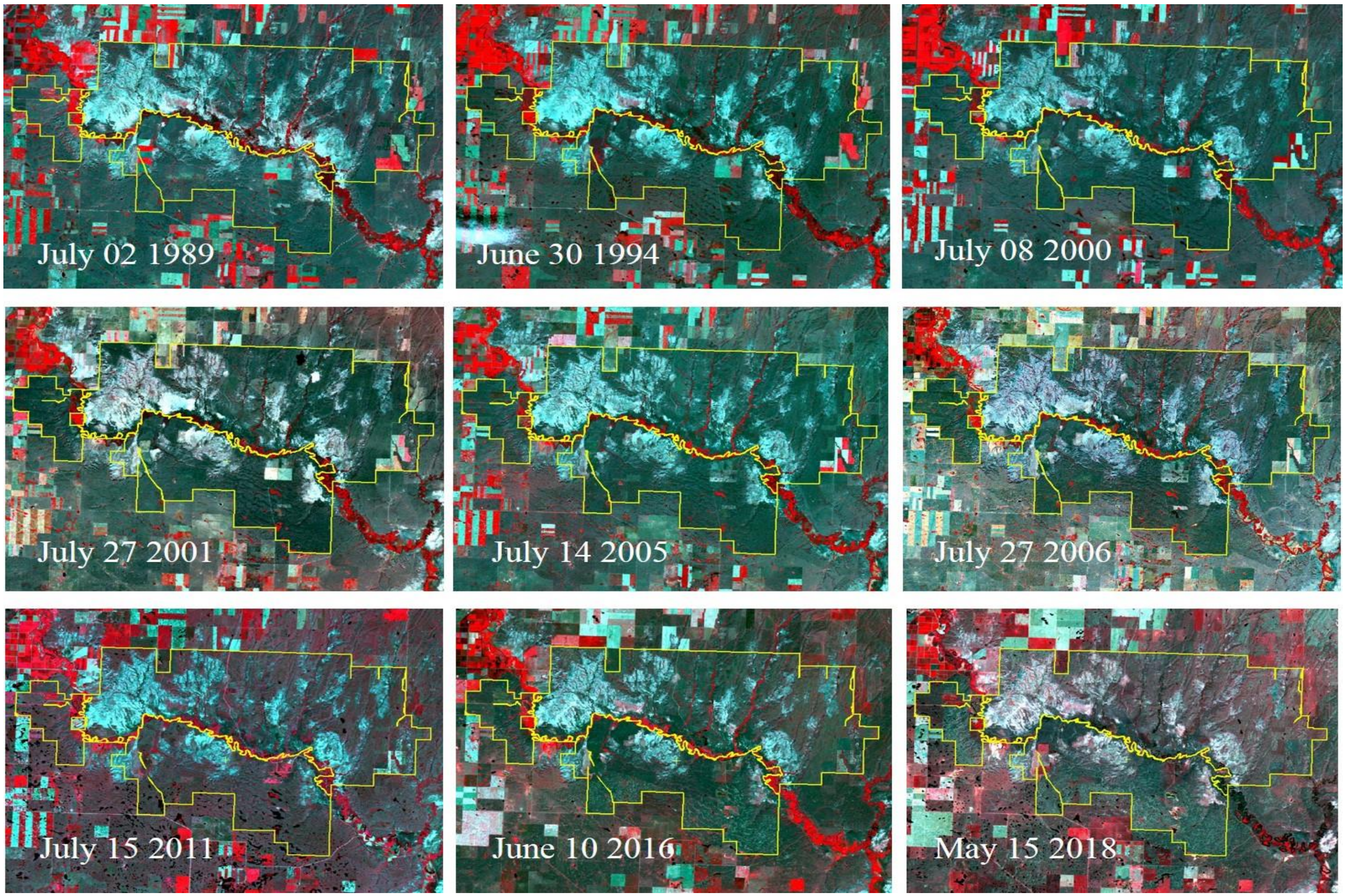

Figure 3-4 Historical Landsat images of the Grasslands National Park West block in growing seasons during 1989-2018. This series of nine standard false-colour composite (RGB: NIR, Red, Green) images represent the diminishing difference between conservation grasslands ecosystem inside Grasslands National Park and surrounding agricultural land after bison reintroduction.

3.2. Research methodology

The overall flowchart of methodology is demonstrated in Figure 3-5.

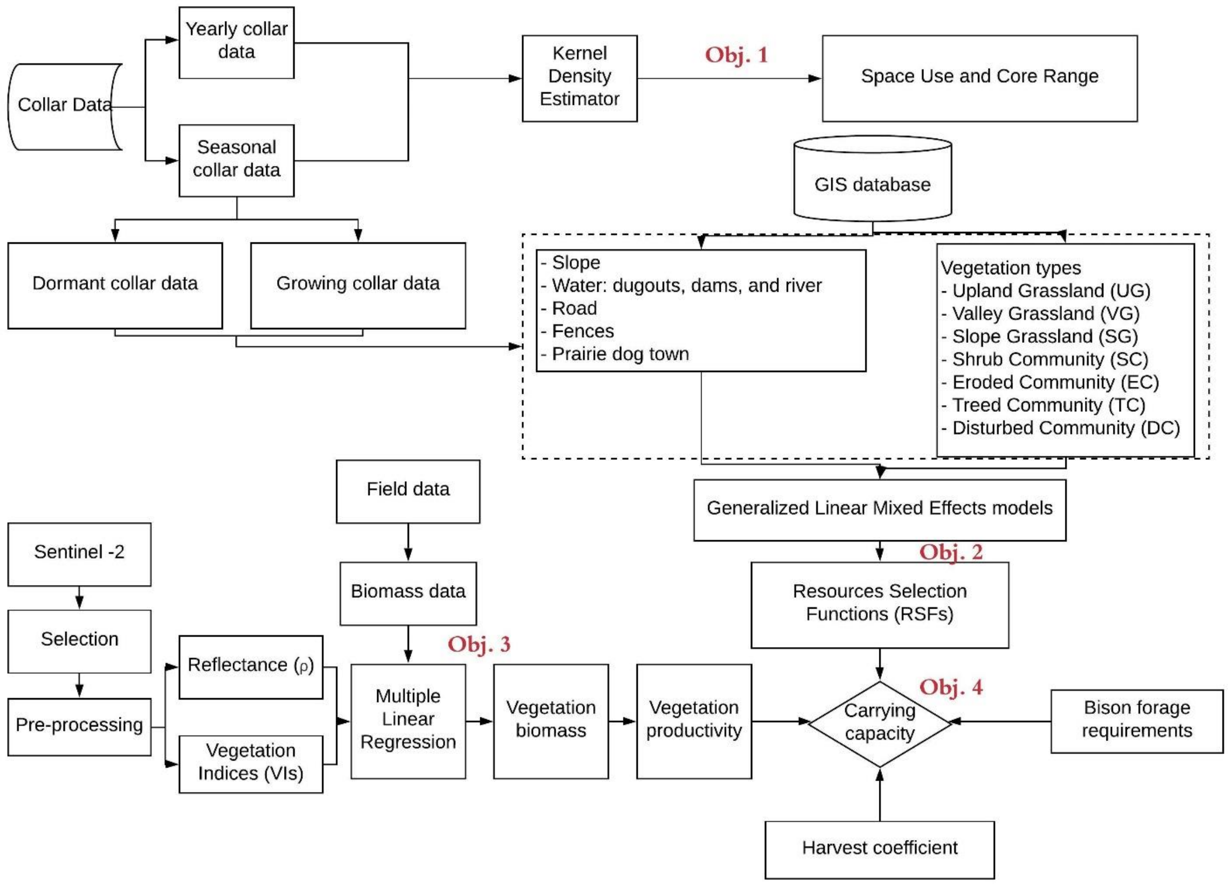

Figure 3-5 Overview of methods used in this research.

3.2.1. Datasets and Preprocessing

3.2.1.1.Bison data

Between 2005 and 2018, 16 female bison > 1 year old were equipped with GPS collars (3300L, 4400M, and Iridiumtrack M; Lotek Engineering Inc., New Market, Ontario, Canada). Each animal was monitored continuously until GPS ran out of battery or bison's health became worse, for a total of 108,617 recorded GPS locations. Collar data was extracted into yearly datasets during 2006-2018 and seasonal datasets (i.e., growing season and dormant season) during 2012-2018. Two main seasons (dormant: 1 October - 31 March; growing: 1 May – 31 August) were defined based on alteration of grassland phenology, as described by Cui, Martz, & Guo (2017). Collar data collected between November 1 and December 15 during surplus years (i.e., 2013, 2015,

2017) were excluded from the analysis, thus removing bias associated with gathering of animals within the holding fields of the bison handling facility.

3.2.1.2.Landscape factors

From literature, relevant landscape factors that influence habitat/resources selection of plains bison include vegetation type, slope, and locations of water sources, roads, fences, and prairie dog colonies. Water sources for plains bison herd include the Frenchman river portion, dams, and dugouts within their containment area. Percent slope was calculated within each 30 m x 30 m pixel from a Digital Elevation Model (DEM) derived from USGS (U.S. Geological Survey, 2018). We measured influences of the remaining landscape factors based on their Euclidean distance (m) from the features to observed locations used by bison and random locations inside bison containment area.

3.2.1.3.Vegetation biomass and productivity

Sampling sites were chosen using stratified random sampling due to generally homogeneous vegetation within each vegetation type. Sampling locations were generated with support of a geographical positioning system (GPS) with UTM 13N (Figure 3-1). In each sampling site, two 100 m perpendicular transects were aligned in north-south and west-east directions (Figure 3-6). Biomass metrics were collected in eight 20 cm x 50 cm quadrats at sampling points located 20 m and 40 m away from the intersection of the two transects (i.e., N2, N4, E2, E4, S2, S4, W2, W4). Vegetation biomass was collected in June-July (2016, 2017, 2018), at the peak of growing season (He, 2008). Samples were collected by traditional agronomic method, kept in labelled paper bags, sorted into different categories (i.e., green grass, forb, shrub, and dead) and dried at 60-65˚C for 48 hours to obtain dried weight (Appendix A Sample Field Form). For each sampling site, vegetation biomass was calculated as the average weight of the eight sampled quadrats. Biomass of different vegetation types with detailed biomass and percentage of green grass, forbs, shrub, and dead are calculated by averaging biomass data of all sampling sites established in corresponding vegetation types. Dead material in the mixed grasslands includes plant litter, accumulated dead plant matter, and standing dead plants from the previous year (Xu et al., 2014). Thus, we assumed that the green portion of vegetation at the peak of the growing season was the maximum vegetation productivity for the year. This maximum vegetation productivity was the total available forage of plains bison for the year. Literature advocated our assumption that herbivores mainly consume the green (live) portion of vegetation when available (Babin et al., 2011).

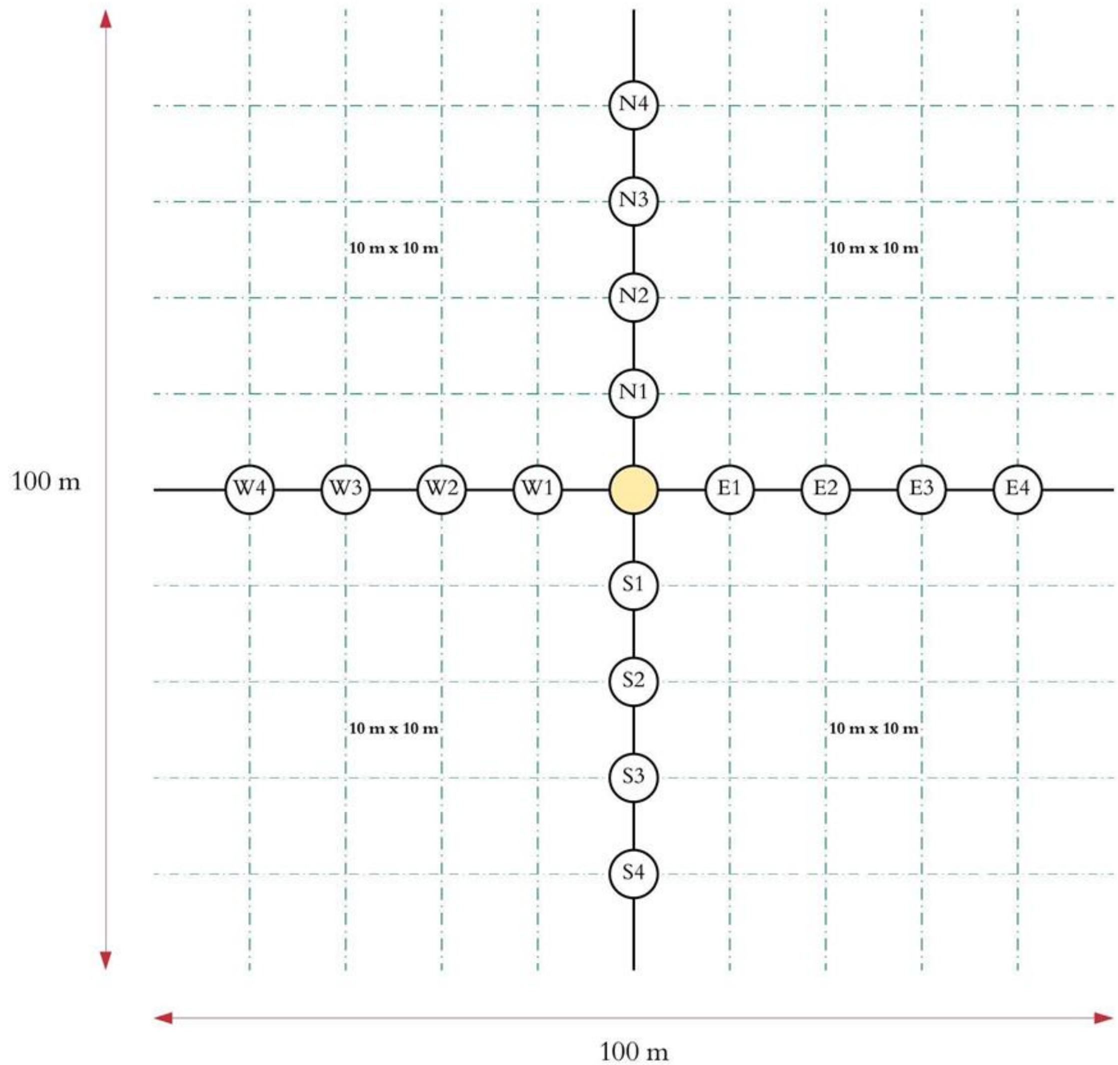

Figure 3-6 Field design used in this study. The background is 100 squares (10 by 10) indicating footprint of pixels covering the field site from Sentinel-2 products of 10 m spatial resolution.

3.2.1.4.Remotely sensed data

Satellite data used in this study were Sentinel-2 Multispectral Imagers (MSI) level-1C images on 22 July 2016, 7 June 2017, and 27 June 2018, downloaded from the website of U.S. Geological Survey (2015). I chose this remotely sensed data because the existence of narrow near-infrared band and three red-edge bands could be useful in estimating vegetation biomass and productivity. Preprocessing steps including atmospheric correction and resampling to 10 m x 10 m spatial resolution were done in Sentinel Application Platform (SNAP) with the support of Sen2COR processor (European Space Agency (ESA), 2018).

3.2.2. Data Analysis

To determine seasonal and annual bison space use, I processed Kernel Density Estimator (KDE) (Downs & Horner, 2008) using Geospatial Modelling Environment (GME) (Beyer, 2012) as the modelling platform and R Studio as its statistical engine (RStudio Team, 2018). KDE is the most recently acceptable method of home-range analysis (Walter, Fischer, Baruch-Mordo, & VerCauteren, 2011), describing the probability of finding an animal in any place (Rodgers, Carr, Beyer, Smith, & Kie, 2007). I created a KDE raster from each collar dataset (bandwidth: least squares cross validation, output cell size: 30m). Following Schuler et al. (2014), 0.95 and 0.50 isopleth contours were created to determine yearly space use boundaries and seasonal core ranges, respectively.

To assess the RSFs of plains bison, I generated an *a priori* model list from all relevant landscape factors. To directly compare the model coefficients, I standardized all continuous variables, then fitted a Generalized Linear Mixed Effect model in which collar ID was included as a random intercept to each model in the list above using the lme4 package in R Studio (Bates, Maechler, Bolker, & Walker, 2014). The best model was selected using second-order Akaike Information Criterion (AICc) with the AICcmodavg package in R Studio (Mazerolle & Linden, 2019). The logistic equation of the final model is:

$$W(x) = \exp(\beta_0 + \beta_1 X_1 + \cdots + \beta_i X_i) \tag{3.1}$$

$W(x)$ is the relative probability of a selected pixel, β_0 is the intercept, and β_i is the estimated coefficient for variable X_i (Manly et al., 2007). Both growing and dormant RSFs were modelled to evaluate the landscape factors' influences on resources selection of bison. I calculated the raster-based RSF surface for growing season only using coefficients of the best model in ArcGIS 10.6 (ESRI, 2018). To create a probability map of bison habitat/resources selection for carrying capacity estimation, the growing season RSF output was displayed by stretching RSF model prediction into the range of 0 (low use) – 1 (high use), which is often used in mapping RSF model (Morris et al., 2016). R Studio Code example for growing season is attached in Appendix B R Studio Code for building R.

To estimate vegetation biomass and productivity, biomass data collected in 33 sampling sites were the sample to build the regression model for predicting vegetation biomass from remote sensing images. At each ground sampling site, surrounding ground sampling center, reflectance (ρ) and Vegetation Indices (VIs) (Table 3-1) were retrieved within 10 x 10 pixels to match the 100 m x 100 m sample plot size. I averaged the ρ and VIs within each sample site to represent the size. Prior to building the regression model, Pearson correlations were calculated for each variable group: ρ and VIs in relation to green biomass (sum of green grass, shrub, and forb), and total biomass. I noticed low correlations between remotely sensed data and green biomass in comparison with the correlations between remotely sensed data and total biomass. Thus, I estimated vegetation biomass first. Correlograms were plotted among variables in each group to detect multicollinearity. Variables were selected in each group based on high coefficients with total biomass and no or little multicollinearity (≤ 0.9). Afterwards, multiple linear regression (MLR) models were built with backward elimination to discard the presence of unimportant variables. A normal Q-Q plot was used to check that the assumption of normality was met and a Breusch-Pagan test was used to test for homoscedasticity. Transformation was used with the VIs group because the homoscedasticity assumption was violated. The coefficient of determination in equation (3.2) and the root-mean-square error (RMSE) in equation (3.3) are calculated to evaluate the performance of the models.

$$r^2 = \frac{\sum(\hat{y} - \bar{y})^2}{\sum(y - \bar{y})^2} \tag{3.2}$$

$\hat{y}$ is the average of the estimated variables, $\bar{y}$ is the average of the predicted variables, and y is the estimated variable.

$$RMSE = \sqrt{\frac{1}{n}\sum(y - y_{actual})^2} \tag{3.3}$$

n is the number of observed variables, and y_{actual} is the observed variables. In addition, relative root mean-square error (rRMSE) which I divided RMSE by the mean observed data also supports the selection of the best prediction model. After estimating vegetation biomass, I multiplied vegetation biomass with average proportion of green vegetation to estimate green biomass which was assumed as maximum vegetation productivity. This calculated vegetation productivity was assumed to be available forage for bison grazing in a year (365 days), because it is expected that bison will consume the green vegetation before the dead vegetation from previous years.

Finally, carrying capacity was estimated by combining the outcomes of the growing RSF as probability of resources selection, available forage, harvest coefficient (to account for other considerations such as wildlife needs, range health), and bison forage requirements (Figure 3-5 & Equation (3.4)). I calculated the forage requirement of a typical herd of bison in our study area based on previous research (Steenweg et al., 2016). The GNP herd is maintained at a ratio of 30 % > 1 year old males (mean weight = 679 kg), 52.5 % > 1 year old females (mean weight = 433 kg), and 17.5 % juveniles (mean weight = 187 kg) (Parks Canada, 2017). The daily dry matter intake of adult male bison, adult female bison, and juvenile bison are 2.5%, 2.75%, and 3% of their body weight (Steenweg et al., 2016). Averaged across the herd, a bison unit requires 12.3 kg of forage daily (or 4,496.8 kg per year). The harvest coefficient chosen for this study was 40% of available forage, recommended as sustainable level for semi-arid mixed-grass prairie (Holechek, 1988).

$$Bison\ carrying\ capacity = \frac{Available\ forage\ \times Resources\ selection\ probability\ \times Harvest\ coefficient}{Forage\ requirement\ per\ bison\ unit} \tag{3.4}$$

Table 3-1 List of Vegetation Indices (VIs) used in this study.

No.	VIs	Definition	Sources
1	Simple Ratio	$SR = \frac{NIR}{Red}$	Jordan (1969)
2	Normalized Difference Vegetation Index	$NDVI = \frac{NIR - Red}{NIR + Red}$	Rouse et al. (1974)
3	Enhanced Vegetation Index	$EVI = 2.5 \times \frac{NIR - Red}{NIR + 6 \times Red - 7.5 \times Green + 1}$	Justice et al. (1998)
4	Ratio Cover Index	$RCI = \frac{SWIR1}{Red}$	Zhang & Guo (2008)
5	Narrow Normalized Difference Vegetation Index	$NDVI_n = \frac{NIR_n - Red}{NIR_n + Red}$	Modified from Rouse et al. (1974)

6	Narrow Perpendicular Vegetation Index	$PVI_n = \frac{NIR_n - a \times Red - b}{\sqrt{1 + a^2}}$ a = 1.95; b = -0.01	Modified from Richardson & Wiegand (1977)
7	Narrow Green Normalized Difference Vegetation Index	$GSAVI_n = 1.5 \times \frac{NIR_n - Green}{NIR_n + Green + 0.5}$	Modified from Tian et al. (2005)
8	Narrow Modified Soil-adjusted Vegetation Index	$MSAVI_n = 0.5 \times \left[(2 \times NIR_n) - \sqrt{(2 \times NIR_n + 1)^2 - 8 \times (NIR_n - Red)}\right]$	Modified from Qi et al. (1994b)
9	Narrow Green Normalized Difference Vegetation Index	$NDVI_{ngreen} = \frac{NIR_n - Green}{NIR_n + Green}$	Modifed from Gitelson et al. (1996)
10	Narrow Enhanced Vegetation Index	$EVI_n = 2.5 \times \frac{NIR_n - Red}{NIR_n + 6 \times Red - 7.5 \times Green + 1}$	(Justice et al. 1998)
11	Narrow Enhanced Vegetation Index 2	$EVI_{2n} = 2.5 \times \frac{NIR_n - Red}{1 + NIR_n + 2.4 \times Red}$	Modified from Jiang et al. (2008)
12	Narrow Modified Triangular Vegetation Index 1	$MTVI_{1n} = 1.2 \times [1.2 \times (NIR_n - Red) - 2.5 \times (Red - Green)]$	Modified from Haboudane et al. (2004)
13	Narrow Normalized Difference Infrared Index 7	$NDII_{7n} = \frac{NIR_n - SWIR_2}{NIR_n + SWIR_2}$	Modified from Hardisky et al. (1983)
14	Narrow Normalized Difference Vegetation Index red-edge 2	$NDVI_{re2n} = \frac{NIR_n - Red - Edge_2}{NIR_n + Red - Edge_2}$	Modified from Rouse et al. (1974)
15	Narrow Normalized Difference Vegetation Index Red-edge 3	$NDVI_{re3n} = \frac{NIR_n - Red - Edge_3}{NIR_n + Red - Edge_3}$	Modified from Rouse et al. (1974)

Chapter 4 RESULTS & DISCUSSION

4.1. Results

4.1.1. Temporal space use of bison family groups

Since reintroduction, the annual home range of bison family groups has been inconsistent, as illustrated in Figure 4-1. From 2006 to 2011, although bison extended their home range into the northwest corner of their containment area, no evidence existed about bison selection in the southwest corner. However, after 2011, bison narrowed their home range into the east half of the containment area. The extension of bison home range into the southwest corner was just revealed from 2016 to 2018. The area of the park used by bison family groups increased as the bison population increased (r^2 = 0.20), but there is almost no linear relationship between number of radiolocations and annual space use of bison family groups (r^2 = 0.01). From the drawn linear relationship between space use and population size, each additional bison needs 5.52 ha on average.

Looking into seasonal space use, bison family groups do not use the available space within their containment area uniformly; most groups concentrate in the northeast corner of their containment area (Figure 4-2). The dormant core range of bison (3,770.6 ha) overlaps most of the growing core range and is about double the area of the growing core range (1,780.0 ha). The growing core range accounts for 9.84% of the bison containment area. The overlapping extent of the seasonal bison core range is 1,618.4 ha (90.1% of growing core range).

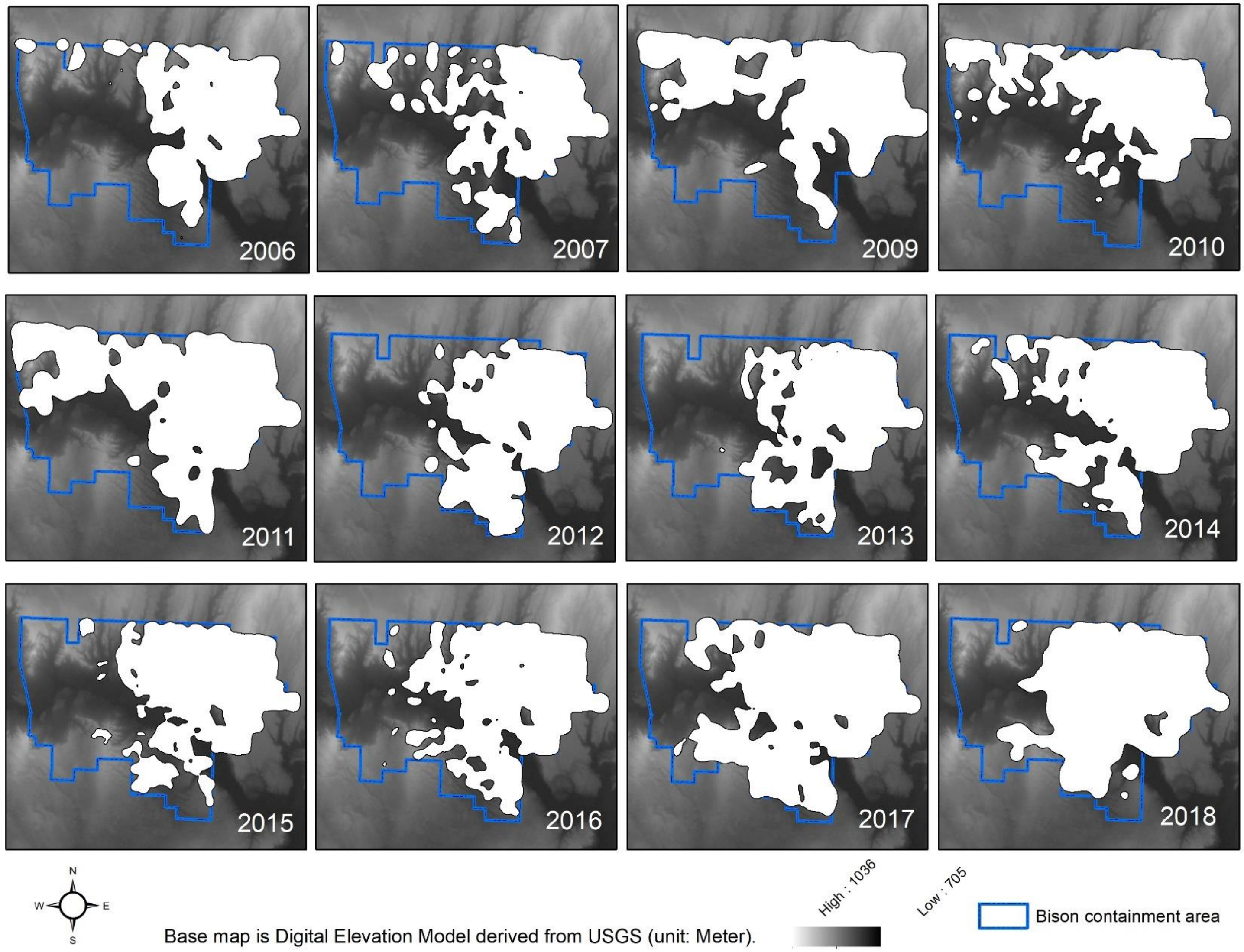

Figure 4-1 Annual space use of bison family groups in Grasslands National Park from 2006 to 2018. White polygons describe the chosen space of bison family groups.

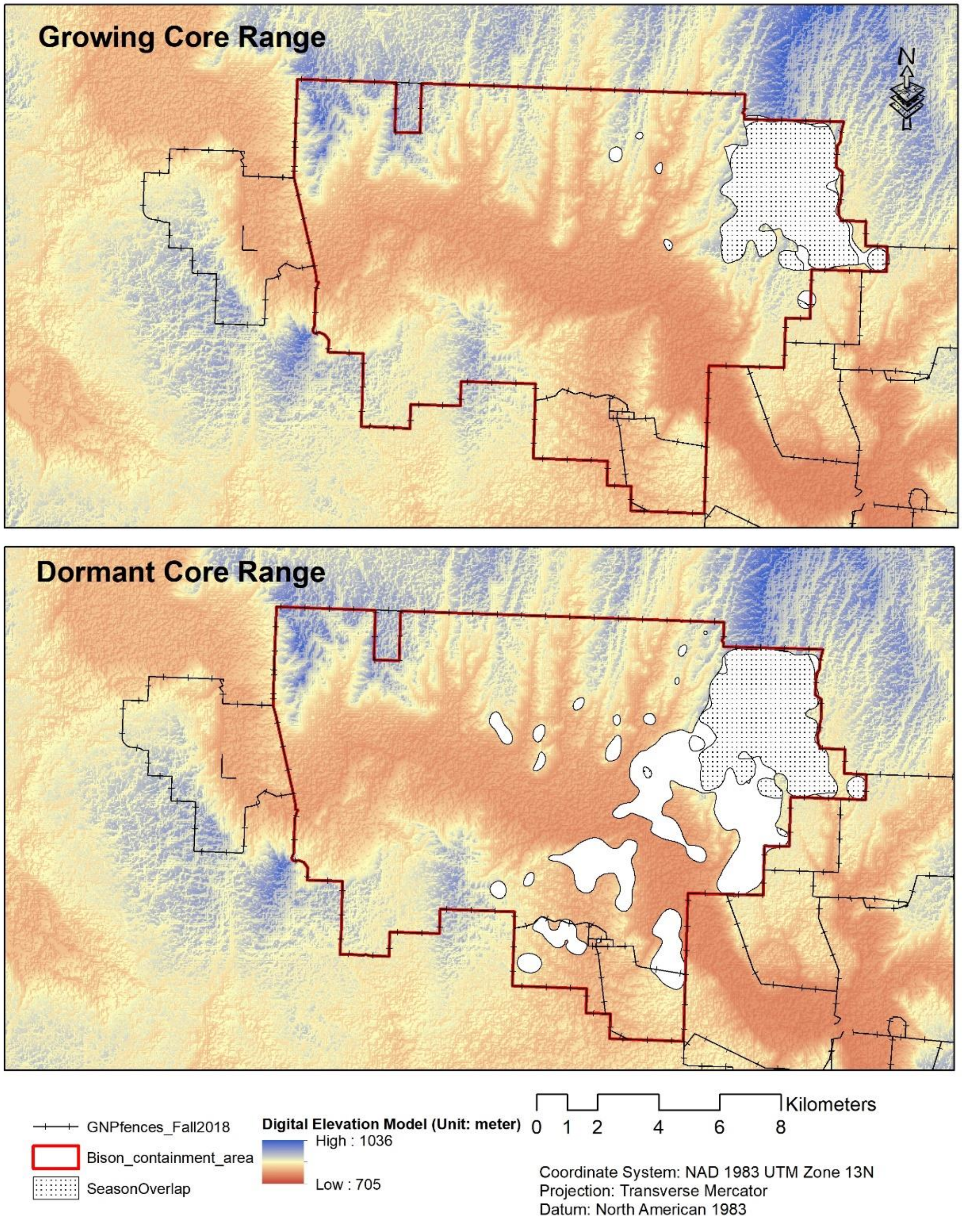

Figure 4-2 Seasonal bison core ranges in Grasslands National Park West block were in the northeast corner, shown in white. The white dotted area indicates overlap of plains bison's core range between growing and dormant seasons.

4.1.2. Seasonal RSFs of bison family groups

In general, vegetation types are more influential to the distribution of bison family groups, in contrast to other landscape factors in both growing and dormant seasons (Table 4-1). RSFs in growing and dormant seasons built from distance to three dominant vegetation types (SG, UG, and VG) shows better performance to habitat/resources selection of bison family groups than the ones built from literature-derived non-vegetation information (slope, road, and water). Estimators of all variables are different between growing and dormant seasons, indicating the seasonal alteration of these factors' impacts to bison groups (Table 4-2). The estimates of model parameters indicate that in both growing and dormant seasons, SG has the strongest influence on the probability of use. A negative estimator of SG explains that the further distance to slope grassland, the lower probability of bison selection. In growing season, UG, EC, and distance to road follow SG respectively regarding the influence on RSF. In dormant season, EC, TC, and distance to water sources are less influential than SG respectively. The growing RSF model prediction is illustrated in Figure 4-3.

Table 4-1 Second-order Akaike Information Criterion (AICc) comparison of the growing RSF models and dormant RSF models. The best model is the candidate model with the smallest AICc, the delta AICc for a candidate model denoted by ΔAICc is the difference between the AICc of that model and the minimum AICc of all candidate models. I selected five candidate models including: all related variables model, vegetation types-model, dominant vegetation types–model (slope grassland (SG), upland grassland (UG), valley grassland (VG)), non-vegetation information-model, and non-vegetation information–model with important factors based on bison grazing literature.

Models	Growing		Dormant	
	AICc	ΔAICc	AICc	ΔAICc
Slope + Water + Fence + Road + Colonies + TC + SG + UG + VG +SC +EC +DC	42,852.0	0.0	77,789.7	0.0
TC + SG + UG + VG +SC +EC +DC	44,504.4	1,652.3	79,226.2	1,436.5
SG + UG + VG	56,519.0	13,667.0	87,416.9	9,627.3
Slope + Water + Fence + Road + Colonies	48,815.6	5,963.6	86,655.9	8,866.2
Slope + Water + Road	59,430.8	16,579.7	89,258.7	11,489.1

Table 4-2 Summary of seasonal RSFs of plains bison use with full variables in Grasslands National Parks. Analysis was calculated within bison containment area in growing and dormant seasons according to vegetation phenology. SE stands for standard error of the regression.

Variables	Growing RSF		Dormant RSF	
	Estimate	SE	Estimate	SE
Intercept	-40.6	3.89	-42.91	2.49
Slope	-0.24	0.01	-0.19	0.01
Water	3.47	0.58	5.40	0.44
Fence	4.81	0.41	3.89	0.26
Road	8.71	0.45	-2.20	0.30
Colonies	8.11	0.35	-1.31	0.23
TC	6.10	0.11	5.60	0.07
SG	-16.25	1.55	-21.18	1.00
UG	-15.79	1.93	-15.62	1.26
VG	1.63	0.97	0.26	0.64
SC	-8.35	0.63	-0.50	0.38
EC	11.27	0.56	-6.49	0.36
DC	-7.40	0.63	0.87	0.40

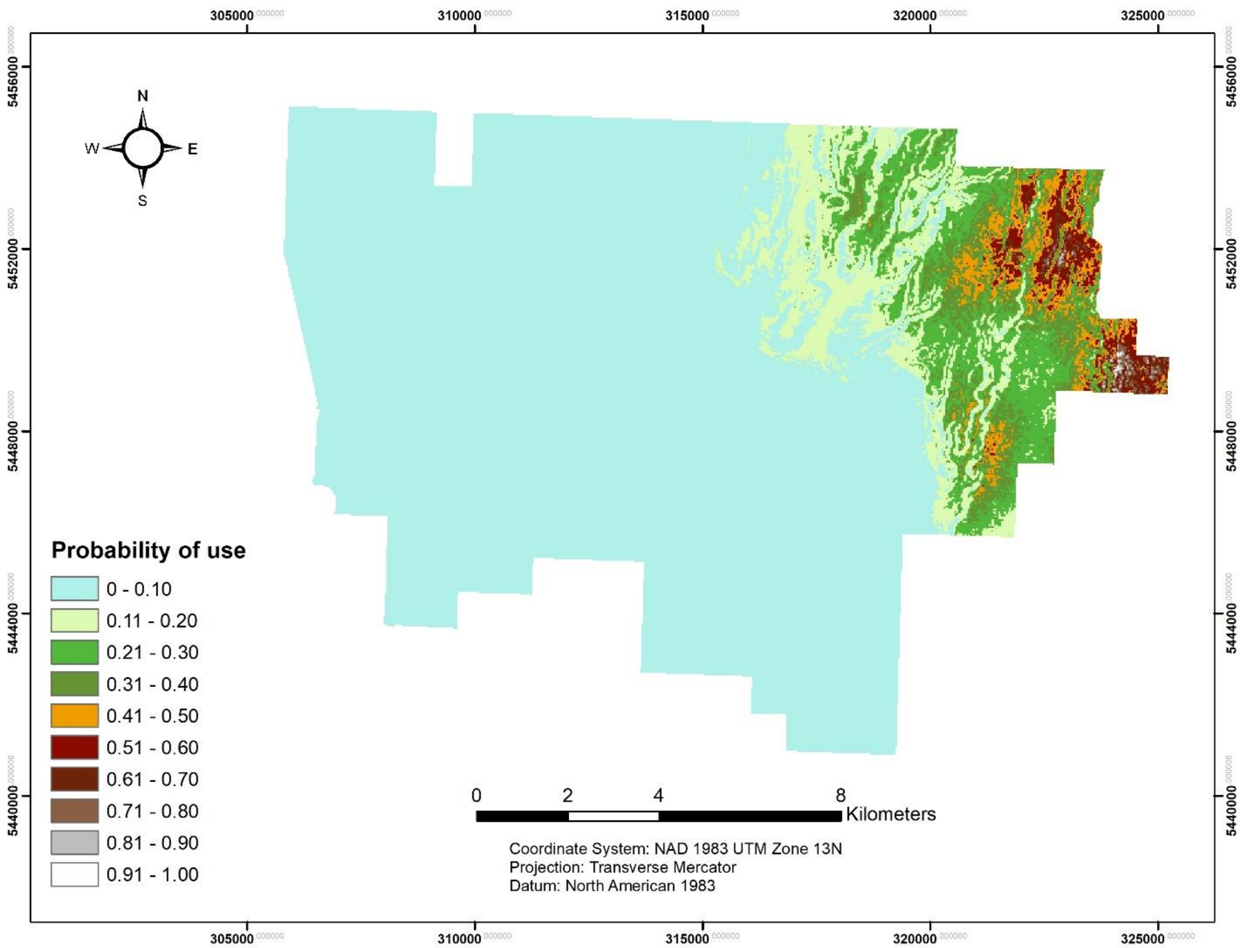

Figure 4-3 Probability of use of plains bison family group in bison containment area in Grasslands National Park West block. Growing Resources Selection Function was built from 22,033 radiolocations of bison during growing season (1 May – 31 August) from 2012 to 2018. The raster output of growing RSF was linear-transformed into the probability of use as shown in this figure to be the probability input for carrying capacity estimation.

4.1.3. Vegetation biomass and productivity

The average composition of aboveground biomass of different vegetation types is depicted in Table 4-3. DC has the largest biomass (total dry weight) but the major component of aboveground biomass is dead vegetation. Having fewer total dry weight than DC, EC has shrub and dead as the major components, accounting for more than 80%. Among three dominant vegetation types (SG, UG, VG) in GNP West block, the most shrub is recorded in VG (12.5%).

Table 4-3 Percentage (%) of aboveground biomass components in Grasslands National Park in summer 2006, 2017, 2018.

Vegetation community	**Green grass**		**Forbs**		**Shrub**		**Dead**		**Total dry weight**
	$g\ m^{-2}$	%	$g\ m^{-2}$	%	$g\ m^{-2}$	%	$g\ m^{-2}$	%	$g\ m^{-2}$
Disturbed community (DC)	204.2	26.0	0.20	0.0	62.5	8.0	518.6	66.0	785.5
Eroded community (EC)	24.9	6.1	16.1	3.9	167.7	40.9	201.8	49.1	410.5
Slope grassland (SG)	70.8	22.4	22.4	7.1	9.3	2.9	214.2	67.6	316.7
Upland grassland (UG)	64.9	19.0	10.2	3.0	2.3	0.0	264.1	78.0	341.5
Valley grassland (VG)	85.2	7.2	10.8	2.9	46.4	12.5	229.2	77.4	371.6

The MLR model build from Sentinel-2 reflectance had better performance in predicting vegetation biomass than the VIs-based model (Table 4-4). Average vegetation biomass of the bison containment area in growing season (May – September) of 2016-2018 is 2,627 kg ha^{-1} (Figure 4-4), smaller than average vegetation biomass of GNP West block during the same period (2,689 kg ha^{-1}). The selected MLR model was shown in Equation (4.1**)** below.

$$\begin{aligned} Biomass = 86.58 - 0.22 \times \mathrm{Blue} + 0.14 \times \mathrm{Green} + 0.35 \times \mathrm{Red-edge1} \\ - 0.45 \times \mathrm{Red-edge2} + 0.07 \times \mathrm{Red-edge3} + 0.03 \\ \times \mathrm{Narrow-NIR} \end{aligned} \tag{4.1}$$

Based on the coverage of green vegetation investigated for different vegetation communities (Table 4-3) and the extent of these vegetation types extracted from GNP's land inventory, green vegetation (green grass, shrub, and forbs) accounts for 27.97% of total vegetation biomass. Thus, average available forage of bison containment area in GNP West block is 734 kg ha^{-1}.

Table 4-4 Results of Multiple Linear Regression (MLR) to the relationship between Sentinel-derived parameters and vegetation biomass in peak growing seasons at the Grasslands National Park West block, 2016 – 2018.

Parameters	r^2	RMSE (g m^{-2})	rRMSE
Reflectance (ρ)	0.57	119.04	0.32
Vegetation Indices (VIs)	0.45	135.28	0.36

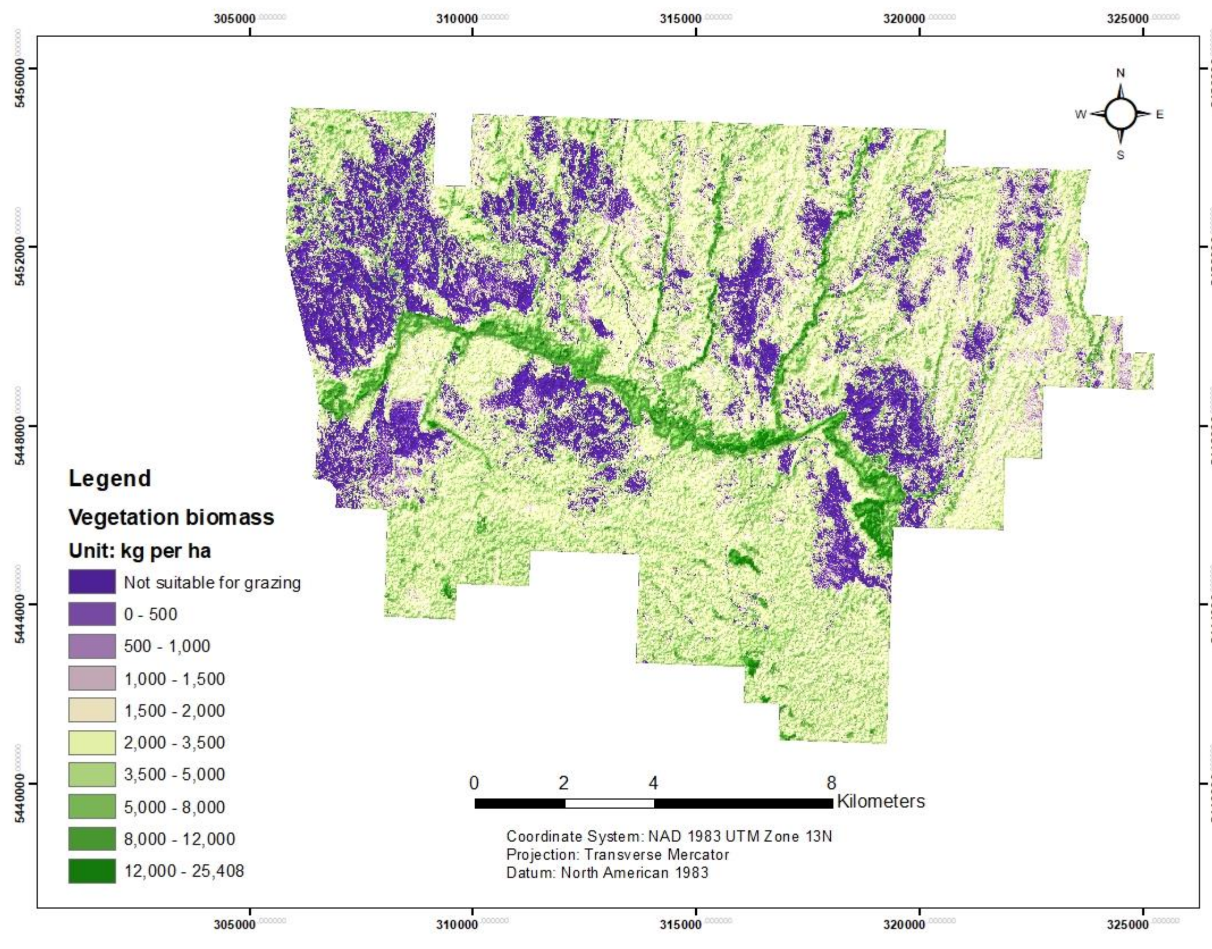

Figure 4-4 Vegetation biomass prediction from Sentinel-2 reflectance (r^2 = 0.57, RMSE = 119.04 g m^{-2}). The category labelled "Not suitable for grazing" indicates extremely low vegetation biomass, resulting in vegetation biomass less than 0 in these areas from MLR model prediction.

4.1.4. *Bison carrying capacity*

The estimated average bison density for the bison containment area inside GNP West block is 0.053 Bison Unit Year ha^{-1} (Figure 4-5).

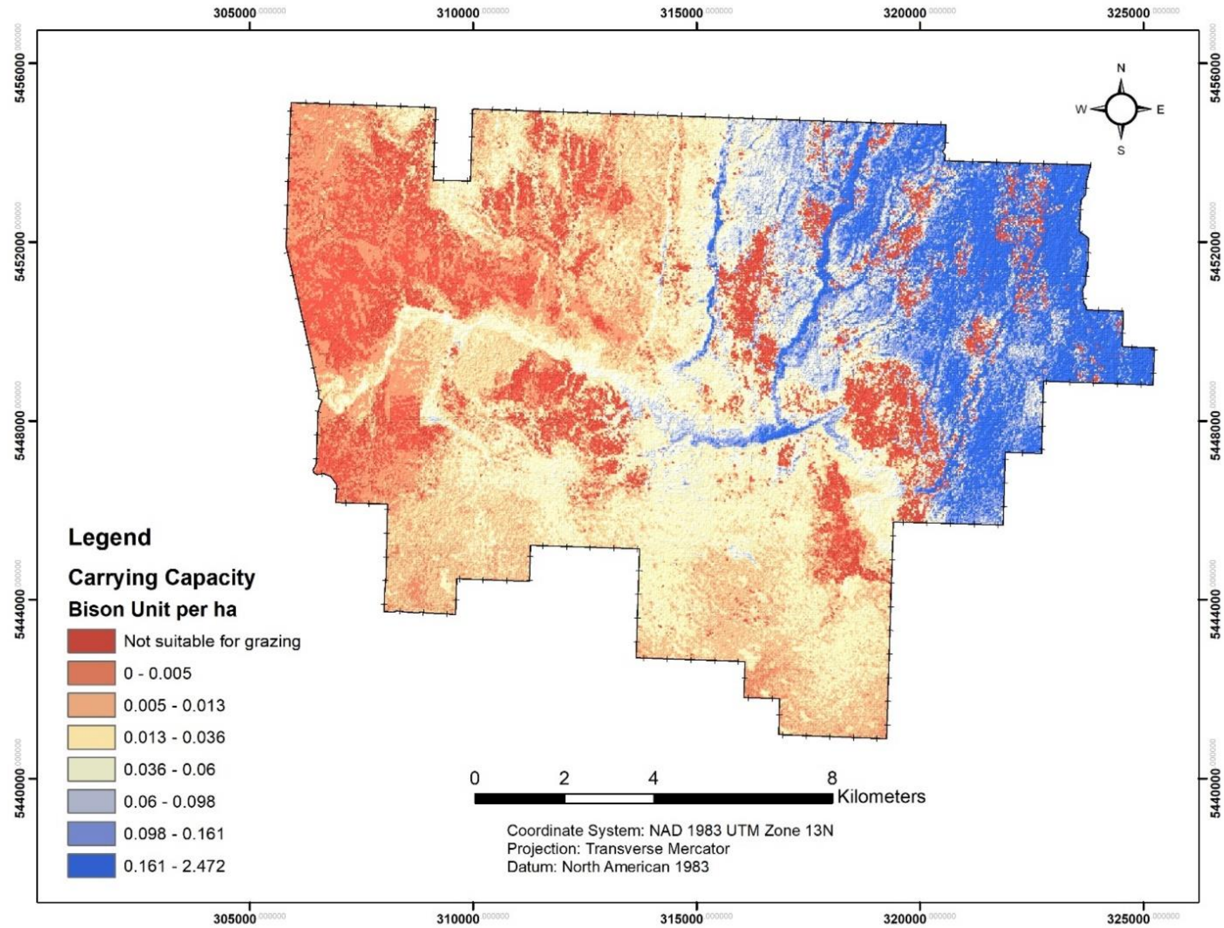

Figure 4-5 Estimated bison carrying capacity (Bison Unit Year per ha) in Grasslands National Park with maximum forage utilization rate of 40%. This carrying capacity estimation was the combination of available forage, bison forage requirements, probability of resources selection, and harvest coefficient of mixed-grass prairie. The areas not suitable for grazing have low vegetation biomass, derived from vegetation biomass prediction.

4.2. Discussion

In GNP West block, I recommend 0.053 Bison Unit Year ha^{-1} to be the carrying capacity of the bison containment area. This is the result of combining carrying capacity's drivers (available forage and bison requirements for food) and adjustment factors (RSFs and harvest coefficient). Without RSF consideration, 0.653 Bison Unit Year ha^{-1} is the estimated carrying capacity which far surpasses my real estimation. With my estimation, the failure recorded in Buffalo National Park due to misguided management efforts (Markewicz, 2018) is not expected to happen in GNP. There were 454 bison in 2018, equal to 544 Bison Unit (the conversion is based on the estimated average sex ratio). Based on my carrying capacity estimates, bison containment area in GNP West block appears to be able to support a greater population size year-round. It would contribute remarkably to the continental conservation status of this emblematic species.

Several scenarios have been considered regarding this estimated carrying capacity. First, the limitation of Sentinel-2 in estimating vegetation components of mixed-grass prairie leads to over-estimation of available food for bison in shrub and tree communities. Major vegetation components of shrub and tree communities are shrub and tree which are unconsumed by bison. Second, visual evaluation of soil erosion in the field based on Adams et al. (2009) indicates light to moderate level in eroded community. Thus, soil erosion in eroded community can stress vegetation production leading unsuitable area for grazing practices (Arnalds & Barkarson, 2003b; Doan & Guo, 2019; Yu et al., 2010). Third, other wildlife conservation programs are in progress in Grasslands National Park. Sliwinski (2011) indicated a linear decrease of some songbird species (Baird's sparrow, grasshopper sparrows, Savannah sparrows, Sprague's pipits) with bison grazing. The nest of these songbird species are related to the distribution of sagebrush, especially in disturbed community. Three afore-mentioned scenarios suggest an exclusion of shrub community, tree community, eroded community, and disturbed community in estimating total number of bison unit supported in Grasslands National Park's West block. Therefore, I suggest a range of 671-959 Bison Unit for bison carrying capacity (671 is the lower limit if upland grassland, slope grassland, and valley grassland are used primarily by bison).

Sentinel-2 reflectance correlated with total biomass by explaining 57% of the variation, significantly better than Landsat with 44% (Zhang, Guo, Wilmshurst, & Sissons, 2005). The improvement comes from the existence of red-edge region which is a chlorophyll absorption-to-leaf scattering transition zone (Clevers et al., 2002). However, this percentage of variation is not great because of accumulated standing dead materials, litter, and biological crust (moss, lichen) in sparse and low vegetation in the mixed grass prairie (Zhang & Guo, 2008).

Relying on my seasonal RSFs, vegetation information is more influential on bison habitat/resources selection in both growing and dormant seasons. SG is the most important to bison selection. The higher average grass biomass of SG (Table 4-3) might be a reason because the major component of bison's diet are graminoids (> 95%) (Steenweg et al. 2016). The findings of this study are consistent with literature that slope and distance to water are significant to bison RSFs (Allred et al., 2011; Babin et al., 2011; Kohl et al., 2013). Additionally, distance to the colonies is important to bison habitat/resources selection in both growing and dormant seasons. There is little vegetation in prairie dog colonies. Weltzin et al. (1997) found that off-colony live herbaceous biomass at least tripled on-colony biomass. Moreover, prairie dogs influence distribution, abundance, and composition of fauna in the southern mixed-grass prairie (Weltzin et al., 1997). Thus, the temporal extension of these colonies can adjust bison's habitat/resources selection.

When growing season changes to dormant season in the mixed-grass prairie, the core range of bison family groups almost doubles in size. There are several possible reasons for this. First, food abundance determines the home ranges of bison (Krasińska, Krasiński, & Bunevich, 2000), thus forage limitations in the growing season forces bison herd to extend their range. Second, due to the reproduction period and new born calves till August (COSEWIC, 2004), bison population increases leading to a reasonable core range extension. From the analysis of annual space use, bison family groups did not use the southwest corner of the containment area without any solid explanation. I suppose that domestic cattle grazing in the Nose and Two Trees paddocks inside the West block and out of bison containment in the west is problematic to bison. Moreover, bison family groups, especially in reproduction period, might consider the safety which deter bison to use the southwest containment area.

Chapter 5 CONCLUSION, IMPLICATIONS, LIMITATIONS, & FUTURE WORKS

To synthesize the whole picture of the research, this final chapter aims to draw all major findings, highlight the implication of this research into Ecological Integrity (EI) management objectives of Parks Canada, and justify existing limitations of this work and determine future directions.

5.1. Conclusion

Since plains bison were reintroduced to the Northern Great Plains, bison carrying capacity estimates have become critical for bison conservation and grasslands protection. The heterogeneity between different ecosystems in the Northern Great Plains requires thorough bison carrying capacity studies in each ecosystem, especially in the mixed-grass prairie. Bison carrying capacity has two main drivers: forage availability and food requirement. Additionally, resource/habitat selection and harvest coefficient should be taken as adjusting factors in bison carrying capacity estimates. Illustrating temporal space use of bison herd highlights their non-uniform resource/habitat selection. GIS techniques support the researchers in examining how bison use their available space and assess bison behaviors in resource selection. Meanwhile, improvements in spatial resolution of remote sensors today helps investigate how much forage is available for bison. Thus, remotely sensed data and GIS can be integrated in estimating bison carrying capacity.

For assessing temporal space use of bison, Kernel Density Estimator (KDE) was used to determine the annual home range and seasonal core range of bison family groups. Subsequently, I used Resources Selection Functions (RSFs) which have been increasingly common due to their better validation than Habitat Suitability Index (Cumulative Environmental Management Association (CEMA), 2011) to quantify the relative importance of different landscape components (Koper & Manseau, 2012). Landscape components influencing bison RSFs include vegetation types, slope, distance to water, distance to roads and fences, climatic factors, and competition. Historical GPS collar data retrieved in Grasslands National Park during 2006-2018 were provided by the park to carry out this research.

Sparse and low vegetation in mixed-grass prairie provided a challenge in estimating the amount of available forage for bison. I used Sentinel-2 MSI, medium spatial resolution imagery instead of coarse spatial resolution data, to improve the performance of predicting vegetation biomass, productivity, and available forage. The arrival of narrow near-infrared band and three red-edge bands in Sentinel-2 demonstrate potential to improve vegetation biomass and productivity estimation.

I found that in GNP, bison use space unevenly. The dormant core range overlaps most of the growing core range, doubles the growing core range in size. Seasonal RSFs resulted in an understanding of the significance of vegetation types and non-vegetation information to bison spatial distribution. The regression model we developed for biomass estimation using medium spatial resolution remotely sensed data was unable to discriminate the green proportion and dead proportion of vegetation in mixed-grass prairie. Nevertheless, the existence of narrow near-infrared band and red-edge bands in Sentinel-2 and its finer spatial resolution improved biomass estimation in comparison to Landsat imagery (Zhang, Guo, Wilmshurst, & Sissons, 2005). With an average productivity of 734 kg ha^{-1}, I suggest 671 - 959 Bison Unit could be sustained by GNP's West Block to promote long-term conservation of this species.

5.2. Implications

Ecological Integrity (EI) is central to ecosystem management in national parks, as suggested by Parks Canada Agency (2017b). Ecosystem management aims to maintain sustainable population levels for species (Parks Canada Agency, 2017b). The carrying capacity estimations in this study follow the EI management objectives of Parks Canada, and are expected to be used in updating GNP's bison management plan. To properly ensure resource management based on my carrying capacity estimation, the logistic growth model of bison population in GNP should be:

$$P(t) = \frac{671 \times e^{0.28t}}{0.23 + e^{0.28t}} \tag{5.1}$$

or

$$P'(t) = \frac{959 \times e^{0.28t}}{0.76 + e^{0.28t}} \tag{5.2}$$

t is time (year), P is population, and P(t) is the population function of time. I applied the logistic growth model, firstly introduced by Verhulst (1845) to the current bison situation in GNP (initial population is 544 Bison Unit, recorded bison population in 2018; carrying capacity is 671 (5.1) -

959 (5.2) Bison Unit; and the growth rate is 0.28). The logistic growth models are illustrated in Figure 5-1.

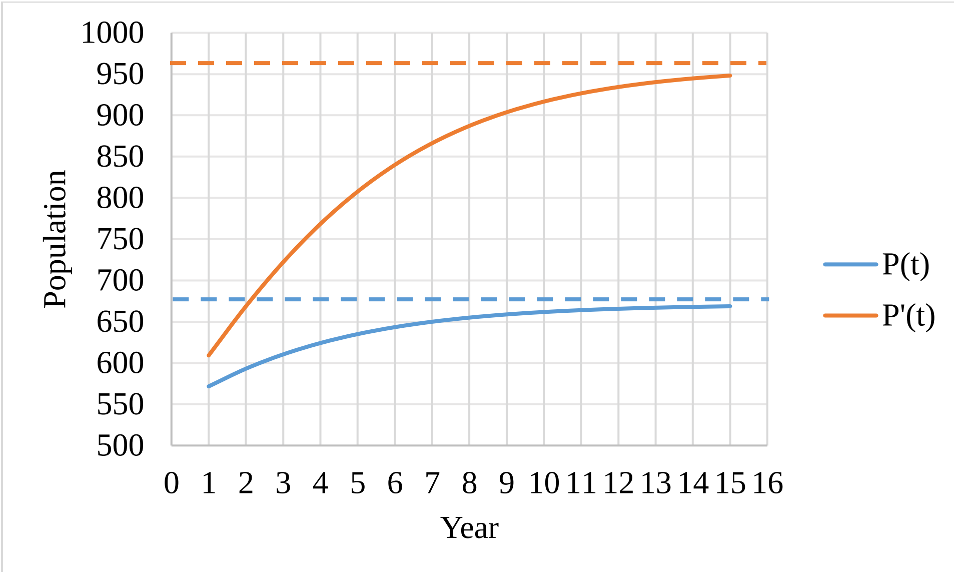

Figure 5-1 Logistic growth models of bison population in Grasslands National Park. Dashed lines represent my estimated carrying capacity values.

The drawn logistic growth models should be applied into bison management plan followed by the modification of biennial surplus removal activities. If male/female/juvenile ratio changes according to the grazing purposes, GNP can use the given approach to estimate bison's requirement forage then re-calculate the carrying capacity. After almost a century of disappearance, bison reintroduction to GNP would restore grazing as a natural driver of grassland plant communities in mixed-grass prairie. My work as part of the reintroduction process of plains bison promises to contribute to long-term and large-scale conservation of this wild species.

5.3. Limitations and future works

In this research, I reveal some limitations, and propose some suggestions corresponding to these limitations for future direction. First, I used medium spatial resolution (10 m x 10 m) remotely sensed data (Sentinel -2 MSI) which is still limited in accuracy when estimating vegetation biomass and productivity. Additionally, it was unable to provide detailed information of specific species and nutrients of vegetation. If fine spatial resolution imagery was used (i.e., GeoEye, IKONOS, Quickbird, SPOT, WorldView, KOMPSAT), this limitation could be addressed. However, the cost for these remotely sensed images and time for their acquisition were beyond this study's budget. The use of Sentinel-2 MSI provided the following challenges: 1) time consuming pre-processing steps, and 2) a lack of similar quality historical data. I suggest future researchers incorporate field hyperspectral data into this work to investigate the suitable spectral indices in understanding not only total available forage but also the food selection and nutrient requirement of plains bison. If possible, some fine scale satellite imagery can be purchased to help refine and evaluate the models.

Second, carrying capacity should be examined based on forage quality in addition to forage quantity, as being discussed in the literature review. The historical dry biomass and the ongoing collection of field measure may include some lab based measures of forage quality including protein, fibre, etc.

Third, climate factors, especially extreme climatic events (snow, drought) have not been considered in RSFs. According to Steenweg et al. (2016), bison prefer not to graze in snow deeper than 40 cm. Snowfall in GNP occasionally reach such depths (Parks Canada, 2012; Parks Canada Agency, 2017a). Snow cover and depth can be significant, especially on the bottoms of valleys and coulees. I suggest the use of Sentinel-2 images to detect snow and investigate the impact of snow on bison dormant RSF due to the capability of this remotely sensed data (Hollstein, Segl, Guanter, Brell, & Enesco, 2016). Modelling of long term climate change impacts on forage quality and quantity is important for the long term conservation purpose.

Subsequently, fire is also an important factor in bison RSFs. There was a large wildfire in GNP West block in April 2013, and this may have altered bison grazing patterns. Future researches can look explicitly at the long term impacts of fire on bison range through examining the existing burn and small scale manipulative experiments to look at the role of fire and potential for controlled burns to maintain and improve bison forage.

Last, soil erosion is one of the adjusting factors of carrying capacity as suggested by literature. Despite this, it is not accounted for in carrying capacity estimates. Remote sensing and GIS integration can help assess the severity of soil erosion by using the Universal Soil Loss Equation (USLE) (Chen et al., 2011; Dabral et al., 2008; Meusburger et al., 2010) and a fuzzy class membership approach (Ahamed et al., 2000). However, I was unable to overcome this limitation because of deficient data and expertise, as well time constraints.

LITERATURE CITED

Adams, B., Ehlert, G., Stone, C., Lawrence, D., Alexander, M., Willoughby, M., … Carlson, J. (2009). *Rangeland health assessment for grassland, forest and tame pasture*. Alberta: Alberta Sustainable Resource Development, Lands Division, Rangeland Management Branch.

Adjorlolo, C., Mutanga, O., Cho, M. A., & Ismail, R. (2012). Challenges and opportunities in the use of remote sensing for C3 and C4 grass species discrimination and mapping. *African Journal of Range & Forage Science*, *29*(2), 47–61. https://doi.org/10.2989/10220119.2012.694120

Adjorlolo, Clement, Mutanga, O., Ismail, R., & Cho, M. A. (2012). Optimizing spectral resolutions for the classification of C3 and C4 grass species, using wavelengths of known absorption features. *Journal of Applied Remote Sensing*, *6*(1), 063560. https://doi.org/10.1117/1.JRS.6.063560

Adler, P. B., & Hall, S. A. (2005). The development of forage production and utilization gradients around livestock watering points. *Landscape Ecology*, *20*(3), 319–333. https://doi.org/10.1007/s10980-005-0467-1

Adler, P., Raff, D., & Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, *128*(4), 465–479. https://doi.org/10.1007/s004420100737

Ahamed, T. N., Rao, K. G., & Murthy, J. S. R. (2000). Fuzzy class membership approach to soil erosion modelling. *Agricultural Systems*, *63*(2), 97–110. https://doi.org/10.1016/S0308-521X(99)00066-9

Ahamed, T., Tian, L., Zhang, Y., & Ting, K. C. (2011). A review of remote sensing methods for biomass feedstock production. *Biomass and Bioenergy*, *35*(7), 2455–2469. https://doi.org/10.1016/j.biombioe.2011.02.028

Alexakis, D. D., Hadjimitsis, D. G., & Agapiou, A. (2013). Integrated use of remote sensing, GIS and precipitation data for the assessment of soil erosion rate in the catchment area of "Yialias" in Cyprus. *Atmospheric Research*, *131*, 108–124. https://doi.org/10.1016/j.atmosres.2013.02.013

Allison, C. D. (1985). Factors Affecting Forage Intake by Range Ruminants: A Review. *Journal of Range Management*, *38*(4), 305–311. https://doi.org/10.2307/3899409

Allred, B. W., Fuhlendorf, S. D., & Hamilton, R. G. (2011). The role of herbivores in Great Plains conservation: Comparative ecology of bison and cattle. *Ecosphere*, *2*(3), art26. https://doi.org/10.1890/ES10-00152.1

American Bison Society. (2019). All about bison. Retrieved June 18, 2019, from All About Bison website: https://allaboutbison.com/bison-in-history/american-bison-society/

Anaya, J. A., Chuvieco, E., & Palacios-Orueta, A. (2009). Aboveground biomass assessment in Colombia: A remote sensing approach. *Forest Ecology and Management*, *257*(4), 1237–1246. https://doi.org/10.1016/j.foreco.2008.11.016

Anderson, G. L., Hanson, J. D., & Haas, R. H. (1993). Evaluating landsat thematic mapper derived vegetation indices for estimating above-ground biomass on semiarid rangelands. *Remote Sensing of Environment*, *45*(2), 165–175. https://doi.org/10.1016/0034-4257(93)90040-5

Anderson, K. E., Glenn, N. F., Spaete, L. P., Shinneman, D. J., Pilliod, D. S., Arkle, R. S., … Derryberry, D. R. (2018). Estimating vegetation biomass and cover across large plots in shrub and grass dominated drylands using terrestrial lidar and machine learning. *Ecological Indicators*, *84*, 793–802. https://doi.org/10.1016/j.ecolind.2017.09.034

Anderson, R. C. (2006). Evolution and origin of the Central Grassland of North America: Climate, fire, and mammalian grazers1. *The Journal of the Torrey Botanical Society*, *133*(4), 626–647. https://doi.org/10.3159/1095-5674(2006)133[626:EAOOTC]2.0.CO;2

Anderson, R. P., Peterson, A. T., & Gómez-Laverde, M. (2002). Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos*, *98*(1), 3–16. https://doi.org/10.1034/j.1600-0706.2002.t01-1-980116.x

Andrew, M. H. (1988). Grazing impact in relation to livestock watering points. *Trends in Ecology & Evolution*, *3*(12), 336–339. https://doi.org/10.1016/0169-5347(88)90090-0

Arnalds, O., & Barkarson, B. H. (2003a). Soil erosion and land use policy in Iceland in relation to sheep grazing and government subsidies. *Environmental Science & Policy*, *6*(1), 105–113. https://doi.org/10.1016/S1462-9011(02)00115-6

Arnalds, O., & Barkarson, B. H. (2003b). Soil erosion and land use policy in Iceland in relation to sheep grazing and government subsidies. *Environmental Science & Policy*, *6*(1), 105–113. https://doi.org/10.1016/S1462-9011(02)00115-6

Arthun, D., & Holechek, J. L. (1982). The North American bison History. *Rangelands Archives*, *4*(3), 123–125.

Aune, K., Jørgensen, D., & Gates, C. (2018). The IUCN Red List of Threatened Species. Retrieved June 13, 2019, from IUCN Red List of Threatened Species website: https://www.iucnredlist.org/en

Avitabile, V., Baccini, A., Friedl, M. A., & Schmullius, C. (2012). Capabilities and limitations of Landsat and land cover data for aboveground woody biomass estimation of Uganda. *Remote Sensing of Environment*, *117*, 366–380. https://doi.org/10.1016/j.rse.2011.10.012

Ayllón, D., Almodóvar, A., Nicola, G. G., Parra, I., & Elvira, B. (2012). Modelling carrying capacity dynamics for the conservation and management of territorial salmonids. *Fisheries Research*, *134–136*, 95–103. https://doi.org/10.1016/j.fishres.2012.08.004

Babin, J.-S., Fortin, D., Wilmshurst, J. F., & Fortin, M.-E. (2011). Energy gains predict the distribution of plains bison across populations and ecosystems. *Ecology*, *92*(1), 240–252. https://doi.org/10.1890/10-0252.1

Baccini, A., Friedl, M. A., Woodcock, C. E., & Zhu, Z. (2007). Scaling field data to calibrate and validate moderate spatial resolution remote sensing models. *Photogrammetric Engineering & Remote Sensing*, *73*(8), 945–954. https://doi.org/10.14358/PERS.73.8.945

Bain, I. (2010). Sustainable Development in Western China: Managing People, Livestock and Grasslands in Pastoral Areas. *Mountain Research and Development*, *30*(1), 59–60. https://doi.org/10.1659/mrd.mm065

Balasubramanian, A. (2017). *Digital Elevation Model (DEM) in GIS* (No. 3). Retrieved from University of Mysore website: 10.13140/RG.2.2.23976.47369

Bannari, A., Haboudane, D., & Bonn, F. (2000). Mid infrared interest for culture residues cartography. *Canadian Journal of Remote Sensing*, *26*(5), 384–393. https://doi.org/10.1080/07038992.2000.10855270

Baptestini, E. M., de Aguiar, M. A. M., Bolnick, D. I., & Araújo, M. S. (2009). The shape of the competition and carrying capacity kernels affects the likelihood of disruptive selection. *Journal of Theoretical Biology*, *259*(1), 5–11. https://doi.org/10.1016/j.jtbi.2009.02.023

Baret, F., Guyot, G., & Major, D. J. (1989). TSAVI: A vegetation index which minimizes soil brightness effects on LAI and APAR estimation. *12th Canadian Symposium on Remote*

Sensing Geoscience and Remote Sensing Symposium, 3, 1355–1358. Vancouver, British Colombia: IEEE.

Baret, Fred, & Guyot, G. (1991). Potentials and limits of vegetation indices for LAI and APAR assessment. *Remote Sensing of Environment*, *35*(2–3), 161–173. https://doi.org/10.1016/0034-4257(91)90009-U

Barker, W. T., & Whitman, W. C. (1988). Vegetation of the Northern Great Plains. *Rangelands*, *10*(6), 266–272. Retrieved from https://www.jstor.org/stable/4000297

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4 (Version 1.7). Retrieved from http://cran.r-project.org/package=lme4

Beck, J. L., Peek, J. M., & Strand, E. K. (2006). Estimates of Elk Summer Range Nutritional Carrying Capacity Constrained by Probabilities of Habitat Selection. *Journal of Wildlife Management*, *70*(1), 283–294. https://doi.org/10.2193/0022-541X(2006)70[283:EOESRN]2.0.CO;2

Belal, A.-A., El-Ramady, H. R., Mohamed, E. S., & Saleh, A. M. (2014). Drought risk assessment using remote sensing and GIS techniques. *Arabian Journal of Geosciences*, *7*(1), 35–53. https://doi.org/10.1007/s12517-012-0707-2

Beyer, H. L. (2012). GME | SpatialEcology.Com. Retrieved August 7, 2019, from Geospatial Modelling Environment website: http://www.spatialecology.com/gme/

Biard, F., & Baret, F. (1997). Crop residue estimation using multiband reflectance. *Remote Sensing of Environment*, *59*(3), 530–536. https://doi.org/10.1016/S0034-4257(96)00125-3

Bjørneraas, K., Moorter, B. V., Rolandsen, C. M., & Herfindal, I. (2010). Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. *The Journal of Wildlife Management, 74*(6), 1361–1366. https://doi.org/10.1111/j.1937-2817.2010.tb01258.x

Boyd, D. P. (2003). *Conservation of North American bison: Status and recommendations* (PhD Thesis). University of Calgary.

Brotons, L., Thuiller, W., Araújo, M. B., & Hirzel, A. H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, *27*(4), 437–448. https://doi.org/10.1111/j.0906-7590.2004.03764.x

Bruggeman, Jason E., Garrott, R. A., White, P. J., Watson, F. G. R., & Wallen, R. (2007). Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecological Applications*, *17*(5), 1411–1423. https://doi.org/10.1890/06-0196.1

Bruggeman, Jason Edward. (2006). *Spatio-temporal dynamics of the central bison herd in Yellowstone National Park* (Doctoral dissertation, Montana State University). Retrieved from https://scholarworks.montana.edu/xmlui/handle/1/995

Bruynooghe, J., & Macdonald, R. (2008). Managing Saskatchewan Rangeland. *Agriculture and Agri-Food Canada, Government of Saskatchewan: Regina, SK, Canada*.

Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2157–2162. https://doi.org/10.1098/rstb.2010.0107

Campbell, C., Campbell, I. D., Blyth, C. B., & McAndrews, J. H. (1994). Bison extirpation may have caused aspen expansion in western Canada. *Ecography*, 360–362.

Cao, X., Chen, J., Matsushita, B., & Imura, H. (2010). Developing a MODIS-based index to discriminate dead fuel from photosynthetic vegetation and soil background in the Asian steppe area. *International Journal of Remote Sensing*, *31*(6), 1589–1604. https://doi.org/10.1080/01431160903475274

Chapman, E. J., & Byron, C. J. (2018). The flexible application of carrying capacity in ecology. *Global Ecology and Conservation*, *13*, e00365. https://doi.org/10.1016/j.gecco.2017.e00365

Che, T., Li, X., Jin, R., Armstrong, R., & Zhang, T. (2008). Snow depth derived from passive microwave remote-sensing data in China. *Annals of Glaciology*, *49*, 145–154. https://doi.org/10.3189/172756408787814690

Chen, J., Gu, S., Shen, M., Tang, Y., & Matsushita, B. (2009). Estimating aboveground biomass of grassland having a high canopy cover: An exploratory analysis of in situ hyperspectral data. *International Journal of Remote Sensing*, *30*(24), 6497–6517. https://doi.org/10.1080/01431160902882496

Chen, T., Niu, R., Li, P., Zhang, L., & Du, B. (2011). Regional soil erosion risk mapping using RUSLE, GIS, and remote sensing: A case study in Miyun Watershed, North China. *Environmental Earth Sciences*, *63*(3), 533–541. https://doi.org/10.1007/s12665-010-0715-z

Ciuti, S., Pipia, A., Grignolio, S., Ghiandai, F., & Apollonio, M. (2009). Space use, habitat selection and activity patterns of female Sardinian mouflon (Ovis orientalis musimon) during the lambing season. *European Journal of Wildlife Research*, *55*(6), 589–595. https://doi.org/10.1007/s10344-009-0279-y

Clevers, J. G. P. W., Jong, S. M. D., Epema, G. F., Meer, F. D. V. D., Bakker, W. H., Skidmore, A. K., & Scholte, K. H. (2002). Derivation of the red edge index using the MERIS standard band setting. *International Journal of Remote Sensing*, *23*(16), 3169–3184. https://doi.org/10.1080/01431160110104647

Cline, D. W., Bales, R. C., & Dozier, J. (1998). Estimating the spatial distribution of snow in mountain basins using remote sensing and energy balance modeling. *Water Resources Research*, *34*(5), 1275–1285. https://doi.org/10.1029/97WR03755

Cook, C. W. (1966). Factors Affecting Utilization of Mountain Slopes by Cattle. *Journal of Range Management*, *19*(4), 200–204. https://doi.org/10.2307/3895647

Cooper, J. R. (2008). *Bison hunting and Late Prehistoric human subsistence economies in the Great Plains* (Ph.D., Southern Methodist University). Retrieved from https://search.proquest.com/docview/276049633/abstract/950C4C62AA894ACAPQ/1

Coppedge, B. R., Leslie Jr, D. M., & Shaw, J. H. (1998). Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management*, *51*(4), 379–382. https://doi.org/10.2307/4003321

Coppedge, B. R., & Shaw, J. H. (2000). American bison Bison bison wallowing behavior and wallow formation on tallgrass prairie. *Acta Theriologica*, *45*, 103–110. https://doi.org/10.4098/AT.arch.00-10

COSEWIC. (2004). *COSEWIC assessment and status report on the plains bison Bison bison bison in Canada* (p. 71). Retrieved from https://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_plains_bison_e.pdf

COSEWIC. (2013). *COSEWIC assessment and status report of the plains bison Bison bison bison and the wood bison Bison bison athabascae in Canada* (p. 109). Retrieved from https://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Plains%20Bison%20and%20Wood%20Bison_2013_e.pdf

Coughenour, M. B. (2005). *Bison and elk in Yellowstone national park—Linking ecosystem, animal nutrition, and population processes*. Bozeman, Montana, USA: Biological Resources Division.

Coupland, R. T. (1961). A Reconsideration of Grassland Classification in the Northern Great Plains of North America. *Journal of Ecology*, *49*(1), 135–167. https://doi.org/10.2307/2257431

Cowlishaw, S. J. (1969). The carrying capacity of pastures. *Grass and Forage Science*, *24*(3), 207–214. https://doi.org/0.1111/j.1365-2494.1969.tb01071.x

Crête, M. (1989). Approximation of K carrying capacity for moose in eastern Quebec. *Canadian Journal of Zoology*, *67*(2), 373–380. https://doi.org/10.1139/z89-055

Crist, E. P. (1985). A TM tasseled cap equivalent transformation for reflectance factor data. *Remote Sensing of Environment*, *17*(3), 301–306. https://doi.org/10.1016/0034-4257(85)90102-6

Croneborg, L., Saito, K., Matera, M., McKeown, D., & van Aardt, J. (2015). *Digital Elevation Models: A Guidance Note on How Digital Elevation models are created and used*. International Bank for Reconstruction and Development.

Cui, T., Martz, L., & Guo, X. (2017). Grassland phenology response to drought in the Canadian prairies. *Remote Sensing*, *9*(12), 1258.

Cumulative Environmental Management Association (CEMA). (2011). Synthesis of habitat models used in the oil sands region. Retrieved August 7, 2019, from CEMA Studying culumative effects in wood buffalo website: http://cemaonline.ca/index.php/tools-a-libraries/habitat-model

Dabral, P. P., Baithuri, N., & Pandey, A. (2008). Soil Erosion Assessment in a Hilly Catchment of North Eastern India Using USLE, GIS and Remote Sensing. *Water Resources Management*, *22*(12), 1783–1798. https://doi.org/10.1007/s11269-008-9253-9

Dasmann, W. (1945). A method for estimating carrying capacity of range lands. *Journal of Forestry*, *43*(6), 400–402. https://doi.org/10.1093/jof/43.6.400

Daughtry, C. S. (2001). Discriminating crop residues from soil by shortwave infrared reflectance. *Agronomy Journal*, *93*(1), 125–131. https://doi.org/10.2134/agronj2001.931125x

DeCalesta, D. S., & Stout, S. L. (1997). Relative deer density and sustainability: A conceptual framework for integrating deer management with ecosystem management. *Wildlife Society Bulletin*, *25*(2), 252–258.

Delgiudice, G. D., Moen, R. A., Singer, F. J., & Riggs, M. R. (2001). Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. *Wildlife Monographs*, *147*, 1–60.

Desmet, P. J. J., & Govers, G. (1996). A GIS procedure for automatically calculating the USLE LS factor on topographically complex landscape units. *Journal of Soil and Water Conservation*, *51*(5), 427–433.

DeYoung, R. W., Hellgren, E. C., Fulbright, T. E., Robbins, W. F., & Humphreys, I. D. (2000). Modeling Nutritional Carrying Capacity for Translocated Desert Bighorn Sheep in Western Texas. *Restoration Ecology*, *8*(4S), 57–65. https://doi.org/10.1046/j.1526-100x.2000.80066.x

Dhondt, A. A. (1988). Carrying capacity: A confusing concept. *ACTA OECOL.(OECOL. GEN.).*, *9*(4), 337–346.

DiTomaso, J. M., Brooks, M. L., Allen, E. B., & Minnichi, R. (2006). *Fire as a tool for controlling invasive plants*. Berkeley, CA.: California Invasive Plant Council.

DiTomaso, J. M., Masters, R. A., & Peterson, V. F. (2010). Rangeland Invasive Plant Management. *Rangelands*, *32*(1), 43–47. https://doi.org/10.2111/RANGELANDS-D-09-00007.1

Doan, T., & Guo, X. (2019). Understanding bison carrying capacity estimation in Northern Great Plains using remote sensing and GIS. *Canadian Journal of Remote Sensing*. https://doi.org/10.1080/07038992.2019.1608518

Donovan, M. L., Rabe, D. L., & Olson, C. E. (1987). Use of geographic information systems to develop habitat suitability models. *Wildlife Society Bulletin (1973-2006)*, *15*(4), 574–579.

Downs, J. A., Gates, R. J., & Murray, A. T. (2008). Estimating carrying capacity for sandhill cranes using habitat suitability and spatial optimization models. *Ecological Modelling*, *214*(2–4), 284–292.

Downs, J. A., & Horner, M. W. (2008). Effects of Point Pattern Shape on Home-Range Estimates. *Journal of Wildlife Management*, *72*(8), 1813–1818. https://doi.org/10.2193/2007-454

Dozier, J., & Frew, J. (1990). Rapid calculation of terrain parameters for radiation modeling from digital elevation data. *IEEE Transactions on Geoscience and Remote Sensing*, *28*(5), 963–969. https://doi.org/10.1109/36.58986

Edwards, R. Y., & Fowle, C. D. (2013). The concept of carrying capacity. In *Essential Readings in Wildlife Management and Conservation* (Krausman P. R., and Bruce, D. L., pp. 279–393). United States of America: The Johns Hopkins University Press.

Eisfelder, C., Kuenzer, C., & Dech, S. (2012). Derivation of biomass information for semi-arid areas using remote-sensing data. *International Journal of Remote Sensing*, *33*(9), 2937–2984. https://doi.org/10.1080/01431161.2011.620034

ESRI. (2018). *ArcGIS 10.6*. Redlands, California.

European Space Agency (EESA). (2018). Sentinel Application Platform (SNAP) (Version 6.0). Retrieved from http://step.esa.int/main/download/snap-download/

Fagen, R. (1988). Population effects of habitat change: A quantitative assessment. *The Journal of Wildlife Management*, *52*(1), 41–46. https://doi.org/10.2307/3801055

Fischer, L. A., & Gates, C. C. (2005). Competition potential between sympatric woodland caribou and wood bison in southwestern Yukon, Canada. *Canadian Journal of Zoology*, *83*(9), 1162–1173. https://doi.org/10.1139/z05-117

Fistikoglu, O., & Harmancioglu, N. B. (2002). Integration of GIS with USLE in assessment of soil erosion. *Water Resources Management*, *16*(6), 447–467. https://doi.org/10.1023/A:1022282125760

Flores, D. (1991). Bison ecology and bison diplomacy: The southern plains from 1800 to 1850. *The Journal of American History*, *78*(2), 465–485.

Fortin, D., & Andruskiw, M. (2003). Behavioral Response of Free-Ranging Bison to Human Disturbance. *Wildlife Society Bulletin (1973-2006)*, *31*(3), 804–813. Retrieved from https://www.jstor.org/stable/3784603

Fortin, D., Fryxell, J. M., O’Brodovich, L., & Frandsen, D. (2003). Foraging ecology of bison at the landscape and plant community levels: The applicability of energy maximization principles. *Oecologia*, *134*(2), 219–227. https://doi.org/10.1007/s00442-002-1112-4

Foster, G. R., McCool, D. K., Renard, K. G., & Moldenhauer, W. C. (1981). Conversion of the universal soil loss equation to SI metric units. *Journal of Soil and Water Conservation*, *36*(6), 355–359.

Frank, D. A., & Groffman, P. M. (1998). Ungulate vs. Landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology*, *79*(7), 2229–2241. https://doi.org/10.1890/0012-9658(1998)079[2229:UVLCOS]2.0.CO;2

Frank, D. A., & McNaughton, S. J. (1992). The Ecology of Plants, Large Mammalian Herbivores, and Drought in Yellowstone National Park. *Ecology*, *73*(6), 2043–2058. https://doi.org/10.2307/1941454

Freeland, W. J., & Choquenot, D. (1990). Determinants of Herbivore Carrying Capacity: Plants, Nutrients, and Equus Asinus in Northern Australia. *Ecology*, *71*(2), 589–597. https://doi.org/10.2307/1940312

Freese, C. H., Aune, K. E., Boyd, D. P., Derr, J. N., Forrest, S. C., Cormack Gates, C., … Redford, K. H. (2007). Second chance for the plains bison. *Biological Conservation*, *136*(2), 175–184. https://doi.org/10.1016/j.biocon.2006.11.019

Friedl, M. A., Schimel, D. S., Michaelsen, J., Davis, F. W., & Walker, H. (1994). Estimating grassland biomass and leaf area index using ground and satellite data. *International Journal of Remote Sensing*, *15*(7), 1401–1420. https://doi.org/10.1080/01431169408954174

Friedl, Mark A., McIver, D. K., Hodges, J. C. F., Zhang, X. Y., Muchoney, D., Strahler, A. H., … Schaaf, C. (2002). Global land cover mapping from MODIS: Algorithms and early results. *Remote Sensing of Environment*, *83*(1–2), 287–302. https://doi.org/10.1016/S0034-4257(02)00078-0

Friedl, Mark A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., & Huang, X. (2010). MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets. *Remote Sensing of Environment*, *114*(1), 168–182. https://doi.org/10.1016/j.rse.2009.08.016

Fu, B. J., Zhao, W. W., Chen, L. D., Zhang, Q. J., Lü, Y. H., Gulinck, H., & Poesen, J. (2005). Assessment of soil erosion at large watershed scale using RUSLE and GIS: A case study in the Loess Plateau of China: ASSESSMENT OF SOIL EROSION USING RUSLE AND GIS. *Land Degradation & Development*, *16*(1), 73–85. https://doi.org/10.1002/ldr.646

Ganskopp, D., & Vavra, M. (1987). Slope use by cattle, feral horses, deer, and bighorn sheep. *Northwest Science*, *61*(2), 74–81.

Gao, B.-C. (1996). NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment*, *58*(3), 257–266. https://doi.org/10.1016/S0034-4257(96)00067-3

Gates, C. C., Freese, C. H., Gogan, P. J., & Kotzman, M. (2010). *American bison: Status survey and conservation guidelines 2010*. Grand, Switzerland: IUCN.

Ge, J., Meng, B., Liang, T., Feng, Q., Gao, J., Yang, S., … Xie, H. (2018). Modeling alpine grassland cover based on MODIS data and support vector machine regression in the headwater region of the Huanghe River, China. *Remote Sensing of Environment*, *218*, 162–173. https://doi.org/10.1016/j.rse.2018.09.019

Gitelson, A. A., Kaufman, Y. J., & Merzlyak, M. N. (1996). Use of a green channel in remote sensing of global vegetation from EOS-MODIS. *Remote Sensing of Environment*, *58*(3), 289–298.

Gjetvaj, B. (2012, November 22). Winter in Grasslands National Park. Retrieved from Branimir Gjetvaj photography website: http://branimirphoto.ca/blog/winter-in-grasslands-national-park/

Grasslands National Park. (2005, Spring). *Grasslands National Park of Canada*. Retrieved from http://parkscanadahistory.com/publications/fact-sheets/eng/grasslands.pdf

Grunow, J. O. (1980). Feed and habitat preferences among some large herbivores on African veld. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, *15*(1), 141–146. https://doi.org/10.1080/00725560.1980.9648901

Guo, X., Wilmshurst, J., McCanny, S., Fargey, P., & Richard, P. (2004). Measuring Spatial and Vertical Heterogeneity of Grasslands Using Remote Sensing Techniques. *JOURNAL OF ENVIRONMENTAL INFORMATICS*, *3*(1), 24–32. Retrieved from http://www.jeionline.org/index.php?journal=mys&page=article&op=view&path%5B%5D=200400024

Guthery, F. S. (1999). Energy-Based Carrying Capacity for Quails. *The Journal of Wildlife Management*, *63*(2), 664–674. https://doi.org/10.2307/3802656

Haboudane, D., Miller, J. R., Pattey, E., Zarco-Tejada, P. J., & Strachan, I. B. (2004). Hyperspectral vegetation indices and novel algorithms for predicting green LAI of crop canopies: Modeling and validation in the context of precision agriculture. *Remote Sensing of Environment*, *90*(3), 337–352.

Hall, D. (2012). *Remote sensing of ice and snow*. Boca Raton: Springer Science & Business Media.

Han, P., Wang, P. X., Zhang, S. Y., & Zhu, D. H. (2010). Drought forecasting based on the remote sensing data using ARIMA models. *Mathematical and Computer Modelling*, *51*(11), 1398–1403. https://doi.org/10.1016/j.mcm.2009.10.031

Handcock, R. N., Swain, D. L., Bishop-Hurley, G. J., Patison, K. P., Wark, T., Valencia, P., … O'Neill, C. J. (2009). Monitoring Animal Behaviour and Environmental Interactions Using Wireless Sensor Networks, GPS Collars and Satellite Remote Sensing. *Sensors*, *9*(5), 3586–3603. https://doi.org/10.3390/s90503586

Hanley, T. A., & Rogers, J. J. (1989). Estimating carrying capacity with simultaneous nutritional constraints. *Res. Note PNW-RN-485. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 31 p*, *485*. https://doi.org/10.2737/PNW-RN-485

Hardisky, M. A., Smart, R. M., & Klemas, V. (1983). Seasonal spectral characteristics and aboveground biomass of the tidal marsh plant. *Spartina Alterniflora, Photogram. Eng. Remote Sens.*, *49*, 85–92.

Hartnett, D. C., Hickman, K. R., & Walter, L. E. (1996). Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Rangeland Ecology & Management / Journal of Range Management Archives*, *49*(5), 413–420. Retrieved from https://journals.uair.arizona.edu/index.php/jrm/article/view/9143

He, Y. (2008). *Modeling grassland productivity through remote sensing products* (PhD Thesis, University of Saskatchewan). Retrieved from http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.974.3584&rep=rep1&type=pdf

He, Y., Guo, X., & Wilmshurst, J. (2006). Studying mixed grassland ecosystems I: Suitable hyperspectral vegetation indices. *Canadian Journal of Remote Sensing*, *32*(2), 98–107. https://doi.org/10.5589/m06-009

Hebblewhite, M., Merrill, E., & McDermid, G. (2008). A Multi-Scale Test of the Forage Maturation Hypothesis in a Partially Migratory Ungulate Population. *Ecological Monographs*, *78*(2), 141–166. https://doi.org/10.1890/06-1708.1

Hemami, M.-R., Esmaeili, S., Brito, J. C., Ahmadi, M., Omidi, M., & Martínez-Freiría, F. (2018). Using ecological models to explore niche partitioning within a guild of desert felids.

Hystrix, the Italian Journal of Mammalogy, *29*(2), 216–222. https://doi.org/10.4404/hystrix-00042-2017

Hendrickson, J. R., Sedivec, K. K., Toledo, D., & Printz, J. (2019). Challenges Facing Grasslands inthe Northern Great Plains and North Central Region. *Rangelands*, *41*(1), 23–29. https://doi.org/10.1016/j.rala.2018.11.002

Henwood, W. D. (1998). An overview of protected areas in the template grasslands biome. *Parks*, *8*(3), 60.

Hirzel, A. H., Helfer, V., & Metral, F. (2001). Assessing habitat-suitability models with a virtual species. *Ecological Modelling*, *145*(2), 111–121. https://doi.org/10.1016/S0304-3800(01)00396-9

Hirzel, Alexandre H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, *199*(2), 142–152.

Hobbs, N. Thompson, & Hanley, T. A. (1990). Habitat evaluation: Do use/availability data reflect carrying capacity? *The Journal of Wildlife Management*, 515–522. https://doi.org/10.2307/3809344

Hobbs, N. Thompson, & Swift, D. M. (1985). Estimates of Habitat Carrying Capacity Incorporating Explicit Nutritional Constraints. *The Journal of Wildlife Management*, *49*(3), 814–822. https://doi.org/10.2307/3801716

Hobbs, N.T., Baker, D. L., Ellis, J. E., Swift, D. M., & Green, R. A. (1982). Energy- and nitrogen-based estimates of elk winter-range carrying capacity. *Journal of Wildlife Management*, *46*(1), 12–21. Retrieved from https://digitalcommons.usu.edu/aspen_bib/4313

Holechek, J. L., Pieper, R. D., & Herbel, C. H. (1995). Range management: Principles and practices. *Range Management: Principles and Practices.*, (Ed. 2). Retrieved from https://www.cabdirect.org/cabdirect/abstract/19950713922

Holechek, Jerry L. (1988). An approach for setting the stocking rate. *Rangelands*, *10*(1), 10–14. Retrieved from https://www.jstor.org/stable/4000362

Holechek, Jerry L., & Galt, D. (2000). Grazing intensity guidelines. *Rangelands*, *22*(3), 11–14. Retrieved from https://www.jstor.org/stable/4001426

Holechek, Jerry L., Gomes, H. de S., Molinar, F., & Galt, D. (1998). Grazing Intensity: Critique and Approach. *Rangelands*, *20*(5), 15–18. Retrieved from https://www.jstor.org/stable/4001290

Hollstein, A., Segl, K., Guanter, L., Brell, M., & Enesco, M. (2016). Ready-to-use methods for the detection of clouds, cirrus, snow, shadow, water and clear sky pixels in Sentinel-2 MSI images. *Remote Sensing*, *8*(8), 666. https://doi.org/10.3390/rs8080666

Horn, B. E. (2005). *Livestock grazing distribution*. Rangeland management educator, University of Wyoming Cooperative Extension Service.

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, *83*(1), 195–213. https://doi.org/10.1016/S0034-4257(02)00096-2

Huete, A. R. (1988). A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment*, *25*(3), 295–309.

Hunt Jr, E. R., Everitt, J. H., Ritchie, J. C., Moran, M. S., Booth, D. T., Anderson, G. L., … Seyfried, M. S. (2003). Applications and research using remote sensing for rangeland management. *Photogrammetric Engineering & Remote Sensing*, *69*(6), 675–693. https://doi.org/10.14358/PERS.69.6.675

Hunt Jr, E. R., & Miyake, B. A. (2006). Comparison of stocking rates from remote sensing and geospatial data. *Rangeland Ecology & Management*, *59*(1), 11–18. https://doi.org/10.2111/04-177R.1

Ingvartsen, K. L. (1994). Models of voluntary food intake in cattle. *Livestock Production Science*, *39*(1), 19–38.

Jansen, V. S., Kolden, C. A., Taylor, R. V., & Newingham, B. A. (2016). Quantifying livestock effects on bunchgrass vegetation with Landsat ETM+ data across a single growing season. *International Journal of Remote Sensing*, *37*(1), 150–175. https://doi.org/10.1080/01431161.2015.1117681

Jędrzejewski, W., Jędrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S., & Mys\lajek, R. W. (2008). Habitat suitability model for Polish wolves based on long-term national census. *Animal Conservation*, *11*(5), 377–390. https://doi.org/10.1111/j.1469-1795.2008.00193.x

Jiang, Y., Tao, J., Huang, Y., Zhu, J., Tian, L., & Zhang, Y. (2015). The spatial pattern of grassland aboveground biomass on Xizang Plateau and its climatic controls. *Journal of Plant Ecology*, *8*(1), 30–40. https://doi.org/10.1093/jpe/rtu002

Jiang, Z., Huete, A. R., Didan, K., & Miura, T. (2008). Development of a two-band enhanced vegetation index without a blue band. *Remote Sensing of Environment*, *112*(10), 3833–3845.

Jin, Y., Yang, X., Qiu, J., Li, J., Gao, T., Wu, Q., … Xu, B. (2014). Remote Sensing-Based Biomass Estimation and Its Spatio-Temporal Variations in Temperate Grassland, Northern China. *Remote Sensing*, *6*(2), 1496–1513. https://doi.org/10.3390/rs6021496

Johnson, C. J., Nielsen, S. E., Merrill, E. H., McDONALD, T. L., & Boyce, M. S. (2006). Resource Selection Functions Based on Use-Availability Data: Theoretical Motivation and Evaluation Methods. *The Journal of Wildlife Management*, *70*(2), 347–357. https://doi.org/10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Jones, R. J., & Sandland, R. (1974). The relation between animal gain and stocking rate: Derivation of the relation from the results of grazing trials. *The Journal of Agricultural Science*, *83*(2), 335–342. https://doi.org/10.1017/S0021859600052035

Jordan, C. F. (1969). Derivation of leaf-area index from quality of light on the forest floor. *Ecology*, *50*(4), 663–666.

Justice, C. O., Vermote, E., Townshend, J. R., Defries, R., Roy, D. P., Hall, D. K., … Strahler, A. (1998). The Moderate Resolution Imaging Spectroradiometer (MODIS): Land remote sensing for global change research. *IEEE Transactions on Geoscience and Remote Sensing*, *36*(4), 1228–1249. https://doi.org/10.1109/36.701075

Kalaitzidis, C., Heinzel, V., & Zianis, D. (2010). *A review of multispectral vegetation indices for biomass estimation*. 201–208. Chania, Greece: IOS Press.

Kawamura, K., Akiyama, T., Yokota, H., Tsutsumi, M., Yasuda, T., Watanabe, O., & Wang, S. (2005). Comparing MODIS vegetation indices with AVHRR NDVI for monitoring the forage quantity and quality in Inner Mongolia grassland, China. *Grassland Science*, *51*(1), 33–40.

Khanif, Y. M. (2010). Improvement of soil carrying capacity for better living. *Journal of International Society for Southeast Asian Agricultural Sciences*, *16*(1), 1–7.

Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Towne, E. G. (1999). The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience*, *49*(1), 39–50.

Knight, E., & Kvaran, G. (2014). Landsat-8 operational land imager design, characterization and performance. *Remote Sensing*, *6*(11), 10286–10305. https://doi.org/10.3390/rs61110286

Kohl, M. T., Krausman, P. R., Kunkel, K., & Williams, D. M. (2013). Bison versus cattle: Are they ecologically synonymous? *Rangeland Ecology & Management*, *66*(6), 721–731. https://doi.org/10.2111/REM-D-12-00113.1

Koper, N., & Manseau, M. (2012). A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. *Rangifer, Special Issue*(20), 195–203.

Kouli, M., Soupios, P., & Vallianatos, F. (2009). Soil erosion prediction using the revised universal soil loss equation (RUSLE) in a GIS framework, Chania, Northwestern Crete, Greece. *Environmental Geology*, *57*(3), 483–497. https://doi.org/10.1007/s00254-008-1318-9

Krasińska, M., Krasiński, Z. A., & Bunevich, A. N. (2000). Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Bia\lowieża Forest. *Acta Theriologica*, *45*(3), 321–334.

Krueger, K. (1986). Feeding Relationships Among Bison, Pronghorn, and Prairie Dogs: An Experimental Analysis. *Ecology*, *67*(3), 760–770. https://doi.org/10.2307/1937699

Kumar, L., & Mutanga, O. (2017). Remote Sensing of Above-Ground Biomass. *Remote Sensing*, *9*(9), 935. https://doi.org/10.3390/rs9090935

Kuzyk, G. W. (2008). *Carrying capacity of sympatric ungulates in central Alberta* (Doctoral dissertation). University of Alberta.

Larson, D. M., Grudzinski, B. P., Dodds, W. K., Daniels, M. D., Skibbe, A., & Joern, A. (2013). Blazing and grazing: Influences of fire and bison on tallgrass prairie stream water quality. *Freshwater Science*, *32*(3), 779–791. https://doi.org/10.1899/12-118.1

Larter, N. C., & Gates, C. C. (1991). Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Canadian Journal of Zoology*, *69*(10), 2677–2685. https://doi.org/10.1139/z91-376

Launchbaugh, K. (2014). *Forage production and carrying capacity: Guidelines for setting a proper stocking rate*. University of Idaho.

Lauver, C. L., Busby, W. H., & Whister, J. L. (2002). Testing a GIS Model of Habitat Suitability for a Declining Grassland Bird. *Environmental Management*, *30*(1), 88–97. https://doi.org/10.1007/s00267-001-2609-z

Lemaître, J., & Villard, M.-A. (2005). Foraging patterns of pileated woodpeckers in a managed Acadian forest: A resource selection function. *Canadian Journal of Forest Research*, *35*(10), 2387–2393. https://doi.org/10.1139/x05-148

Leslie Jr, D. M., Bowyer, R. T., & Jenks, J. A. (2008). Facts from feces: Nitrogen still measures up as a nutritional index for mammalian herbivores. *The Journal of Wildlife Management*, *72*(6), 1420–1433. https://doi.org/10.2193/2007-404

Li, M., & Guo, X. (2014). Long Term Effect of Major Disturbances on the Northern Mixed Grassland Ecosystem—A Review. *Open Journal of Ecology*, *4*(4), 214–233. https://doi.org/10.4236/oje.2014.44021

Li, Z., & Guo, X. (2018). Non-photosynthetic vegetation biomass estimation in semiarid Canadian mixed grasslands using ground hyperspectral data, Landsat 8 OLI, and Sentinel-2 images. *International Journal of Remote Sensing*, *39*(20), 6893–6913. https://doi.org/10.1080/01431161.2018.1468105

Loarie, S. R., van Aarde, R. J., & Pimm, S. L. (2009). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, *142*(12), 3099–3107. https://doi.org/10.1016/j.biocon.2009.08.021

Long, Y. U., Li, Z., Wei, L. I. U., & Hua-Kun, Z. (2010). Using remote sensing and GIS technologies to estimate grass yield and livestock carrying capacity of alpine grasslands in Golog Prefecture, China. *Pedosphere*, *20*(3), 342–351.

Lu, D., Li, G., Valladares, G. S., & Batistella, M. (2004). Mapping soil erosion risk in Rondônia, Brazilian Amazonia: Using RUSLE, remote sensing and GIS. *Land Degradation & Development*, *15*(5), 499–512. https://doi.org/10.1002/ldr.634

Lu, Dengsheng. (2006). The potential and challenge of remote sensing-based biomass estimation. *International Journal of Remote Sensing*, *27*(7), 1297–1328. https://doi.org/10.1080/01431160500486732

Luo, T., Li, W., & Zhu, H. (2002). Estimated Biomass and Productivity of Natural Vegetation on the Tibetan Plateau. *Ecological Applications*, *12*(4), 980–997. https://doi.org/10.1890/1051-0761(2002)012[0980:EBAPON]2.0.CO;2

Lyons, R. K., & Machen, R. V. (2002, January 4). *Livestock Grazing Distribution: Considerations and Management*. Retrieved from http://hdl.handle.net/1969.1/87089

Maclin, E. (2018, April 23). Carrying capacity in a ecosystem. *Sciencing*. Retrieved from https://sciencing.com/carrying-capacity-ecosystem-5201.html

Manel, S., Williams, H. C., & Ormerod, S. J. (2001). Evaluating presence–absence models in ecology: The need to account for prevalence. *Journal of Applied Ecology*, *38*(5), 921–931. https://doi.org/10.1046/j.1365-2664.2001.00647.x

Manly, B. F., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. United States of America: Springer Science & Business Media.

Marabel, M., & Alvarez-Taboada, F. (2013). Spectroscopic Determination of Aboveground Biomass in Grasslands Using Spectral Transformations, Support Vector Machine and Partial Least Squares Regression. *Sensors*, *13*(8), 10027–10051. https://doi.org/10.3390/s130810027

Markewicz, L. (2018). *Like Distant Thunder: Canada's Bison Conservation Story - Elk Island National Park*. Retrieved from https://www.pc.gc.ca/en/pn-np/ab/elkisland/nature/eep-sar/bison

Marsett, R. C., Qi, J., Heilman, P., Biedenbender, S. H., Carolyn Watson, M., Amer, S., … Marsett, R. (2006). Remote Sensing for Grassland Management in the Arid Southwest. *Rangeland Ecology & Management*, *59*(5), 530–540. https://doi.org/10.2111/05-201R.1

Mazerolle, M. J., & Linden, D. (2019). AICcmodavg (Version 2.2-2). Retrieved from https://cran.r-project.org/package=AICcmodavg

McCall, T. C., Brown, R. D., & Bender, L. C. (1997). Comparison of Techniques for Determining the Nutritional Carrying Capacity for White-Tailed Deer. *Journal of Range Management*, *50*(1), 33–38. https://doi.org/10.2307/4002702

McLeod, S. R. (1997). Is the concept of carrying capacity useful in variable environments? *Oikos*, 529–542.

McLoughlin, P. D., Morris, D. W., Fortin, D., Wal, E. V., & Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, *79*(1), 4–12. https://doi.org/10.1111/j.1365-2656.2009.01613.x

McMillan, N. A., Kunkel, K. E., Hagan, D. L., & Jachowski, D. S. (2019). Plant community responses to bison reintroduction on the Northern Great Plains, United States: A test of the keystone species concept. *Restoration Ecology*, *27*(2), 379–388. https://doi.org/10.1111/rec.12856

McNairn, H., & Protz, R. (1993). Mapping corn residue cover on agricultural fields in Oxford County, Ontario, using Thematic Mapper. *Canadian Journal of Remote Sensing*, *19*(2), 152–159. https://doi.org/10.1080/07038992.1993.10874543

Meagher, M. (1989). Evaluation of Boundary Control for Bison of Yellowstone National Park. *Wildlife Society Bulletin (1973-2006)*, *17*(1), 15–19. Retrieved from https://www.jstor.org/stable/3782030

Meehan, M., Sedivec, K. K., Printz, J., & Brummer, F. (2018). *Determining carrying capacity and stocking rates for range and pasture in North Dakota*. Retrieved from www.ag.ndsu.edu

Menke, J. W. (1992). GRAZING AND FIRE MANAGEMENT FOR NATIVE PERENNIAL GRASS RESTORATION IN CALIFORNIA GRASSLANDS. *Journal of the California Native Plant Society*, *20*(2), 22–25.

Mentis, M. T. (1977). Stocking rates and carrying capacities for ungulates on African rangelands. *South African Journal of Wildlife Research-24-Month Delayed Open Access*, *7*(2), 89–96.

Merzlyak, M. N., Gitelson, A. A., Chivkunova, O. B., & Rakitin, V. Y. (1999). Non-destructive optical detection of pigment changes during leaf senescence and fruit ripening. *Physiologia Plantarum*, *106*(1), 135–141. https://doi.org/10.1034/j.1399-3054.1999.106119.x

Meusburger, K., Konz, N., Schaub, M., & Alewell, C. (2010). Soil erosion modelled with USLE and PESERA using QuickBird derived vegetation parameters in an alpine catchment. *International Journal of Applied Earth Observation and Geoinformation*, *12*(3), 208–215. https://doi.org/10.1016/j.jag.2010.02.004

Michalsky, S. J., & Ellis, J. E. (1994). *Vegetation of Grasslands National Park*. Calgary, Alberta: D.A. Westworth & Associates, Ltd.

Millspaugh, J. J., Nielson, R. M., McDONALD, L., Marzluff, J. M., Gitzen, R. A., Rittenhouse, C. D., … Sheriff, S. L. (2006). Analysis of Resource Selection Using Utilization Distributions. *The Journal of Wildlife Management*, *70*(2), 384–395. https://doi.org/10.2193/0022-541X(2006)70[384:AORSUU]2.0.CO;2

Mishra, A. K., & Singh, V. P. (2011). Drought modeling – A review. *Journal of Hydrology*, *403*(1), 157–175. https://doi.org/10.1016/j.jhydrol.2011.03.049

Monte-Luna, P. D., Brook, B. W., Zetina-Rejón, M. J., & Cruz-Escalona, V. H. (2004). The carrying capacity of ecosystems. *Global Ecology and Biogeography*, *13*(6), 485–495. https://doi.org/10.1111/j.1466-822X.2004.00131.x

Morris, L. R., Proffitt, K. M., & Blackburn, J. K. (2016). Mapping resource selection functions in wildlife studies: Concerns and recommendations. *Applied Geography*, *76*, 173–183. https://doi.org/10.1016/j.apgeog.2016.09.025

Mott, G. O. (1960). Grazing pressure and the measurement of pasture production. *Grazing Pressure and the Measurement of Pasture Production.*, 606–611. United Kingdom.

Mueggler, W. F. (1965). Cattle Distribution on Steep Slopes. *Journal of Range Management*, *18*(5), 255–257. https://doi.org/10.2307/3895492

Nippert, J. B., Fay, P. A., & Knapp, A. K. (2007). Photosynthetic traits in C3 and C4 grassland species in mesocosm and field environments. *Environmental and Experimental Botany*, *60*(3), 412–420. https://doi.org/10.1016/j.envexpbot.2006.12.012

Norton, B. E. (1986). Guidelines for determining stocking rates for saline shrubland. *Reclamation and Revegetation Research (Netherlands)*, *5*, 403–422.

Numata, I., Roberts, D. A., Chadwick, O. A., Schimel, J. P., Galvão, L. S., & Soares, J. V. (2008). Evaluation of hyperspectral data for pasture estimate in the Brazilian Amazon using field and imaging spectrometers. *Remote Sensing of Environment*, *112*(4), 1569–1583. https://doi.org/10.1016/j.rse.2007.08.014

Oesterheld, M., DiBella, C. M., & Kerdiles, H. (1998). Relation between NOAA-AVHRR satellite data and stocking rate of rangelands. *Ecological Applications*, *8*(1), 207–212. https://doi.org/0.1890/1051-0761(1998)008[0207:RBNASD]2.0.CO;2.

Oswald, J., & Harris, S. (2016). Desertification. In *Biological and Environmental Hazards, Risks and Disasters* (pp. 229–256). Netherlands, UK, and USA: Elsevier.

Otgonbayar, M., Atzberger, C., Chambers, J., & Damdinsuren, A. (2019). Mapping pasture biomass in Mongolia using Partial Least Squares, Random Forest regression and Landsat 8 imagery. *International Journal of Remote Sensing*, *40*(8), 3204–3226. https://doi.org/10.1080/01431161.2018.1541110

Parks Canada. (n.d). *Black-Tailed Prairie Dog Cynomys ludovicianus*. Retrieved from https://www.earthrangers.com/content/wildwire/22-PC-Black-tail-prairie-dog-EN-revised.pdf

Parks Canada. (2005). *Plains bison (Bison bison bison) reintroduction plan for Grasslands National Park*.

Parks Canada. (2012). *Grasslands National Park of Canada Visitor Guide*. Retrieved from http://parkscanadahistory.com/brochures/grasslands/booklet-e-2012.pdf

Parks Canada. (2014, April 1). Grasslands National Park. Retrieved from https://www.pc.gc.ca/en/pn-np/sk/grasslands/visit/visit3

Parks Canada. (2017). *Plains Bison Management Plan*.

Parks Canada Agency. (2016). *Multil-species action plan for Grasslands National Park*. Parks Canada Agency.

Parks Canada Agency, G. of C. (2017a, February 8). Weather—Grasslands National Park. Retrieved July 2, 2019, from https://www.pc.gc.ca/en/pn-np/sk/grasslands/visit/visit3

Parks Canada Agency, G. of C. (2017b, July 18). Ecological Integrity—Science and conservation. Retrieved August 16, 2019, from https://www.pc.gc.ca/en/nature/science/conservation/ie-ei

Parks Canada Agency, G. of C. (2018, March 23). Park history—Grasslands National Park. Retrieved September 20, 2019, from https://www.pc.gc.ca/en/pn-np/sk/grasslands/culture/histoire_du_parc-park_history

Paruelo, J. M., & Lauenroth, W. K. (1996). Relative Abundance of Plant Functional Types in Grasslands and Shrublands of North America. *Ecological Applications*, *6*(4), 1212–1224. https://doi.org/10.2307/2269602

Paton, D., Nuñez-Trujillo, J., Díaz, M. A., & Muñoz, A. (1999). Assessment of browsing biomass, nutritive value and carrying capacity of shrublands for red deer (Cervus elaphus L.) management in Monfragüe Natural Park (SW Spain). *Journal of Arid Environments*, *42*(2), 137–147. https://doi.org/10.1006/jare.1999.0501

Pearce, J. L., & Boyce, M. S. (2006). Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, *43*(3), 405–412. https://doi.org/10.1111/j.1365-2664.2005.01112.x

Peden, D. G. (1976). Botanical composition of bison diets on shortgrass plains. *American Midland Naturalist*, 225–229.

Peden, D. G., Van Dyne, G. M., Rice, R. W., & Hansen, R. M. (1974). The trophic ecology of Bison bison L. on shortgrass plains. *Journal of Applied Ecology*, 489–497.

Piao, S., Fang, J., Zhou, L., Tan, K., & Tao, S. (2007). Changes in biomass carbon stocks in China's grasslands between 1982 and 1999. *Global Biogeochemical Cycles*, *21*(2), 10. https://doi.org/10.1029/2005GB002634

Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., … Blair, R. (1995). Environmental and Economic Costs of Soil Erosion and Conservation Benefits. *Science*, *267*(5201), 1117–1123. https://doi.org/10.1126/science.267.5201.1117

Pradhan, B., Chaudhari, A., Adinarayana, J., & Buchroithner, M. F. (2012). Soil erosion assessment and its correlation with landslide events using remote sensing data and GIS: A case study at Penang Island, Malaysia. *Environmental Monitoring and Assessment*, *184*(2), 715–727. https://doi.org/10.1007/s10661-011-1996-8

Prince, S. D. (1991). Satellite remote sensing of primary production: Comparison of results for Sahelian grasslands 1981-1988. *International Journal of Remote Sensing*, *12*(6), 1301–1311. https://doi.org/10.1080/01431169108929727

Pringle, H. J. R., & Landsberg, J. (2004). Predicting the distribution of livestock grazing pressure in rangelands. *Austral Ecology*, *29*(1), 31–39. https://doi.org/10.1111/j.1442-9993.2004.01363.x

Psomas, A., Kneubühler, M., Huber, S., Itten, K., & Zimmermann, N. E. (2011). Hyperspectral remote sensing for estimating aboveground biomass and for exploring species richness patterns of grassland habitats. *International Journal of Remote Sensing*, *32*(24), 9007–9031. https://doi.org/10.1080/01431161.2010.532172

Qi, J., Chehbouni, A., Huete, A. R., Kerr, Y. H., & Sorooshian, S. (1994a). A modified soil adjusted vegetation index. *Remote Sensing of Environment*, *48*(2), 119–126. https://doi.org/10.1016/0034-4257(94)90134-1

Qi, J., Chehbouni, A., Huete, A. R., Kerr, Y. H., & Sorooshian, S. (1994b). A modified soil adjusted vegetation index. *Remote Sensing of Environment*, *48*(2), 119–126.

Raes, N., & Steege, H. ter. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography*, *30*(5), 727–736. https://doi.org/10.1111/j.2007.0906-7590.05041.x

Redfearn, D. D., & Bidwell, T. G. (2003). *Stocking rate: The key to successful livestock production*. Oklahoma Cooperative Extension Service.

Reeves, M. C., Winslow, J. C., & Running, S. W. (2001). Mapping weekly rangeland vegetation productivity using MODIS algorithms. *Journal of Range Management*, *54*, A90.

Reid, C., Slotow, R., Howison, O., & Balfour, D. (2007). Habitat changes reduce the carrying capacity of Hluhluwe-Umfolozi Park, South Africa, for critically endangered black rhinoceros Diceros bicornis. *Oryx*, *41*(2), 247–254. https://doi.org/10.1017/S0030605307001780

Ren, H., & Zhou, G. (2012). Estimating senesced biomass of desert steppe in Inner Mongolia using field spectrometric data. *Agricultural and Forest Meteorology*, *161*, 66–71. https://doi.org/10.1016/j.agrformet.2012.03.010

Ren, H., & Zhou, G. (2014a). Determination of green aboveground biomass in desert steppe using litter-soil-adjusted vegetation index. *European Journal of Remote Sensing*, *47*(1), 611–625. https://doi.org/10.5721/EuJRS20144734

Ren, H., & Zhou, G. (2014b). Estimating aboveground green biomass in desert steppe using band depth indices. *Biosystems Engineering*, *127*, 67–78. https://doi.org/10.1016/j.biosystemseng.2014.08.014

Renard, K. G., Foster, G. R., Weesies, G. A., McCool, D. K., & Yoder, D. C. (1997). *Predicting soil erosion by water: A guide to conservation planning with the Revised Universal Soil Loss Equation (RUSLE)* (Vol. 703). United States Department of Agriculture Washington, DC.

Renschler, C. S., & Harbor, J. (2002). Soil erosion assessment tools from point to regional scales—The role of geomorphologists in land management research and implementation. *Geomorphology*, *47*(2), 189–209. https://doi.org/10.1016/S0169-555X(02)00082-X

Richardson, A. J., & Everitt, J. H. (1992). Using spectral vegetation indices to estimate rangeland productivity. *Geocarto International*, *7*(1), 63–69. https://doi.org/10.1080/10106049209354353

Richardson, A. J., & Wiegand, C. L. (1977). Distinguishing vegetation from soil background information. *Photogrammetric Engineering and Remote Sensing*, *43*(12), 1541–1552.

Roath, L. R., & Krueger, W. C. (1982). Cattle Grazing and Behavior on a Forested Range. *Journal of Range Management*, *35*(3), 332–338. https://doi.org/10.2307/3898312

Rodgers, A. R., Carr, A. P., Beyer, H. L., Smith, L., & Kie, J. G. (2007). *HRT: Home range tools for ArcGIS*. Version.

Rondeaux, G., Steven, M., & Baret, F. (1996). Optimization of soil-adjusted vegetation indices. *Remote Sensing of Environment*, *55*(2), 95–107. https://doi.org/10.1016/0034-4257(95)00186-7

Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., … Boitani, L. (2011). Global habitat suitability models of terrestrial mammals | Philosophical Transactions of the Royal Society B: Biological Sciences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2633–2641. https://doi.org/10.1098/rstb.2011.0113

Rondinini, C., Stuart, S., & Boitani, L. (2005). Habitat Suitability Models and the Shortfall in Conservation Planning for African Vertebrates. *Conservation Biology*, *19*(5), 1488–1497. https://doi.org/10.1111/j.1523-1739.2005.00204.x

Roujean, J.-L., & Breon, F.-M. (1995). Estimating PAR absorbed by vegetation from bidirectional reflectance measurements. *Remote Sensing of Environment*, *51*(3), 375–384. https://doi.org/10.1016/0034-4257(94)00114-3

Rouse, J. W., Haas, R. H., Schelle, J. A., & Deering, D. W. (1974, January 1). *Monitoring vegetation systems in the Great Plains with ERTS*. *1*, 309–317. Retrieved from https://ntrs.nasa.gov/search.jsp?R=19740022614

Rouse, J. W., Haas, R. H., Schelle, J. A., Deering, D. W., & Harlan, J. C. (1974). *Monitoring the vernal advancement or retrogradation of natural vegetation* (No. E73-10302, NASA-CR-130385, PR-1). Greenbelt, MD, USA: NASA/GSFC.

Royle, J. A., & Nichols, J. D. (2003). Estimating Abundance from Repeated Presence–Absence Data or Point Counts. *Ecology*, *84*(3), 777–790. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

RStudio Team. (2018). RStudio. Retrieved August 7, 2019, from RStudio website: https://www.rstudio.com/

Samson, F. B., Knopf, F. L., & Ostlie, W. R. (2004). Great Plains ecosystems: Past, present, and future. *Wildlife Society Bulletin*, *32*(1), 6–15. https://doi.org/10.2193/0091-7648(2004)32[6:GPEPPA]2.0.CO;2

Sanderson, E. W., Redford, K. H., Weber, B., Aune, K., Baldes, D., Berger, J., … Dobrott, S. (2008). The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conservation Biology*, *22*(2), 252–266. https://doi.org/10.1111/j.1523-1739.2008.00899

Sandland, R. L., & Jones, R. J. (1975). The relation between animal gain and stocking rate in grazing trials: An examination of published theoretical models. *The Journal of Agricultural Science*, *85*(1), 123–128. https://doi.org/10.1017/S002185960005348X

Santos, X., Brito, J. C., Sillero, N., Pleguezuelos, J. M., Llorente, G. A., Fahd, S., & Parellada, X. (2006). Inferring habitat-suitability areas with ecological modelling techniques and GIS: A contribution to assess the conservation status of Vipera latastei. *Biological Conservation*, *130*(3), 416–425. https://doi.org/10.1016/j.biocon.2006.01.003

Scaramuzza, P., & Barsi, J. (2005). Landsat 7 scan line corrector-off gap-filled product development. *Proceeding of Pecora*, *16*, 23–27. Sioux Falls, South Dakota.

Scarnecchia, D. L. (1990). Concepts of carrying capacity and susbstitution ratios: A systems viewpoint. *Rangeland Ecology & Management/Journal of Range Management Archives*, *43*(6), 553–555.

Schmidt, K. S., & Skidmore, A. K. (2001). Exploring spectral discrimination of grass species in African rangelands. *International Journal of Remote Sensing*, *22*(17), 3421–3434. https://doi.org/10.1080/01431160152609245

Schönbach, P., Wan, H., Schiborra, A., Gierus, M., Bai, Y., Müller, K., … Taube, F. (2009). Short-term management and stocking rate effects of grazing sheep on herbage quality and productivity of Inner Mongolia steppe. *Crop and Pasture Science*, *60*(10), 963–974. https://doi.org/0.1071/CP09048

Schuler, K. L., Schroeder, G. M., Jenks, J. A., & Kie, J. G. (2014). Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges. *Wildlife Biology*, *20*(5), 259–266. https://doi.org/10.2981/wlb.12117

Scurlock, J. M., Johnson, K., & Olson, R. J. (2002). Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology*, *8*(8), 736–753. https://doi.org/10.1046/j.1365-2486.2002.00512.x

Shaw, J. H., & Meagher, M. (2000). Bison. In *Ecology and management of large mammals in North America* (Demarais, S., and Krausman, P. R., pp. 447–466). Upper Saddle River, N. J : Prentice Hall: Pearson Education.

Shoko, C., Mutanga, O., & Dube, T. (2016). Progress in the remote sensing of C3 and C4 grass species aboveground biomass over time and space. *ISPRS Journal of Photogrammetry and Remote Sensing*, *120*, 13–24. https://doi.org/10.1016/j.isprsjprs.2016.08.001

Silleos, N. G., Alexandridis, T. K., Gitas, I. Z., & Perakis, K. (2006). Vegetation Indices: Advances Made in Biomass Estimation and Vegetation Monitoring in the Last 30 Years. *Geocarto International*, *21*(4), 21–28. https://doi.org/10.1080/10106040608542399

Sliwinski, M. (2011). *Changes in grassland songbird abundance and diversity in response to grazing by bison and cattle in the northern mixed-grass prairie*.

Smith, A. D. (1965). Determining common use grazing capacities by application of the key species concept. *Journal of Range Management*, *14*(4), 196–201. https://doi.org/10.2307/3895597

Starks, P. J., Coleman, S. W., & Phillips, W. A. (2004). Determination of Forage Chemical Composition Using Remote Sensing. *Rangeland Ecology and Management*, *57*(6), 635–640. https://doi.org/10.2111/1551-5028(2004)057[0635:DOFCCU]2.0.CO;2

Steenweg, R., Hebblewhite, M., Gummer, D., Low, B., & Hunt, B. (2016). Assessing Potential Habitat and Carrying Capacity for Reintroduction of Plains Bison (Bison bison bison) in Banff National Park. *PLOS ONE*, *11*(2), e0150065. https://doi.org/10.1371/journal.pone.0150065

Stephenson, T. R., Van Ballenberghe, V., Peek, J. M., & MacCracken, J. G. (2006). Spatio-temporal constraints on moose habitat and carrying capacity in coastal Alaska: Vegetation succession and climate. *Rangeland Ecology & Management*, *59*(4), 359–372. https://doi.org/10.2111/04-063.1

Still, C. J., Berry, J. A., Collatz, G. J., & DeFries, R. S. (2003). Global distribution of C $_3$ and C $_4$ vegetation: Carbon cycle implications: C $_4$ Plants and carbon cycle. *Global Biogeochemical Cycles*, *17*(1), 6-1-6–14. https://doi.org/10.1029/2001GB001807

Store, R., & Jokimäki, J. (2003). A GIS-based multi-scale approach to habitat suitability modeling. *Ecological Modelling*, *169*(1), 1–15. https://doi.org/10.1016/S0304-3800(03)00203-5

Store, R., & Kangas, J. (2001). Integrating spatial multi-criteria evaluation and expert knowledge for GIS-based habitat suitability modelling. *Landscape and Urban Planning*, *55*(2), 79–93. https://doi.org/10.1016/S0169-2046(01)00120-7

Stumpp, M., Wesche, K., Retzer, V., & Miehe, G. (2005). Impact of Grazing Livestock and Distance from Water Source on Soil Fertility in Southern Mongolia. *Mountain Research and Development*, *25*(3), 244–251. https://doi.org/10.1659/0276-4741(2005)025[0244:IOGLAD]2.0.CO;2

Svejcar, T., & Vavra, M. (1985). The Influence of Several Range Improvements on Estimated Carrying Capacity and Potential Beef Production. *Journal of Range Management*, *38*(5), 395–399. https://doi.org/10.2307/3899706

Taylor Jr., C. A. (2006). Targeted grazing to manage fire risk. In *Targeted grazing: A natural approach to vegetation management and landscape enhancement* (pp. 107–112). United States of America: National Sheep Industry Improvement Center (NSIIC) and American Sheep Industry Association (ASI).

Taylor, R. D., & Walker, B. H. (1978). Comparisons of Vegetation Use and Herbivore Biomass on a Rhodesian Game and Cattle Ranch. *Journal of Applied Ecology*, *15*(2), 565–581. https://doi.org/10.2307/2402611

Tian, Y., Zhu, Y., & Cao, W. (2005). Monitoring soluble sugar, total nitrogen & its ratio in wheat leaves with canopy spectral reflectance. *Zuo Wu Xue Bao*, *31*(3), 355–360.

Todd, S. W., Hoffer, R. M., & Milchunas, D. G. (1998). Biomass estimation on grazed and ungrazed rangelands using spectral indices. *International Journal of Remote Sensing*, *19*(3), 427–438.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2163–2176. https://doi.org/10.1098/rstb.2010.0090

Trombulak, S. C., & Frissell, C. A. (2000). Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities. *Conservation Biology*, *14*(1), 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

Truett, J., Phillips, M., Kunkel, K., & Miller, R. (2001). Managing Bison to Restore Biodiversity. *Great Plains Research: A Journal of Natural and Social Sciences*, *11*(1), 123–144. Retrieved from https://digitalcommons.unl.edu/greatplainsresearch/541

Turner, L. W., Udal, M. C., Larson, B. T., & Shearer, S. A. (2000). Monitoring cattle behavior and pasture use with GPS and GIS. *Canadian Journal of Animal Science*, *80*(3), 405–413. https://doi.org/10.4141/A99-093

US Fish and Wildlife Service. (2014). Timeline of the American Bison. Retrieved June 18, 2019, from National Bison Range Wildlife Refuge Complex: Mountain-Prairie Region website: https://www.fws.gov/bisonrange/timeline.htm

U.S. Geological Survey. (2015). USGS Earth Resources Observation and Science (EROS) Center. Retrieved August 8, 2019, from https://earthexplorer.usgs.gov/

U.S. Geological Survey. (2018). National Land Cover Database. Retrieved August 7, 2019, from https://earthexplorer.usgs.gov/

Valipour, M. S. (2012). *Number of Required Observation Data for Rainfall Forecasting According to the Climate Conditions*.

Vallentine, J. F. (2000). *Grazing Management*. United States of America: Academic Press.

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, *143*(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005

Verhulst, P. F. (1845). La loi d'accroissement de la population. *Nouv. Mem. Acad. Roy. Soc. Belle-Lettr. Bruxelles*, *18*(1).

Vescovo, L., & Gianelle, D. (2008). Using the MIR bands in vegetation indices for the estimation of grassland biophysical parameters from satellite remote sensing in the Alps region of Trentino (Italy). *Advances in Space Research*, *41*(11), 1764–1772. https://doi.org/10.1016/j.asr.2007.07.043

Vrieling, A. (2006). Satellite remote sensing for water erosion assessment: A review. *Catena*, *65*(1), 2–18.

Vuren, D. H. V. (2001). Spatial relations of American bison Bison bison and domestic cattle in a montane environment. *Animal Biodiversity and Conservation*, *24*(1), 117-124–124. https://doi.org/57579

Walter, W. D., Fischer, J. W., Baruch-Mordo, S., & VerCauteren, K. C. (2011). What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: The initial step. *Modern Telemetry*, 249–268.

Watkinson, A. R., & Ormerod, S. J. (2001). Grasslands, Grazing and Biodiversity: Editors' Introduction. *Journal of Applied Ecology*, *38*(2), 233–237. Retrieved from https://www.jstor.org/stable/2655793

Weisberg, P. J., Thompson Hobbs, N., Ellis, J. E., & Coughenour, M. B. (2002). An ecosystem approach to population management of ungulates. *Journal of Environmental Management*, *65*(2), 181–197. https://doi.org/10.1006/jema.2002.0543

Weltzin, J. F., Dowhower, S. L., & Heitschmidt, R. K. (1997). Prairie Dog Effects on Plant Community Structure in Southern Mixed-Grass Prairie. *The Southwestern Naturalist*, *42*(3), 251–258. Retrieved from https://www.jstor.org/stable/30055275

White, R., Murray, S., & Rohweder, M. (2000). *Pilot Analysis of Global Ecosystems Grassland Ecosystems Grassland Ecosystems*. Washington, DC, United States of America: World Resources Institute.

Woodhouse, C. A., Lukas, J. J., & Brown, P. M. (2002). Drought in the Western Great Plains, 1845–56. *Bulletin of the American Meteorological Society*, *83*(10), 1485–1494. https://doi.org/10.1175/BAMS-83-10-1485

World Wildlife Fund. (2013, June 5). Saving the Grasslands of the Northern Great Plains. Retrieved June 15, 2019, from World Wildlife Fund website: https://www.worldwildlife.org/stories/saving-the-grasslands-of-the-northern-great-plains

World Wildlife Fund. (2018). Understanding grassland loss in the Northern Great Plains. Retrieved June 15, 2019, from World Wildlife Fund website: https://www.worldwildlife.org/magazine/issues/winter-2018/articles/understanding-grassland-loss-in-the-northern-great-plains

World Wildlife Fund. (n.d.). Plains Bison | Species | WWF. Retrieved June 12, 2019, from World Wildlife Fund website: https://www.worldwildlife.org/species/plains-bison

Xia, J., Liu, S., Liang, S., Chen, Y., Xu, W., & Yuan, W. (2014). Spatio-temporal patterns and climate variables controlling of biomass carbon stock of global grassland ecosystems from 1982 to 2006. *Remote Sensing*, *6*(3), 1783–1802. https://doi.org/10.3390/rs6031783

Xie, Y., Sha, Z., Yu, M., Bai, Y., & Zhang, L. (2009). A comparison of two models with Landsat data for estimating above ground grassland biomass in Inner Mongolia, China. *Ecological Modelling*, *220*(15), 1810–1818. https://doi.org/10.1016/j.ecolmodel.2009.04.025

Xu, D., & Guo, X. (2015). Some Insights on Grassland Health Assessment Based on Remote Sensing. *Sensors*, *15*(2), 3070–3089. https://doi.org/10.3390/s150203070

Xu, D., Guo, X., Li, Z., Yang, X., & Yin, H. (2014). Measuring the dead component of mixed grassland with Landsat imagery. *Remote Sensing of Environment*, *142*, 33–43. https://doi.org/10.1016/j.rse.2013.11.017

Yang, F., Li, J., Gan, X., Qian, Y., Wu, X., & Yang, Q. (2010). Assessing nutritional status of Festuca arundinacea by monitoring photosynthetic pigments from hyperspectral data. *Computers and Electronics in Agriculture*, *70*(1), 52–59. https://doi.org/10.1016/j.compag.2009.08.010

Yang, Y. H., Fang, J. Y., Pan, Y. D., & Ji, C. J. (2009). Aboveground biomass in Tibetan grasslands. *Journal of Arid Environments*, *73*(1), 91–95.

Yu, L., Zhou, L., Liu, W., & Zhou, H.-K. (2010). Using Remote Sensing and GIS Technologies to Estimate Grass Yield and Livestock Carrying Capacity of Alpine Grasslands in Golog Prefecture, China. *Pedosphere*, *20*(3), 342–351. https://doi.org/10.1016/S1002-0160(10)60023-9

Zhang, B., Zhang, L., Xie, D., Yin, X., Liu, C., & Liu, G. (2016). Application of synthetic NDVI time series blended from Landsat and MODIS data for grassland biomass estimation. *Remote Sensing*, *8*(1), 10. https://doi.org/10.3390/rs8010010

Zhang, C., & Guo, X. (2008). Monitoring northern mixed prairie health using broadband satellite imagery. *International Journal of Remote Sensing*, *29*(8), 2257–2271. https://doi.org/10.1080/01431160701408378

Zhang, C., Guo, X., Wilmshurst, J., & Sissons, R. (2005). The evaluation of broadband vegetation indices on monitoring northern mixed grassland. *Prairie Perspectives*, *8*, 23–36.

Zhang, H., Sun, Y., Chang, L., Qin, Y., Chen, J., Qin, Y., … Wang, Y. (2018). Estimation of grassland canopy height and aboveground biomass at the quadrat scale using unmanned aerial vehicle. *Remote Sensing*, *10*(6), 851. https://doi.org/10.3390/rs10060851

Zhao, F., Xu, B., Yang, X., Jin, Y., Li, J., Xia, L., … Ma, H. (2014). Remote sensing estimates of grassland aboveground biomass based on MODIS net primary productivity (NPP): A case study in the Xilingol grassland of Northern China. *Remote Sensing*, *6*(6), 5368–5386. https://doi.org/10.3390/rs6065368

Zhao, G., Mu, X., Wen, Z., Wang, F., & Gao, P. (2013). Soil Erosion, Conservation, and Eco-Environment Changes in the Loess Plateau of China. *Land Degradation & Development*, *24*(5), 499–510. https://doi.org/10.1002/ldr.2246

Appendices

Appendix A Sample Field Form

SAMPLING RECORD IN GNP, 2018 GROWING SEASON

Site Name:	Date of collection:
Dominant species:	

Quad	# bags[i]	∑Fresh weight (g)	Dry weight (g)							Note
			Green grass	Shrub	Forb	Lichen	Moss	Dead	Others	
N2										
N4										
E2										
E4										
S2										
S4										
W2										
W4										

i: Detail number of paper bags for each quadrat

Appendix B R Studio Code for building RSFs

Code of the script:

```
############################################################################

library(sp)

## Warning: package 'sp' was built under R version 3.5.3

library(lattice)

## Warning: package 'lattice' was built under R version 3.5.3

library(rgdal) # readOGR

## Warning: package 'rgdal' was built under R version 3.5.3

## rgdal: version: 1.4-3, (SVN revision 828)
##  Geospatial Data Abstraction Library extensions to R successfully loaded
##  Loaded GDAL runtime: GDAL 2.2.3, released 2017/11/20
##  Path to GDAL shared files: \\cabinet/work$/ttd745/My Documents/R/win-libr
ary/3.5/rgdal/gdal
##  GDAL binary built with GEOS: TRUE
##  Loaded PROJ.4 runtime: Rel. 4.9.3, 15 August 2016, [PJ_VERSION: 493]
##  Path to PROJ.4 shared files: \\cabinet/work$/ttd745/My Documents/R/win-li
brary/3.5/rgdal/proj
##  Linking to sp version: 1.3-1

library(rgeos) #gIntersection

## Warning: package 'rgeos' was built under R version 3.5.3

## rgeos version: 0.4-2, (SVN revision 581)
##  GEOS runtime version: 3.6.1-CAPI-1.10.1
##  Linking to sp version: 1.3-1
##  Polygon checking: TRUE

library(raster) # to use "raster" function

## Warning: package 'raster' was built under R version 3.5.3

library(adehabitatHR)

## Warning: package 'adehabitatHR' was built under R version 3.5.3

## Loading required package: deldir

## Warning: package 'deldir' was built under R version 3.5.3

## deldir 0.1-16

## Loading required package: ade4
```

```
## Warning: package 'ade4' was built under R version 3.5.3

## Loading required package: adehabitatMA

## Warning: package 'adehabitatMA' was built under R version 3.5.3

##
## Attaching package: 'adehabitatMA'

## The following object is masked from 'package:raster':
##
##     buffer

## Loading required package: adehabitatLT

## Warning: package 'adehabitatLT' was built under R version 3.5.3

## Loading required package: CircStats

## Warning: package 'CircStats' was built under R version 3.5.3

## Loading required package: MASS

## Warning: package 'MASS' was built under R version 3.5.3

##
## Attaching package: 'MASS'

## The following objects are masked from 'package:raster':
##
##     area, select

## Loading required package: boot

##
## Attaching package: 'boot'

## The following object is masked from 'package:lattice':
##
##     melanoma

library(maptools) #readAsciiGrid

## Warning: package 'maptools' was built under R version 3.5.3

## Checking rgeos availability: TRUE

summer.bison <- read.csv("E:/Master thesis/CompiledData(2019)/GISdatabase/Res
ourceSelectioFunction/SeasonalCollarData/SummerCollar2012_2018.csv", header =
T)
str(summer.bison)

## 'data.frame':    22072 obs. of  17 variables:
##  $ ID       : int  46509 46510 46511 46512 46513 46514 46515 46516 46517 4
```

```
6518 ...
##  $ No       : Factor w/ 1 level "#N/A": 1 1 1 1 1 1 1 1 1 1 ...
##  $ Collar_ID: int  32732 32733 33248 32732 32733 33248 32732 32733 33248 3
2732 ...
##  $ Date     : Factor w/ 664 levels "#N/A","1/5/2013",..: 2 2 2 2 2 2 2 2 2
2 ...
##  $ YYYY     : int  2013 2013 2013 2013 2013 2013 2013 2013 2013 2013 ...
##  $ MM       : int  5 5 5 5 5 5 5 5 5 5 ...
##  $ DD       : int  1 1 1 1 1 1 1 1 1 1 ...
##  $ Time     : Factor w/ 4454 levels "0.125173611",..: 868 861 886 1267 123
0 1224 1440 1451 1432 4337 ...
##  $ HH       : int  0 0 0 2 2 2 4 4 4 6 ...
##  $ LATITUDE : Factor w/ 120 levels "#N/A","49.102",..: 102 112 79 103 112
81 103 112 82 102 ...
##  $ LONGITUDE: Factor w/ 230 levels "-107.398","-107.399",..: 80 89 51 79 9
1 53 78 91 54 77 ...
##  $ Elevation: Factor w/ 10003 levels "-180.14","-484.70",..: 8054 5248 680
1 5845 2260 7427 6161 2206 8157 7820 ...
##  $ DOP      : num  0.6 2 0.6 3.4 3.2 1.8 2.2 1.8 0.6 5 ...
##  $ VALIDATED: Factor w/ 1 level "#N/A": 1 1 1 1 1 1 1 1 1 1 ...
##  $ TEMP     : int  6 8 12 4 7 7 4 3 0 0 ...
##  $ X        : Factor w/ 9126 levels "#N/A","301025",..: 4452 3977 6315 449
5 3849 6227 4536 3855 6159 4626 ...
##  $ Y        : Factor w/ 7670 levels "#N/A","5441799",..: 5923 7011 3409 60
43 7083 3646 6035 7026 3750 5953 ...

summer.bison$Collar_ID = as.factor(summer.bison$Collar_ID)
levels(summer.bison$Collar_ID)

## [1] "32732" "32733" "33248" "34204" "37551" "37552" "37553"

summer.bison$X = as.integer(as.character(summer.bison$X))

## Warning: NAs introduced by coercion

summer.bison$Y = as.integer(as.character(summer.bison$Y))

## Warning: NAs introduced by coercion

summer.bison$LATITUDE = as.integer(as.character(summer.bison$LATITUDE))

## Warning: NAs introduced by coercion

summer.bison$LONGITUDE = as.integer(as.character(summer.bison$LONGITUDE))

## Warning: NAs introduced by coercion

summer.bison$Elevation = as.integer(as.character(summer.bison$Elevation))

## Warning: NAs introduced by coercion

str(summer.bison)
```

```
## 'data.frame':    22072 obs. of  17 variables:
##  $ ID       : int  46509 46510 46511 46512 46513 46514 46515 46516 46517 4
6518 ...
##  $ No       : Factor w/ 1 level "#N/A": 1 1 1 1 1 1 1 1 1 1 ...
##  $ Collar_ID: Factor w/ 7 levels "32732","32733",..: 1 2 3 1 2 3 1 2 3 1 .
..
##  $ Date     : Factor w/ 664 levels "#N/A","1/5/2013",..: 2 2 2 2 2 2 2 2 2
2 ...
##  $ YYYY     : int  2013 2013 2013 2013 2013 2013 2013 2013 2013 2013 ...
##  $ MM       : int  5 5 5 5 5 5 5 5 5 5 ...
##  $ DD       : int  1 1 1 1 1 1 1 1 1 1 ...
##  $ Time     : Factor w/ 4454 levels "0.125173611",..: 868 861 886 1267 123
0 1224 1440 1451 1432 4337 ...
##  $ HH       : int  0 0 0 2 2 2 4 4 4 6 ...
##  $ LATITUDE : int  49 49 49 49 49 49 49 49 49 49 ...
##  $ LONGITUDE: int  -107 -107 -107 -107 -107 -107 -107 -107 -107 -107 ...
##  $ Elevation: int  859 829 845 835 789 852 839 788 860 856 ...
##  $ DOP      : num  0.6 2 0.6 3.4 3.2 1.8 2.2 1.8 0.6 5 ...
##  $ VALIDATED: Factor w/ 1 level "#N/A": 1 1 1 1 1 1 1 1 1 1 ...
##  $ TEMP     : int  6 8 12 4 7 7 4 3 0 0 ...
##  $ X        : int  319595 318983 321580 319647 318806 321489 319696 318812
321418 319806 ...
##  $ Y        : int  5452815 5453959 5450202 5452935 5454045 5450448 5452927
5453974 5450560 5452845 ...

newsummer.bison <- subset(summer.bison, summer.bison$Y <= 5455127)
summer.bison <- newsummer.bison

slope <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/ResourceSele
ctioFunction/ASCII_August/Slope_perc_std_bison.asc")
distancetowater <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Re
sourceSelectioFunction/ASCII_August/EucDis_water_std_bison.asc")
distancetoroad <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Res
ourceSelectioFunction/ASCII_August/EucDis_road_std_bison.asc")
distancetofence <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Re
sourceSelectioFunction/ASCII_August/EucDist_fence_std_bison.asc")
distancetodogtown <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/
ResourceSelectioFunction/ASCII_August/EucDist_dog_std_bison.asc")
distancetoDC <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_DC_std_bison.asc")
distancetoVG <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_VG_std_bison.asc")
distancetoTC <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_TC_std_bison.asc")
distancetoSG <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_SG_std_bison.asc")
distancetoEC <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_EC_std_bison.asc")
distancetoUG <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_UG_std_bison.asc")
```

```
distancetoSC <- raster("E:/Master thesis/CompiledData(2019)/GISdatabase/Resou
rceSelectioFunction/ASCII_August/EucDist_SC_std_bison.asc")

coords <- data.frame(x=summer.bison$X, y=summer.bison$Y)
summer.bison.spdf <- SpatialPointsDataFrame(coords = coords, data = summer.bi
son, proj4string = CRS("+init=epsg:26913"))
proj4string(summer.bison.spdf)

## [1] "+init=epsg:26913 +proj=utm +zone=13 +datum=NAD83 +units=m +no_defs +e
llps=GRS80 +towgs84=0,0,0"

projection(slope) <- CRS("+init=epsg:26913")
projection(distancetowater) <- CRS("+init=epsg:26913")
projection(distancetoroad) <- CRS("+init=epsg:26913")
projection(distancetofence) <- CRS("+init=epsg:26913")
projection(distancetodogtown) <- CRS("+init=epsg:26913")
projection(distancetoDC) <- CRS("+init=epsg:26913")
projection(distancetoVG) <- CRS("+init=epsg:26913")
projection(distancetoTC) <- CRS("+init=epsg:26913")
projection(distancetoSG) <- CRS("+init=epsg:26913")
projection(distancetoEC) <- CRS("+init=epsg:26913")
projection(distancetoUG) <- CRS("+init=epsg:26913")
projection(distancetoSC) <- CRS("+init=epsg:26913")

slo <- as.data.frame(as(slope, "SpatialGridDataFrame"))
water <- as.data.frame(as(distancetowater, "SpatialGridDataFrame"))
road <- as.data.frame(as(distancetoroad, "SpatialGridDataFrame"))
fence <- as.data.frame(as(distancetofence, "SpatialGridDataFrame"))
colonies <- as.data.frame(as(distancetodogtown,"SpatialGridDataFrame"))
DC <- as.data.frame(as(distancetoDC, "SpatialGridDataFrame"))
VG <- as.data.frame(as(distancetoVG, "SpatialGridDataFrame"))
TC <- as.data.frame(as(distancetoTC, "SpatialGridDataFrame"))
SG <- as.data.frame(as(distancetoSG, "SpatialGridDataFrame"))
EC <- as.data.frame(as(distancetoEC, "SpatialGridDataFrame"))
UG <- as.data.frame(as(distancetoUG, "SpatialGridDataFrame"))
SC <- as.data.frame(as(distancetoSC, "SpatialGridDataFrame"))

str(slo)

## 'data.frame':    201054 obs. of  3 variables:
##  $ Slope_perc_std_bison: num  1.95 3.28 4.46 5.09 5.1 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...

str(water)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDis_water_std_bison: num  -1.53 -1.53 -1.53 -1.54 -1.54 ...
##  $ s1                    : num  305941 305971 306001 306031 306061 ...
##  $ s2                    : num  5455104 5455104 5455104 5455104 5455104 ..
.
```

```
str(road)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDis_road_std_bison: num  -1.08 -1.08 -1.08 -1.08 -1.08 ...
##  $ s1                   : num  305941 305971 306001 306031 306061 ...
##  $ s2                   : num  5455104 5455104 5455104 5455104 5455104 ...

str(fence)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_fence_std_bison: num  -1.39 -1.39 -1.39 -1.39 -1.39 ...
##  $ s1                     : num  305941 305971 306001 306031 306061 ...
##  $ s2                     : num  5455104 5455104 5455104 5455104 5455104 .
..

str(colonies)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_dog_std_bison: num  -1.3 -1.3 -1.3 -1.3 -1.3 ...
##  $ s1                   : num  305941 305971 306001 306031 306061 ...
##  $ s2                   : num  5455104 5455104 5455104 5455104 5455104 ...

str(DC)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_DC_std_bison: num  -1.38 -1.38 -1.38 -1.38 -1.38 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...

str(VG)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_VG_std_bison: num  -1.36 -1.36 -1.36 -1.36 -1.36 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...

str(TC)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_TC_std_bison: num  -1.86 -1.86 -1.86 -1.86 -1.86 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...

str(SG)

## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_SG_std_bison: num  -1.41 -1.41 -1.41 -1.41 -1.41 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...

str(EC)
```

```
## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_EC_std_bison: num  -1.46 -1.46 -1.46 -1.46 -1.46 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...
```

```r
str(UG)
```

```
## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_UG_std_bison: num  -1.41 -1.42 -1.42 -1.42 -1.42 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...
```

```r
str(SC)
```

```
## 'data.frame':    201054 obs. of  3 variables:
##  $ EucDist_SC_std_bison: num  -1.35 -1.36 -1.36 -1.36 -1.36 ...
##  $ s1                  : num  305941 305971 306001 306031 306061 ...
##  $ s2                  : num  5455104 5455104 5455104 5455104 5455104 ...
```

```r
layers = cbind(slo, water, road, fence, colonies, DC, VG, TC, SG, EC, UG, SC)
head(layers)
```

```
##     Slope_perc_std_bison       s1      s2 EucDis_water_std_bison       s1
## 653             1.949744 305941.4 5455104              -1.532012 305941.4
## 654             3.284744 305971.4 5455104              -1.533175 305971.4
## 655             4.462911 306001.4 5455104              -1.534337 306001.4
## 656             5.093839 306031.4 5455104              -1.535500 306031.4
## 657             5.096044 306061.4 5455104              -1.536662 306061.4
## 658             3.931757 306091.4 5455104              -1.537824 306091.4
##          s2 EucDis_road_std_bison       s1      s2 EucDist_fence_std_bison
## 653 5455104             -1.078981 305941.4 5455104               -1.392017
## 654 5455104             -1.078797 305971.4 5455104               -1.392017
## 655 5455104             -1.078586 306001.4 5455104               -1.392017
## 656 5455104             -1.078346 306031.4 5455104               -1.392017
## 657 5455104             -1.078080 306061.4 5455104               -1.392017
## 658 5455104             -1.077786 306091.4 5455104               -1.392017
##           s1      s2 EucDist_dog_std_bison       s1      s2
## 653 305941.4 5455104             -1.298781 305941.4 5455104
## 654 305971.4 5455104             -1.299578 305971.4 5455104
## 655 306001.4 5455104             -1.300372 306001.4 5455104
## 656 306031.4 5455104             -1.301162 306031.4 5455104
## 657 306061.4 5455104             -1.301950 306061.4 5455104
## 658 306091.4 5455104             -1.302734 306091.4 5455104
##     EucDist_DC_std_bison       s1      s2 EucDist_VG_std_bison       s1
## 653            -1.384072 305941.4 5455104            -1.360258 305941.4
## 654            -1.383931 305971.4 5455104            -1.360922 305971.4
## 655            -1.383780 306001.4 5455104            -1.361577 306001.4
## 656            -1.383619 306031.4 5455104            -1.362226 306031.4
## 657            -1.383447 306061.4 5455104            -1.362890 306061.4
## 658            -1.383265 306091.4 5455104            -1.363667 306091.4
##          s2 EucDist_TC_std_bison       s1      s2 EucDist_SG_std_bison
```

```
## 653 5455104            -1.856900 305941.4 5455104            -1.409528
## 654 5455104            -1.857376 305971.4 5455104            -1.409750
## 655 5455104            -1.857836 306001.4 5455104            -1.409924
## 656 5455104            -1.858280 306031.4 5455104            -1.410049
## 657 5455104            -1.858709 306061.4 5455104            -1.410125
## 658 5455104            -1.859121 306091.4 5455104            -1.410150
##            s1      s2 EucDist_EC_std_bison       s1      s2
## 653 305941.4 5455104            -1.457864 305941.4 5455104
## 654 305971.4 5455104            -1.457864 305971.4 5455104
## 655 306001.4 5455104            -1.457864 306001.4 5455104
## 656 306031.4 5455104            -1.457864 306031.4 5455104
## 657 306061.4 5455104            -1.457864 306061.4 5455104
## 658 306091.4 5455104            -1.457864 306091.4 5455104
##     EucDist_UG_std_bison       s1      s2 EucDist_SC_std_bison       s1
## 653            -1.414413 305941.4 5455104            -1.354990 305941.4
## 654            -1.415493 305971.4 5455104            -1.355658 305971.4
## 655            -1.416556 306001.4 5455104            -1.356317 306001.4
## 656            -1.417580 306031.4 5455104            -1.356968 306031.4
## 657            -1.418490 306061.4 5455104            -1.357610 306061.4
## 658            -1.418948 306091.4 5455104            -1.358243 306091.4
##          s2
## 653 5455104
## 654 5455104
## 655 5455104
## 656 5455104
## 657 5455104
## 658 5455104
```

```
layers = layers[,-c(2,3,5,6,8,9,11,12,14,15,17,18,20,21,23,24,26,27,29,30,32,
33)]
names(layers) = c("slope", "water", "road", "fence","colonies", "DC", "VG", "
TC", "SG", "EC", "UG", "SC", "x", "y")
head(layers)
```

```
##        slope     water      road     fence  colonies        DC        VG
## 653 1.949744 -1.532012 -1.078981 -1.392017 -1.298781 -1.384072 -1.360258
## 654 3.284744 -1.533175 -1.078797 -1.392017 -1.299578 -1.383931 -1.360922
## 655 4.462911 -1.534337 -1.078586 -1.392017 -1.300372 -1.383780 -1.361577
## 656 5.093839 -1.535500 -1.078346 -1.392017 -1.301162 -1.383619 -1.362226
## 657 5.096044 -1.536662 -1.078080 -1.392017 -1.301950 -1.383447 -1.362890
## 658 3.931757 -1.537824 -1.077786 -1.392017 -1.302734 -1.383265 -1.363667
##            TC        SG        EC        UG        SC        x       y
## 653 -1.856900 -1.409528 -1.457864 -1.414413 -1.354990 305941.4 5455104
## 654 -1.857376 -1.409750 -1.457864 -1.415493 -1.355658 305971.4 5455104
## 655 -1.857836 -1.409924 -1.457864 -1.416556 -1.356317 306001.4 5455104
## 656 -1.858280 -1.410049 -1.457864 -1.417580 -1.356968 306031.4 5455104
## 657 -1.858709 -1.410125 -1.457864 -1.418490 -1.357610 306061.4 5455104
## 658 -1.859121 -1.410150 -1.457864 -1.418948 -1.358243 306091.4 5455104
```

```
# grab values for hexagonal sample of points (taken above)
grab.values = function(layer, x,y){
  # layer is data.frame of spatial layer, with values "x", "y", and -?
  # x is a vector
  # y is a vector
  if(length(x) != length(y)) stop("x and y lengths differ")
  z = NULL
  for(i in 1:length(x)){
    dist = sqrt((layer$x - x[i])^2 + (layer$y-y[i])^2)
    #Could adjust this line or add another line to calculate moving window or
distance to nearest feature
    z = rbind(z, layer[dist == min(dist),][1,])
  }
  return(z)
}

summer.bison <- as.data.frame(summer.bison.spdf)
str(summer.bison)

## 'data.frame':    22033 obs. of  19 variables:
##  $ ID       : int  46509 46510 46511 46512 46513 46514 46515 46516 46517 4
6518 ...
##  $ No       : Factor w/ 1 level "#N/A": 1 1 1 1 1 1 1 1 1 1 ...
##  $ Collar_ID: Factor w/ 7 levels "32732","32733",..: 1 2 3 1 2 3 1 2 3 1 .
..
##  $ Date     : Factor w/ 664 levels "#N/A","1/5/2013",..: 2 2 2 2 2 2 2 2 2
2 ...
##  $ YYYY     : int  2013 2013 2013 2013 2013 2013 2013 2013 2013 2013 ...
##  $ MM       : int  5 5 5 5 5 5 5 5 5 5 ...
##  $ DD       : int  1 1 1 1 1 1 1 1 1 1 ...
##  $ Time     : Factor w/ 4454 levels "0.125173611",..: 868 861 886 1267 123
0 1224 1440 1451 1432 4337 ...
##  $ HH       : int  0 0 0 2 2 2 4 4 4 6 ...
##  $ LATITUDE : int  49 49 49 49 49 49 49 49 49 49 ...
##  $ LONGITUDE: int  -107 -107 -107 -107 -107 -107 -107 -107 -107 -107 ...
##  $ Elevation: int  859 829 845 835 789 852 839 788 860 856 ...
##  $ DOP      : num  0.6 2 0.6 3.4 3.2 1.8 2.2 1.8 0.6 5 ...
##  $ VALIDATED: Factor w/ 1 level "#N/A": 1 1 1 1 1 1 1 1 1 1 ...
##  $ TEMP     : int  6 8 12 4 7 7 4 3 0 0 ...
##  $ X        : int  319595 318983 321580 319647 318806 321489 319696 318812
321418 319806 ...
##  $ Y        : int  5452815 5453959 5450202 5452935 5454045 5450448 5452927
5453974 5450560 5452845 ...
##  $ x        : num  319595 318983 321580 319647 318806 ...
##  $ y        : num  5452815 5453959 5450202 5452935 5454045 ...

# grab all values for used and available points based on combined layer data
set
used = grab.values(layers, summer.bison$x, summer.bison$y)
used$x = summer.bison$x
```

```
used$y = summer.bison$Y
used$collar_id = summer.bison$Collar_ID
used$use = 1
head(used)

##             slope     water       road     fence  colonies        DC
## 50356  1.80721998 -1.500867 -0.9593339 -1.342803 -1.339755 -1.362313
## 25712  5.31487799 -1.510279 -0.9234957 -1.367351 -1.313293 -1.327109
## 106798 2.30867505 -1.555426 -1.0907880 -1.328031 -1.366622 -1.481287
## 47766  0.16812690 -1.497923 -0.9621189 -1.347446 -1.334852 -1.363433
## 23762  0.06720451 -1.515570 -0.9255857 -1.370128 -1.313719 -1.325282
## 101611 0.68794358 -1.563263 -1.0815600 -1.319263 -1.365604 -1.471968
##               VG        TC        SG        EC        UG        SC      x
## 50356  -1.459142 -1.416017 -1.434538 -1.402286 -1.418490 -1.422443 319595
## 25712  -1.460933 -1.439987 -1.434538 -1.400626 -1.416735 -1.443159 318983
## 106798 -1.461189 -1.322297 -1.434538 -1.402896 -1.405672 -1.443765 321580
## 47766  -1.461322 -1.413625 -1.434538 -1.399396 -1.418490 -1.427054 319647
## 23762  -1.464795 -1.447173 -1.434538 -1.401716 -1.410667 -1.450439 318806
## 101611 -1.459422 -1.327820 -1.434538 -1.409454 -1.409559 -1.448214 321489
##              y collar_id use
## 50356  5452815     32732   1
## 25712  5453959     32733   1
## 106798 5450202     33248   1
## 47766  5452935     32732   1
## 23762  5454045     32733   1
## 101611 5450448     33248   1

# Available habitat for bison is bison containment area of the West block of
Grasslands National Park
library(rgdal)
library(raster)
GNP_boundary <- shapefile("E:/Master thesis/CompiledData(2019)/GISdatabase/Re
sourceSelectioFunction/ASCII_August/BisonContainmentArea.shp")

## Warning in rgdal::readOGR(dirname(x), fn, stringsAsFactors =
## stringsAsFactors, : Z-dimension discarded

projection(GNP_boundary) <- CRS("+init=epsg:26913")
str(GNP_boundary)

## Formal class 'SpatialPolygonsDataFrame' [package "sp"] with 5 slots
##   ..@ data       :'data.frame':  1 obs. of  3 variables:
##   .. ..$ OBJECTID  : chr "1"
##   .. ..$ Shape_Leng: num 72497
##   .. ..$ Shape_Area: num 1.81e+08
##   ..@ polygons   :List of 1
##   .. ..$ :Formal class 'Polygons' [package "sp"] with 5 slots
##   .. .. .. ..@ Polygons :List of 1
##   .. .. .. .. ..$ :Formal class 'Polygon' [package "sp"] with 5 slots
##   .. .. .. .. .. .. ..@ labpt  : num [1:2] 314796 5449313
##   .. .. .. .. .. .. ..@ area   : num 1.81e+08
```

```
##   .. .. .. .. .. .. ..@ hole    : logi FALSE
##   .. .. .. .. .. .. ..@ ringDir: int 1
##   .. .. .. .. .. .. ..@ coords : num [1:85, 1:2] 309165 309111 309937 3099
89 310008 ...
##   .. .. .. ..@ plotOrder: int 1
##   .. .. .. ..@ labpt    : num [1:2] 314796 5449313
##   .. .. .. ..@ ID       : chr "0"
##   .. .. .. ..@ area     : num 1.81e+08
##   ..@ plotOrder  : int 1
##   ..@ bbox       : num [1:2, 1:2] 305811 5440892 325244 5455127
##   .. ..- attr(*, "dimnames")=List of 2
##   .. .. ..$ : chr [1:2] "x" "y"
##   .. .. ..$ : chr [1:2] "min" "max"
##   ..@ proj4string:Formal class 'CRS' [package "sp"] with 1 slot
##   .. .. ..@ projargs: chr "+init=epsg:26913 +proj=utm +zone=13 +datum=NAD8
3 +units=m +no_defs +ellps=GRS80 +towgs84=0,0,0"

# Plot the home ranges
plot(GNP_boundary)

# ... And the relocations
plot(summer.bison.spdf, col=as.data.frame(summer.bison.spdf)[,2], add=TRUE)
```

```
# First create random sample of points with in available polygon
random.points <- spsample(GNP_boundary, 22033, "random")

# can take 5+ minutes
```

```r
available = grab.values(layers, random.points$x, random.points$y)
available$x = random.points$x
available$y = random.points$y
available$collar_id = summer.bison$Collar_ID
available$use = 0
head(available)
```

```
##              slope     water      road     fence  colonies        DC
## 117151 -0.06497882 -1.550184 -1.073547 -1.325566 -1.389158 -1.473840
## 168812  0.93060398 -1.589360 -1.150325 -1.301231 -1.421300 -1.503119
## 201909  0.30747461 -1.558038 -1.115248 -1.342613 -1.466885 -1.496367
## 118947  1.74740005 -1.521431 -1.056090 -1.219440 -1.487373 -1.451624
## 68769   3.70852208 -1.536373 -1.046563 -1.331162 -1.434667 -1.420647
## 160767 -0.14924170 -1.554211 -1.135960 -1.350428 -1.481707 -1.489615
##               VG        TC        SG        EC        UG        SC
## 117151 -1.465907 -1.336285 -1.432059 -1.413211 -1.414097 -1.446992
## 168812 -1.448323 -1.503975 -1.434538 -1.405205 -1.417580 -1.447945
## 201909 -1.452469 -1.417948 -1.432321 -1.368132 -1.420054 -1.410376
## 118947 -1.450781 -1.511928 -1.431213 -1.457864 -1.408504 -1.445541
## 68769  -1.465907 -1.869224 -1.387089 -1.456284 -1.380151 -1.449327
## 160767 -1.463420 -1.717973 -1.419748 -1.456747 -1.409855 -1.452664
##               x       y collar_id use
## 117151 321131.9 5449733     32732   0
## 168812 315751.5 5447341     32733   0
## 201909 317225.8 5445797     33248   0
## 118947 316669.9 5449642     32732   0
## 68769  308213.4 5451966     32733   0
## 160767 307679.5 5447709     33248   0
```

```r
data = rbind(available, used)
str(data)
```

```
## 'data.frame':    44066 obs. of  16 variables:
##  $ slope    : num  -0.065 0.931 0.307 1.747 3.709 ...
##  $ water    : num  -1.55 -1.59 -1.56 -1.52 -1.54 ...
##  $ road     : num  -1.07 -1.15 -1.12 -1.06 -1.05 ...
##  $ fence    : num  -1.33 -1.3 -1.34 -1.22 -1.33 ...
##  $ colonies : num  -1.39 -1.42 -1.47 -1.49 -1.43 ...
##  $ DC       : num  -1.47 -1.5 -1.5 -1.45 -1.42 ...
##  $ VG       : num  -1.47 -1.45 -1.45 -1.45 -1.47 ...
##  $ TC       : num  -1.34 -1.5 -1.42 -1.51 -1.87 ...
##  $ SG       : num  -1.43 -1.43 -1.43 -1.43 -1.39 ...
##  $ EC       : num  -1.41 -1.41 -1.37 -1.46 -1.46 ...
##  $ UG       : num  -1.41 -1.42 -1.42 -1.41 -1.38 ...
##  $ SC       : num  -1.45 -1.45 -1.41 -1.45 -1.45 ...
##  $ x        : num  321132 315751 317226 316670 308213 ...
##  $ y        : num  5449733 5447341 5445797 5449642 5451966 ...
##  $ collar_id: Factor w/ 7 levels "32732","32733",..: 1 2 3 1 2 3 1 2 3 1 .
..
##  $ use      : num  0 0 0 0 0 0 0 0 0 0 ...
```

```r
# Model considered
library(lme4)

## Warning: package 'lme4' was built under R version 3.5.3

## Loading required package: Matrix

library(AICcmodavg)

## Warning: package 'AICcmodavg' was built under R version 3.5.3

##
## Attaching package: 'AICcmodavg'

## The following object is masked from 'package:lme4':
##
##     checkConv

fit1 = glmer(use ~ (1|collar_id) + slope + water + fence
             +road + colonies + TC + SG + UG + VG
             + SC + EC + DC, data = data, family = binomial(link = "logit"),
nAGQ = 0)
fit2 = glmer(use ~ (1|collar_id) + TC + SG + UG + VG
             + SC + EC + DC, data = data, family = binomial(link = "logit"),
nAGQ = 0)

fit3 = glmer(use ~ (1|collar_id) + SG + UG + VG, data = data, family = binomi
al(link = "logit"), nAGQ = 0)

fit4 = glmer(use ~ (1|collar_id) + slope + water + fence + road + colonies,
             data = data, family = binomial(link = "logit"), nAGQ = 0)
fit5 = glmer(use ~ (1|collar_id) + slope + water + road,
             data = data, family = binomial(link = "logit"), nAGQ = 0)

mynames <- paste("fit", as.character(1:5), sep = "")
myaicc <- aictab(list(fit1,fit2,fit3,fit4,fit5), modnames = mynames)
print(myaicc, LL = FALSE)

##
## Model selection based on AICc:
##
##       K     AICc Delta_AICc AICcWt Cum.Wt
## fit1 14 42852.03       0.00      1      1
## fit2  9 44504.37    1652.34      0      1
## fit4  7 48815.63    5963.60      0      1
## fit3  5 56519.01   13666.98      0      1
## fit5  5 59430.77   16578.74      0      1

summary(fit1)

## Generalized linear mixed model fit by maximum likelihood (Adaptive
##   Gauss-Hermite Quadrature, nAGQ = 0) [glmerMod]
```

```
##  Family: binomial  ( logit )
## Formula:
## use ~ (1 | collar_id) + slope + water + fence + road + colonies +
##     TC + SG + UG + VG + SC + EC + DC
##    Data: data
##
##      AIC      BIC   logLik deviance df.resid
##  42852.0  42973.7 -21412.0  42824.0    44052
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -3.7011 -0.4948  0.0936  0.5558  5.4541
##
## Random effects:
##  Groups    Name        Variance Std.Dev.
##  collar_id (Intercept) 0.01668  0.1292
## Number of obs: 44066, groups:  collar_id, 7
##
## Fixed effects:
##               Estimate Std. Error z value Pr(>|z|)
## (Intercept) -40.600336   3.885196 -10.450  < 2e-16 ***
## slope        -0.240738   0.009936 -24.228  < 2e-16 ***
## water         3.466566   0.581654   5.960 2.52e-09 ***
## fence         4.814528   0.408214  11.794  < 2e-16 ***
## road          8.707077   0.448382  19.419  < 2e-16 ***
## colonies      8.107733   0.351971  23.035  < 2e-16 ***
## TC            6.109628   0.107765  56.694  < 2e-16 ***
## SG          -16.254404   1.550860 -10.481  < 2e-16 ***
## UG          -15.792475   1.934001  -8.166 3.20e-16 ***
## VG            1.628405   0.967682   1.683   0.0924 .
## SC           -8.351368   0.621620 -13.435  < 2e-16 ***
## EC          -11.272070   0.564173 -19.980  < 2e-16 ***
## DC           -7.404092   0.626264 -11.823  < 2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##
## Correlation matrix not shown by default, as p = 13 > 12.
## Use print(x, correlation=TRUE)  or
##     vcov(x)        if you need it
```