2014-09-04

Forest stand management and implications for elk selection in Jasper National Park, Alberta

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by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF ENVIRONMENTAL DESIGN

FACULTY OF ENVIRONMETNAL DESIGN

CALGARY, ALBERTA

SEPTEMBER, 2014

ABSTRACT

Seasonal resource selection patterns of elk in Jasper National Park, Alberta revealed elk select for areas that would be enhanced by natural or anthropogenic disturbance as they prefer herbaceous, shrub, and open conifer habitat types as well as burn sites. The FireSmart-ForestWise Community program was designed to mimic natural disturbance, such as fire, and consisted of timber removal to protect the community of Jasper from wildfires and improve ecological conditions for wildlife. Following timber removal, forage availability and cover for ungulates increased including grass and forb biomass, cover and diversity along with shrub cover. This thesis demonstrates that changes in human alterations to the landscape can benefit herbivores. If Parks Canada mandate continues to focus on maintaining and enhancing ecological integrity, programs such as this should be encouraged and continued.

Key Words: Elk (*Cervus elaphus*), Forest Stand Management, Habitat Modification, National Park, Resource Selection Functions, Plant Community Diversity, Generalized Linear Mixed Models

Acknowledgements

I would like to thank the numerous faculty members, my professional colleagues, friends, and family members who provided guidance and encouragement throughout my process of discovering and exploring my thesis topic.

This thesis would not have been possible without the support and guidance of my supervisor, Dr. Marco Musiani. I would also like to thank my committee members, Dr. Paul Galpern and Dr. Kathreen Ruckstuhl for their contribution and support.

Thank you for the help of my colleagues and friends at Jasper National Park, in particular to Dr. John Whilmhust, Mark Bradley, Layla Neufeld, and Saakje Hazenberg; for all the scientific guidance, support, inspiration and many enjoyable moments playing music. Thanks are also due to the many Parks Canada specialists, local naturalists, and citizens of Jasper who offered information, constructive comments, and idea. As well, to Alan Westhaver and everyone involved in developing, implementing and collecting baseline data for the FireSmart-ForestWise monitoring program. The basis of this thesis refers directly to your hard work. Thanks to Jesse Whittington for providing the script to validate my models and Dr. Paul Galpern and Dr. Pablo Pina for all the tedious help and advice creating and debugging my scripts. Thank you to Mike Alexander of the Government of Alberta Range Resource Management Department in Pincher Creek, Alberta for providing grazing exclusion cages.

My field work could not have been completed without the help of my field volunteers including the 2012 Jasper National Park summer students, as well as Leanne Arnison and Maria Fe Saraiva.

Thank you to all of my friends: your support, encouragement, insights, hugs and laughs have made this experience enjoyable. Especially my fellow EVDSers (Cheryl Clieff, Mary Benjamin, Kathleen Pilfold and Cynthia Nemeth) and my lab mates (Joe Kermish-Wells, Christa Dubesky, Crysoula Gubili, Tyler Jessen, and Dr. Byron Weckworth).

Finally and most importantly, I would like to thank my family, Mom, Dad and Leanne, for their unwavering support and love. Their confidence in me never wavered, even when mine did. I could not have done this without your help. And finally to Matt, whose love and support helped me through this process every day. There are no words big enough to express what your support has meant to me.

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Chapter 1: Introduction

1.1 Background

The first national parks in Canada were developed in the late 1800s to preserve spaces for tourism and economic development (Hall & Shultis, 1991). Canada's first national park, Banff Hot Springs Reserve (today called Banff National Park), was established in 1885 due to the potential tourism opportunity following the completion of the Canadian Pacific Railway through the area. Yoho and Glacier National Parks soon followed, and were developed along the same transcontinental mainline in an attempt to promote railway tourism. Without the elements of transportation and potential hot springs spa the idea of a national park system may not have been created so early in Canada (Marty, 1984).

A transition towards developing parks as a place of preservation began in 1930 with the *Canadian National Parks Act* (Parks Canada, 2000a). This event marked a shift in park management practices and placed greater emphasis on preserving natural areas in an unimpaired state through ecological integrity, as opposed to development based heavily on tourism profit (Woodley, 1994). The concept of ecological integrity is intended to enhance the protection of biological and ecological resources against the threat of human activities. Specifically it refers to the system's wholeness, including the presence of all appropriate elements and occurrence of all processes at appropriate rates (Angermeier & Karr, 1994; Callicott & Mumford, 1997; Noss, 1995). According to the *Canada National Parks Act*, *ecological integrity* means ". . . a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes" (Parks Canada, 2000a). Thus, an ecological system has integrity when its dominant ecological characteristics (e.g., elements of composition, structure, function, and ecological processes) occur within their natural range of variation and can withstand and recover from modifications imposed by natural environmental dynamics or human disruptions (Parks Canada, 2000b; Parrish, Braun, & Unnasch, 2003). However, the definition of "ecological integrity" is frequently vague (Cronin, 2010) as it can include ethical, political, and economical elements (Cairns, 1977; Cairns, McCormick, & Niederlehner, 1993; Cronin, 2010; Karr & Dudley, 1981; Karr, Fausch, Angermeier, Yant, & Schlosser, 1986; Regier, 1993). Ecological integrity (unlike variables such as species abundance or composition) is not an objective, quantifiable property of ecosystems, as it is comprised of a multitude of components and their functions and processes that maintain the system as a whole. In order to monitor and assess ecological integrity, individual variables, which are often based on selected measures of major ecosystems (e.g. forest, wetlands), must be measured using ecological indicators such as native biodiversity as in the *Jasper National Park Management Plan* (Parks Canada, 2010).

Achieving and maintaining ecological integrity would mean that there is an optimal condition for the ecosystem in question, however defining this optimal condition is often difficult (Cronin, 2010). Historical conditions have been used as a reference for optimal conditions and can provide a frame of reference for assessing modern patterns and processes, however these can be problematic as they are often limited or fragmentary to be useful (Swetnam, Allen, & Betancourt, 1999). For example, scientific knowledge of most ecological systems and species has a relatively short history, as does the preserved record of most environmental regimes (e.g. weather and fire). Additionally, in some areas, the ecological system has been so thoroughly transformed by direct human alterations, such as anthropogenic development or introduced species, that the current ecological systems may not have a historic equivalent (Parrish et al., 2003). It can be argued that no ecosystems in existence today are in a natural, pristine, or untouched state, therefore, the maintenance of these states is an unrealizable goal (Wicklum & Davies, 1995). For example, the concentration of millions of visitors each year to Canada's national parks ensures that the pristine and untouched qualities for which they are often celebrated will not exist.

Maintaining ecological integrity in protected areas may be achieved through human-induced alterations on the landscape. For example, in the early 1900s, Canadian officials perceived forest fires as an undesirable phenomenon that destroyed forest resources and, instead, concentrated on eliminating natural fire and traditional native practices of fire use while placing a high priority on fire suppression (Murphy, 1985). Fire protection and suppression were implemented in Jasper National Park (hereafter referred to as JNP) from 1913-1980 (Kay & White, 1995; Rhemtulla, Hall, Higgs, & Macdonald, 2002; Tande, 1979; Wagner, Finney, & Heathcott, 2006) which resulted in parks managers mandated to suppress fires before they spread in size or to an intensity that was difficult to control to protect park's infrastructure and resources.

Today, the impacts of fire suppression on wildlife and vegetation are well known, including the in-growth of forests, and can been observed with the decline of fire dependent ecosystems and species that depend on them (Risbrudt, 1995; Westhaver, 2003). Consequently, land managers have adapted measures to counteract fire suppression impacts such as prescribe burning or manual thinning. In 2004, Jasper National Park's FireSmart- ForestWise Program (hereafter referred to as the FireSmart Program) was implemented and consisted of manual, mechanical and fire treatments for the dual purposes of protecting the community of Jasper from wildfire and improving ecological conditions, including ungulate habitat (Westhaver, 2003). To date, 350 ha have been cleared or thinned.

Timber removal, such as in the FireSmart Program, has direct effects on vegetation and indirect effects on animals. Herbivores respond to changes in plant abundance and distribution and their predators follow. In this study, I focus on the dominate herbivore species in the system, Rocky Mountain elk (*Cervus elaphus*), and its potential response. I also briefly discuss other ecosystem effects involving other herbivores and predators. Further, elk are an ideal focal species as they are likely to respond to timber removal treatments, abundant enough to be adequately sampled, and are known to quickly adapt to landscape changes (Shepherd & Whittington, 2006).

Elk are ubiquitous magafauna of the Canadian and United States Rocky Mountains where they are esteemed for sport hunting and conservation value (Van Dyke et al., 2012). Maintenance of elk populations provides ecological, social and economic benefits. Wildlife viewing and hunting generate millions of dollars annually in Alberta; in 2008 Albertan hunters spent more than $102.5 million in direct hunting expenditures (Econometric Research Limited, 2008). Ecologically, elk contribute to maintaining early successional habitat conditions, which have declined in some areas due to influences such as fire suppression. However, elk also cause concerns from potential damage, nuisance activity and disease transmission. Within protected areas, damage caused by elk includes over-browsing of timber resources, vehicle collisions, nuisances and safety concerns due to habituation close to human developments.

Since the early 1900s, the elk population in JNP has significantly fluctuated due to changes in ecological processes, such as predation, herbivory, fire suppression and climate variation (see figure 1-1). Elk were widely distributed in North America prior to European settlement, however their abundance and distribution was greatly reduced by the early 20th century (Hicks, Rachlow, Rhodes, Williams, & Waits, 2007; O'Gara & Dundas, 2002). To counter the decline, numerous translocations were used to restore free-ranging elk populations to locations within their historic range, including JNP (Beschta & Ripple, 2007; Bradley & Neufeld, 2012; Conard, Statham, Gipson, & Wisely, 2010; Hicks et al., 2007; Polziehn, 2000; Wolfe, Kimball, & Schildwachter, 2002). In JNP, elk were few in number prior to their reintroduction in 1920 with 88 individual elk from Yellowstone National Park (Dekker, Bradford, & Gunson, 1995). Following this reintroduction, the elk population experienced much variability, as was documented by Bradley and Neufeld (2012) and Beschta and Ripple (2007). By 1936, elk numbers were up to over 2000 individuals (Beschta & Ripple, 2007; Flook, 1962) due to the low wolf population at the time as a result of Parks Canada's predator control practices. Predator control in JNP started in 1900 and continued until 1959.

Severe winter die offs caused a rapid decline in the population in the late 1940s, however the population was able to rebound to pre-1948 numbers by 1969. As elk increased in numbers, some habituated to the town of Jasper, and became a nuisance to the residents. As a result, 2200 elk were culled between 1942 and 1970 (approximately 80 elk/year). In the winter of 1972-1973, extreme cold weather and exceptionally deep snowpack resulted in a major die off of elk (Bradley & Neufeld, 2012). This time, however, predators were re-established in JNP and forage availability was reduced due to consumption by the large numbers of elk and horses. The elk population was not able recover to the same level, however stabilized from 1973 to

1995 at approximately 1000 individuals (Dekker, 1985). Since 1995, the elk population has been in a consistent annual decline of 8% (figure 1-2) due to unknown causes.

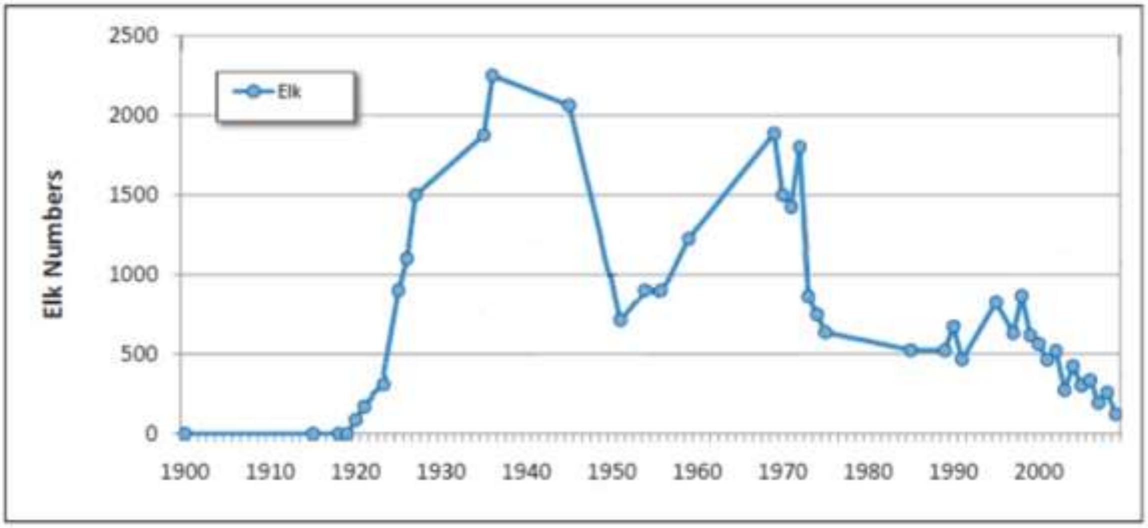

Figure 1-1: Trends in approximate abundance of elk in Jasper National Park from 1900 to 2012, adapted from Bradley and Neufeld (2012).

Habitat and resource selection is a fundamental ecological process which impact population dynamics and ecosystem structure (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). Understanding which factors drive selection is vital for effective species- and landscape-level management. Numerous methods have been developed to characterize and predict how species use space and resources. These include relatively simple comparisons between expectations of used and available resources, such as foraging or selection indices from Manley et al. (2002) to more complicated techniques such as compositional analysis (Aebischer, Robertson, & Kenward, 1993), K-select analysis (Calenge, Dufour, & Maillard, 2005), species distribution models (Phillips, Anderson, & Schapire, 2006), mechanistic home range models (Moorcroft & Barnett, 2008), habitat suitability models (Hirzel & Le Lay, 2008), and related resource selection and resource selection probability functions (Manly, McDonald et al., 2002). Of the available procedures that quantify relative use of habitat resources, the resource selection function (RSF) is arguably the most popular and most widely used (Manly, McDonald et al., 2002) as they provide quantitative, spatially explicit, predictive models for animal occurrence.

An RSF is a model that estimates the probability of an animal using a specific set of resources. Fundamentally, an RSF compares the use of resources to their availabilities on the landscape (Manly, McDonald et al., 2002). Often, an RSF is developed to evaluate critical resources to animals and to determine whether the current landscape is providing the needed components for the targeted animal. As such, resource selection functions are increasingly used as a tool in natural resource management, cumulative effects assessment, land-management planning, and population viability analysis (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Johnson, Seip, & Boyce, 2004; Richardson, Stirling, & Hik, 2005).

1.2 Purpose and objectives

I studied resource selection patterns of 10 individual elk and determined how they responded to forest alteration in Jasper National Park, Alberta. More specifically, I developed spatially explicit habitat models by examining the factors leading to elk habitat occupancy within the study area for two seasons. To accomplish this goal, I used resource selection function methods for characterizing and predicting elk habitat relationships (Boyce & McDonald, 1999; Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006; Manly, 1993a; McDonald et al., 2002) which also accounted for individual elk behavior. After understanding habitat selection, I examined the response of elk to the intentional and managed timber removal program (the FireSmart Program) and its associated increase in forage biomass production and other vegetation characteristics.

Specific research questions are as follows:

1. What landscape characteristics do elk select within their home range?

2. How does tree removal affect stand and vegetation composition?

3. If elk habitat requirements are enhanced following tree removal, will elk increase their use of sites with enhanced forage opportunities?

My specific research objectives were to:

1. Identify elk patterns of selection with respect to landscape variables in summer and winter;

2. Determine vegetation responses to the FireSmart Program's timber removal;

3. Verify whether:

    a) The FireSmart program produced changes in the direction of the landscape features selected by elk (see point 1);

    b) Elk select for areas managed within the FireSmart program.

1.3 Thesis Structure and Content

In Chapter 2, telemetry data from 10 individual elk is used to relate environmental variables to habitat use patterns across the study area. Resource selection functions for summer and winter were developed which incorporate random effects in order to account for multiple sampling within each individual elk and elk habituated to the town of Jasper. The resource selection function is used to determine what features of the landscape is being used by elk and whether these features were enhanced by the FireSmart Program.

In Chapter 3, I examine how elk habitat features and vegetation responded to the FireSmart Program around the town of Jasper. To do this, I use nonparametric and mixed modeling analyses to determine how stand density, vegetation diversity, grass and forb biomass, ungulate usage and other ecological characteristics changed following timber removal over a 9 year period in three different stand types.

In chapter 4, I discuss the effect of the FireSmart Program on vegetation and elk habitat selection and make suggestions for future research. Further, I make recommendations for the management of ecological integrity in Jasper National Park based on the theoretical and empirical implications of my research. It is my hope that the ecological information contained in this document will be used by managers in Jasper National Park, and elsewhere where FireSmart practices are implemented, to develop sound science-based management practices to promote the preservation of wildlife and its habitat.

1.4 Thesis Significance

This thesis provides information regarding elk response to habitat modification. To my knowledge, I provided the first detailed assessment of vegetation response to a FireSmart Program in Canada. Results from this study are intended to inform future conservation and management approaches within the Canadian Rockies and to provide a comparative measure for future research in the area. The knowledge gathered will enhance the efficiency of habitat management of human-altered landscapes as well as provide better predictions of the effects of future development in previously unaltered environments.

Chapter 2: Elk Resource Selection in Jasper National Park

2.1 Introduction

Understanding how wildlife use their surrounding habitats is of paramount importance to ecology and wildlife management (Boyce & McDonald, 1999; Mcclean, Rumble, King, & Baker, 1998). Habitat selection studies usually compare assessments of habitat use to habitat availability, showing how animals actively select the environments where they spend most of their time (Manly, 1993a). Resource selection models can be used to analyze intensity of resource use and predict the geographical distribution of a particular species by combining information from point occurrence data and environmental variables (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Manly, 1993b).

This chapter will detail elk response to landscape variables in Jasper National Park (hereafter referred to as JNP), a protected area in Alberta, Canada, using mixed-model resource selection functions (RSFs). Development of RSFs is one approach to describing patterns of space-use and environmental associations. While causation cannot be inferred from correlative RSFs, magnitude and sign of coefficients as well as strength of prediction can reveal responses to environmental components (Austin, 2002). In certain situations, RSFs can be a critical tool in conservation and management because they allow for interpolated distributions based on current or future scenarios (Boyce et al., 2002). Thus, detailing patterns of elk response to current landscape features, whether anthropogenic or natural, can provide resource practitioners opportunities to predict outcomes of future landscape changes.

2.1.1 Known patterns of elk habitat selection

Many studies have shown that ungulate distributions are primarily influenced by the distribution of forage resources, competition, terrain conditions, and predators (Anderson et al., 2005; Boyce, Mao, Merrill, Fortin, & Turner, 2003; Cook, 2002; Hebblewhite, Pletscher, & Paquet, 2002; Jones & Hudson, 2002; Mccullough & Mccullough, 1999; Morgantini & Hudson, 1989; Skovlin, Zager, & Johnson, 2002; White, Feller, & Bayley, 2003; Wilmshurst, Fryxell, & Hudson, 1995). Additionally, human management practices and climate play an important role in habitat selection (Bradley & Neufeld, 2012; Robinson et al., 2010). A literature review of elk habitat studies in North America was conducted to determine potential spatial variables to use and understand the habitat selection of elk in JNP.

Available forage resources change seasonally; therefore elk habitat selection may also change depending on the season. In the summer, forage is typically plentiful, however, in the winter, forage is often limited (Robinson, Hebblewhite, & Merrill, 2010). As well, winter weather, especially snow depth can have a very strong influence on selection (Beier & McCullough, 1990; Creel & Creel, 2009).

<u>Elk response to vegetation</u>

Although, elk are considered a generalist herbivore and are often flexible in their choice of foods and habitats (Christianson & Creel, 2007; Cook, 2002; Geist, 2002), forage acquirement and forage quality still affects their habitation selection (Langvatn & Hanley, 1993; Van Dyke et al., 2012; Wilmshurst et al., 1995). Many elk models have shown a direct link between elk forage and resource selection (Hebblewhite, Merrill, & McDermid, 2008; Mao et al., 2005; Robinson et al., 2010). Research by Hebblewhite et al. (2008) and Mao et al. (2005) showed that in summer, elk habitat selection is driven by the availability of high-quality herbaceous forage which is often at higher elevations in mountainous terrain. Thus, elk have the ability to move away from predators with low consequences to their fitness when forage is typically plentiful. In winter, however, where forage is limited, elk may risk being exposed to higher predation risk in favor of forage availability (Robinson et al., 2010).

Studies have also shown elk prefer certain land cover types, such as a mix of open grasslands and conifer cover (Mao et al., 2005; Peck & Peek, 1991; Skovlin et al., 2002; Unsworth, Kuck, Garton, & Butterfield, 1998). Robinson et al. (2010) created RSFs for both migratory and non-migratory elk in summer and winter and found that elk selection for various land cover types changed depending on the season, however, in each season, grasslands and shrublands were selected more frequently. More specifically, in summer, migratory elk selected for high elevation grasslands and shrublands, while non-migratory elk selected for low and alpine grasslands as well as open conifer, closed conifer stands and low barren areas (river flats) and wetlands/water areas. Winter elk selected for low elevation habitats that provided winter forage, as well as low snow cover, low elevation, herbs and shrublands.

Elk response to predation

The risk of predation drives many behavioral responses in prey (Creel & Winnie, 2005; Winnie, Christianson, Creel, & Maxwell, 2006). Prey, such as elk, use a number of strategies to reduce the risk of predation and, in turn, increase survival (Winnie et al., 2006). In order to reduce predation risk, elk have been known to increase vigilance, reduce foraging time or movements, change group size and move to less risky areas or refuges (Creel & Winnie, 2005; Lima & Dill, 1990; Proffitt et al., 2010). In JNP, wolves (*Canis lupus*) are elk's primary predator and their alternative prey species include mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*) and woodland caribou (*Rangifer tarandus caribou*). Unlike many other ungulate species, wolf predation is known to drive elk movements in JNP, as well as other protected areas of the Canadian Rockies (Dekker & Bradford, 2001; Hebblewhite, Munro, & Merrill, 2009).

Previous studies have shown that predation by wolves influence elk habitat selection; thus, leading to elk avoiding areas with high predation risk (Burcham, Edge, & Marcum, 1999; Frair et al., 2005; Hebblewhite & Merrill, 2009b; Lyon, 1983; Rowland, Wisdom, Johnson, & Kie, 2000). In areas of well-established elk and wolf populations, wolves have been found to be the strongest limitation to elk population growth (Creel, Christianson, Liley, & Winnie, 2007; Creel & Christianson, 2008). Alternatively, human development and activities tend to displace wolves, thereby locally reducing predation risk experienced by elk and providing a fine-scale refuge from predation (Beschta & Ripple, 2007). It could be argued that elk which are habituated to the town of Jasper have reduced predation risk compared to those residing outside of town due to the refuge of the town. In Banff National Park, as wolves were recolonizing in areas, elk increasingly utilized habitats close to and within areas of human development (Hebblewhite et al., 2002; Hebblewhite & Merrill, 2009b; White et al., 2003). Although wolves are not the only species which predate on elk, wolves are considered to be particularly important carnivores because they affect prey populations (Hebblewhite et al., 2002; Hebblewhite et al., 2005) and can cause ripple down effects in ecosystems (Hebblewhite et al., 2005; McLaren & Peterson, 1994).

<u>Elk response to anthropogenic features</u>

As of 2009, there were 31,000 kilometres of provincial highways in Alberta (Government of Alberta, 2009). Studies have shown that roads are one of the most widespread human alterations of the natural landscape and are one of the primary causes of wildlife habitat fragmentation (Forman et al., 2003). Roads are known to affect wildlife in several ways including changing animal behavior, increasing wildlife mortality, altering the physical environment, reducing the gene flow, spreading and introducing exotic species of plants, as well as limiting animal dispersal (Epps et al., 2005; Proctor, McLellan, Strobeck, & Barclay, 2005). Further studies have shown that when animals avoid roads, there can be a reduction in permeability of landscape which may cause population fragmentation (Dodd, Gagnon, Boe, & Schweinsburg, 2007; Gibeau, Herrero, McLellan, & Woods, 2001).

Roads are considered to be a major factor influencing distribution of elk across the landscape (Roloff, 1998; Rowland, Wisdom, Johnson, & Penninger, 2005; Thomas & Toweill, 1982). Roland et al. (2005) identified areas with high road density may not have forest cover patches large enough to be effective habitat for elk. Further, elk higher levels of stress and increased movement rates have been documented in elk in areas of high road density compared to areas with lower road density (Frair, Merrill, Beyer, & Morales, 2008; Lyon, 1979; Rost & Bailey, 1979). Additionally, roads can also affect elk mortality rates; in JNP from 1980 to 2004, an average of <1 elk per/year died from vehicle collisions.

Elk selection close to roads varies between studies, some studies have shown elk avoid roads (Lyon, 1983; Naylor, Wisdom, & Anthony, 2009; Rost & Bailey, 1979; Rowland et al., 2000) while other studies found elk to select areas close to roads (Dodd et al., 2007; Gagnon, Theimer, Dodd, Boe, & Schweinsburg, 2007), however this often varied with traffic volume, road density, and adjacent habitat type. Elk in fact may be attracted to roads for foraging availability or important habitat close to roads (Dodd et al., 2007; Gagnon et al., 2007) and not the road itself, therefore it is the adjacent habitat that determines elk selection of roads.

Further, studies have shown that the selection of trails by elk depends on the season. Elk have been found to avoid trails in the winter, possibly because of stronger selection by wolves for trails during this season (Hebblewhite, Merrill, & Mcdonald, 2005; Whittington, St. Clair, & Mercer, 2005) or because of human activity (Frair et al., 2005; Hebblewhite et al., 2005; Kloppers, St Clair, & Hurd, 2005; Rowland et al., 2000).

Elk response to terrain conditions

Elk preference for terrain conditions is often due to slope, elevation and other topographic features. Previous studies have indicated that elk tend to select west and south facing slopes as well as areas that have mild to medium steepness (Mao et al., 2005; Peck & Peek, 1991; Robinson et al., 2010; Skovlin et al., 2002; Unsworth et al., 1998). Robinson et al. (2010) found that elk usage of areas declined with increasing slope as well as in areas with high snowpack in winter. Additionally, the amount of snowfall can influence the amount and spatial distribution of herbivory within plant communities (Beschta & Ripple, 2007). In terms of elevation, Robinson et al. (2010) found elk to select low elevation montane valleys, specifically at lower to moderate elevations in Banff and Jasper National Parks.

Deep snow and severe winter weather are known to be detrimental to elk reproduction and survival (Creel & Creel, 2009; Munro, Hebblewhite, Visscher, Hamilton, & Merrill, 2002; Post & Stenseth, 1999; Taper & Gogan, 2002). Creel and Creel (2009) found that elk population growth was negatively related to winter snow accumulation, even more so than wolf presence.

Elk response to fire and stand management

Natural forest fires and prescribed burns have shown to strongly increase herbaceous forage biomass (Hebblewhite et al., 2008; Sachro, Strong, & Gates, 2005) due to the increase of light on the ground. Elk diet typically consists of herbaceous vegetation, therefore, they often select for burns (Hebblewhite et al., 2008; Irwin & Peek, 1983; Peck & Peek, 1991). Further, fire can create a mosaic of stand ages whose overall dynamics and forage availability depends on both initial conditions and fire severity (Bormann & Likens, 1979; Kohm & Fraklin, 1997).

Openings created from timber removal are thought to benefit ungulates as it increases forage opportunities, creates edges as well as cover habitat (Basile & Jensen, 1971; Harper, 1971; Hershey & Leege, 1976; Irwin & Peek, 1983; Krefting, 1962; Lyon & Jensen, 1980). Lyon and Jensen (1980) found that ungulates often use openings to search for better quality or greater quantities of forage. However, this is often influenced by security requirements during the feeding period. Elk and deer prefer clear-cuts with cover in the opening except where such cover inhibited forage growth. Both preferred openings in which logging slash was not a barrier to movement. Elk preferred smaller openings than deer, but were more tolerant of large openings in areas with natural openings already present. However, other studies have indicated that the openings from timber removal can be detrimental because it reduces available cover and produces slash, thus increasing big game vulnerability to hunting and harassment (Beall, 1976; Hershey & Leege, 1976; Lyon & Jensen, 1980; Marcum, 1976; Pengelly, 1972). Beier and McCullough (1990) found that ungulates move into openings more often at night or when there is fog, suggesting ungulates use openings when there is a lower chance of visual detection.

2.1.2 Resource selection function

Resource selection functions (RSFs) are models that estimate the probability of use of a resource by animals. Fundamentally, they compare resource use to the availability of those resources on the landscape (McDonald, Thomas, McDonald, & Erickson, 2002). By combining information from point occurrence data and environmental variables, RSFs can be used to analyze intensity of resource use and predict the geographic distribution of a particular species in an area (Boyce et al., 2002). Although causation cannot be inferred from RSFs, magnitude and sign of coefficients as well as strength of prediction can reveal responses to environmental components (Austin, 2002). Often, they are developed to understand critical resources to animals and to determine whether the current landscape is providing the needed components. As such, RSFs are increasingly used as a tool in natural resource management, cumulative effects assessment, land-management planning, and population viability analysis (Boyce et al., 2002; Johnson, Seip, & Boyce, 2004; Richardson, Stirling, & Hik, 2005).

RSFs are estimated from observations of presence/absence (often called used vs. unused) or presence/available (used vs. available) resource units (Boyce et al., 2002). As well, there are three selection study designs that incorporates used versus available data, as described by Manly et al. (2002). Design 1: available and used resource units are both defined for the complete population of the studied animals. Design 2: available resource units are assumed to be the same for the whole animal population but the used units are set at the individual level. Design 3: available and used resource units are identified for individual animals. According to Johnson (1980a), Design 1 and 2 are considered second order selection (i.e., selection of individual home ranges within its geographic range) and Design 3 is third order selection (i.e., selection of resources within the home ranges).

A resource unit is defined as a sampling unit of the landscape, for example, a pixel or a grid cell. It can consist of various predictor variables (i.e., covariates) which are habitat attributes that can be used to predict the relative probability of use for a resource unit (McDonald et al., 2002). Response variables (i.e., dependent variables) can be resource selection, home range use or survival. Predictor variables (i.e., independent variables) are often environmental conditions, such as elevation, land cover type, and distance to linear features.

The most common statistical model for developing an RSF is a binomial generalized linear model (GLM), usually logistic regression (Augustin, Mugglestone, & Buckland, 1996; Boyce et al., 2002; Buckland & Elston, 1993; Miller, Franklin, & Aspinall, 2007; Walker, 1990). A GLM provides a method to estimate a function of the mean response of a dependent variable as a linear combination of a set of predictors. GLMs are particularly useful for species distribution modeling because they provide a solid statistical foundation for realistically modeling ecological relationships (Austin, 2002). Further, generalized linear mixed-effects modeling (GLMM) (Gillies et al., 2006) allows models to include random effects such as variability of each individual animal's behavior and to control for groups of animals that behave similarly, such as elk that are habituated to human development.

The process of model selection allows the user to determine the most parsimonious model from a collection of possible models. The most parsimonious model is the model with sufficient parameters to avoid bias, but not too many that precision is lost (Burnham & Anderson, 2002). Parsimony can be measured by statistical indices such as Akaike's Information Criterion (AIC) and the model with the lowest AIC is deemed to be the most parsimonious model from a group of models (Burnham & Anderson, 2002).

To evaluate RSFs, Boyce et al. (2002) indicates that the most important consideration is its ability to make predictions. If a model reliably predicts the locations of animals, it is a good model. Other measures for model evaluation is how well a model fits the data, however receiver operator characteristics (ROC curves) and likelihood-ratio test are not appropriate for use-availability designs (Boyce et al., 2002). Models can be validated using a testing-to-training k-fold partitioning procedure (Fielding & Bell, 1997). K-fold cross validation allows to test prediction success and the model's ability to predict different levels of suitability (predicted to expected ratio). As described by Fielding and Bell (1997), the k-fold procedure involves calculating the correlation between RSF ranks and area-adjusted frequencies for a withheld sub-sample of data.

The RSF can be used in a GIS to plot the relative probability of animal use across the study area or other areas with similar environmental characteristics (Boyce et al., 2002; Kie, Ager, & Bowyer, 2005). This method allows for a complex understanding of the patterns of habitat use and allows the researcher to depict habitats that are probably occupied by the study animal (Boyce & McDonald, 1999).

2.2 Methods

2.2.1 Study Area

The study area for the elk habitat selection analysis is the entire boundary of Jasper National Park (figure 2-1), which is located along the western provincial boundary of Alberta and within the central Canadian Rocky Mountains. The Continental Divide marks the western boundary of the park, sharing its border with the Alberta-British Columbia provincial boundary line. The Brazeau River and Sunwapta River drainage basin mark the southern boundary, which is partially shared with the northern boundary of Banff National Park. The summit ridges of the first major mountain range of the eastern slopes of the Rockies mark the eastern boundary. The northern boundary of JNP is largely comprised of a collection of mountain summits and passes which delineate a rough east-west boundary line, also, shared by the southern border of Willmore Wilderness Provincial Park.

In total, the park encompasses 10,878 km^2 of the Canadian Rocky Mountains (MacLaren, 2007). Its width (i.e., southwest to north east) is approximately 80 km, and its length (i.e., southeast to northwest) measures roughly 200 kilometres. Numerous mountain ranges and valley drainage systems are found within this region. The topography is rugged and has a local vertical relief averaging 1000 to 2000 meters from valley bottom to summit top. However, the landscape surrounding the river valley is generally characterized by broad glacier-eroded valleys associated with more gradual and subtle changes in relief, which provides a wildlife corridor through the Rockies.

Typical of continental climate within the Canadian Rockies, JNP has highly variable seasonal, annual precipitation, and temperature patterns (Janz & Storr, 1977), while its vegetation landscape is classified into montane, subalpine, and alpine ecoregions (Holland, Coen, Holroyd, Van Tighem, & Pedology, 1983). Open shrub-forb meadows dominate the alpine ecoregion. The mid-elevation subalpine ecoregion is comprised mainly of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and lodgepole pine (*Pinus contorta*) forests with a small amount of open grasslands. Both alpine and subalpine ecoregions can have avalanche terrain, non-vegetated ridgetops, and areas of rock and ice. The lower elevation montane ecoregion is mainly composed of lodgepole pine, with some Douglas fir (*Pseudotsuga menziesii*), willow (*Salix* spp.), aspen (*Populus tremuloides*), and riparian white spruce (*Picea glauca*) areas. The area also has fragments of grasslands throughout it. Although this ecoregion consists of only 7% of JNP's total land mass, it is considered the most productive and biologically diverse area (Holland et al., 1983).

In addition to elk, the ungulate community consists of caribou (*Rangifer tarandus caribou*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Wolves (*Canis lupus*) prey on all of these ungulates, but Huggard (1993) and Hebblewhite

(2000) documented that elk abundance has been considered to be a primary driver of wolf density in the Rocky Mountains. Other predators of large mammals include cougar (*Felis concolor*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos*). In total, 69 mammal species are known to reside in JNP (Parks Canada, 2010).

Due to the recreation activity and development restrictions placed on the park, the only major land use activities include transportation by highway and railway, as well as non-motorized outdoor recreation (hiking, horse travel, camping, and fishing). Access into the area include one major highway (Highway 16 - the Yellowhead), a railroad, all weather and gravel roads, and official and unofficial hiking trails.

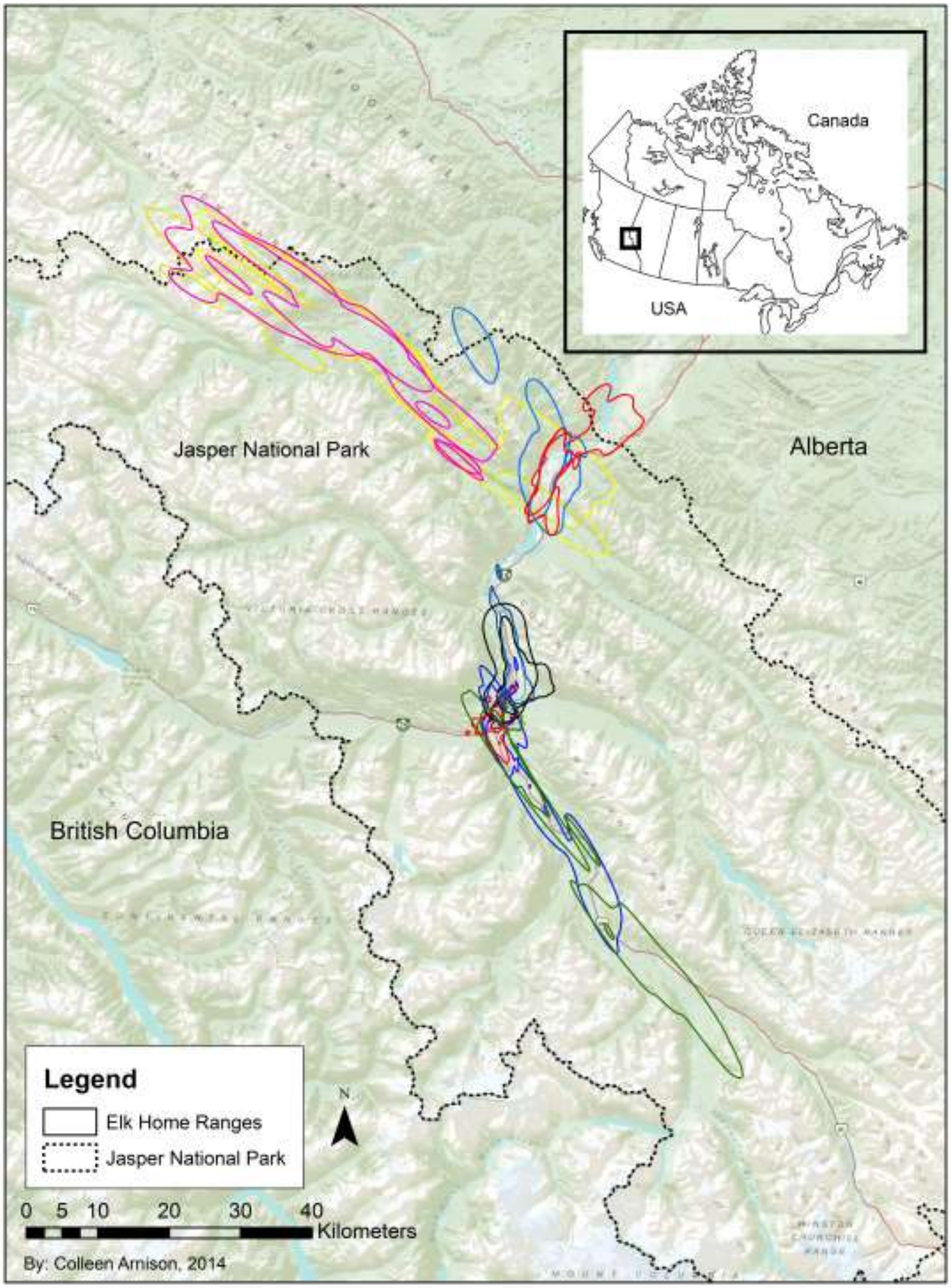

Figure 2-1: Study area of elk habitat selection study, Jasper National Park, Alberta. Summer and winter home ranges of elk analysed in this study (95% kernel density polygons, each colour represents one individual) from 2008 to 2011. Topography and major roads also indicated.

2.2.2 Capture, collaring and data collection

From 2008 to 2011 Parks Canada captured and collared 10 female adult elk within JNP using either ground chemical immobilization (n=5) or aerial netting (n=5). The capture and handling protocol used by Parks Canada was approved by Parks Canada Animal Care Committee. Each elk was fitted with a 4400m Lotek GPS collars (Lotek Engineering Systems, Newmarket, Ontario), and programmed to acquire locations every 2 hours (12 locations per day). Two hours is considered to accurately estimate movement parameters of wildlife (Jerde & Visscher, 2005) and has been used in other ungulate RSFs studies (Hebblewhite & Merrill, 2009a; Robinson et al., 2010). Location data was collected for up to 3 years (September 2008 to December 2011), however due to collar failure and animal death, the number of locations varied by each individual animal (table 2-1). For example, one elk had much less location data points and had low seasonal representation (Elk 139, n=2395 over 200 days) compared to the rest of the elk. To counteract these discrepancies, I used a conservative statistical analysis approach to account for this variability (see section 2.2.4). As well, I validated the resource selection models by testing how well the models predict each individual elk occurrence on the landscape, which protected against overestimating the capacity of the models to predict individual behavior (see section: 2.2.4 on k-fold validation).

Table 2-1: Data summary for elk GPS locations for Jasper National Park, Alberta, from September 2008 to December 2011

Elk ID	Capture Date	End Date	Aprox. No. Days	No. locations
139	04-Mar-11	5-Oct-11	200	2395
106	15-Feb-09	12-Jul-11	698	8380
105	15-Feb-09	09-Dec-11	1069	12829
104	28-Nov-08	09-Dec-11	1000	13223
103	15-Feb-09	24-Jan-11	855	10261
102	15-Feb-09	10-Dec-11	1075	12901
97	31-Oct-08	23-Dec-10	556	6677
96	26-Sep-08	04-Feb-11	1055	12666
94	10-Sep-08	19-May-10	776	9323
95	15-Sep-08	20-Nov-11	1309	15716

Elk locations were imported into a geographic information system (GIS) and all locations were screened for large positional outliers. For example, location points with an horizontal dilution of precision (HDOP) greater than 12, may indicate probable erroneous location accuracy and were removed prior to analysis (Eon & Delparte, 2005). As well, erroneous locations that were beyond the possible ability of elk movement within a given time period (i.e., 2 hours) were removed (Eon, Serrouya, Smith, & Kochanny, 2002). Distances that were above 30 kilometers within each two hour period were examined for errors. Additionally, positions collected within 24 hours of capture were excluded, which is typically carried out when assessing fine-scale animal movements (Bjørneraas, Moorter, Rolandsen, & Herfindal, 2010).

Elk locations were divided into separate seasons to account for the variation in pattern of resource selection through time (Schooley, 1994). I stratified elk population data into two seasons following a study on elk in a similar area done by Hebblewhite et al., (2005). I considered winter to be from October 15 to April 15. Each elk home range for the season was developed using a 95% kernel density process (Felix, Walsh, Hughey, Campa, & Winterstein, 2007; Seaman & Powell, 1996; Worton, 1989). Kernel ranges were produced using a fixed smoothing factor and were used in lieu of MCPs, which tended to overestimate the area potentially utilized by these wide-ranging animals (Frair et al., 2005). Any area of the home range found to be 2700 meters in elevation and above was eliminated, as elk in JNP are not found above that threshold (Neufeld, 2013, pers. comm.). As well, any location point found outside the home range was eliminated. The home ranges were developed to delineate the extent of the available (i.e., random) locations. Ten 'available' points were randomly created for every individual 'used' location (i.e., actual known location) within the home range, thus the measure of availability was unique to each animal. Due to this, my analysis corresponded to analyzing resource selection at the third order scale of selection (i.e., home range) (Johnson, 1980a). ArcGIS 10.1 (ESRI, 2011) and Geospatial Modeling Environment (Beyer, 2012) were used to develop the home range analysis and 'available' points.

Animals that are habituated to human developed areas may exhibit different behavior and habitat selection than non-habituated animals. In JNP habituation of elk to the town site of Jasper started in the early 1940s. This is common in protected areas as the lack of hunting by humans allows elk to lose their natural fear of humans (Murie, 1951; Thompson & Henderson, 1998). Elk are considered to be readily domesticated and may habituate to human activity if disturbance is predictable and harmless (Lyon & Ward, 1982). The advantage of this to elk is a reduction in predation risk, as wolves are more reluctant to use human developed areas (Beschta & Ripple, 2007). This habituation can cause a public safety threat from aggressive elk and can result in localized over-browsing of plants such as willow and aspen (Kloppers et al., 2005; Thompson & Henderson, 1998).

2.2.3 Data layer consolidation

Spatial resources to define each resource unit for the development of the RSF were obtained from Parks Canada and DeCesare (2012b). Each covariate, described below, acted as a potential covariate in the analysis, and an overview of each variable can be found in table 2-2.

Table 2-2: Potential covariates used to develop elk RSFs in Jasper National Park, Alberta from 2008 to 2011. 'No data (cloud/shadow)' was used as the reference category (indicator contrast) for comparisons with in the 'cover' variable, 'No Water' was the reference category for 'Waterbodies' variable, 'No Linear Feature' was the reference category for 'Type of Linear Feature' variable, and 'No Burn' was the reference category for 'Burn Category' variable.

Variable	Description	Variable Type	Ranges of Values	Resolution	Source
Forage Resources and Predation					
Cover	0: No Data (Cloud/Shadow) 1: Dense Conifer Forest 2:Moderate Conifer Forest 3:Open Conifer Forest 4: Mixed Forest 5:Broadleaf Forest 6: Treed Wetland 7: Open Wetland 8: Shrubs 9:Herbaceous 10: Agriculture 12: Barren Land 13: Water 14: Snow/Ice	Categorical	0-14	N/A	DeCesare et al. 2012
NDVI (greenness)	Index of productivity (greenness) to characterize the green forage biomass (2008)	Continuous	0 - 9060	30 m	DeCesare et al. 2012
Water bodies	Water bodies (lakes, rivers, wetland) 0: No Water 1: Water Feature	Categorical	0, 1	N/A	JNP
Dist_Water	Distance to water bodies (m)	Categorical	0, 1	30m	JNP
Burn Category	0: No burn in the past 59 years 1: Recent Burns (0-4 years old) 2:Past Burns (5-25 years old) 3:Historic Burns (25 to 60 years old) 4: FireSmart treatments	Categorical	0-4	N/A	DeCesare et al. 2012/JNP
Burn Age	Years since burn occurred (0 means no burn)	Categorical	0 - 59	30 m	DeCesare et al, 2012
FireSmart Age	Years since Fire smart treatment (0 means no treatment)	Categorical	0 - 20	30 m	JNP
Predation Risk (winter and summer)	Predation risk by wolves	Continuous	0 - 1	30 m	DeCesare et al. 2012
Terrain and Climatic Conditions					
Elevation	Elevation (meters)	Continuous	556-3949	30 m	DeCesare et al. 2012
Slope	Percent slope	Continuous	0 - 86.57	30 m	Derived from 'Elevation'
Aspect	South aspect represented as cosine aspect (i.e., N-S indices)	Continuous	- 1 to 1	30 m	Derived from 'Elevation'
Snow coverage (winter and summer)	Percent of days each pixel was covered by snow between Julian days 321 (Nov 17th) and 144 (May 24th) for winter and between Julian days 145 (May 25th) and 320 (Nov 16th) for summer averaged for each year between January 2000 and December 2009	Continuous	0 - 1	250 m	DeCesare et al. 2012

Variable	Description	Variable Type	Ranges of Values	Resolution	Source
Anthropogenic Factors					
Dist_linear	Distance to all linear features (roads, railways, trails) (meters)	Continuous	0-7595.39	30 m	JNP
Human activity level (winter and summer)	Human activity level (average people per month) of the linear feature closest to location point, for summer and winter	Continuous	0-1000000	30 m	JNP
Linear Type	Type of closest linear feature, 1:Official Trail, 2: Unofficial Trail, 3: Road, 4: Railway	Categorical	1,2,3,4	N/A	JNP

Topographic condition was derived from a digital elevation model (DEM) and included elevation, slope percent, and aspect. Aspect was transformed to a south-to-north index between -1 to 1 using a cosine transformation. Land cover was a composite product generated from land cover, crown closure, species composition and an agricultural mask (for more details refer to McDermid (2006) and DeCesare (2012)). This was reclassified into 14 categories, including (0) No Data (i.e., shadow/cloud cover), (1) Dense Conifer Forest (>70% crown closure; >80% coniferous), (2) Moderate Conifer Forest (31-69% crown closure; >80% coniferous), (3) Open Conifer Forest (<30% crown closure; >80% coniferous), (4) Mixed Forest (21-79% coniferous), (5) Broadleaf Forest (<20% coniferous), (6) Treed Wetland, (7) Open Wetland, (8) Shrubs (9) Herbaceous (10) Agriculture, (12) Barren Land, (13) Water, (14) Snow/Ice. The 'No data (cloud/shadow)' category was used as the reference category (indicator contrast) for comparisons within the land cover variable.

An average Normalized Difference Vegetation Index (NDVI) was used as a measure of productivity of green forage and correlates to primary productivity and biomass (DeCesare, 2012b; Hebblewhite et al., 2008; Pettorelli et al., 2005). NDVI was spatially modeled during the summer to represent the growing season based on 16 day composites between 2000 and 2009. It was derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) and had a 250m^2 resolution. Summer was defined as May 3rd (123rd Julian day) to October 9th (273nd Julian day) (Hebblewhite et al., 2008).

Vector geodatabases of roads, railway, official and unofficial trails were obtained by Parks Canada and used to create a raster of Euclidean distance to linear feature. The maximum distance to a linear features which can influence elk's behavior, according to the literature, range from 800m to 1,800m (800m: Rogala et al. (2011), Hillis et al. (1991); 1000m: Preisler et al. (2006); 1600m: Montgomery et al. (2012); 1800m: Rowland et al. (2000)). Therefore, 1,300 meters (average of the range) was used as the breakpoint distance of road influence on elk. All pixels at a distance beyond 1,300 meters were designated as having no linear feature influence on elk selection. Further a categorical layer was developed to determine what type of linear feature (i.e., trail, road, or railway) was closest to the elk location. This was to determine if elk selection varied by the type of linear feature it was close to, as elk and a variety of other species perceive road types and vehicle use differently (Ager, Johnson, Kern, & Kie, 2003; Clark, Clark, Johnson, & Haynie, 2001; Dickson & Beier, 2002; Dodd et al., 2007). Categories included (1) no linear features (i.e., beyond 1300 meters of a linear feature), (2) official trail, (3) unofficial trail, (3) road, and (4) railway. 'No linear feature' was used as the reference category for comparisons. Additionally, data on the number of people who use each linear feature for summer and winter was incorporated. Data was estimated by Parks Canada in 2005 and represent the number of humans or vehicles per month along each linear feature.

To evaluate elk selection or avoidance of burned areas, fire layers were obtained from Parks Canada. Post fire vegetation biomass is known to fluctuate over time (Schimmel & Granström, 1996) and elk have been found to select burned areas as they consume plant species that increase following fire (Bailey & Whitham, 2002). Because I wanted to determine if elk select burn sites based on how many years since the fire occurred, a continuous 'year since burn' raster layer was derived.

Additionally, it has been documented that herb-dominated vegetation can persist on burned forest sites for up to 25 years (Sachro et al., 2005). Therefore, I created a categorical data layer of different burn ages to determine if elk select for recent, past and historic burns differently. Five categories, based on literature of how elk response to past burn areas, were created (table 2.1). The 'no burn' category was used as the reference category.

Snow cover was derived from Moderate Resolution Imaging Spectroradiometer (MODIS) to characterize the percent of days each pixel within the study area was covered by snow between Julian days 145 (May 25th) and 320 (Nov 16th) for summer and between 321 (Nov 17th) and 144 (May 24th) for winter from January 2000 and December 2009.

Other studies of ungulate resource selection functions use the frequency of a predator's occurrence across the landscape as a measure of predation risk (e.g. Kittle, Fryxell, Desy, & Hamr, 2008). However, this is limited as it does not account for predator search effort (i.e., aggressive response) or the rate which predators successful kill prey while searching (i.e., functional response) (DeCesare, 2012a). DeCesare (2012a) incorporated both wolf resource selection and proportional hazard time-to-event modelling for west central Alberta. The resource selection characterized wolf search effort and the proportional hazard modeling was used to incorporate the effect of time on predation efficiency by accounting for a non-static underlying probability of a kill occurring (DeCesare, 2012a). Kill site analysis was used to define species wolves predated on and locations of successful kills. Prey species included elk, moose, woodland caribou, mule deer, white-tailed deer, bighorn sheep, mountain goat and beaver (*Castor canadensis*). The predation risk layer did not take into account prey distribution or density therefore it is independent from the elk selection analysis. Additionally, this layer was not specific to elk, and took into account an averaged pool of ungulates killed by wolves in the area. This is a more realistic prediction of risk for elk in JNP, as wolves are opportunistic in their prey selection and are not limited to only hunting elk.

All covariate data were in ESRI GIS Grid format and projected to UTM zone 11 with a grid cell resolution of 30 m by 30 m with the exception of snow percentage (250 m resolution).

2.2.4 Model development and comparison

My design corresponded to the third order (Johnson, 1980b), within home range scale, and incorporated the used versus available design in which the resource units are represented by the characteristics of the environment (e.g. elevation, predation risk, and distance to linear feature, described above) at locations actually used by an animal (i.e., the telemetry locations of the 10 collared elk) and at locations randomly picked within the home range of each elk (i.e available locations). Available locations represent the variability of the environment that is within reach of the tracked elk. The spatial extent of available locations (i.e., elk home ranges) was delineated with 95% kernel density for summer and winter. Ten available locations were randomly placed within each home range for every one used location.

Used and available points were contrasted using an availability-use design with the following log-linear form:

$$w^*(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k)$$

Where w(x) represents the relative use function and β_i is the coefficient estimate from the environmental predictor x_i (Manly, 1993a). Coefficients for the model were estimated using logistic regression.

Independence among observation is an assumption of logistic regression (Hosmer & Lemeshow, 2004). While independence is feasible in some RSF designs, it was not assumed in this study, as multiple individuals for the same herd were used for the analysis, which can be a form of pseudo replication. Autocorrelation among observations produces incorrect variance estimates (Otis & White, 1999) and an increased chance of making a Type I error (Leban, Wisdom, Garton, Johnson, & Kie, 2001). To avoid pseudo replication, individual elk were identified in the model as a random effect. Additionally, the number of observations from each elk ranged from 6,677 to 15,716 location points (see table 2-1). This unbalanced sample could create error in the models by influencing model coefficients. However, including a random effect of individual elk accounts for the unbalanced observations among individuals (Bennington & Thayne, 1994; Gillies et al., 2006; Skrondal & Rabe-Hesketh, 2004) and provide for more robust ecological inferences (Pendergast et al., 1996).

Random effects are also used to accommodate non-independence within groups. Elk that are habituated to human development may select for resources differently than elk that do not use these areas. To account for the variation of elk that are habituated compared to those that are not, I incorporated this as a random effect. Elk were considered to be habituated if their home range overlapped with the Jasper town site boundary by a minimum of 30%, which occurred in 40% of the elk (see figure 2-2).

In order to incorporate random effects of individual elk to reduce autocorrelation (Pendergast et al., 1996) and habituated elk to account for the potential variation differences, I used a generalized linear mixed-effects modeling (GLMM) framework (Gillies et al., 2006).

Large GPS data sets and large log-likelihood values are known to inadequately penalize AIC calculations (Boyce et al., 2002). This can result in selection of the global model (i.e., model with all variables) over other candidate models. Therefore, first an initial analysis was conducted to determine each variable's influence on predicting elk presence (table 2-3). Variables that were found to be significant (α=0.05), were used to develop candidate models. All variables were found to be significant, except for human activity level in the winter model. Then, all predictive habitat variables were tested for pairwise correlation using Pearson correlation coefficients. Variables were excluded from use in the same model where the correlation index (r) was ≥ 0.7 (Nielsen, Boyce, Stenhouse, & Munro, 2002). Most variables were found not to be correlated to each other, however, in the summer model, 'snow cover' correlated with 'elevation' (r = 0.79) and in the winter, 'distance to water' was correlated with 'elevation' (r = 0.80). Since all of these variables are likely biologically important for elk habitat selection, none of the variables were eliminated from the model selection process, however, correlated variables were never placed into the same model. The explanatory power of each variable was then evaluated individually using logistic regression. Variables were ranked for their significance (i.e., their influence on habitat selection). Multi-variable logistic regression candidate models were developed based on the variable's individual significance level. These models were then tested using Aikaike's Information Criterion (AIC) to determine the best and most parsimonious model among candidate models and to discourage 'over fitting' by penalizing models with too many variables. Parsimonious models are more numerically stable, subject to less bias, and more accurately extrapolated. The wide difference in ΔAIC and w_i between the different models confirmed the strength of the best model.

I validated the top seasonal models using a testing-to-training k-fold partitioning procedure (Fielding & Bell, 1997), which involves calculating the spearman's rank correlation between RSF ranks and area-adjusted frequencies for a withheld sub-sample of data. All GPS location data by individual elk (n=10) was partitioned so that all locations from 1 elk was withheld as the test dataset and the remaining locations for 9 elk were used as the model training data. Spearman rank correlations (r_s) between training and test data grouped with ten bins was calculated to determine the predictive capacity of the partitioned models (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Fielding & Bell, 1997).

The top models for each season were then used to create an elk resource selection map which provided a relative probability of elk occurrence in JNP. They were constructed using coefficients from the equation above and then the original RSF values, $w(x)$, were standardized by dividing by $(1+w(x))$ to facilitate RSF classification. Resultant maps provided a relative assessment of animal occurrence, ranging from 0 (low relative index of use) to a maximum value of 1 (high relative index of use).

2.3 Results

2.3.1 Elk ranges in summer and winter

A total of 86,705 used location points were retrieved from 10 individual female elk over the 3 year period in the study area. When locations were partitioned into summer and winter (winter: October 15-April 15), average number of observations per elk were similar (paired $t(9)=-0.62$, $p=0.55$), however there was a wide range (summer: $\mu=4291$ observations/elk, range= 1885-6434; winter $\mu=4531$ observations/elk, range 610-6547). This range was due to animal death and collar failure of some individuals. Size of seasonal home range also varied considerably (summer: 8.9km^2 to 396 km^2, winter: 11.5km^2 to 527km^2) and was found to significantly differ across home ranges ($F(9, 10) = 9.68$, $p = 0.0007$). However summer and winter home ranges did not differ significantly for each elk (paired $t(9) = 1.67$. $p=0.06$).

Four elk were considered to be habituated to the town where the town boundary overlaped with the home range by 30% (figure 2-2). In the winter, home ranges of habituated elk were significantly smaller (μ = 26.9 km^2) than elk that resided out of town (μ = 198.6 km^2) ($t(7) = -3.40$ $p=0.01$).

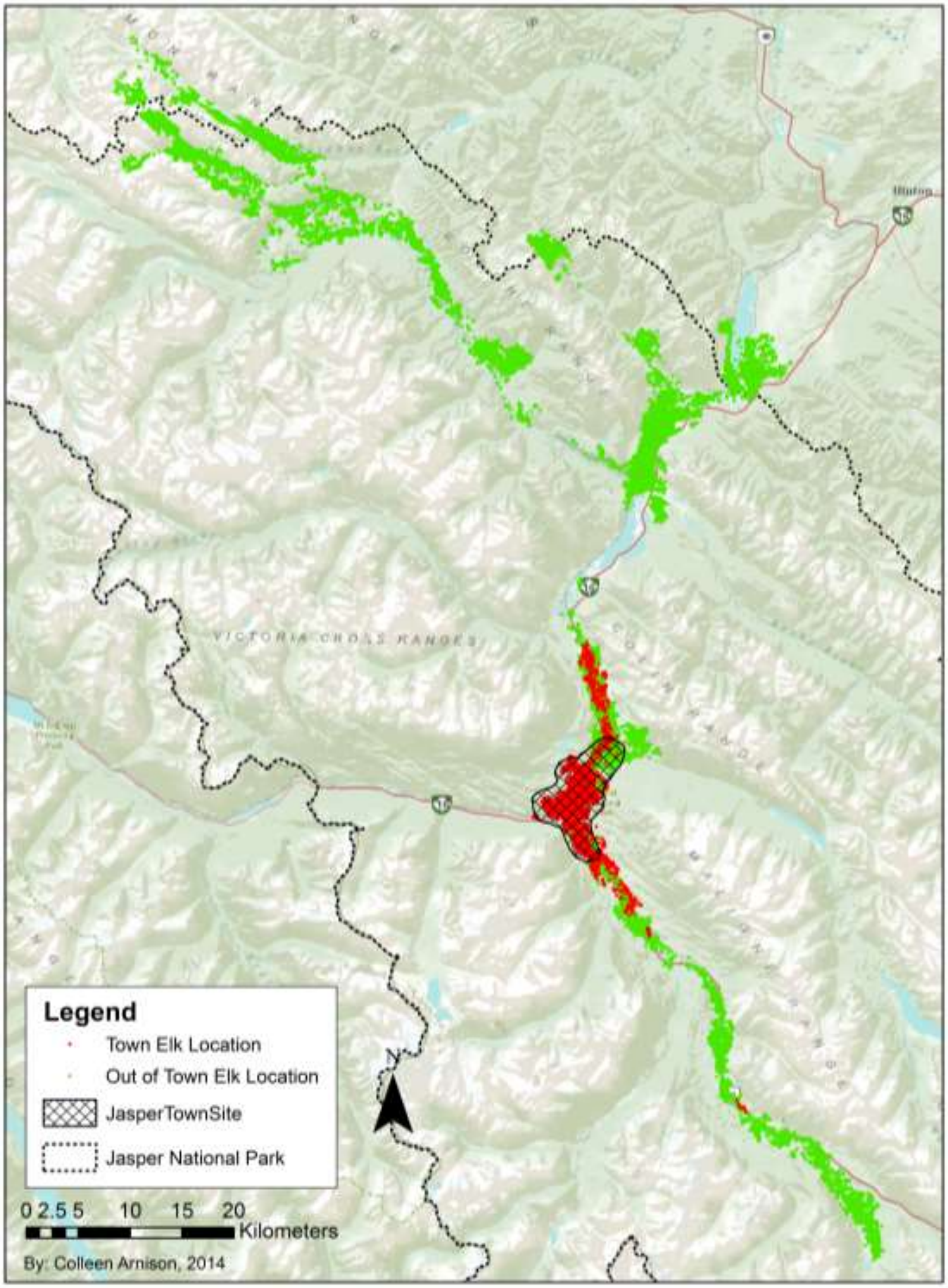

Figure 2-2: Individual elk locations for ten elk in Jasper National Park from 2008 to 2011, colours based on habituated (red) versus elk residing outside of town (green). Boundary of the town of Jasper, topography, and major roads indicated.

2.3.2 Elk resource selection function model building and result

All variables were significantly correlated with elk use, except for human activity level in the winter (table 2-3), therefore this was the only covariate not included in the candidate models. Based on statistical significance level of the initial correlation, candidate models were developed for winter and summer (tables 2-8 and 2-9). AIC was used to select the most parsimonious model and ΔAIC and w_i confirmed the strength of the best model. Table 2-4 and 2-5 presents the highest ranking models for each season. See table 2-8 and table 2-9 for all candidate models and their ranking.

Coefficients and their significance values for variables in the final top models are shown in table 2-7. It was found that both the top summer and winter model had land cover (cover), elevation, percent slope, predation risk (prisk), year since FireSmart treatment (FireSmt), year since burn (BrnAge), burn category (BurnCat) and an interaction of closest linear feature type (Type) and distance to nearest linear features (DistLinear). In addition, the top summer model also contained greenness (NDVI) and distance to water (Dwater), while the top winter model also included a waterbody category (WatrBndy), aspect (Cosaspect) and human activity level (SummerUse).

The results showed that the selection of land cover types within the study area was similar in both seasons for elk, with the exception of when elk avoided treed wetlands and snow/ice in summer. In the winter, no land cover class was avoided. In the summer, elk preferably selected for broadleaf forests, open wetland, herbaceous, and open conifer land cover. In the winter, the most common land cover types that were selected were herbaceous, shrubs, open conifer and barren land. Flatter slopes were preferred year round by elk. In the summer elk selected for lower elevations with a southern aspect, while in the winter they preferred higher elevations. Additionally, elk selected for lower snow cover in the winter and selected areas of high predation risk from wolves year round.

Elk preferred older FireSmart treated areas. In the winter, they preferred older burns, however in the summer, elk preferred newer burn sites. In the summer, elk selected for all burn categories (recent, past, and historic), however, in the winter, elk avoided past and historic burn areas (5-59 years since fire), but selected for recent burn areas (less than 5 years since fire). Further, elk also avoided areas of high human use while being closer to linear features. Within 1.3 kilometres, elk avoided all linear features (trails, roads and railway) in the summer, however in the winter selected each feature.

Elk resource selection maps provided a relative probability of elk occurrence for summer and winter in Jasper National Park (figure 2-3). The maps indicate that elk are restricted to the valley bottoms in the winter and more evenly distributed across the study area in the summer, while avoiding areas of high human use.

The summer model resulted in an average Spearman's rho of 0.951 and winter model resulted in an average rho of 0.935 (table 2- 6). These averages indicated that the coefficients in both models were robust and accurately predicted elk use. When predicting individual elk occurrence, all animals but 1 had a spearman rho above 0.90 for both summer and winter. One elk (Elk ID = 105) was predicted at a lower level (summer rho = 0.793, winter rho = 0769), however this is above the critical threshold value of 0.648. Therefore, the season models predicted the relative probability of occurrence of elk on the landscape.

Table 2-3: Individual relationships between elk occurrence and each potential variable, assessed individually using generalized linear mixed model with individual elk as a random effect

	Winter			Summer		
Variable	**Estimate**	**Std. Error**	***P***	**Estimate**	**Std. Error**	***P***
Land Cover class (Categorical, reference: No data (cloud/shadow))						
Dense Conifer Forest	1.2769	0.1265	<2E-16	1.14269	0.04975	<2E-16
Moderate Conifer Forest	2.0804	0.1249	<2E-16	1.84384	0.0444	<2E-16
Open Conifer Forest	2.8218	0.1254	<2E-16	2.47645	0.04781	<2E-16
Mixed Forest	2.1598	0.125	<2E-16	2.06516	0.04498	<2E-16
Broadleaf Forest	2.6539	0.1269	<2E-16	2.54764	0.05052	<2E-16
Treed Wetland	-12.1374	3172.686	0.997	-8.83439	1.38225	1.64E-10
Open Wetland	2.7977	0.1306	<2E-16	2.68232	0.06714	<2E-16
Shrubs	2.7491	0.125	<2E-16	2.47224	0.0448	<2E-16
Herbaceous	3.1431	0.1251	<2E-16	2.72903	0.04548	<2E-16
Barren Land	2.2919	0.1252	<2E-16	1.74139	0.04598	<2E-16
Water	1.0916	0.1278	<2E-16	0.92063	0.05417	<2E-16
Snow/Ice	-12.1858	368.3272	0.974	-14.7012	1.20014	<2E-16
Elevation	-1.05E-03	2.02E-05	<2E-16	-6.54E-04	2.32E-05	<2E-16
Slope	-0.04755	0.000651	<2E-16	-0.04611	0.000802	<2E-16
Cosaspect (S-N;-1 to 1)	-0.02871	0.004932	5.81E-09	0.107646	0.007221	<2E-16
Snow cover	-1.33559	0.03435	<2E-16	-2.81339	0.08975	<2E-16
NDVI	-	-	-	-2.93E-05	7.71E-06	0.000142
Predation risk (prisk)	4.00179	0.03611	<2E-16	14.70292	0.17244	<2E-16
Year since FireSmart (FireSmt)	0.035662	0.002349	<2E-16	0.009738	0.004314	0.024
Year since burn (BrnAge)	0.00808	0.001269	1.91E-10	0.009525	0.001806	1.33E-07
Burns (Categorical, reference: No burn)						
Recent Burn	1.16709	0.045148	<2E-16	2.06811	0.090535	<2E-16
Past Burn	0.179574	0.015657	<2E-16	0.370688	0.023518	<2E-16
Historic Burn	-1.00549	0.058076	<2E-16	-0.80725	0.142032	1.32E-08
FireSmart	0.190802	0.012838	<2E-16	0.075002	0.020548	0.000262
WaterBody (Categorical, reference: No water)						
WaterBodies	-0.52759	0.015187	<2E-16	-	-	-
Distance to water	-5.00E-05	3.58E-06	<2E-16	-1.26E-05	3.72E-06	0.000711
Human activity level	1.29E-07	7.34E-08	0.0791	3.76E-07	1.40E-08	<2E-16
Distance to Linear features	-6.04E-04	8.84E-06	<2E-16	-5.92E-04	1.11E-05	<2E-16
Closest Linear Feature (Categorical, reference: No linear feature)						
Official Trail	0.74671	0.01654	<2E-16	0.70636	0.02137	<2E-16
Unofficial Trail	0.64904	0.01626	<2E-16	0.50465	0.02073	<2E-16
Road	1.24112	0.01653	<2E-16	1.24407	0.02099	<2E-16
Railway	1.22299	0.01939	<2E-16	1.18061	0.02561	<2E-16

Table 2-4: Summer model selection results for elk resource selection function in Jasper National Park, Alberta, 2008-2011, includes the model's overall rank, AIC, △AIC and AIC weights

Model	Rank	AIC	ΔAIC	w_i
Cover + Elevation + Slope + Prisk_s + SummerUse + LinearType * DistLinear + BrnAge + NDVI + FireSmt + BurnCat + DistWater	**1**	268682.2	0	0.323
Cover + Elevation + Slope + Prisk_s + SummerUse + LinearType * DistLinear + BrnAge + NDVI + BurnCat + DistWater	**2**	268685.6	3.4	0.0590
Cover + Elevation + Slope + Prisk_s + SummerUse + LinearType * DistLinear + BrnAge + NDVI + BurnCat + DistWater + Cosaspect	**3**	268686.2	4	0.0437
Cover + Elevation + Slope + Prisk_s + SummerUse + LinearType * DistLinear + BrnAge + FireSmart + BurnCat + DistWater	**4**	268703.1	20.9	<0.0001

Table 2-5: Winter model selection results for elk resource selection function in Jasper National Park, Alberta, 2008-2011, includes the model's overall rank, AIC, △AIC and AIC weights

Model	Rank	AIC	ΔAIC	w_i
Cover + Elevation + Slope + Prisk_w + Snow_w + BrnAge + BurnCat + FireSmt + LinearType * DistLinear + WatrBndy + Cosaspect	**1**	276119.9	0	0.429
Cover + Elevation + Slope + Snow_w + BrnAge + BurnCat + FireSmt + LinearType * Distlinear + WatrBndy + Cosaspect	**2**	276122.1	2.2	0.143
Cover + Elevation + Slope + Prisk_w + Snow_w + BrnAge + BurnCat + FireSmt + LinearType + DistLinear + WatrBndy + Cosaspect	**3**	276425	305.1	<0.0001

Table 2-6: Spearman rank correlations (*rho*) and associated *P*-values for top seasonal elk resource selection function model predictions and observed frequencies of use using external training data (one animal at a time) for validation in Jasper National Park, Alberta, 2008–2011.

	Winter		Summer	
Elk ID	*rho*	*P*	*rho*	*P*
94	0.9878788	9.31E-08	0.9878788	9.31E-08
95	0.9878788	9.31E-08	1	1.06E-62
96	0.830303	2.94E-03	0.9272727	1.12E-04
97	0.9272727	1.12E-04	0.9636364	7.32E-06
102	0.9393939	5.48E-05	0.9151515	0.000204472
103	0.9878788	9.31E-08	0.9636364	7.32E-06
104	0.9875776	1.03E-07	1	1.06E-62
105	0.769697	9.22E-03	0.7939394	6.10E-03
106	0.9515152	2.28E-05	0.9878788	9.31E-08
139	0.9878788	9.31E-08	0.9757576	1.47E-06
Average	0.93572746	0.001235008	0.95151516	0.000643273

Table 2-7: Coefficient values and stand errors for the top seasonal elk resource selection functions models with data collected in Jasper National Park, Alberta from 2008 to 2011.

Variable	Winter			Summer		
	Estimate	Std. Error	P	Estimate	Std. Error	P
Intercept	-2.258	0.4599	9.14E-07	-3.372	0.1737	< 2e-16
Land Cover class (Categorical)*						
Dense Conifer Forest	1.987	0.3811	1.84E-07	0.9854	0.1357	3.80E-13
Moderate Conifer Forest	2.664	0.3792	2.12E-12	1.353	0.1337	< 2e-16
Open Conifer Forest	3.456	0.3794	< 2e-16	1.801	0.1349	< 2e-16
Mixed Forest	2.662	0.3793	2.23E-12	1.624	0.1338	< 2e-16
Broadleaf Forest	2.956	0.3822	1.04E-14	2.305	0.1363	< 2e-16
Treed Wetland	-	-	-	-9.369	702.8	0.98936
Open Wetland	3.331	0.3837	< 2e-16	2.036	0.1442	< 2e-16
Shrubs	3.487	0.3795	< 2e-16	1.794	0.1338	< 2e-16
Herbaceous	3.966	0.3795	< 2e-16	2.021	0.134	< 2e-16
Barren Land	3.373	0.3793	< 2e-16	1.293	0.1339	< 2e-16
Water	1.928	0.3814	4.29E-07	0.3199	0.1386	0.02094
Snow/Ice	-	-	-	-12.51	376.9	0.97353
Elevation	-0.00178	6.17E-05	< 2e-16	0.000706	3.61E-05	< 2e-16
Slope	-0.03028	0.001429	< 2e-16	-0.03434	0.001282	< 2e-16
CosAspect (S-N;-1 to 1)	-0.235	0.007858	< 2e-16	-	-	-
Snow_cover	-1.44	0.07614	< 2e-16	-	-	-
NDVI	-	-		-2.30E-05	5.22E-06	1.49E-05
Predation risk (prisk)	0.2019	0.0981	0.03953	3.931	0.3144	< 2e-16
Year since FireSmart (FireSmt)	0.02322	0.004239	4.34E-08	0.01645	0.007018	0.01909
Year since burn (BrnAge)	0.04661	0.00439	< 2e-16	-0.03582	0.005415	3.72E-11
Burn Category*						
Recent Burn	0.4829	0.1103	1.20E-05	1.919	0.09585	< 2e-16
Past Burn	-0.8617	0.04876	< 2e-16	0.7072	0.05406	< 2e-16
Historic Burn	-2.929	0.2311	< 2e-16	0.2722	0.2263	0.22919
FireSmart	0.436	0.02564	< 2e-16	0.1054	0.03512	0.00268
WaterBody (Categorical)*	-0.4188	0.02414	< 2e-16	-	-	-
Distance to water	-	-		7.87E-05	5.43E-06	< 2e-16
Human activity level	-	-	-	-2.40E-07	1.85E-08	< 2e-16
Distance to Linear features	-0.00028	3.69E-05	4.28E-14	-0.00102	4.36E-05	< 2e-16
Closest Linear Feature Category*						
Official Trail	-0.1765	0.08132	0.03001	-1.296	0.08246	< 2e-16
Unofficial Trail	0.04372	0.08109	0.58976	-1.411	0.8192	< 2e-16
Road	0.2243	0.08138	0.00585	-0.7711	0.08274	< 2e-16
Railway	0.0898	0.08315	0.28013	-0.852	0.0845	< 2e-16
Official Trail * Dist_Linear	0.000484	5.37E-05	< 2e-16	0.001091	5.69E-05	< 2e-16
Unofficial Trail * Dist_Linear	2.02E-05	5.44E-05	0.71059	0.000703	5.56E-05	< 2e-16
Road * Dist_Linear	-0.00037	5.67E-05	4.38E-11	0.000753	5.49E-05	< 2e-16
Railway * Dist_Linear	0.000496	6.83E-05	3.78E-13	0.000957	7.04E-05	< 2e-16

*'No data (cloud/shadow)' was used as the reference category (indicator contrast) for comparisons with in the 'cover' variable, 'no Water' was the reference category for 'Waterbodies' variable, 'No Linear Feature' was the reference category for 'Type of Linear Feature' variable, and 'No Burn' was the reference category for 'Burn Category' variable

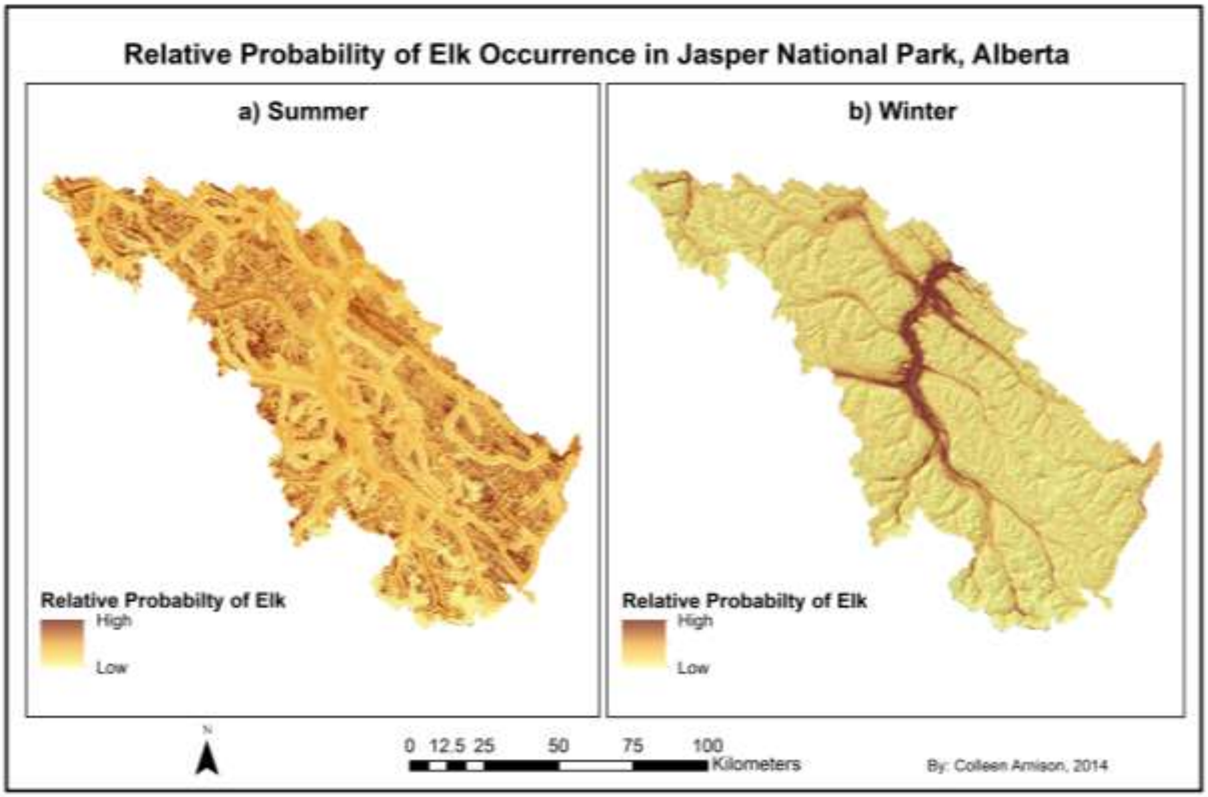

Figure 2-3: Relative probability of occurrence of elk throughout Jasper National Park based on park-wide RSF models for a) summer and b) winter distributions.

2.4 Discussion

The JNP elk resource selection models for summer and winter were validated; indicating that the models predicted elk occurrence accurately. Due to this result, actual elk distribution within JNP can be explained by examining these models in detail. These findings indicate that elk preferentially use areas with different environmental characteristics and this selection changes seasonally.

The resulting relative probability of occurrence of elk in JNP map (figure 2-3) shows elk distribution restricted to the valley bottoms in the winter, which was also found in many other studies (Fryxell & Sinclair, 1988; Sawyer, Kauffman, Nielson, & Horne, 2009). In comparison, in the summer, elk are more evenly distributed across the study area. Elk frequent the study area more evenly because vegetation is more evenly distributed following green up in higher elevation areas. However, it is noticeable that elk avoid areas that people intensively use, including roads and trails in the summer.

Land Cover

Compared to the reference category for land cover (i.e., no data such as cloud or shadow), elk selected for all cover types, except for treed wetland and snow/ice. This broad selection may have been due to the limited size of the reference category compared to all other land cover types. Regardless, the results indicated that certain land cover types were more favored over others. In the summer, elk selected highly for broadleaf forests, herbaceous and open wetland, however, in the winter, herbaceous, shrubs, open conifer, and barren land were the strongest selected type compared to the reference category. As elk are considered a generalist herbivore and are often flexible in their choice of foods and habitat (Christianson & Creel, 2007; Cook, 2002; Geist, 2002), they may select a variety of land cover types to acquire forage. Herbaceous land cover (i.e., grass and forbs) was highly selected in each season as it contains the highest forage availability compared to all other land cover types. In the winter this is particularly important as 90% of elk diet can consist of graminoids (Hebblewhite, 2006). Open conifer forests may be attractive to elk in winter because snow depth tends to be lower under coniferous forest canopy than in open areas (Huot, 1974), and elk are known to avoid areas of deep snow (Pauley, Peek, & Zager, 1993; Sweeney & Sweeney, 1984). Broadleaf forests are characterized as being composed of more than 80% deciduous species, including aspen, which is a major browse species for elk (White, Olmsted, & Kay, 1998).

Dense and moderate conifer forest, which are characterized as having more than 30% crown closure and are composed of 80% conifer species were selected less often by elk throughout the year. Both of these land cover types are typical of landscapes that have been exposed to fire suppression management practices. Without the fire disturbance, open areas can slowly become in-grown with conifer trees, which has been documented in JNP (Mitchell, 2006; Rhemtulla, 1999). More details on this process can be found in section 3.1.3.

Throughout the year, elk avoided treed wetlands as well as snow and ice areas. Whereas the avoidance of snow and ice areas is obvious, taking into consideration the scarcity of food resources in those areas, the avoidance of treed wetlands is perhaps explained by its limited distribution. Within JNP, no areas were classified as treed wetland, however, there was a small patch (0.46 ha in size), located just east of the parks boundary where elk are located. Therefore, its avoidance may simply be its small size relative to all other land cover types.

Other natural features

Regarding natural features, elk preferred less steep slopes year round; however elevation preference changed depending on the season. Elk preferred lower elevation and low snow cover in the winter and a higher elevation in the summer. This seasonal preferential difference for elevation may be due to the fact that temperature and precipitation often change with elevation, which directly relates to snow accumulation and plant phenology (Morgantini & Hudson, 1989; Singh, Grachev, Bekenov, & Milner-Gulland, 2010). It is common in herbivore species to follow retreating snow cover and greater food availability in higher elevations in the summer, and choose lower elevation for their winter range (Fryxell & Sinclair, 1988; Sawyer et al., 2009). Moving to lower elevation in the winter is a strategy to find wintering areas with shallow snow depth (Boyce, 1991; White et al., 2010). Further, in the winter, elk were found to prefer south facing slopes, which are often free of snow due to the effect of wind and solar radiation (Eon & Delparte, 2005).

Wolf Predation

Regardless of the season, elk selected areas where they are at risk to wolf predation, however this was more so in the summer than in the winter. This is contrary to many studies which have indicated that elk avoid areas with high predation risk (Burcham et al., 1999; Frair et al., 2005; Hebblewhite & Merrill, 2009b; Lyon, 1983; Rowland et al., 2000). This may indicate that wolf predation risk in JNP does not limit elk habitat use or distribution and that wolves searching for prey may select for similar landscape features as elk, such as low elevation in the winter. It is important to note that predation risk in this model did not include elk density but was a combination of wolf kill sites and wolf resource selection functions for the area. Additionally, the predation risk layer was not limited to elk, but all prey species that wolves target (e.g. elk, deer, and bighorn sheep). Since my model demonstrates that there is an overlap of high occurrence of elk and higher predation risk of wolves, wolves may be following elk. Although many studies have indicated that wolf predation drives elk movements in JNP and other protected areas in the Canadian Rockies (Dekker & Bradford, 2001; Hebblewhite et al., 2009), perhaps it is elk movements that drives wolves predation strategies and behavior.

FireSmart forest stand management and burn areas

Year round, elk selected for FireSmart timber removal treatment areas and prefer treatments that are older. Openings created by logging and thinning operations are considered to be beneficial to ungulates because they generally increase forage production and edge habitat (Basile & Jensen, 1971; Harper, 1971; Krefting, 1962; Lyon & Jensen, 1980). However, other studies have indicated that created opening can be detrimental as it reduces available cover and produces slash, thus increasing elk vulnerability to predation (Beall, 1976; Hershey & Leege, 1976; Lyon & Jensen, 1980; Marcum, 1976; Pengelly, 1972). The size of each logged area in the FireSmart program was limited, with an average of 10.91 ha in size for each treatment site. As well, slash was piled and burned. This would limit ungulate vulnerability by allowing elk to move freely though the logged areas (because of limited slash pile up) and have adequate cover close by, due to the small size.

There was a seasonal difference in elk's selection of burned areas. In the summer, elk selected for all ages of burns, however, preferred areas that had been burned more recently. In the winter, elk selected for more recent burn (<5 years) sites and avoided older burn sites (5-59 years). Increase in herbaceous forage biomass occurs within the first few years following a fire, which is when the area is most attractive for elk (Hebblewhite et al., 2008; Irwin & Peek, 1983; Peck & Peek, 1991; Sachro et al., 2005). Since overall forage resources are limited in the winter, elk may concentrate on these areas which contain the most forage and avoid older burn areas which have lower forage availability and high snow cover due to the open canopy.

Anthropogenic features

Elk preferred areas close to linear features in both the summer and winter, however, when considering areas within 1.3 km of linear features (the assumed distance of influence of linear features) elk preference differed seasonally. In the winter, elk preferred areas close to roads, but not close to official and unofficial trails, and the railway line. In the summer, elk did not prefer any linear feature over another within 1.3 km of linear features. Many studies have shown that elk distribute away from roads (Lyon, 1983; Naylor et al., 2009; Rost & Bailey, 1979; Rowland et al., 2000) while others found them to select areas close to roads (Dodd et al., 2007; Gagnon et al., 2007). This selection often varied with traffic volume, road density, and adjacent habitat type. In the winter in JNP the traffic is lower due to a lower number of tourists visiting the area and elk may be more attracted to roads for foraging availability or important adjacent habitat during this time (Dodd et al., 2007; Gagnon et al., 2007). In the summer, elk may avoid linear features due to the higher amount of traffic volume on roads and trails and may choose suitable habitat with adequate forage in other areas. Additionally, elk avoidance of trails in the winter may be due to a stronger selection of wolves for trails during this season (Hebblewhite et al., 2005; Whittington et al., 2005).

Model validation

Although the number of observations for each elk ranged considerably from 6,677 to 15,716 location points (see table 2-1), my approach to modeling was conservative from a statistical point of view in order to take into account this imbalance. Firstly, using individual elk as a random effect in the RSF model accounted for the unbalanced observations among individuals by representing individual differences in the overall mean level of the response (Bennington & Thayne, 1994; Gillies et al., 2006; Skrondal & Rabe-Hesketh, 2004). Additionally, the k-fold validation method, as described in section 2.2.4, tested the model's predictability for each individual elk occurrence (Fielding & Bell, 1997). Specifically, all locations from 1 elk were withheld as the test dataset and the remaining locations for 9 elk were used as the model training data. Results indicated that the models predicted all animal occurrences above the critical threshold, however 1 elk (elk 105) was predicted at a lower level (summer rho = 0.793, winter rho = 0769). Elk 105 had the largest home range for both winter and summer (summer: 395.7 km^2, winter: 527.7 km^2) compared to all other elk and, unlike the majority of other collared elk, increased its home range in the winter. Perhaps the landscape within Elk 105 home range is of lower quality and needed to be larger for the animal to acquire all of its forage needs.

2.5 Conclusion

Considering the rate of decline in the JNP elk population there is a clear need to understand the key habitat requirements for elk in order to examine the current conditions in JNP. I have provided the first step towards evaluating habitat requirements and constraints by highlighting elk response to various landscape attributes. Key findings that may be of importance to managers include elk preference to land cover types which are more open and their preference towards burns and FireSmart treatment areas throughout the year.

Elk were shown to prefer open habitat, such as herbaceous, shrub and open conifer land cover types. These land cover habitats may be enhanced by natural and/or human-made disturbance. If park management is dedicated to maintaining ecological integrity, than whenever it is feasible, management should continue to allow for natural disturbances, such as fire, on the landscape. Additionally, human induced disturbances like the FireSmart treatments program and prescribed burning need to be maintained in order to increase the heterogeneity of the landscape and promote herbivore habitat.

Elk's preference to burn and FireSmart treatment areas is most likely due to their increased forage availability, including an increase in the diversity and biomass of grass and forbs (see Chapter 3). However, over time these areas will naturally colonize with trees and shrub species. It is therefore recommended that this open habitat be maintained through prescribed burning or thinning of colonizing trees to allow for favourable elk habitat to persist.

Table 2-8: Winter elk resource selection function candidate model, including their ranking, AIC values, ΔAIC, model weights and model selection outcome in Jasper National Parks, Alberta from 2008 to 2011.

Model	**Rank**	**AIC**	**ΔAIC**	***W*i**
Cover + Elevation + Slope + Prisk_w + Snow_w + BrnAge + WatrBndy + FireSmt + Cosaspect + LinearType * DistLinear + BurnCat	**1**	276119.9	0	4.29E-01
Cover + Elevation + Slope + Snow_w + BrnAge + WatrBndy + FireSmt + Cosaspect + LinearType * Distlinear + BurnCat	**2**	276122.1	2.2	1.43E-01
Cover + Elevation + Slope + Prisk_w + Snow_w + BrnAge + WatrBndy + FireSmt + Cosaspect + LinearType + DistLinear + BurnCat	**3**	276425	305.1	2.40E-67
Cover + Elevation + Slope + Prisk_w + Snow_w + BrnAge + WatrBndy + FireSmt + Cosaspect + LinearType * DistLinear + BurnCat	**4**	276983.5	863.6	1.27E-188
Cover + Elevation + Slope + Prisk_w + BrnAge + FireSmt + BurnCat + LinearType + DistLinear + Cosaspect + WatrBndy + Snow_w	**5**	277183	1063.1	6.07E-232
Cover + Elevation + Slope + Prisk_w + Snow_w + BurnAge + WatryBndy + FireSmt + Cosaspect + LinearType * Distlinear	**6**	277604.8	1484.9	1.482197e -323
Cover + Elevation + Slope + Snow_w + BrnAge + FireSmt + Cosaspect + BurnCat	**7**	278070.5	1950.6	0.00E+00
Cover + Slope +Prisk_w + BrnAge + FireSmt + BurnCat + LinearType + DistLinear + Cosaspect + WatrBndy + Snow_w + DistWater	**8**	278267.7	2147.8	0.00E+00
Cover + Elevation + Slope + Prisk_w + Snow_w + WatrBody + LinaerType * DistLinear	**9**	278496.9	2377	0.00E+00
Cover + Elevation + Slope + Prisk_w + Snow_w + WatrBndy + FireSmt + Cosaspect + DistLinear + BrnAge	**10**	279184.5	3064.6	0.00E+00
Cover + Slope + Snow_w + BrnAge + FireSmart + Cosaspect + BurnCat +Distwater	**11**	279326	3206.1	0.00E+00
Cover + Elevation + Slope + Prisk_w + Snow_w + WatrBndy + DistLinear	**12**	279703.9	3584	0.00E+00
Cover + Elevation + Slope + Prisk_w + Snow_w	**13**	280816.9	4697	0.00E+00
Cover + Elevation + Slope + Snow_w	**14**	280818	4698.1	0.00E+00
Cover + Slope + Prisk_w + Snow_w + WatrBndy + DistLinear + Distwater	**15**	280861.3	4741.4	0.00E+00

Table 2-9: Summer elk resource selection function candidate model, including their ranking, AIC values, ΔAIC, model weights and model selection outcome in Jasper National Parks, Alberta from 2008 to 2011.

Model	**Rank**	**AIC**	**ΔAIC**	$\boldsymbol{W_i}$
Cover + Elevation + Slope + Prisk_s + BrnAge + FireSmt + NDVI + BurnCat + SummerUse + LinearType * DistLinear + Distwater	**1**	268682.2	0	3.23E-01
Cover + Elevation + Slope + Prisk_s + BrnAge + NDVI + BurnCat + SummerUse + LinearType * DistLinear + DistWater	**2**	268685.6	3.4	5.90E-02
Cover + Elevation + Slope + Prisk_s + BrnAge + NDVI + BurnCat + SummerUse + LinearType*DistLinear + DistWater + Cosaspect	**3**	268686.2	4	4.37E-02
Cover + Elevation + Slope + Prisk_s + BrnAge + FireSmart + BurnCat + SummerUse + LinearType *DistLinear + DistWater	**4**	268703.1	20.9	9.35E-06
Cover + Elevation + Slope + Prisk_s + BrnAge + FireSmart + BurnCat + SummerUse + LinearType * DistLinear + DistWater + Cosaspect	**5**	268703.5	21.3	7.65E-06
Cover + Snow_s + Slope + Prisk_s + BrnAge + FireSmt + NDVI + BurnCat + SummerUse + LinearType * DistLinear + DistWater + Cosaspect	**6**	268866.7	184.5	2.79E-41
Cover + Elevation + Slope + Prisk_s + BrnAge + FireSmt + NDVI + BurnCat + SummerUse + LinearType * DistLinear + DistWater	**7**	269087.4	405.2	3.32E-89
Cover + Elevation + Slope + Prisk_s + BrnAge + FireSmt + NDVI +BurnCat + SummerUse + LinearType + DistLinear + DistWater + Cosaspect	**8**	269087.4	405.2	3.32E-89
Cover + Snow_s + Slope + Prisk_s + BrnAge + FireSmt + NDVI + BurnCat + SummerUse + LinearType + DistLinear +DistWater + Cosaspect	**9**	269242.9	560.7	5.68E-123
Cover + Elevation + Slope + Prisk_s + BrnAge + NDVI + SummerUse + LinearType * DistLinear + DistWater	**10**	269344.2	662	5.72E-145
Cover + Elevation + Slope + SummerUse + LinearType * DistLinear + DistWater	**11**	269514	831.8	7.69E-182
Cover + Snow_s + Prisk_s + BrnAge + FireSmt + NDVI + LinearType * DistLinear + DWater	**12**	270215.4	1533.2	0.00E+00
Cover + Elevation + Slope + Prisk_s + BurnCat + SummerUse + DistLinear + Distwater	**13**	270845.1	2162.9	0.00E+00
Cover + Elevation + Slope + BrnAge + FireSmt + NDVI + BurnCat + DistWater + Cosaspect	**14**	272011.3	3329.1	0.00E+00
Cover + Elevation + Slope + BrnAge + FireSmt + NDVI + DistWater	**15**	272614.2	3932	0.00E+00

Chapter 3: Vegetation and ungulate response to FireSmart treatments in Jasper National Park

3.1 Introduction

Human-induced alterations on the landscape can be a management strategy to maintain ecological integrity in protected areas. In the early 1900s, Canadian officials perceived fire as an undesirable phenomenon that destroyed forests. Therefore, beginning in the early 1900s, park management efforts concentrated on eliminating traditional First Nation's practices of fire use and placed a high priority on fire suppression, a policy in place from 1907 to 1980 (Murphy, 1985). Once the impacts of fire suppression on wildlife and vegetation became known, land managers adapted measures to counteract fire suppression impacts with practices such as prescribe burning or manual thinning. In 2004, Jasper National Park's FireSmart- ForestWise Program (FireSmart Program) was implemented and consisted of manual, mechanical and burning treatments on forest stands adjacent to the town of Jasper for the dual purposes of protecting the community from wildfire and improving ecological conditions (Westhaver, 2003).

I examined how vegetation and ungulates responded to the FireSmart Program around the town of Jasper. I used nonparametric and mixed modeling analyses to determine how stand density, vegetation cover, species richness and diversity, grass and forb biomass, ungulate usage and other ecological characteristics changed following timber removal over a 9-year period in three different stand types.

3.1.1 Fire history in Canada and Jasper National Park

Fire is an important disturbance mechanism in forest ecosystems. It influences species composition and age structure, stand structure, heterogeneity, regulates forest insects and diseases, affects nutrient cycling and energy fluxes, and maintains the productivity, diversity, and stability of different habitats. Most forests in Canada have evolved with fire since the last ice age, and many species are adapted to fire or are dependent upon it for their survival (Volney & Hirsch, 2005).

For more than 10,000 years, the majority of fires were ignited by First Nation peoples (White, 2001), who used fire as a management tool to facilitate the growth of plants, improve forage for grazers, drive animal movement when hunting, clear vegetation, and to reduce wildfire hazards around communities (Chavardès, 2014; Kay, 1995; Miller, 2010). Lightning ignitions additionally played a role in establishing the current ecosystem patterns, processes and plant composition (Wierzchowski, Heathcott, & Flannigan, 2002). As more Europeans arrived and settled in North America, First Nation's people were displaced to reserves (Neu & Graham, 2006) and their traditional use of fire on the land declined (White, 2001).

In Canada, since 1980 there has been an average of 8,600 forest fires reported each year. Approximately 60% are human caused, however, lightning fires, in some areas, exceed those caused by people. The mean annual area burned nationwide is 2.5 million hectares (ha) (Stocks, 1991), but this can vary from year to year, for example, in 1978, 0.3 million ha burned and in 1989, 7.5 million ha burned (Stocks et al., 2002). Ninety-five to ninety-nine percent of all wildfires are relatively small in size (i.e., <200 ha) but those that do escape, account for over 97% of the area burned (Weber & Stocks, 1998). The most common forests burned is in the boreal forest of western and northern Canada (Stocks et al., 2002).

Natural disturbances, particularly fire, played a fundamental role in shaping the pattern, structure and function of Jasper National Park (JNP) ecosystems over thousands of years. This is particularly true in the low elevation montane ecoregion where frequent low intensity surface fires maintained non-forest habitats such as grasslands, shrub lands and open forest communities like Douglas fir stands (Chavardès, 2014). Higher intensity, stand replacing crown fires prevailed in moister continuous pine stands on the valley sides (Volney & Hirsch, 2005).

Further, the montane ecoregion is estimated to have a <40 year fire cycle as its historic regime, depending on the stand type (Arno, 1980; Tande, 1979). Specifically, mean historic fire cycles are estimated to range from 50 years for the lodgepole pine and Douglas fir stands to 10 years for shrub lands and grasslands. A compilation of multiple fire history studies in the Alberta Rocky Mountains based on dendrological data from the 1500's to present found that the average annual burn area for the entire park was forty-two square kilometres (4,163 hectares) (Achuff, Westhaver, & Mitchell, 2001). Therefore, the average annual area burned in the montane ecoregion should be approximately 1,500 hectares, roughly 2% of the ecoregion each year; however, since 1931 only 0.5% has been burned in total due to fire suppression practices (see section 3.1.2).

3.1.2 Fire suppression in Jasper National Park

By the early twentieth century, Canadian officials perceived fire as an undesirable phenomenon that destroyed precious forests resources. By 1913, park management efforts concentrated on eliminating traditional First Nation practices of fire use and placed a high priority on fire suppression in JNP (Kay & White, 1995; Murphy, 1985; Rhemtulla, Hall, Higgs, & Macdonald, 2002; Tande, 1979; Wagner, Finney, & Heathcott, 2006). This resulted in parks managers mandated to suppress fires before they spread in size or to an intensity that was difficult to control to protect park's infrastructure and resources. Parks Canada records show that the fire suppression policy was very effective as less than 42 km^2 has burned in all wildfires since 1930. Andison and Forest (2000) determined that less than 0.5% of the total montane area has burned since 1931. This represents a low rate of burning which is historically unprecedented, as the natural range of variability for burning is between 6% and 54% of the montane forests in a single 20-year period. Analysis of all available data from Rocky Mountain fire history studies by Van Wagner (1995) determined that the "fire free" period (between 1930-1995) was unique in the 500-year dendrological fire record. Further, after studying more than 100 years of weather data Van Wagner et al. (2006) showed that this fire free period was not the result of reduced fire weather conditions. Fire control polices were maintained until 1980 (Murphy, 1985).

3.1.3 Impact of fire suppression on wildlife and vegetation

There are many impacts of fire suppression on wildlife and vegetation, especially in ecosystems that were shaped and evolved with fire, such as the montane ecoregion. Using remote sensing and ground plots, Rhemtulla (1999) and Mitchell (2006) determined that fire suppression efforts in JNP have significantly changed forest stand and vegetation composition. The cumulative effects of fire suppression have resulted in the artificial process of forest encroachment or *in-growth*, where gradually the forest canopy closes, altering the internal stand conditions and eliminating habitat elements required by native species (Risbrudt, 1995). Consequently, ecosystems that depend on fire have significantly declined in number and sizes and are becoming rare, for example open grasslands. As frequent low-intensity surface fires clean up the forest floor of fine fuels and removes regenerating conifers (Covington & Moore, 1994), studies have found that fire suppression results in increased fuel loads, increased fuel continuity, and enhanced probabilities of crown fire (Daigle, 1996; Graham, McCaffrey, & Jain, 2004; Scott & Reinhardt, 2001). This can be detrimental to local communities and their infrastructure if an unexpected fire moves through the area.

3.1.4 Fuel Management Standards in Canada

Fuel management standards in Canada are based on the National Fire Protection Association code, *NFPA 1144 Standard for Protection of Life and Property from Wildfire* (2013). This standard code provides a methodology for assessing wildland fire ignition hazards around infrastructure and provides requirements for new construction to reduce the potential of structure ignition from wildland fires. Current Canadian standards for communities to manage fuels, such as the FireSmart-ForestWise Program, was developed by the Partners in Protection organization and sets Canadian preventative standards for management of forest fuels by individual homeowners or agencies working to protect communities. Communities across Canada, United States, and Australia have implemented the FireSmart-ForestWise program.

3.1.5 FireSmart-ForestWise Community project in Jasper National Park

The FireSmart – ForestWise project in JNP was initiated to reduce the risk of wildfire losses to the town and adjacent developments, and to improve ecological health by restoring a more natural structure to adjacent forests and to enhance wildlife habitat, including ungulates (Municipality of Jasper and Parks Canada, 2011; Westhaver, 2003)

To achieve these objectives, manual and mechanical vegetation treatments such as selective thinning, pruning and burning took place on approximately 350 hectares of forest that surround the town of Jasper and the nearby Lake Edith Cottage development. These treatments reduced forest density as well as decreased fuel accumulations on the forest floor. Unique prescriptions were developed for each of the distinct vegetation types found within the project area in order to prescribe treatments for the unique characteristics of each site and to ensure that critical habitat elements such as habitat trees were maintained. Size of each prescription varied, however averaged 10.91 ha in size.

3.1.6 Vegetation and wildlife response to timber removal

Vegetation response following timber removal has been well documented in the literature (Babbitt & Hungerford, 1987; Clark, Antos, & Bradfield, 2003; Keenan & Kimmins, 1993; Prescott, 1997; Ramovs & Roberts, 2003; Roberts & Gilliam, 1995; Roberts & Zhu, 2002; Visscher & Merrill, 2009; Yarie, 1993). Research has shown that removing timber and opening up the forest canopy can affect diversity, distribution, and richness of species (Franklin & Forman, 1987).

Removal of overstory trees changes the microclimate on the ground surface, by increasing temperature and surface soil moisture, and decreasing relative humidity due to the increase in solar radiation (Keenan & Kimmins, 1993; Ramovs & Roberts, 2003). This can result in higher rates of photosynthesis leading to a faster growth of species, especially those which take advantage of unshaded conditions (i.e., shade intolerant species). It can, however, have negative impacts on seedling survival and growth, depending on the impact of the logging operation on the ground surface (Keenan & Kimmins, 1993). Many interacting factors determine the success of understory vegetation following timber removal, including light, water, nutrients, seed source, vegetation regeneration and plant and animal competition (Crawford, 1976; Halpern, 1988; Kemball, Wang, & Dang, 2005; Morgan & Neuenschwander, 1988). Additionally, understory vegetation production is related to stand type, stand structure, and stand disturbance. Although cutting the stand often increases the diversity and quantity of certain understory vegetation, this increase varies by site quality, stand type, and structure (Crawford, 1976).

Following timber removal, pioneer species, that find the disturbed, open environment suitable for colonization, such as certain grasses, often increase in diversity and biomass (Franklin & Forman, 1987). Haeussler and Bergeron (2004) found that clearcuts had more understory tall shrubs, forbs, bryophytes and lichens compared to uncut site. Visscher and Merrill (2009) also determined that herbaceous biomass consisting of forbs and graminoids recovered rapidly following timber removal. On the other hand, species loss may be the result of an unsuitable forest microenvironment, competitive interactions with edge or opening species, or an insufficient total area of suitable foraging habitat (Franklin & Forman, 1987). Clear-cutting also causes structural simplification of forests and may negatively impact the forest floor, which may not be suitable to some species (Prescott, Maynard, & Laiho, 2000).

The impact of wildlife from timber removal is closely related to the change in structure and composition of their habitat from the disturbance. The response of wildlife varies greatly depends on their life history characteristics, habitat requirements, and relationships with forest species composition and structure (Keenan & Kimmins, 1993; Leopold, 1987). Forests are used by animals to obtain energy, nutrients, and water, to shelter temporarily from wind, snow, or heat and to escape from predators (Cannell, 1999). Many species have evolved to adapt to periodic changes in forest structure from natural disturbances (Denslow, 1980; Keenan & Kimmins, 1993).

Previous studies have shown that ungulates use areas after they have had their overstory removed. Vegetation associated with early successional stages after timber removal often provides forage for ungulates and numerous habitat niches for other wildlife (Frair et al., 2005; Thomas, 1979; Visscher & Merrill, 2009). Ungulates favor the open, early stages of forest succession due to the increased availability of forage (Keenan & Kimmins, 1993; Leopold, 1987). Many ungulates also heavily use forest edges (i.e., areas where forest and open areas meet) for feeding or shelter (Franklin & Forman, 1987; Keenan & Kimmins, 1993). Additionally, overtime as the stand recolonizes, thermal and hiding cover may be provided for ungulates, especially when trees become 10 m tall and canopy closures reaches 70% (Irwin & Peek, 1983; Thomas, 1979).

3.2 Methods

3.2.1 Study Area

The study area surrounds the town of Jasper and nearby cottage subdivision at Lake Edith, approximately 3 km north east of town, within Jasper National Park (figure 3-1). For a detailed account of JNP, refer to section 2.2.1. It extends outwards from the perimeter of these urban developments and is composed of approximately 36 square kilometers of forests near the confluence of the Athabasca, Maligne, and Miette Rivers.

This area has highly variable precipitation and temperature patterns (Janz & Storr, 1977). Annual precipitation is less than 30 cm mainly due to a rain shadow effect creating a warmer, drier climate (Tande, 1979). In 2013, total annual precipitation was 28.8 cm (22.2 cm falling as rain) with a mean annual temperature of 4 degrees Celsius (13 degrees Celsius in the summer) (Environment Canada, 2013). Snow often covers the ground at lower elevations from late October through late March (Soper, 1970).

The area is in the montane ecoregion which is mainly composed of closed forests with fragments of grassland, and open and trembling aspen forests. It is considered the most productive and biologically diverse area within JNP as it contains much of the critical ungulate winter range and other specialized wildlife habitats (Holroyd & Van Tighem, 1983).

Dominate forest stands include mature lodgepole pine, smaller Douglas fir, mixed conifer stands and small grasslands interspersed throughout the area. Lodgepole pine (*Pinus contorta*) often dominates with some Douglas fir (*Pseudotsuga menziesii*), willow (*Salix spp.),* and aspen (*Populus tremuloides*). Coniferous regeneration includes white spruce in mesic and hydric sites as it is a typical late-successional species, whereas on dryer xeric sites lodgepole pine and Douglas fir regeneration is more common. White spruce (*Picea glauca*) is found in riparian areas. Historically, these stands evolved in a regime of frequent, low-intensity (stand maintaining) surface fires and infrequent high intensity (stand replacing) crown fires (Andison & Forest, 2000; Tande, 1979). Currently, the structure of the forest is an artifact of recent fire suppression management practices, rather than a reflection of natural fire cycle processes. Due to the absence of fire from fire suppression management practices, formerly open, savannah-like Douglas-fir and lodgepole pine forests in the study area have changed significantly. They are now characterized by a scattering of dominant widely spaced, large diameter Douglas-fir old growth trees (200-300 years old) that are in-grown with dense multilayered canopy of shorter, smaller-diameter lodgepole pine and Douglas fir trees. Westhaver (2006) found that the dense tree understory is younger than 75 years old and originated from the start of fire suppression policies within the park.

Westhaver (2006) identified five forest stand types in the study area, which was in accordance with Holland and Coen (1982). These include: (1) fire-maintained upland pine forest, (2) fire-maintained Douglas fir forest on level terrain, (3) dense even-aged lodgepole pine originating from stand replacing fire, (4) fire-maintained Douglas fir on steep slopes, and (5) mixed conifer forests. The first three stand types are the focus of this study and are hereafter referred to as Open Pine, Douglas fir, and Closed Pine.

Open Pine stands have open canopy tree cover and are multi-layered in structure. They are found on dry to mesic sites in valley bottoms. Lodgepole pine is the dominant tree species; however it also includes Douglas fir, white spruce, and mature trembling aspen.

Douglas fir stands have very large-diameter old growth Douglas fir trees that are up to 400 years old and widely spaced apart. In between the large Douglas fir trees, multi-aged lodgepole pines and Douglas fir trees are found that are less than 70 years old and grow at high stem densities of regeneration trees (over 1000 stems per hectare). Additionally, infrequent small grassland patches and openings with young conifer trees are found. This stand occurs on dry, level to mildly undulating sites in the valley bottom and on lower glacial terraces.

Closed pine stands occur on stony, dry, lower slope sites with deep soil. It has a dense, even-aged lodgepole pine canopy with trees similar in age (90-110 years old), height, and diameter (Tande, 1979). A few mature aspen and Douglas fir trees grow as well as white spruce and balsam fir (*Abies balsamea)* sampling and regeneration trees. Tree density is the highest compared to the other stands (850-1040 stems per hectare), especially on mesic sites.

The ungulate community in the study area includes elk (*Cervus Ccanadensis*), moose (*Alces alces*), white-tailed (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis Canadensis*) and mountain goats (*Oreamnos americanus*). Wolves (*Canis lupus*), cougar (*Puma concolor*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), black (*Ursus americanus*) and grizzly bear (*Ursus arctos*) prey on all of these ungulates, however wolves are considered to be a primary predator (Hebblewhite, 2000; Huggard, 1993).

The town of Jasper is a community of approximately 5000 permanent residents and 500 businesses. It has been established as a service center for park visitors, Parks Canada administration, and the Canadian National Railway. Three kilometres north east of the town of Jasper lies the Lake Edith cottage subdivision which was established in the 1920's and includes 54 seasonally occupied homes situated along the shores of Lake Edith on individually leased lands. JNP receives approximately 2 million visitors a year (mostly in the summer season) and the town area commonly has 20,000 overnight visitors (Parks Canada, 2000c).

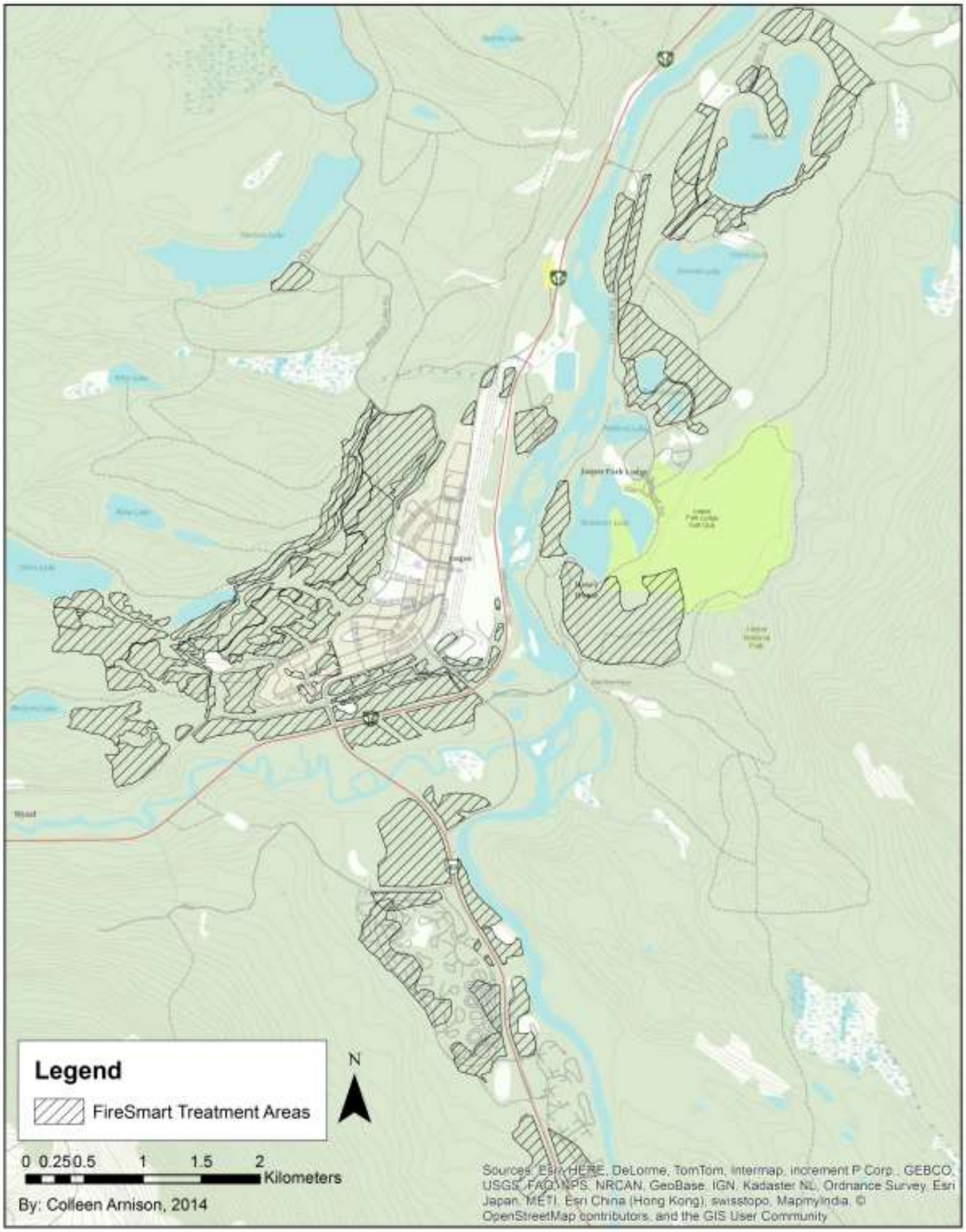

Figure 3-1: FireSmart-ForestWise program study area in Jasper National Park, Alberta. Treatment areas, topography, and major roads indicated.

3.2.2 Monitoring the FireSmart Program

The FireSmart-ForestWise program in JNP created an opportunity to monitor wildlife and vegetation responses to vegetation management treatments. Treatments included timber removal and a small prescribed burn surrounding the town of Jasper and the Lake Edith cottage subdivision to reduce the risk of fires encroaching on urban infrastructure. Treatments occurred between 2004 and 2009 on approximately 350 hectares (figure 3-1).

Westhaver (2006) designed and implemented a long-term monitoring program for the FireSmart program in 2003 to determine how treatments affect wildlife and vegetation over time. Permanent monitoring sites (hereafter referred to as grids) were established in the study area (figure 3-2) and included associated treated and control grids to compare the effects of the treatment and to discern the effect from natural variability, stochastic events, and underlying trends in the larger area. Grids were permanent marked in the field using 30 cm rebar rods (1 cm in diameter) driven into the ground on each corner (labeled with an aluminum cap) and each grid point (labeled with a red plastic cap). Grids were surveyed before and after treatments to determine how the treatments changed over time. Treated grids were selected based on the planned original FireSmart-ForestWise program plan and associated control grids were placed in areas with similar environmental and vegetation characteristics. All grids were evaluated for homogeneity, uniformity and adequacy of size (for more details on selection of sites see Westhaver, 2006). Surveys were conducted in 2003 (before treatment) and 2004 and 2012 (after treatment) and recorded various parameters including stand density, vegetation cover, richness and diversity, biomass production and ungulate relative abundance.

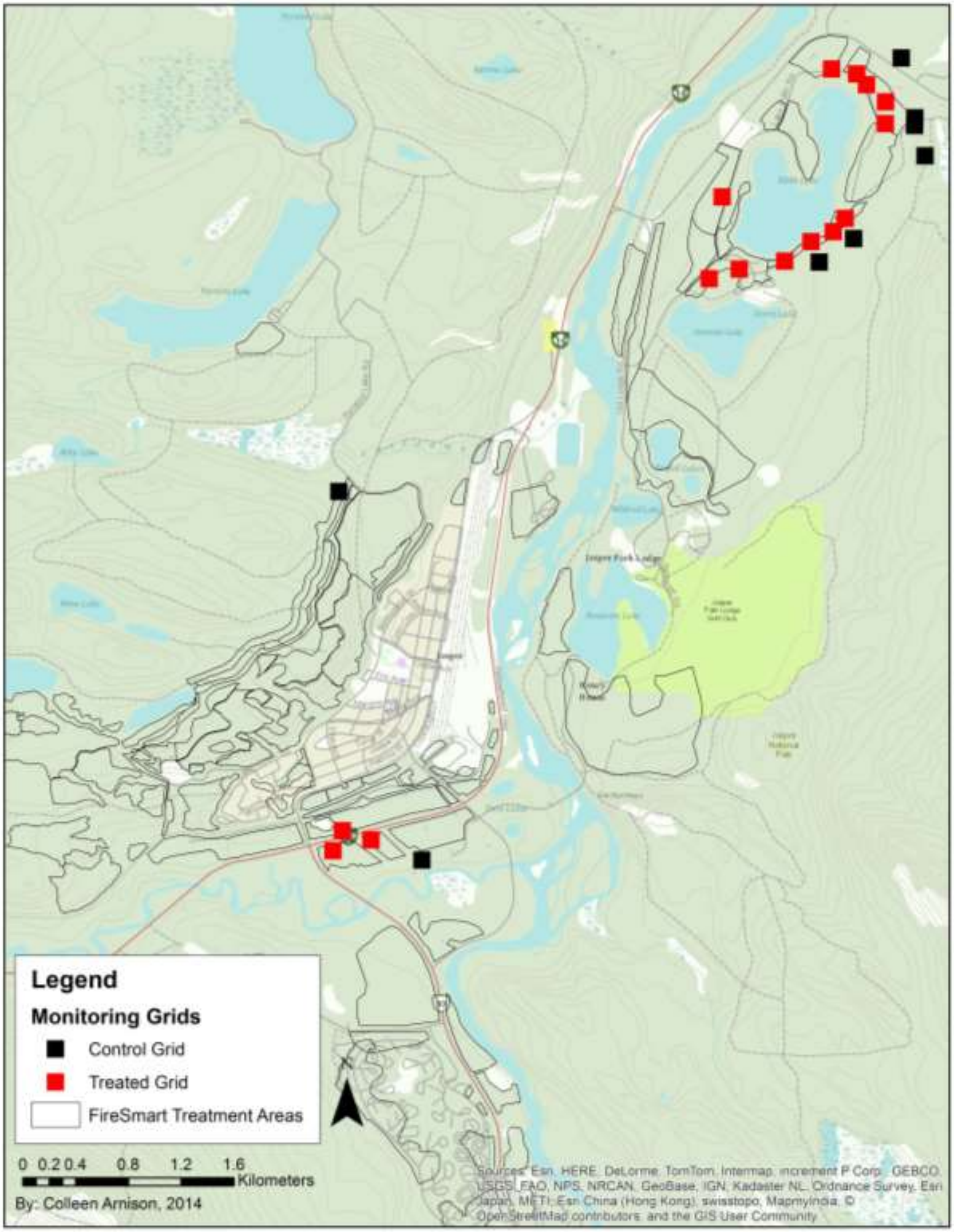

Figure 3-2: Site locations of grids around the town of Jasper and the Lake Edith development in Jasper National Park, Alberta for monitoring the FireSmart-ForestWise program, 2003-2012.

The monitoring program was originally designed to survey two types of treatments (thin only, thin and burn) in three stand types (Open Pine, Closed Pine and Douglas fir) with an equal number of treated and untreated control grids in each stand type thereby comparing pre and post-treatment conditions at each grid (i.e., same grid over time) and comparisons between treated and untreated (control) grids of the same forest stand (Westhaver, 2006). However, the FireSmart-ForestWise program is adaptive to allow for operational changes on the ground in order to effectively mitigate unanticipated ecological effects that are recognized as the work is being completed. Since 2003, the boundaries and size of some of the treated areas deviated from the original plan. As a consequence, the original equal distribution of monitoring grids changed.

By 2012, one grid had a treatment of thin and burn and 6 grids were half logged. Data collected in plots that were half treated or burned were eliminated from the analysis. Further, timber removal occurred from 2004 to 2009, one stand at a time, causing different stands to be treated at different times (table 3-1). In order to comprehend the vegetation response to the FireSmart program, it was important to be able to incorporate the number of years since treatment occurred into the analysis to be able to capture this variability. In total, 23 grids were monitored in the study area, which represented three stand types. The Open Pine stand had 6 treatment grids and 3 control grids, Closed Pine stand had 3 treatment and 3 control grids, and Douglas Fir stand had 5 treatment and 3 control grids, for a total of 14 treated and 9 control grids (table 3-1).

Table 3-1: Distribution of monitoring grids for each stand type in the FireSmart monitoring program in Jasper National Park, 2003-2012; including the number of treatment and control grids and date of treatment for each

Stand Type	**Treatment (No. of grids)**	**Control (No. of grids)**	**Treatment Date**
Open Pine (OP)	6	3	2004
Closed Pine (CP)	3	3	2004
Douglas Fir (DF)	5	3	2009
Total	14	9	

Monitoring first occurred in the summer of 2003, prior to any treatment, to develop a baseline for the parameters surveyed. The following winter, timber removal began and was completed in the Open Pine and Closed Pine stands. In the summer of 2004, grids were resampled for those stands which were treated previously. In 2009, the timber removal was completed in the Douglas fir stand. All sites were then resampled in 2012. All operations involving timber removal occurred in the winter and each treatment area had its own prescription based on site characteristics to minimalize environmental damage.

3.2.3 Data collection

The sampling design was based on an integrated grid-based approach adapted from the U.S. Joint Fire Science Program for the National Study of the Consequences of Fire and Fire Surrogate Treatments (Weatherspoon & McIver, 2000; Westhaver, 2006). This approach allowed for point, line, and area data collection within a grid. Each grid was 90 m × 90 m square which allowed for three 90 m linear sample lines (30 m apart), nine 30 m by 30 m plots, and 49 intersection points (called ‘grid points’), 15 m apart. Plots, line, and points were consistently numbered for each grid to be able to resample the exact location over time (see figure 3-3). Points were used to collect data on grass and forb biomass and horizontal site distance. Lines were used for pellet counts and plots were used for vegetation composition and site characteristics.

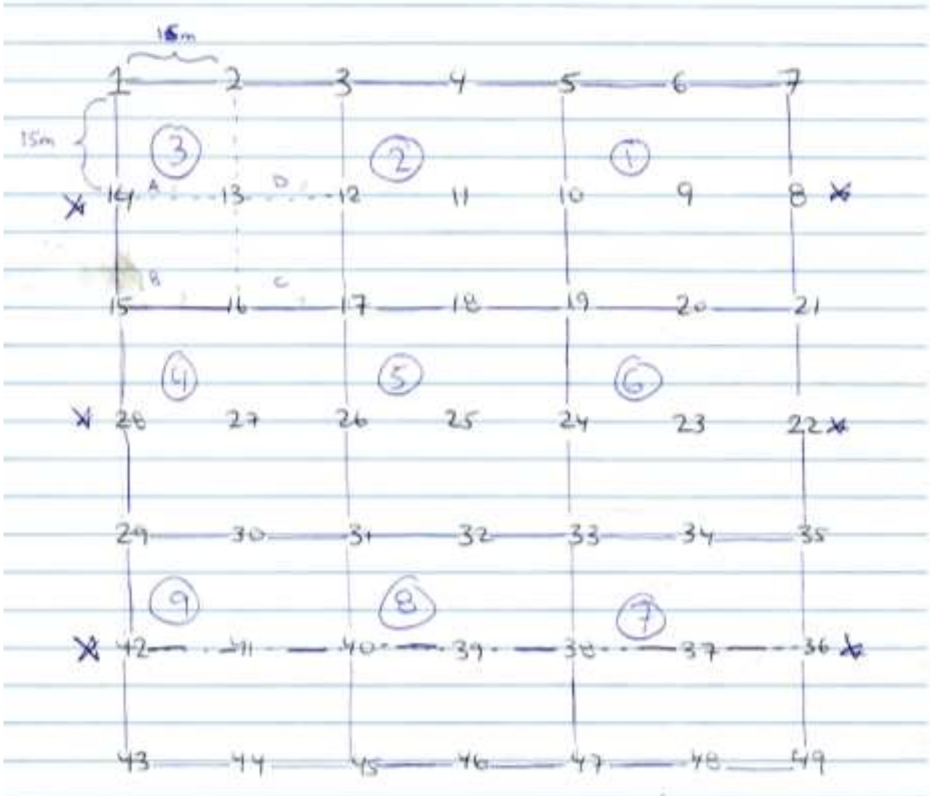

Figure 3-3: Survey layout for each grid for the FireSmart monitoring program in Jasper National Park, Alberta, 2003-2012. Each number corresponds to a gird point, circled number corresponds to 30 m x 30 m plots and lines between stars represents transects for ungulate pellet counts.

Surveys of each parameter were replicated, either randomly or in the same location, within each grid over time. Each measured parameter used a different sampling design within the grid, depending on the nature of the variable itself (table 3-2). Parameters included plot and vegetation characteristics, including grass and forb biomass, horizontal cover, and pellet counts.

Table 3-2: Variables measured for the FireSmart monitoring program in Jasper National Park, Alberta, 2003-2012, includes types of survey, area size for each survey within each grid, number of replicates per grid and how it will be replicated over time.

Measured Variables	Size within each grid	No. replicates (per grid)	Replicated
Plot characteristics Slope Aspect	30 x 30 m	3	Random
Vegetation Composition Percent Cover Tree Density	 30 x 30 m 15 x 15 m	 3 6	 Random Random
Grass and Forb Biomass	1 x 1 m	10	Random
Horizontal Cover	4 sample, 15 m apart	9	Same Location
Pellet Count	90 m transect	3	Same Location

The following section describes how each variable was surveyed, based on Westhaver (2006):

For each vegetation plot (i.e., three randomly chosen 30 x 30 m plots within each grid), general characteristics were recorded, including ecoregion classification (based on Holland & Coen, (1982)), percent slope, aspect (i.e., slope orientation), elevation, UTM co-ordinate of the grid center, topographic position (i.e., where it is located on the landscape), relief shape of the plot (i.e. concave, convex, rolling, flat, or steep slope) and moisture regime. Moisture regime is the presence or absence of either ground water or water held in the soil (Holland & Coen, 1982). For analysis, moisture regime was categorized into 1-5 scale based on Beckingham et al. (1996). Surveys were conducted in June and July of 2003 (pre-treatment), and 2004 and 2012 (post-treatment of treatment and control grids), for a total of 143 plots. Further, within each plot, vegetation composition within each forest strata was determined. Each species was identified and percent cover estimated. Plant nomenclature was based on Kershaw, Mackinnon and Pojar (1998), Duft (1989), and Williams (1992). Forest strata included trees, shrubs, herbs and grasses, and bryoids (figure 3-4). If more than one canopy tree layer existed, it was split into two categories: overstory and understory trees. The shrub layer was split into three categories: shrubs 2-5 m tall and sampling trees, shrubs 0.5-2 m tall and regeneration trees, and dwarf shrubs < 0.5 m tall. Grasses and forbs were grouped together, while mosses and lichens were separated within the bryoid layer. Ground cover, other than vegetation, was also estimated in eight categories: ground litter, rocks and stones, exposed mineral soil, deadfall, water, ash, slash and unburned debris piles.

Species richness is a qualitative description and measures the number of species in a given area, it does not account for the overall diversity of species or species evenness. Vegetation diversity for each forest strata was determined using Simpson's diversity index (*D*) (Simpson, 1949). It takes into account both richness and the proportion of each species relative to the total area (i.e., percent cover) in a given forest strata (Pielou, 1975).

The formula for calculating D is:

$$D = 1 - \frac{\sum_{i=1}^{s} n_i (n_i - 1)}{N(N-1)}$$

Where *S* is the number of species, *N* is the total percentage cover or total number of organisms and *n* is the percentage cover of a species or number of organisms of a species. Simpson's diversity index (*D*) ranges from 0 (no diversity or homogeneous) to 1 (highly diverse or heterogeneous).

For each of the dominant tree species identified, tree height, height of live crown and the diameter at breast height (1.3 m above ground) was determined for an average, randomly selected tree. Tree density was estimated by counting each tree within each forest layer (i.e., overstory trees, understory, sapling (30 cm to 5 m) and regeneration trees (3 cm to 30 cm)) in two randomly sampled 15 m by 15 m sub-plots within each plot. Surveys were conducted from July to September 2003 (n=30, pre-treatment, treatment grids only) and August 2004 (n=46, post-treatment, treatment and control grids) and June to August 2012 (n=66, post-treatment, treatment and control grids), for a total of 143 plots. Further, in 2003 and 2004, tree age structure information was obtained by taking tree cores from representative individuals in the overstory and understory layer using a standard increment corer and a 10-power hand lens.

Cores were taken at 45 cm above ground and a correction factor of five years was added to account for time to reach that height. See appendix A-1 for the field data collection form.

Figure 3-4 Forest strata diagram of overstory tree, understory tree, shrub, herbs and grass, byrophytes, and ground cover for vegetation composition survey in Jasper National Park, 2003-2012.

Understory vegetation structure is a measure of net primary productivity, an indicator of ecosystem health, and important for ungulate habitat cover (Knapp, Briggs, Childers, Sala, & Fahey, 2007). One method to measure vegetation structure is a visual obstruction technique (also known as Robel height), which has been used extensively in grassland and wetland assessments as a rapid, reliable and effective vegetation assessment technique (Rabb, Rooney, & Bayley, 2013; Robel, Briggs, Dayton, & Hulbert, 1970). This technique involved using a modified Robel Pole which was a 2 m long pole with alternating red and white sections (25 cm in length) (Robel et al., 1970; Westhaver, 2006). An observer estimates the visual percentage of each section (i.e., not occluded by vegetation) 15 m away at four readings (taken north, south, east and west from the observer) at 9 grid points in each grid. This survey was conducted starting in July, when summer vegetation is at its peak volume and before foliage begins to senesce or leaf-shed begins. From this data, height of understory vegetation and average visual percentage along the Robel pole was determined for analysis. This occurred in 2003 (control and treatment grids), 2004 and 2012 (post-treatment in control and treatment grids). See Appendix A-2 for field data collection form.

Grass and forb biomass is an indicator of forage availability for ungulates. Its sampling method was adopted from Arizona (2002) and was conducted from mid-August to mid-September, when biomass is at its peak. In each grid, 10 random grid points and an associated direction from the grid point were determined using a random number table. A 1 x 1 m wooded frame was placed 3 m from a selected grid point using the selected direction. The plot was rejected if > 4% (i.e., 20 X 20 cm) of the framed area was obstructed by a tree, stump, unburned brush pile, ash pile, or dense shrub patch. If rejected, the frame was repositioned at a distance of 5 m and attempted again. If rejected, the frame was placed at 7 m. If rejected a third time, the direction was changed (clockwise) and the process was restarted at 3 m. A photo of the frame was taken for future reference prior to clipping (Troxel & White, 1989). All grass and forbs were clipped at 1 cm above the ground and separated into different paper bags in the field. In the lab, initial weights were measured with a precision of 0.1 grams prior to drying and final weights were measured after being placed into a drying oven for a minimum of 24 hours at 40 °C. The average weight of an empty paper bag was then subtracted from the final weight (7.1 grams). This survey was completed in 2004 and 2012 (control and treatment sites).

To determine forage use by ungulates, in June 2012, two grazing enclosures (1 m × 1 m × 2.5 m) were randomly placed within each grid. Cages were obtained from the Government of Alberta Range Resource Management Department in Pincher Creek, Alberta. Cages were made of rebar (outside frame) and wire mesh within the frame. Biomass collection occurred from August 30 to September 12, 2012 and followed the same protocol above except plots were place inside and outside of the cage (3 m away from the cage in a random direction).

Relative ungulate habitat use can be estimated by conducting pellet counts which is considered to be as accurate as those obtained by radio tracking and direct observation (Edge & Marcum, 1989; Loft & Kie, 1988). Pellet data collection followed methods described by Edge and Macum (1989) and White (2001). Three 90 m transects were sampled within each grid. Sampling was conducted twice per year to reduce error due to age of pellets. Sampling occurred prior to spring green-up and before plant senescence in the fall (Stelfox, 1995). Further, sampling was not conducted if rain fell within 18 hours, which can cause the pellet surface to be moist, and colours altered, reducing the accuracy to determine the age and species of pellets. Species and age of pellet groups (i.e., 'summer' or 'winter' and 'current' or 'old') was identified separately for each 25 m section of the transect. Pellet piles were counted when more than 50% of the pellets were within 1 m of the transect center line. Pellet piles with less than 20 pellets were not recorded. Pellet surveys were collected in the fall of 2003 (September 17 to October 27; n= 23), summer of 2004 (June 29 to July 15, n=23) and fall of 2004 (September 27 to October 27; n=23), for a total of 6,210 m each year.

3.2.4 Data analysis

Data analysis for understanding the response of vegetation and ungulate usage to the FireSmart program occurred in two parts. Part one involved using non-parametric tests to determine (1) how similar the control and treatments grids were, (2) how site conditions and vegetation characteristics differed among the three stand types, and (3) how vegetation and ungulate usage changed following timber removal. Although part one gives a basic understanding of what variables changed after the treatment, it was not able to account for the nested nature of the FireSmart monitoring design (i.e., multiple plots within each grid and multiple grids representing one stand type). In order to account for the variation within each stand type and grid, as well as to account for the repeated measures over time, linear regression models with mixed effects were developed.

3.2.4.1 Part 1

In order to determine if the associated treatment and control grids were similar in vegetation characteristics prior to treatment, I evaluated the difference of treated and control sites using pair-wise comparisons of Mann-Whitney U-tests (Mann & Whitney, 1947). However, only ungulate pellet counts and vertical sight distance was reported as these surveys were the only variables in which data was collected for both treatment and control grids prior to timber removal.

Site conditions and vegetation characteristics that were different among stand types prior to timber removal were determined using nonparametric Kruskal-Wallis tests (Breslow, 1970). Post hoc Mann-Whitney U-tests with Bonferroni correction were used to distinguish statistically different groups within each stand type that was found to have significant differences. Three stand types included: Open Pine, Closed Pine and Douglas fir.

Vegetation characteristics and ungulate forage usage that changed following timber removal (i.e., comparison between same grids before and after treatment) were examined with pair-wise Mann-Whitney U-tests. Bonferroni correction was not used because each variable was evaluated independently in the direction that was expected. However, if the bonferroni correction was applied, the level of correction would be $p=0.001042$ (48 tests total), which exceeds the level I used to describe in the results. Only results which were highly significant statistically ($p<0.001$) and biologically significant to ungulates were reported; for all other results refer to Appendix B, table B-2.

Unless stated otherwise, the significance level for tests was set to 0.05 and R (R Core Team, 2012) was used for the analysis.

3.2.4.2 Part 2

Linear regression models with mixed effects were developed to examine the relationship between vegetation response and elk use to various site characteristics (such as treatment stage and stand type). Linear mixed models are statistically rigorous and used to describe a relationship between a response variable and covariates that have been measured or observed along with the response. Further, they include random effects to account for a repeated measured design (Baayen, Davidson, & Bates, 2008). Vegetation cover, biodiversity, biomass and structure as well as ungulate relative presence were modeled. Fix effects included the number of years since treatment, treatment phase (i.e., control grids before and after timber removal, and treatment grids before and after timber removal), and stand type (Open Pine, Closed Pine and Douglas fir). Treatment phase and stand type used dummy variables to account for their categorical nature. The reference category for ‘treatment phase’ was *pre-control* or *pre-treatment* depending on the variable. *Open Pine* was the reference category for ‘stand type'. Stand type was incorporated into the linear models as it is known to impact the response of vegetation following timber removal as it influences the seed bank for regenerating species and is related to understory vegetation production (Crawford, 1976; Kramer & Johnson, 1987). Before integrating stand types into the model, it is essential to determine if and how stand types differ from each other, which will be competed in part 1 of the analysis (see above).

Prior to the development of the models, all predictive variables were tested for pairwise correlation using Pearson correlation coefficients. Variables were excluded when the correlation index (r) was ≥ 0.7. For random effects, I assigned *grid number* to account for the repeated measures among years. As well, I assigned *plot number* as nested within *grid number* to account for autocorrelation arising from the spatial hierarchy of the sampling design and to capture the variability within each grid.

Models were selected following a forward stepwise procedure using likelihood ratio tests with the effect in question against the model without the effect in question, to determine which variables should be used in the final model (Pinheiro & Bates, 2000). Normality of the residuals and the coefficient of determination (R^2) were examined to check the models assumptions and determine model fit (Nagelkerke, 1991). I used R (R Core Team, 2012) and the package *lme4* (Bates, Maechler, & Bolker, 2012) for the analysis as it offers reliable algorithms for parameter estimation (Bates, 2005).

3.3 Results

General characteristics of the grids confirmed that the study area is in the montane ecoregion, at the valley bottom and with an elevation of 1050 m (range of 1019 m - 1175 m). The slope ranged from 0-22% with a mean of 4.73%, as most grids were flat or gentle (see table 3-3). Seventy percent of grids had a mesic moisture regime while the rest were distributed among xeric and hydric regime, as indicated in table 3-3.

Table 3-3: Physical attributes (topographic position and moisture regime) of treatment and control grids in the FireSmart area of Jasper National Park, Alberta, 2003-2012.

Physical attributes	**Percent of grids**
Topographic Position	
Flat	32.90%
Gentle Slope	38.60%
Mild Slope	8.57%
Irregular	5.71%
Rolling	4.29%
Concave	4.29%
Convex	1.43%
Gentle Rolling	1.43%
Irregular Rolling	1.43%
Steep Slope	1.43%
Moisture Regime	
Mesic	69.99%
Xeric	14.28%
Mesic/Hydric	7.17%
Hydric	4.28%
Mesic/Xeric	4.28%

In total, 164 plant species were identified, however, the number of species found varied by forest stratum. Five tree species were found including *Pseudotsuga menziesii* (Douglas fir), *Pinus contorta* (lodgepole pine), *Picea glauca* (white spruce), *Populus tremuloides* (trembling aspen), as well as few unidentified salix species. On treatment grids before timber removal, there was 55.20% (SD: 12.90) tree cover. Lodgepole pine accounted for 75% of trees present on treatment grids, while only 48% of trees on pre-treated control grids. Douglas fir, white spruce and trembling aspen accounted for the remaining percent cover. The average number of tree species found in each plot of the overstory layer was 1.65, while more tree species were found in the understory layer (μ=2.36). Overstory tree ages ranged from 39 to 250 years old and understory tree ages range from 32 to 102 years old. Overall, Douglas fir was found to be the oldest species (μ=143.1 years), followed by trembling aspen (μ=97.6 years), lodgepole pine (μ =

94.1 years) and white spruce (μ=88.7 years). The oldest Douglas fir trees were found on treatment grids before timber was removed (μ=197.5 years old).

Twenty shrub species were found in total; the most common were *Shepherdia canadensis* (Buffaloberry), *Symphoricarpos albus* (common snowberry), *Rosa acicularis* (prickly rose), *Juniperus communis* (common Juniper), and *Alnus viridis* (green alder). Five dwarf shrubs were found, including *Arctostaphylos uva-ursi* (bearberry), *Vaccinium caespitosum* (dwaft blueberry) and *Juniperus horizontalis* (creeping juniper). Prior to timber removal, shrub cover was 39.43% (SD: 16.63). On average, 3.42 shrub species were found in each plot, with a range of 1- 11. The highest species richness was found in shrubs that were 0.5 m to 2 m tall (μ=6.95, SD = 1.71), while the lowest number of species was found in the dwarf shrub layer (μ=1.09, SD = 0.40).

Overall, 113 species of grass and forbs were identified with the most common being in the *Poa* spp. (bluegrass), *Elymus innovatus* (hairy wildrye), *Agropyron* spp. (Crusted wheatgrass), *Viola adunca* (early blue violet), *Linnaea borealis* (twinflower), and *Epilobium angustifolium* (fireweed). Grass and forb cover was 39.67% (SD: 18.42) on treatment sites prior to timber removal. On average, 13.38 grass and herb species were identified in each plot with a range of 3-25. Nine species of moss were found with the most common being *Hylocomium splendens* (star step moss), *Pleurozium schreberi* (feather moss) and *Ptilium crista-castrensis* (knights plume moss). Five species of lichen were identified, including *Peltigera aphthosa* (Freckle pelt lichen), *Peltigera canina* (dog pelt), and *Peltigera collina* (lichen tree pelt). More moss species were identified than lichen species (moss: μ=2.62, SD = 1.10, lichen: μ=1.59, SD = 0.78). 43.70% (SD: 24.11) of the ground surface was covered with mosses and lichen on grids before tree removal occurred.

3.3.1 Similarity of sites before treatment

Elk and deer pellet groups were present on all sites prior to tree removal (i.e. treatment), confirming prior ungulate usage of the entire study area. Although elk present was higher on all sites than deer, elk and deer usage was similar on treated (Elk: μ=71.50 (3.05); Deer: μ=66.67 (5.57) and control (Elk: μ=80.67(4.42); Deer: μ=64.99(2.29) sites prior to tree removal (Elk: U = 9048.5, P = 0.1637; Deer: U = 2468, P = 0.5761).

Additionally, before treatment occurred, average vertical sight distance percent in control sites was 47.24% (SE: 2.00) and in treatment site was 47.52% (SE: 1.98). Control and treatment sites prior to any treatment were not significantly different (U = 5347.50, P = 0.987).

Table 3-4: Mean ungulate usage and understory forage structure (SE) prior to timber removal in control and treatment grids, in Jasper National Park, Alberta, 2003-2012.

	Control	Treatment	*U*	*P*
Ungulate Usage				
Elk (pellet groups/ha)	80.67 (4.42)a	71.50(3.05)a	9048.5	0.164
Deer (pellet groups/ha)	64.99 (2.29)a	66.67 (5.75)a	2468	0.576
Forage Cover/Structure				
Foliage Cover*	47.24 (2.00)a	47.52 (1.98)a	5347.5	0.987
*percent that can be seen within a 2 m vertical rod 15 away from observer				

3.3.2 Differences in stand types prior to timber removal

Topographic features did not differ significantly among stand types except for elevation. All stands were in the valley bottom, with a mean slope of 4.07%, a mean aspect of 226.85 degrees, and at a submesic moisture regime. Elevation was significantly lower on Open Pine (μ=1037.6 m) and Douglas fir (μ = 1029.0 m) stands than on Closed Pine stands (μ = 1058.3 m, H = 13.19, p=0.001). Ground cover did not significantly differ among stand types, except for litter and humus. Open Pine (μ = 67.7%) and Douglas fir (μ = 45.0%) stands had a significantly higher percentage of litter and humus than the Closed Pine stand (μ = 24.6%).

Overstory tree density was significantly higher in Closed Pine (μ = 644.4 stems/ha) stands compared to Open Pine (μ = 306.2 stems/ha) and Douglas fir (μ = 214.8 stems/ha) stands. Douglas fir stands, on the contrary, had significantly higher regeneration trees (μ = 3474.07 stems/ha) compared to Open and Closed Pine stands (549.39 stems/ha). Understory and sampling tree density did not significantly differ among stand types (178.6 and 335.8 stems/ha respectively).

Mean diameter of trees was significantly higher on Open Pine and Douglas fir stands (μ = 26.1 cm) compared to the Closed Pine stand (μ = 21.6 cm). Douglas fir stand had the tallest trees (μ = 27.0 m), followed by Closed Pine (μ = 22.5 m) and Open Pine (μ = 20.5 m) stands. Overstory tree age also differed among stands; Douglas fir stand had the oldest trees (μ = 196.7 years), compared to Closed Pine (μ = 112.0 years) and Open Pine (μ = 111.0 years) stand. Understory tree age did not differ among stand types and was an average of 75 years old. Open Pine and Douglas fir had significantly lower tree and bryoid cover (tree cover: μ = 48.3%, bryoid cover: μ = 38.4%) compared to Closed Pine (tree cover: μ = 65.9%, bryoid cover: μ = 72.6%). Additionally, Open Pine and Closed Pine stands had significantly higher grass and forb cover (μ = 41.3%) than Douglas fir (μ = 16%) stand. Shrub cover did not differ significantly among stand types.

Open Pine and Douglas fir stands had significantly higher total tree richness (μ = 2.39), overstory trees (μ = 2.20), shrubs 2 m to 5 m (μ = 1.81); however, lower total bryoid (μ = 1.26), and moss (μ = 1.35) compared to the Closed Pine stand. Open Pine and Closed Pine stands had significantly higher grass and forb richness (μ = 7.74) than the Douglas fir stand (μ = 3.5).

Open Pine and Douglas fir stands had significantly higher biodiversity in overstory trees (average of 0.30), shrubs (2-5m) and sampling trees (average of 0.46), compared to the Closed Pine stand (overstory: 0.10; shrubs (2-5m) and sampling trees: 0.02). Open Pine stand had a higher biodiversity of shrubs (0.40) than Douglas Fir and Closed Pine stands (0.19). Closed Pine stand had the highest biodiversity of grass and forbs (0.62), bryoid (0.20) and lichen (0.10), while the lowest biodiversity was found in Open Pine stand (0.39, 0.05, and 0.04 respectively).

Open Pine stand had the highest grass and forb biomass (grass: 35.17 g/m^2; forb: 4.88 g/m^2) compared to Closed Pine (grass: 30.39 g/m^2; forb: 3.17 g/m^2) and Douglas fir stands (grass: 29.30 g/m^2; forb: 3.17 g/m^2).

Elk and deer used each stand type similarly prior to timber removal. On average, 71.25 elk pellet groups/ha and 65.35 deer pellet groups/ha were found. Further, average visual sight distance did not differ significantly among stand types (μ=49.2%) however Closed Pine stand did have a significantly higher understory vegetation height (μ=112.5 cm) compared to the Open Pine stand (μ=61.32 cm).

3.3.3 Changes in plant community following timber removal

As mentioned above, unless otherwise stated, only results which were highly significant statistically (p<0.001) and biologically significant to ungulates were reported; for all other results refer to Appendix B, table B-2.

Tree characteristics

As expected, overstory tree density decreased after timber removal by 63% to 145.27 stems per ha (U = 5898.5, P < 0.0001), while understory tree density decreased by 39% to 111.11 stems per ha (U = 4915.5, P < 0.0001) (figure 3-5). On the other hand, sapling tree density increased by 53% to 543.88 stems per ha (U = 4368.5, P = 0.01) following thinning. Although tree density decreased, mean overstory tree diameter increased following timber removal from 23.98 cm to 28.41, an increase of 18% (U = 415.5, P <0.001). As well, overstory tree age decreased by 16% from 116.37 to 96.93 years old (U = 2193, P <0.001), while understory tree age did not change with tree removal (average 59.25 years old).

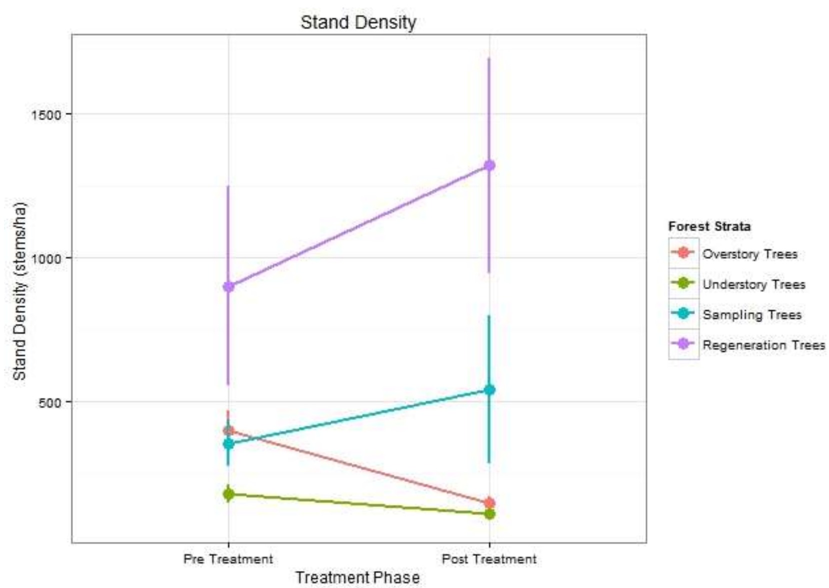

Figure 3-5: Stand density (stems/ha) before and after timber removal in overstory, understory, sampling and regeneration trees in Jasper National Park, Alberta.

Timber removal only caused a significant change in the litter and humus layer of ground cover, which decreased by 49% (from 53.4% to 26.8). All other ground cover layers were not affected by the logging operation.

Species composition

Timber removal resulted in a significant change in vegetation cover of trees, grasses and forbs and byroids (figure 3-6). Although tree cover declined by 47% (from 55% to 29%) (U = 1555.5, p < 0.0001), timber removal lowered tree cover by 34.8% ± 3.8 ($\chi^2(1)$ = 56.506, p<0.001), while the number of years since treatment increased tree cover by 1.8% ± 0.5 ($\chi^2(1)$ = 14.0, p<0.001).

Even though the Mann-Whitney U-test revealed that there was no change in shrub cover following timber removal (U = 925.5, p = 0.728), models showed that stand type affected shrub cover ($\chi^2(2)$ = 6.8377, p<0.032), increasing it by 15.21% ± 5.71 in the Douglas Fir stand and increasing it by 1.4% ± 3.36 in the Closed Pine Stand, compared to Open Pine stand. As the number of years since treatment increases, shrub cover increases by 3.2% ± 0.39 ($\chi^2(1)$ = 50.092, p<0.001). Tree cover also affected shrub cover ($\chi^2(1)$ = 44.88, p<0.001), increasing it by 0.59% ± 0.07.

Grass and forb cover was shown to increase by 50% (U = 446.5, p < 0.0001) following timber removal. Models indicate that it was affected by stand type ($\chi^2(2)$ = 9.5034, p<0.008637), lowering it by 21.1% ± 7.25 in the Douglas Fir Stand and lowering it by 15.6% ± 5.48 in the Closed Pine Stand. Also, years since treatment affected grass and forb cover ($\chi^2(1)$ = 83.399, p<0.0000001), increasing it by 4.2% ± 0.34.

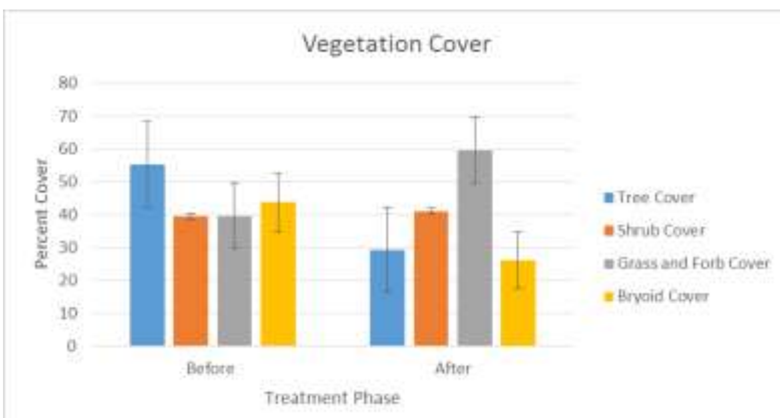

Figure 3-6: Tree, shrub, grass and forb and bryoid vegetation cover before and after FireSmart program's timber removal in Jasper National Park 2003-2012.

Species richness and diversity

Tree, grass and forb and moss species richness also changed significantly following timber removal. Tree species richness (in both overstory and understory layer) declined by 20% to an average of 1.8 species (U = 4488.5, p < 0.001). Grass and forb species increased by 102% to 15.1 species (U = 1.6, p < 0.001), while moss increased by 53.33% (U = 283.5, p < 0.001) to 2.53 species.

Following timber removal both shrub (0.5-2 m) and regeneration tree and grass and forb layers increased significantly in diversity (figure 3-7). Shrub and regeneration tree diversity increased by 27% to 0.66 (Simpson diversity index) and was affected by both treatment phase and the number of years since treatment. Number of years since treatment ($\chi^2(1) = 4.808$, p = 0.028) increased shrub diversity by 0.009 ± 0.004, while treatment phase ($\chi^2(2) = 11.298$, p=0.004), increased it after timber removal by 0.12 ± 0.04 on control grids and by 0.09 ± 0.04 on treatment grids, compared to pre-treated treatment grids.

Grass and forb diversity increased by 50% to 0.69 (Simpson diversity index) and was affected by both stand type and treatment phase. Stand type ($\chi^2(2) = 8.984$, p = 0.011), increased grass and forb diversity by 0.07 ± 0.3 in the Douglas fir stand and increased it by 0.07 ± 0.02 in the Closed Pine stand compared to Open Pine (figure 3-7). Treatment phase ($\chi^2(2) = 70.698$, p < 0.001), increased diversity after timber removal by 0.25 ± 0.03 on control sites and by 0.23 ± 0.03 on treatment sites.

The coefficient of determination (R^2) for the species diversity models ranged from 0.34 to 0.49 (Table 3-5).

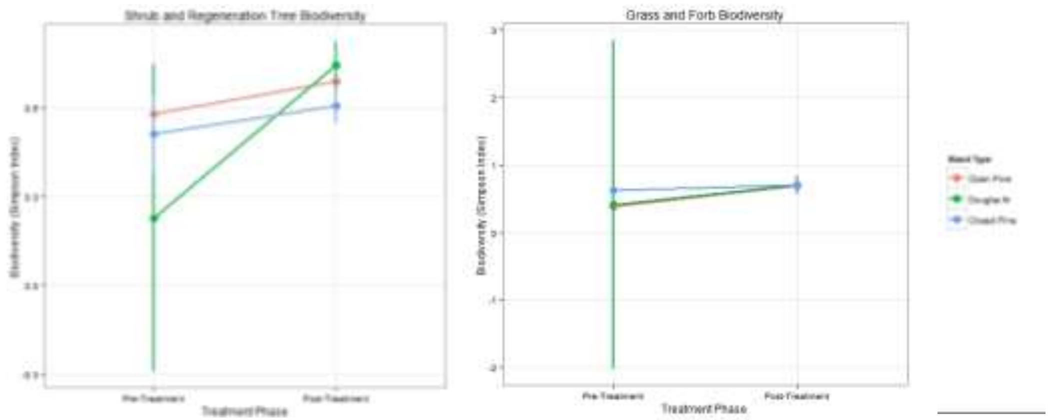

Figure 3-7: Shrub and regeneration tree and grass and forb diversity before and after timber removal of the FireSmart treatments according to stand type (Open Pine, Douglas fir, and Closed Pine) in Jasper National Park, Alberta, 2003-2012

Grass and forb biomass

Biomass of grass and forbs both increased significantly following thinning (figure 3-8). Grass increased by 333% from 7.53 g/m^2 to 32.61 g/ m^2 (U = 1749.5, P < 0.001). Forb biomass increased by 548% from 0.59 g/ m^2 to 4.05 g/ m^2 (U = 2153.5, P < 0.001). Total grass and forb biomass was not only dependent on the treatment itself, but also on stand type. Stand type affected biomass ($\chi2(2) = 15.672$, p<0.001), lowering it by 20.6 g/ m^2 in the Douglas fir stand and lowering it by 14.0 g/ m^2 in the Closed Pine stand compared to Open Pine. Treatment phase affected total biomass ($\chi2(3) = 22.199$, p<0.001), compared to pre-thinned treatment sites, biomass is increased by 4.1 g/ m^2 ± 6.4 on control sites prior to timber removal, increased by 7.6 g/m2 ± 5.1 on control sites after timber removal and increased it by 17.1 g/ m^2± 3.9 on treatment after tree removal (figure 3-9). The coefficient of determination (R^2) for the grass and forb model was 0.38.

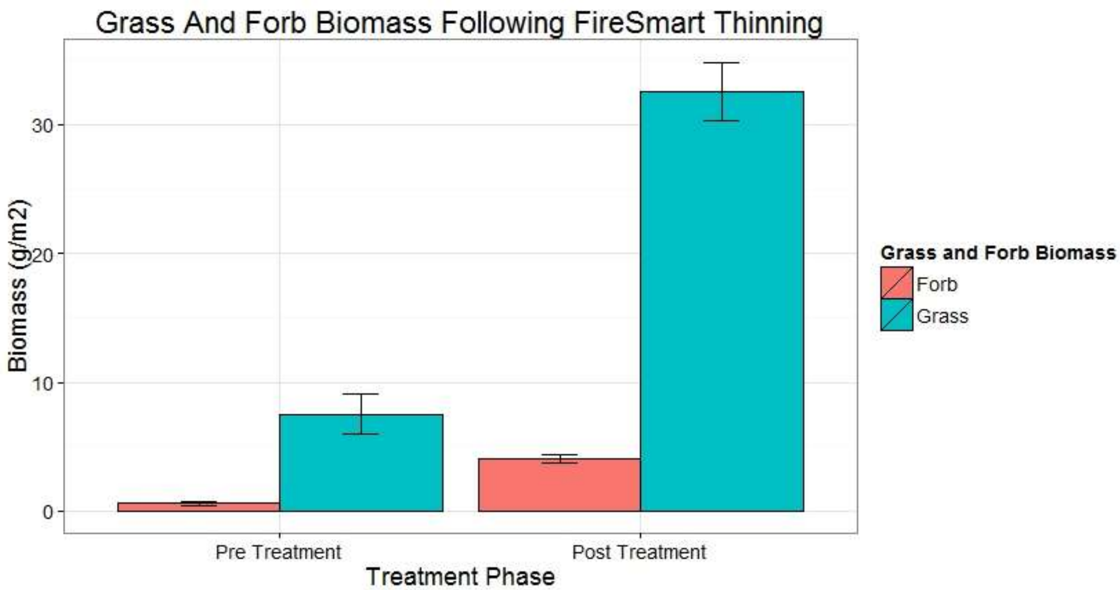

Figure 3-8: Grass and forb biomass (g/m^2) before and after FireSmart timber removal on treatment in Jasper National Park, Alberta, 2003-2012

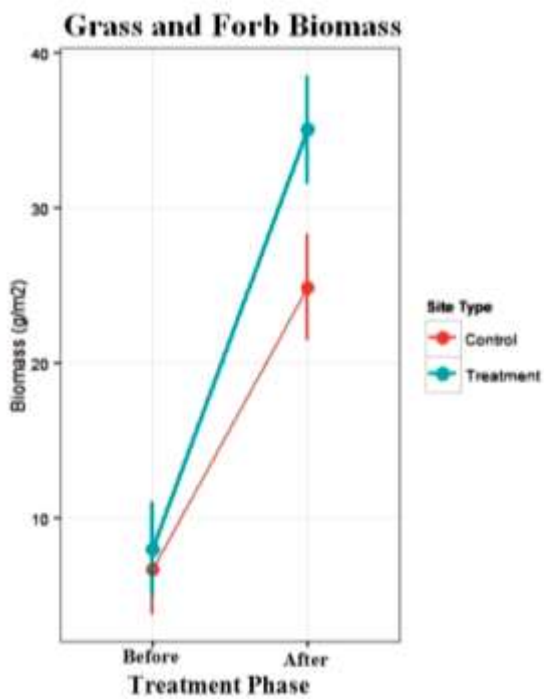

Figure 3-9: Total biomass (grass and forb) before and after FireSmart timber removal on treatment and control sites in Jasper National Park, Alberta, 2003-2012

Ungulate usage

Following timber removal, elk and deer usage increased on all sites (figure 3-10). On average, the elk relative usage increased by 42% to an average of 101.6 pellet groups per ha ($U = 7494$, $p < 0.001$). Elk usage was dependent on treatment phase and season. Treatment phase ($\chi2(3) = 22.3$, $p<0.001$) on control sites increased elk usage by 7.50 pellet groups/ha ± 6.94 prior to tree removal and increased it by 27.51 pellet groups/ha ± 11.05 after tree removal. Treatment sites increased by 28.65 pellet groups/ha ± 6.72 after treatment occurred compared to pre-treated treatment sites. Season affected elk usage ($\chi2(1) = 15.262$, $p<0.001$), increasing it by 21.25 pellet groups/ha ± 5.40 in winter, compared to summer.

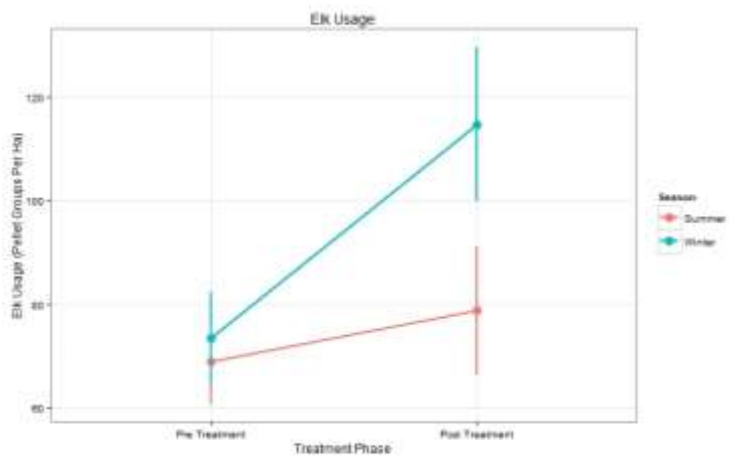

Figure 3-10: Elk relative usage (pellet groups/ha) before and after FireSmart timber removal in summer and winter seasons in Jasper National Park, Alberta, 2003-2012.

Vegetation structure

Timber removal significantly increased the understory vegetation height ($U = 82357.0$, $p < 0.001$) from 52.55 cm to 78.35 cm, a change of 49.0%. Due to the nature of the survey, random effects for forage cover was changed to center points nested in grids compared to plots within grids for the other models. Treatment phase affected minimum forage height ($\chi^2(3) = 118.8$, $p < 0.001$), lowering it by 27.05 cm ± 6.47 on control sites before tree removal occurred, increasing it by 30.772 cm ± 5.41 on control sites after tree removal, and increasing it by 25.81 cm ± 5.24 on treatment sites after treatment occurred compared to pre-treated treatment sites (table 3-5).

Table 3-5: Linear regression mixed models for vegetation cover, biomass, ungulate usage, forage height, and species biodiversity for the FireSmart program in Jasper National Park, Alberta, 2003-2012, includes covariate estimates (standard error) and R^2.

Model	No. years since treatment	Treatment Phase*¹			Stand Type*²				
		Pre-Control	Post-Control	Post-Treatment	Douglas fir	Closed Pine	Tree Cover	Season (winter)*³	R^2
Vegetation Cover									
Tree	1.78 (0.5)			-34.76 (3.8)					0.54
Shrub	3.21 (0.39)				15.21 (5.71)	1.41 (3.36)	0.59 (0.07)		0.57
Grass and Forb	4.14 (0.34)				-21.41 (7.25)	15.54 (5.48)			0.74
Biomass									
Grass and Forb		4.10 (6.4)	7.61 (5.1)	17.1 (3.9)	-20.57 (6.45)	-13.97 (3.21)			0.38
Ungulate Usage									
Elk		7.50 (6.94)	27.51 (11.05)	28.65 (6.72)				21.25 (5.40)	0.08
Deer		-0.74 (6.93)	2.81 (11.39)	21.97 (7.05)				17.22 (5.78)	0.09
Forage Structure									
Understory forage height		-27.05 (6.47)	30.77 (5.41)	25.81 (5.24)					0.07
Biodiversity									
Overstory Trees			-0.14 (0.05)	-0.07 (0.04)					0.36
Understory Trees	-0.01 (0.005)								0.34
Shrubs and sampling trees			0.35 (0.10)	-0.01 (0.08)					0.43
Shrubs and regeneration Trees	0.009 (0.004)		0.12 (0.04)	0.095 (0.04)					0.42
Grass and Forbs			0.25 (0.03)	0.023 (0.03)	0.073 (0.30)	0.067 (0.02)			0.46
Moss (Db)			0.24 (0.05)	0.19 (0.04)	0.127 (0.5)	0.210 (0.03)			0.38
Lichen (Dl)	0.02 (0.01)								0.49

*¹Treatment sites prior to timber removal was used as the reference category for comparisons within the Treatment Phase variable

*²Open Pine was used as the reference category for Stand Type variable *³Summer was used as the reference category for Season variable

3.3.4 Elk forage consumption

Grazing cages excluded ungulates from grazing inside the cages in order to determine the amount of grazing intensity of grass and forbs in the area. No grazing effect on grasses was found on control and treatment grids, however, grass biomass was higher on treated grids (average=26.5 g/m^2) compared to control grids (average=16.1 g/m^2) (table 3-6). Forbs, however, were found to be grazed on both treated and control grids. On treated grids, there was a 34.2% forb consumption rate, while on controls grids the forb consumption rate was 33.7%.

Table 3-6: Grass and forb biomass (g/m^2) (SE) for inside and outside grazing cages in Control and Treatment areas within Jasper National Park using pair-wise comparisons by Mann-Whitney U-tests.

	Inside Grazing Cage	**Outside Grazing Cage**	**Consumption Rate***	***U***	***P***
Control Grids					
Grass (g/m^2)	15.26 (4.26)	16.92 (5.16)	-10.89%	146.5	0.526
Forb (g/m^2)	4.62 (1.27)	3.06 (0.85)	33.76%	64	0.04
Treated Grids					
Grass (g/m^2)	25.55 (3.55)	27.51 (5.09)	-7.67%	119	0.919
Forb (g/m^2)	3.19 (0.91)	2.10 (0.80)	34.17%	22.5	0.02
*Consumption rate based on Bonham (1989), % consumption = 100 * (B_i - B_0)/ B_i where B_i = dry weight of biomass inside grazing cage, and B_0=dry weight of biomass outside cage					

3.4 Discussion

Control and treatment sites prior to timber removal were found to be similar in both ungulate usage and understory vegetation height, confirming all sites were equally used by elk and had similar understory vegetation structure prior to the logging operation. Further, these characteristics were similar across all stand type examined. Other vegetation characteristics were different among stand types prior to timber removal, including tree height and width, vegetation cover, species richness and diversity as well as grass and forb biomass. Since vegetation characteristics were found to be different among stand types examined, it was incorporated into the linear modeling in order to determine how the stand type influences vegetation response to the FireSmart program.

3.4.1 Responses of vegetation communities to timber removal

The most detrimental effects of timber harvesting on soils result from forest floor removal and soil compaction (Keenan & Kimmins, 1993). Ground cover, including deadfall, exposed mineral soil, rock and stone, did not change following the FireSmart program timber removal. This indicates that operational practices were conducted with minimal damage to the ground cover. Operations occurred in winter, which is known to reduce the impact on the forest floor and the in situ seed bank as the ground is frozen (Keenan & Kimmins, 1993; Outcalt & White, 1981). Additionally, logging on flat terrain, such as in the study area, often results in insignificant soil erosion, depending on the type of logging operation (Keenan & Kimmins, 1993). The percentage of litter and humus, however, significantly decreased following timber removal. Litter and humus are the surface accumulation of organic matter on the forest floor and are made up of plant remains as well as by-products of decomposition (Prescott et al., 2000). It is considered important to the sustainability of long-term forest productivity as it is the main source of nutrients and contributes to moisture retention and soil structure (Prescott et al., 2000). Following timber removal, Jurgensen et al. (1997) found that the decomposition of humus recovered in the short term (<5 year) due to the increase in soil temperature and moisture (Covington, 1981; Keenan & Kimmins, 1993). Damage from the logging operation in the FireSmart program should fully recover back to pre-logged levels within <5 years to 80 years depending on the degree of disturbance and forest type (Covington, 1981; D'Antonio & Vitousek, 1992; Prescott et al., 2000).

The growth of understory species following a disturbance is a dynamic process. Establishment and growth is influenced by available vegetative regeneration (Buse & Bell, 1992; Kemball et al., 2005), seed banks (Halpern, 1988; Morgan & Neuenschwander, 1988), precipitation, solar radiation, soil nutrients (Crawford, 1976; Ford, 1984), and varies with the type, intensity, and frequency of the disturbance, stand structure, and stand type (Keenan & Kimmins, 1993). The question on how the FireSmart program timber removal operation affected stand and vegetation composition was answered with clarity. Within a nine-year period following logging, plant communities decreased in stand density but increased in herbaceous biomass, diversity and species richness, and shrub cover, all of which are key components of forage for ungulates (Kufeld, 1973).

A direct result of timber removal was the decline in overstory and understory tree density, height, age, cover, and overstory tree richness, due to the loss of overstory trees from logging. Simultaneously there was no change in overstory or understory diversity, indicating that although logging practices targeted certain species (i.e., lodgepole pine), it did not change their relative species abundance. At the same time, sampling tree density increased following tree removal, which mainly included lodgepole pine (65.6% average percent cover) and Douglas fir (57.6% average percent cover). Lodgepole pine is a shade intolerant, early seral species (Daniel, Helms, & Baker, 1979) while Douglas fir is considered to be moderately shade-tolerant (Burns & Honkala, 1990). In low light, shade-intolerant species often have greater height growth than more shade-tolerant species (Beaudet & Messier, 1998). However, the sudden increase in light from the opening of the canopy would promote the rapid increase in seedling growth, especially for shade-intolerant species, like lodgepole pine (Kemball et al., 2005; Wright, Canham, & Coates, 2000).

Grass and forbs cover, biomass, richness, and diversity all increased following timber removal. Herbaceous forage, especially grasses, are physiologically adapted to grow rapidly in high light situations; as well they can regenerate rapidly from underground rhizomes, from seed buried in the soil or be dispersed by wind (Keenan & Kimmins, 1993). Other studies have shown that following timber removal, grass and forbs have increased in biomass for approximately 10 years then slowly decline as the cut block age and the canopy closure increases (Visscher & Merrill, 2009).

Grass and forb biomass was influenced by the timber removal process as well as stand type. Post-treated grids were significantly higher in biomass than on control sites, indicating the change in biomass was not a result of improved environmental conditions, for example more precipitation. Grass and forb biomass in the Open Pine stands was the highest, followed by the Douglas fir stand. Open Pine stands has a more open overstory structure and may promote more herbaceous growth before timber removal compared to other stand types; this may have resulted in the higher increase in grass and forb biomass following logging.

Stand type was found to influence grass and forb biomass, cover, and diversity following timber removal. Many other studies have also found that forest characteristics, such as stand type, influence vegetation response to disturbances (Bergeron, Harvey, Luduc, & Gauthier, 1999; Crawford, 1976; Keenan & Kimmins, 1993). Although this study focused on certain stand types that were located in the area, the applicability of these results is not limited to areas with similar stand characteristics. Regardless of the stand type, logging increased all aspects of forage for ungulates. Therefore it is expected that if logging operation, like the FireSmart program, is applied to other areas with different cover types, it will cause an increase in forage availability, however the magnitude of response will be determined by the stand characteristics, such as stand type.

3.4.2 Responses of elk in changes in plant communities

As demonstrated in chapter 2, elk are influenced by the distribution and quality of forage resources on the landscape (Langvatn & Hanley, 1993; Thomas & Toweill, 1982; Van Dyke et al., 2012; Wilmshurst, Fryxell, & Hudson, 1995). Logging operations, which creates openings in forests are considered to be beneficial to ungulates as they often increase forage production and edge habitat (Basile & Jensen, 1971; Harper, 1971; Krefting, 1962; Lyon & Jensen, 1980). Lyon and Jensen (1980) found that ungulates often use the opening in search of better quality or greater quantities of forage. However, this is often influenced by security requirements during the feeding period to protect against predators. Elk and deer were also found to prefer openings with cover in the opening except where such cover inhibited forage growth.

Results showed that both elk and deer increased their use of the treated areas one year after timber removal. Ungulate presence was influenced by season (i.e., summer or winter). Compared to the summer, winter elk usage was higher, indicating that ungulates use these open areas more often during the winter. Elk may need to access the openings where forage abundance is higher in the winter when forage availability is limited (Robinson, Hebblewhite, & Merrill, 2010). Additionally, increases in the diversity index, richness and overall cover had the largest change in magnitude in grass and forbs layer, which is the most important component of elk forage (Van Dyke et al., 2012), especially in winter (Hebblewhite, 2006).

Although both grass and forb biomass increased on treated sites, only forbs were found to be consumed by ungulates during the two month period the grazing cages were set up. In early spring, elk are known to consume species that begin to grow early in the season (i.e., grasses) and may increase their consumption of forbs during the summer (Kufeld, 1973; Thomas & Toweill, 1982). Since the grazing cages were only set up during the summer, they maybe not have captured the spring feeding of grasses.

Ungulate populations have been known to disperse or even decline when forests mature and increase in crown closure (Peek, Dennis, & Hershey, 2002). However, ungulate populations can be maintained or increased when forage is provided during times of limited resource (Boyce, 1988). Therefore, an increase of grass and forb biomass is critical to ungulates on forested landscapes (Irwin & Peek, 1983; Visscher & Merrill, 2009) especially those that have been ingrown from fire suppression policies in the past.

3.5 Conclusions

The goal of the FireSmart – ForestWise program in Jasper National Park is to reduce the risk of wildfire losses to the town and adjacent development as well as to restore the ecological condition of the fire-dependent areas and to enhance wildlife habitats (Parks Canada and Municipality of Jasper 2011). FireSmart programs have been implemented across North America and Australia; however a detailed account on the impact of vegetation characteristics following this program has not been documented. To my knowledge, I provided the first detailed assessment of vegetation response to a FireSmart Program in Canada and results are intended to inform future conservation and management approaches within the Canadian Rockies and to provide a comparative measure for future research in the area. The knowledge gathered will enhance the efficiency of habitat management of human-altered landscapes as well as provide better predictions of the effects of future development in previously unaltered environments.

In conclusion, the FireSmart program in Jasper National Park increased forage availability for ungulates by increasing grass and forb biomass, cover and diversity and shrub cover, all key components of elk diet. Magnitude of the vegetation response was found to depend on not only the logging operation of the time since it occurred, but also stand characteristics, such as stand type.

Chapter 4: Synthesis and Management Implications

4.1 Summary

I studied forest stand management and implications for elk forage selection in Jasper National Park, Alberta. Seasonal resource selection patterns of 10 individual elk were developed by examining the factors leading to elk habitat occupancy within the study area for winter and summer. Resource selection function methods were used to characterize and predict elk habitat relationships (Boyce & McDonald, 1999; Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006; Manly, 1993a; McDonald, Thomas, McDonald, & Erickson, 2002) using generalized linear mixed models to account for individual elk behavior. In the summer, elk preferably selected for broadleaf forests, open wetland, herbaceous, and open conifer land cover while in the winter, the most common land cover types that were selected were herbaceous, shrubs, open conifer and barren land. Additionally, elk selected for lower snow cover in the winter and selected areas with high predation risk from wolves. Older FireSmart treated areas were preferred year round and in the winter, elk preferred older burns, however in the summer, elk preferred newer burn sites.

The resource selection models indicated that elk select for areas that would be enhanced by natural or human made disturbance as they selected for herbaceous, shrub and open conifer habitat types as well as FireSmart treated areas and burn sites. The FireSmart – ForestWise program in Jasper National Park was designed to mimic natural disturbance, such as fire, and consisted of timber removal and prescribed fire. Vegetation response to timber removal was examined and it was found to result in a decrease in stand density but an increase in herbaceous biomass, diversity and species richness, and shrub cover, all of which are key components of forage for ungulates (Kufeld, 1973). Magnitude of the vegetation response was found to depend on not only the logging operation itself, but also on stand characteristics, such as stand type. Overall, the FireSmart program increased forage availability for ungulates surrounding the town of Jasper as it promoted multiple aspects of ungulate forage.

Additionally, deer and elk increased their use of the treated areas one year following timber removal. This was especially true in the winter, however also occurred in the summer season.

This finding was in direct agreement with the developed resource selection function models, as FireSmart areas were selected more often in the winter than in the summer.

4.2 Study limitations

Regardless of the general trends and implications of this study, there are a number of limitations. Resource selection functions only offer one method for examining animal response to landscape features. One of its shortcomings is that patterns of selection cannot be related to habitat quality. Although habitats that elk select were identified, the quality of these sites was not measured. Elk may be selecting for habitats that are of lower quality for processes such as reproduction or survival and which may ultimately result in negative growth rates (Battin 2004).

Nevertheless, resource selection functions are valuable because they are spatially explicit, predictive, and simultaneously quantify response to multiple landscape variables. As such, they are often used in conservation and wildlife planning (Boyce et al., 2002) and provide an assessment of important attributes of areas utilised by targeted animals. Maps, such as the one developed, could be used by managers when considering developing permits, conservation planning and or used to identify important areas for habitat enhancement.

RSF maps which were developed in this study may identify areas that meet the habitat requirements for elk, but does not necessarily mean that elk occupy those areas. Nor does it provide any information regarding elk density or carrying capacity for elk on the landscape. However, the in-sample validation and variation explained through inclusion of a random effect for individuals revealed that elk response was similar across each individual that was examined within the study area. Therefore, it can be inferred that if elk are present in areas without collared animals, they would select areas predicted by the RSF model.

In terms of the FireSmart project, limitations were mainly based on inconsistent or incomplete data collection. Collection of data prior to timber removal on control grids would have allowed to accurately determine if control and treatment sites were statistically different prior to logging. With this data, a more traditional Before-After-Control-Impact (BACI) design could have been followed in order to detect change after the logging occurred and make sure that the detected change was due to the logging itself and because of a more favorable climate condition during the time of monitoring.

Additionally, although it is beneficial to have the FireSmart program adaptive to operational changes that need to occur, it makes it difficult when using permanently marked plots in the field. Due to operational changes, six of the 23 grids were only half logged, causing some data to be eliminated entirely from the dataset. Therefore, it is recommended that the grids also be adaptive to operational changes on the ground and be able to shift in space when needed.

4.3 Future research

There are many possible avenues for future research that can be developed from this study, as it was the first examination of vegetation response to FireSmart operations that is known. Since the FireSmart program was developed to mimic natural fire disturbance, comparing vegetation response of the timber removal to a natural and/or prescribed burn would be helpful in determine how effective these goals were being achieved. This could be accomplished by establishing and surveying similar monitoring grids in comparable stand types which have recently been burned or will be burned in the future using prescribed burning. Further, the elk RSFs developed in this survey found that elk select for both the FireSmart treatment areas as well as burn sites, depending on age of the burn. Comparing multiple burn sites which have been burned at different periods in the past may reveal what particular characteristics elk are attracted to or avoid in those areas. Since elk are in decline in JNP any additional knowledge on their habitat requirements and behaviour could help park managers make effective decisions.

The FireSmart program was also designed to be monitored over the long term. Over time, trees will recolonize the treated area and forage availability for ungulates will change. It would be beneficial to continue to monitor these changes every five years, as was suggested by Westhaver (2003), to capture the fine scale changes in vegetation response to these treatments. This would allow managers to understand when it will be important to actively remove trees from these areas again in order to maintain effective wildlife habitat.

Additionally, although the predicted outcomes for the elk RSFs were generally consistent with other studies, the underlying mechanisms can only be inferred. Sampling at a finer scale might identify factors driving larger-scale habitat selection. More detailed sampling could include examination of critical factors neglected in the research presented, such as forage quality. Fine scale variables could then be included in larger scale models to increase their predictive capabilities.

As well, updating spatial layers, such as the human activity level, would make the models more accurate to the current conditions. The data that was used for this analysis was estimated in 2005 and should be updated. Additionally, since, monitoring of elk continues in Jasper National Park, it would be interesting to examine whether future elk response is consistent with model predictions. This could also be examined using previous telemetry data from VHF collars, however there would be a much lower number of observations.

Further, once more GPS data collection has been done on elk in Jasper National Park, RSF could be created separately for elk habituated to town compared to non-habituated elk. I was unable to complete this analysis, unfortunately, due to the small sample size of collared elk which were habituated to the town of Jasper (n=4). Once more data becomes available, models could be developed to compare these two different groups to determine if they have different habitat selection strategies and requirements. Habituated elk continue to cause problems for residents, such as vehicle collisions and aggressive encounters, and understanding their particular habitat requirements would be beneficial for managers to be able to provide what they need outside of town.

This study only examined female elk habitat selection, as they represent the segment of the population which is most responsible for driving overall population dynamics (Eberhardt, 2002). However, male elk behavior may be different as past studies have indicated that female and male elk selected for different landscape characteristics especially cover types, topographic features and distance to humans (Mccorquodale, Raedeke, & Taber, 1986; Mccorquodale, 2003; Unsworth, Kuck, Garton, & Butterfield, 1998). As well, RSFs could be developed on a finer scale to understand the complexity of elk behavior in more detail. For example, during calving season, female elk may have different habitat requirements compared to the rest of the year. As well, the results of the RSF could be combined with other herbivore species in Jasper National Park, such as white tailed and mule deer, to further understand herbivore selection and to identify prime ungulate habitat.

4.4 Management implications and recommendations

Parks Canada is mandated to maintain and enhance ecological integrity in our protected areas for all Canadians. This is to ensure the protection of biological and ecological resources against the threat of human activities for future generations. However the concentration of millions of visitors each year to Canada's National Parks limits the pristine and untouched qualities for which they are often celebrated. Further, Parks Canada mandate is also to foster public understanding, appreciation and enjoyment of National Parks. Parks managers must balance the activities that promote ecological integrity while also protecting people, their property and provide recreational access. Although promoting natural disturbances, such as fire would benefit landscape heterogeneity and enhanced ecological integrity, it is not always feasible when adjacent to urban developments. Programs such as the FireSmart-ForestWise provide an alternative to this dilemma.

FireSmart-ForestWise programs have been implemented across North America and Australia; however a detailed account on the impact of vegetation characteristics following this program has not been documented. These results will inform future conservation and management approaches within the Canadian context. Additionally, this study helps to resolve knowledge gaps regarding the relationships and response of various wildlife and habitat elements to vegetation management treatments, which were identified during the design process for the FireSmart monitoring program (see Westhaver (2003)).

Fire suppression has had a lasting effect on the landscape in Jasper National Park, especially in the montane ecoregion which evolved and is adapted to fire disturbance. Long term restoration efforts are necessary to reduce the multiple negative effects of fire suppression, including forest ingrowth and a reduction of grassland areas. The FireSmart-ForestWise program is only one initative which can be used to mitigate these fire suppression effects and it is recommended that the program is continued in Jasper National Park as it fulfills many aspects of Parks Canada's mandate, including maintaining ecological integrity, by promoting wildlife habitat and restoring disturbance to the landscape. It is recommended that the area continues to be monitored whenever possible in order to determine how vegetation will respond in the long term to changes in the environment, which is a known gap of knowledge in the literature.

Bibliography

Achuff, P. L., Westhaver, A. L., & Mitchell, M. (2001). *Fire/vegetation groups, fire cycles, fire behavior prediction fuel types, and annual burn areas in Jasper National Park* (p. 20).

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, *74*(5), 1313–1325.

Ager, A. A., Johnson, B. K., Kern, J. W., & Kie, J. G. (2003). Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy*, *84*(3), 1076–1088.

Anderson, D. P., Forester, J. D., Turner, M. G., Frair, J. L., Merrill, E. H., Fortin, D., Boyce, M. S. (2005). Factors influencing female home range sizes in elk (Cervus elaphus) in North American landscapes. *Landscape Ecology*, *20*(3), 257–271.

Andison, D. W., & Forest, F. M. (2000). *Landscape-level fire activity on foothills and mountain landscapes of Alberta*. Foothills Model Forest.

Angermeier, P. L., & Karr, J. R. (1994). Biological integrity versus biological diversity as policy directives: protecting biotic resources. *BioScience*, *44*(10), 690–697.

Arno, S. F. (1980). Forest fire history in the northern Rockies. *Journal of Forestry*, *78*(8), 460–465.

Association, N. F. P. NFPA 1144–Standard for protection of life and property from wildfire, 2002 edition. , NFPA. Batterymarch Park, MA. 19p (2013).

Augustin, N. H., Mugglestone, M. A., & Buckland, S. T. (1996). An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology*, 339–347.

Austin, M. P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, *157*(2), 101–118.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412.

Babbitt, R. E., & Hungerford, R. D. (1987). Overstory removal and residue treatments affect soil surface, air, and soil temperature : implications for seedling survival.

Bailey, J. K., & Whitham, T. G. (2002). Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. *Ecology*, *83*(6), 1701–1712.

Basile, J. V, & Jensen, C. E. (1971). Grazing potential on lodgepole pine clearcuts in Montana.

Bates, D. (2005). Fitting linear mixed models in R. *R News*, *5*(1), 27–30.

Bates, D. M., Maechler, M., & Bolker, B. M. (2012). lme4: Linear mixed-effects models using S4 classes.

Beall, R. C. (1976). Elk habitat selection in relation to thermal radiation. In *Proc. Elk-logging Roads Symp., Univ. Idaho, Moscow, ID* (pp. 97–100).

Beaudet, M., & Messier, C. (1998). Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Canadian Journal of Forest Research*, *28*(7), 1007–1015.

Beckingham, J. D., Corns, I. G. W., & Archibald, J. H. (1996). *Field guide to ecosites of west-central Alberta*.

Beier, P., & McCullough, D. R. (1990). Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs*, (109).

Bennington, C., & Thayne, W. (1994). Use and Misuse of Mixed Model Analysis of Variance in Ecological Studies. *Ecology*, *75*(3), 717–722.

Bergeron, Y., Harvey, B., Luduc, A., & Gauthier, S. (1999). Forest management guidelines based on natural disturbance dynamics: stand and forest level considerations. *The Forestry Chronicle*, *75*(1), 49–54.

Beschta, R. L., & Ripple, W. J. (2007). Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research*, *37*(10), 1873–1885.

Beyer, H. L. (2012). Geospatial Modelling Environment (Version 0.7.2.0). (software). Retrieved from URL: http://www.spatialecology.com/gme.

Bjørneraas, K., Moorter, B., 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.

Bonham, C. D. (1989). *Measurements for terrestrial vegetation*. New York: John Wiley & Sons.

Bormann, F. H., & Likens, G. E. (1979). *Pattern and process in a forested ecosystem*. Springer-Verlag.

Boyce, M. S. (1988). Elk winter feeding dampens population fluctuations at the national elk refuge. *Western States and Provinces Elk Workshop Proceedings*.

Boyce, M. S. (1991). Migratory behavior and management of elk (< i> Cervus elaphus</i>). *Applied Animal Behaviour Science*, *29*(1), 239–250.

Boyce, M. S., & McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, *14*(7), 268–272.

Boyce, M. S., Mao, J. S., Merrill, E. H., Fortin, D., & Turner, M. G. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, *10*(4), 421–431.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, *157*, 281–300.

Bradley, M., & Neufeld, L. (2012). Climate and management interact to explain the decline of woodland caribou (Rangifer tarandus caribou) in Jasper National Park. *Rangifer*, *32*(2).

Breslow, N. (1970). A Generalized Kruskal-Wallis Test for Comparing K Samples Subject to Unequal Patterns of Censorship. *Biometrika*, *57*(3), 579.

Buckland, S. T., & Elston, D. A. (1993). Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology*, 478–495.

Burcham, M., Edge, W. D., & Marcum, C. Les. (1999). Elk use of private land refuges. *Wildlife Society Bulletin*, *27*(3), 833–839.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer.

Burns, R. M., & Honkala, B. H. (1990). *Silvics of North America. Volume 1. Conifers* (p. 675). Washington: Agriculture Handbook.

Buse, L. J., & Bell, F. W. (1992). *Critical silvics of selected crop and competitor species in northwest Ontario*. *Forest Technology Development Unit*.

Cairns Jr, J., McCormick, P. V, & Niederlehner, B. R. (1993). A proposed framework for developing indicators of ecosystem health. *Hydrobiologia*, *263*(1), 1–44.

Cairns, J. (1977). *Quantification of biological integrity*. US Government Printing Office.

Calenge, C., Dufour, A. B., & Maillard, D. (2005). K-select analysis: a new mathod to analyse habitat selection in radio-tracking studies. *Ecological Modelling*, *186*(2), 143–153.

Callicott, J. B., & Mumford, K. (1997). Ecological as a Conservation Concept Sustainability. *Conservation Biology*, *11*(1), 32–40.

Cannell, M. G. R. (1999). Environmental impacts of forest monocultures : water use , acidification , wildlife conservation , and carbon storage. *New Forests*, *17*, 239–262.

Chavardès, R. D. (2014). *Fire history and climate-fire relations in Jasper National Park, Alberta, Canada*. University of British Columbia.

Christianson, D. A., & Creel, S. (2007). A review of environmental factors affecting elk winter diets. *The Journal of Wildlife Management*, *71*(1), 164–176.

Clark, B. K., Clark, B. S., Johnson, L. A., & Haynie, M. T. (2001). Influence of Roads on Movements of Small Mammals. *The Southwestern Naturalist*, *46*(3), 338–344.

Clark, D. F., Antos, J. A., & Bradfield, G. E. (2003). Succession in sub-boreal forests of West-Central British Columbia. *Journal of Vegetation Science*, *14*(5), 721–732.

Conard, J. M., Statham, M. J., Gipson, P. S., & Wisely, S. M. (2010). The influence of translocation strategy and management practices on the genetic variability of a reestablished elk (Cervus elaphus) population. *Restoration Ecology*, *18*(1), 85–93.

Cook, J. G. (2002). Nutrition and food. *North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, DC, USA*, 259–349.

Covington, W. W. (1981). Changes in Forest Floor Organic Matter and Nutrient Content Following Clear Cutting in Northern Hardwoods. *Ecological Society of America*, *62*(1), 41–48.

Covington, W. W., & Moore, M. M. (1994). Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry*, *2*(1-2), 153–181.

Crawford, H. S. (1976). Relationships between forest cutting and understory vegetation: an overview of eastern hardwood stands. *USDA Forest Service Reserach Paper*.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, *23*(4), 194–201.

Creel, S., & Creel, M. (2009). Density dependence and climate effects in Rocky Mountain elk: an application of regression with instrumental variables for population time series with sampling error. *Journal of Animal Ecology*, *78*(6), 1291–1297.

Creel, S., & Winnie Jr, J. A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, *69*(5), 1181–1189.

Creel, S., Christianson, D., Liley, S., & Winnie, J. a. (2007). Predation risk affects reproductive physiology and demography of elk. *Science (New York, N.Y.)*, *315*(5814), 960.

Cronin, J. K. (2010). *Manufacturing National Park Nature: Photography, Ecology, and the Wilderness Industry of Jasper*. UBC Press.

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, *23*(1), 63–87.

Daigle, P. (1996). *Fire in the dry interior forests of British Columbia*. British Columbia Ministry of Forests Research Program.

Daniel, T. W., Helms, J. A., & Baker, F. S. (1979). *Principles of silviculture* (2nd ed.). New York: McGraw-Hill Book Company.

DeCesare, N. J. (2012a). Separating spatial search and efficiency rates as components of predation risk Separating spatial search and efficiency rates as components of predation risk. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1747), 4626–4633.

DeCesare, N. J. (2012b). Separating spatial search and efficiency rates as components of predation risk. *Proceedings. Biological Sciences / The Royal Society*, *279*(1747), 4626–33.

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., … Morgantini, L. E. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, *22*(4), 1068–1083.

Dekker, D. (1985). Elk population fluctuations and their probable causes in the Snake Indian Valley of Jasper National Park: 1970–85. *Alta. Nat*, *15*, 49–54.

Dekker, D., & Bradford, W. (2001). Two decades of wildlife investigations at Devona, Jasper National Park, 1981–2001. *Jasper National Park, Jasper, Alta*.

Dekker, D., Bradford, W., & Gunson, J. R. (1995). Elk and wolves in Jasper National Park, Alberta, from historical times to 1992. *Ecology and Conservation of Wolves in a Changing World (Occasional Publication No. 35). Canadian Circumpolar Institute, Edmonton, Alberta, Canada*, 85–94.

Denslow, J. S. (1980). Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia*, *46*(1980), 18–21.

Dickson, B. G., & Beier, P. (2002). Home-range and habitat selection by adult cougars in southern Califrnia. *Journal of Wildlife Management*, *66*(4), 1235–1245.

Dodd, N. L., Gagnon, J. W., Boe, S., & Schweinsburg, R. E. (2007). Assessment of elk highway permeability by using global positioning system telemetry. *Journal of Wildlife Management*, *71*(4), 1107–1117.

Duft, J. F. (1989). *Alpine wildflowers of the Rocky Mountains* (p. 200). Mountain Press.

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology*, *83*(10), 2841–2854.

Econometric Research Limited. (2008). *Hunting in Alberta in 2008: Performance, value and socioeconomic impacts*, 1–45.

Edge, W. D., & Marcum, C. Les. (1989). Determining elk distribution with pellet-group and telemetry techniques. *The Journal of Wildlife Management*, 621–624.

Eon, R. G. D., & Delparte, D. (2005). Effects of radio-collar position and orientation on GPS radio-collar performance , and the implications of PDOP in data screening. *Journal of Applied Ecology*, *42*(2), 383–388.

Eon, R. G. D., Serrouya, R., Smith, G., & Kochanny, C. O. (2002). GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, *30*(2), 430–439.

Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., Ramey, R. R., & McCullough, D. R. (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters*, *8*(10), 1029–1038.

ESRI. (2011). ArcGIS Desktop: Release 10.1. Redlands, CA: Environmental Systems Research Institute.

Felix, A. B., Walsh, D. P., Hughey, B. D., Campa, H., & Winterstein, S. R. (2007). Applying Landscape-Scale Habitat-Potential Models to Understand Deer Spatial Structure and Movement Patterns. *The Journal of Wildlife Management*, *71*(3), 804–810.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, *24*(01), 38–49.

Flook, D. R. (1962). Range relationships of some ungulates native to Banff and Jasper National Parks, Alberta. In *Grazing in terrestrial and marine environments: a symposium of the British Ecological Society* (11), 1–14.

Ford, E. D. (1984). Dynamics of plantation growth. In *Nutrition of plantation forest*. GD Bowen, ESK Nambiar.

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., … Heanue, K. (2003). *Road ecology*. Island Press Washington, DC.

Frair, J. L., Merrill, E. H., Beyer, H. L., & Morales, J. M. (2008). Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology*, *45*(5), 1504–1513.

Frair, J. L., Merrill, E. H., Visscher, D. R., Fortin, D., Beyer, H. L., & Morales, J. M. (2005). Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, *20*(3), 273–287.

Franklin, J. E., & Forman, R. T. T. (1987). Creating landscape patterns by forest cutting : Ecological consequences and principles. *Landscape Ecology*, *1*(1), 5–18.

Fryxell, J. M., & Sinclair, A. R. E. (1988). Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, *3*(9), 237–241.

Gagnon, J. W., Theimer, T. C., Dodd, N. L., Boe, S., & Schweinsburg, R. E. (2007). Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management*, *71*(7), 2318.

Geist, V. (2002). Adaptive behavioral strategies. *North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, DC, USA*, 219–277.

Gibeau, M. L., Herrero, S., McLellan, B. N., & Woods, J. G. (2001). Managing for grizzly bear security areas in Banff National Park and the Central Canadian Rocky Mountains. *Ursus*, 121–129.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., … Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, *75*(4), 887–898.

Government of Alberta. (2009). *2008-2009 Transporation Annual Report*. Edmonton, Alberta.

Graham, R. T., McCaffrey, S., & Jain, T. B. (2004). *Science basis for changing forest structure to modify wildfire behavior and severity* (p. 43 pp).

Haeussler, S., & Bergeron, Y. (2004). Range of variability in boreal aspen plant communities after wildfire and clear-cutting1. *Canadian Journal of Forest Research*, *34*(2), 274–288.

Hall, C. M., & Shultis, J. (1991). Railways, tourism and worthless lands: the establishment of national parks in Australia, Canada, New Zealand and the United States. *Australian Canadian Studies*, *8*(2), 57–74.

Halpern, C. B. (1988). Early successional pathways and the resistance and resilience of forest communities. *Ecology*, *69*(6), 1703–1715.

Harper, J. A. (1971). *Ecology of Roosevelt elk*. Portland, Oregon.

Hebblewhite, M. (2000). *Wolf and elk predator-prey dynamics in Banff National Park*. University of Montana Missoula, Montana.

Hebblewhite, M. (2006). *Linking Predation Risk and Forage to Ungulate Population Dynamics.* University of Alberta.

Hebblewhite, M., & Merrill, E. H. (2009a). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, *90*(12), 3445–3454.

Hebblewhite, M., & Merrill, E. H. (2009b). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, *90*(12), 3445–54.

Hebblewhite, M., Merrill, E. H., & Mcdonald, T. L. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos*, *1*(February), 101–111.

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.

Hebblewhite, M., Munro, R. H., & Merrill, E. H. (2009). Tropic consequences of postfire logging in a wolf-ungulate system. *Forest Ecology and Management*, *257*, 1053–1062.

Hebblewhite, M., Pletscher, D. H., & Paquet, P. C. (2002). Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, *80*(5), 789–799.

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., … Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, *86*(8), 2135–2144.

Hershey, T. J., & Leege, T. A. (1976). Influences of logging on elk on summer range in northcentral Idaho. In *Proceedings, Elk logging roads symposium* (pp. 73–80).

Hicks, J. F., Rachlow, J. L., Rhodes Jr, O. E., Williams, C. L., & Waits, L. P. (2007). Reintroduction and genetic structure: Rocky Mountain elk in Yellowstone and the western states. *Journal of Mammalogy*, *88*(1), 129–138.

Hillis, J. M., Thompson, M. J., Canfield, J. E., Lyon, L. J., & Lonner, T. N. (1991). Defining elk security: the Hillis paradigm. *Proceedings Elk Volunerability Symposium*, 38–43.

Hirzel, A. H., & Le Lay, G. (2008). Habitat suitability modeling and niche theory. *Journal of Applied Ecology*, *45*(2), 1372–1381.

Holland, W. D., & Coen, G. M. (1982). *Ecological (Biophysical) Land Classification of Banff and Jasper National Parks. Volume II. Soil and Vegetation Resources. Alberta Institute of Pedology Publication No*. SS-82-44, Edmonton, Alberta.

Holland, W., Coen, G., Holroyd, G., Van Tighem, K., & Pedology, A. I. O. (1983). *Ecological (biophysical) landclassification of Banff and Jasper National Parks.* (p. 540). Alberta, Canada: Alberta Institute of Pedology Publication.

Holroyd, G. L., & Van Tighem, K. J. (1983). Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 3. The wildlife inventory. *Canadian Wildlife Service, Edmonton, Alberta, Canada*.

Hosmer Jr, D. W., & Lemeshow, S. (2004). *Applied logistic regression*. John Wiley & Sons.

Huggard, D. J. (1993). Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology*, *71*(1), 130–139.

Huot, J. (1974). Winter habitat of white-tailed deer at Thirty-one Mile Lake, Quebec. *Canadian Field Naturalist*, *88*, 293–301.

Irwin, L. L., & Peek, J. M. (1983). Elk habitat use relative to forest succession in Idaho. *The Journal of Wildlife Management*, 664–672.

Janz, B., & Storr, D. (1977). *The climate of the Contiguous Mountain Parks: Banff, Jasper, Yoho, Kootenay*.

Jerde, C. L., & Visscher, D. R. (2005). GPS measurement error influences on movement model parameterization. *Ecological Applications*, *15*(3), 806–810.

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. *Journal of Wildlife Management*, *70*(2), 347–357.

Johnson, C. J., Seip, D. R., & Boyce, M. S. (2004). A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*, *41*(2), 238–251.

Johnson, D. H. (1980a). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71.

Johnson, D. H. (1980b). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*(1), 65–71.

Jones, P. F., & Hudson, R. J. (2002). Winter habitat selection at three spatial scales by American elk, Cervus elaphus, in west-central Alberta. *Canadian Field-Naturalist*, *116*(2), 183–191.

Jurgensen, M. F., Harvey, A. E., Graham, R. T., Page-Dumroese, D. S., Tonn, J. R., Larsen, M. J., & Jain, T. B. (1997). Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland northwest forests. *Forest Science*, *43*(2), 234–251.

Karr, J. R., & Dudley, D. R. (1981). Ecological perspective on water quality goals. *Environmental Management*, *5*(1), 55–68.

Karr, J. R., Fausch, K. D., Angermeier, P. L., Yant, P. R., & Schlosser, I. J. (1986). Assessing biological integrity in running waters. *A Method and Its Rationale. Illinois Natural History Survey, Champaign, Special Publication*, *5*.

Kay, C. E. (1995). Aboriginal overkill and native burning : Implications for modern ecosystem management. *Western Journal of Applied Forestry*, *10*, 121–126.

Kay, C. E., & White, C. A. (1995). Long-term ecosystem states and processes in the Central Canadian Rockies: A new perspective on ecological integrity and ecosystem management. In *Contributed Papers of the 8th Conference on Research and Resource Management in Parks and on Public Lands*, 17–21.

Keenan, R. J., & Kimmins, J. P. (1993). The ecological effects of clear-cutting. *Environmental Reviews*, *1*(2), 121–144.

Kemball, K. J., Wang, G. G., & Dang, Q.-L. (2005). Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. *Canadian Journal of Botany*, *83*(12), 1550–1560.

Kershaw, L., MacKinnon, A., & Pojar, J. (1998). *Plants of the Rocky Mountains* (p. 384). Lone Pine Publishing.

Kie, J. G., Ager, A. A., & Bowyer, R. T. (2005). Landscape-level movements of North American elk (<i>Cervus elaphus): effects of habitat patch structure and topography. *Landscape Ecology*, *20*(3), 289–300.

Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, *157*(1), 163–75.

Kloppers, E. L., St Clair, C. C., & Hurd, T. E. (2005). Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society*, *10*(1), 31.

Knapp, A. K., Briggs, J. M., Childers, D. L., Sala, O. E., & Fahey, T. J. (2007). Estimating aboveground net primary production in grassland-and herbaceous-dominated ecosystems. *Principles and Standards for Measuring Primary Production*, 27–48.

Kohm, K. A., & Fraklin, J. F. (Eds.). (1997). *Creating a forestry for the 21st century: The science of ecosystem mangement*. Island Press.

Kramer, N. B., & Johnson, F. D. (1987). Mature forest seed banks of three habitat types in central Idaho. *Canadian Journal of Botany*, *65*(9), 1961–1966.

Krefting, L. W. (1962). Use of silvicultural techniques for improving deer habitat in the Lake States. *Journal of Forestry*, *60*(1), 40–42.

Kufeld, R. C. (1973). Foods eaten by the Rocky Mountain. *Journal of Range Management*, *26*(2), 106–113.

Langvatn, R., & Hanley, T. A. (1993). Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia*, *95*, 164–170.

Leban, F. A., Wisdom, M. J., Garton, E. O., Johnson, B. K., & Kie, J. G. (2001). Effect of sample size on the performance of resource selection analyses. *Radio Tracking and Wildlife Populations*, 291–307.

Leopold, A. (1987). *Game management*. University of Wisconsin Press.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640.

Loft, E. R., & Kie, J. G. (1988). Comparison of pellet-group and radio triangulation methods for assessing deer habitat use. *The Journal of Wildlife Management*, *52*(3), 524–527.

Lyon, L. J. (1979). Habitat effectivness for elk as influenced by roads and cover. *Journal of Forestry*, *77*(10), 658–660.

Lyon, L. J. (1983). Road density models describing habitat effectiveness for elk. *Journal of Forestry*, *81*(9), 592–613.

Lyon, L. J., & Jensen, C. E. (1980). Management implications of elk and deer use of clear-cuts in Montana. *The Journal of Wildlife Management*, 352–362.

Lyon, L. J., & Ward, A. L. (1982). Elk and land management. In *Elk of North America* (pp. 443–477). Harrisburg, Pennsylvania: Stackpole Books.

MacLaren, I. S. (2007). *Culturing wilderness in Jasper National Park: studies in two centuries of human history in the Upper Athabasca River Watershed*. University of Alberta.

Manly, B. F. J. (1993a). Comments on design and analysis of multiple-choice feeding-preference experiments. *Oecologia*, *93*(1), 149–152.

Manly, B. F. J. (1993b). *Resource selection by animals*. London: Chapman and Hall.

Manly, B. F. McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). Resource selection by animals: statistical analysis and design for field studies. *Nordrecht, The Netherlands: Kluwer*.

Mann, H. B., & Whitney, D. R. (1947). On a test of whether one or two random variables is stochastically larger than the other. *The Annals of Mathematical Statistics*, *18*(1), 50–60.

Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M., & Merrill, E. H. (2005). Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management*, *69*(4), 1691–1707.

Marcum, C. Les. (1976). Habitat selection and use during summer and fall months by a western Montana elk herd. In *Proceedings of the elk-logging-roads symposium. Forestry Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho* (pp. 91–96).

Marty, S. (1984). *A grand and fabulous notion: the first century of Canada's parks*. NC press.

Mcclean, S. A., Rumble, M. A., King, R. M., & Baker, W. L. (1998). Evaluation of Resource Selection Methods with Different Definitions of Availability. *The Journal of Animal Ecology*, *62*(2), 793–801.

Mccorquodale, S. M. (2003). Sex-Specific Movements and Habitat Use by Elk in the Cascade Range of Washington. *The Journal of Wildlife Management*, *67*(4), 729–741.

Mccorquodale, S. M., Raedeke, K. J., & Taber, R. D. (1986). Elk Habitat Use Patterns in the Shrub-Steppe of Washington. *The Journal of Wildlife Management*, *50*(4), 664–669.

Mccullough, D. R., & Mccullough, R. (1999). Density Dependence and Life-History Strategies of Ungulates. *Journal of Mammalogy*, *80*(4), 1130–1146.

McDermid, G. J. (2006). *Remote sensing for large-area, multi-jurisdictional habitat mapping.* . University of Waterloo.

McLaren, B. E., & Peterson, R. O. (1994). Wolves, moose, and tree rings on Isle Royale. *SCIENCE-NEW YORK THEN WASHINGTON-*, 1555.

Miller, A. M. (2010). *Living with Boreal forest fires: Anishinaabe perspectivies on disturbance and collaborative forest planning, Pikangikum First Nation, Northwestern Ontario*.

Miller, J., Franklin, J., & Aspinall, R. (2007). Incorporating spatial dependence in predictive vegetation models. *Ecological Modelling*, *202*(3), 225–242.

Mitchell, M. P. (2006). *Montane landscape heterogeneity and vegetation change in Jasper National Park, Alberta (1949--1997)*. University of Northern British Columbia (Canada).

Montgomery, R. a., Roloff, G. J., & Millspaugh, J. J. (2012). Importance of visibility when evaluating animal response to roads. *Wildlife Biology*, *18*(4), 393–405.

Moorcroft, P. R., & Barnett, A. (2008). Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology*, *89*(4), 1112–1119.

Morgan, P., & Neuenschwander, L. F. (1988). Seed-bank contributions to regeneration of shrub species after clear-cutting and burning. *Canadian Journal of Botany*, *66*, 169–172.

Morgantini, L. E., & Hudson, R. J. (1989). Nutritional significance of wapiti (Cervus elaphus) migrations to alpine ranges in western Alberta, Canada. *Arctic and Alpine Research*, 288–295.

Municipality of Jasper and Parks Canada. *Jasper community sustainability plan*. (2011). Jasper, Alberta.

Munro, R., Hebblewhite, M., Visscher, D., Hamilton, S., & Merrill, E. (2002). Preliminary Evaluation of Elk Forage Dynamics After Harvest and Fire in the Central East Slopes of Alberta, *69*(5), 1977.

Murie, O. J. (1951). *The elk of North America*. Harrisburg: Stackpole Company.

Murphy, P. J. (1985). History of forest and prairie fire control policy in Alberta.

Nagelkerke, N. J. D. (1991). A Note on a General Definition of the Coefficient of Determination. *Biometrika*, *78*(3), 691–692.

Naylor, L. M., J. Wisdom, M., & G. Anthony, R. (2009). Behavioral responses of North American elk to recreational activity. *Journal of Wildlife Management*, *73*(3), 328–338.

Neu, D., & Graham, C. (2006). The birth of a nation: Accounting and Canada's first nations, 1860–1900. *Accounting, Organizations and Society*, *31*(1), 47–76.

Nielsen, S. E., Boyce, M. S., Stenhouse, G. B., & Munro, R. H. M. (2002). Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*, 45–56.

Noss, R. (1995). *Maintaining ecoloigcal integrity in representative reserve networks: A world wildlife Fund Canada/World Wildlife Fund United States Discussion Paper*.

O'Gara, B. W., & Dundas, R. G. (2002). Distribution: past and present. *North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, DC, USA*, 67–119.

Otis, D. L., & White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *The Journal of Wildlife Management*, 1039–1044.

Outcalt, K. W., & White, E. H. (1981). Phytosociological changes in understory vegetation following timber harvest in northern Minnesota. *Canadian Journal of Forest Research*, *11*(1), 175–183.

Parks Canada. (2000b). Unimpaired for future generations? Protecting Ecological Integrity with Canada's National Parks. Vol I. A Call to Action. Vol. II Setting a New Direction for Canada's National Parks. Report of the Panel on the Ecological Integrity (EI) of Canada's Nationa. Ottawa, ON.

Parks Canada. (2000c). Jasper National Park of Canada management plan. Catalogue Number R64-105/28-2000E. (D. of C. Heritage, Ed.). Ottawa, Canada.

Parks Canada. (2010). *Jasper National Park Management Plan*. Ottawa, Canada, 1-132.

Parks Canada. Canada National Parks Act. (Parks Canada, Ed.) (2000a). Ottawa, ON: Minsiter of Justice.

Parrish, J. D., Braun, D. P., & Unnasch, R. S. (2003). Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience*, *53*(9), 851–860.

Pauley, G. R., Peek, J. M., & Zager, P. (1993). Predicting white-tailed deer habitat use in Northern Idaho. *The Journal of Wildlife Management*, *57*(4), 904–913.

Peck, V. R., & Peek, J. M. (1991). Elk, Cervus elaphus, habitat use related to prescribed fire, Tuchodi River, British Columbia. *Canadian Field-Naturalist. Ottawa ON*, *105*(3), 354–362.

Peek, J. M., Dennis, B., & Hershey, T. (2002). Predicting population trends of mule deer. *Journal of Wildlife Management*, *66*(3), 729–736.

Pendergast, J. F., Gange, S. J., Newton, M. A., Lindstrom, M. J., Palta, M., & Fisher, M. R. (1996). of Methods Survey Data Response Binary for Analyzing Clustered. *INternational Statistical Review*, *64*(1), 89–118.

Pengelly, W. L. (1972). Clearcutting: detrimental aspects for wildlife resources. *Journal of Soil and Water Conservation*.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, *20*(9), 503–510.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3), 231–259.

Pielou, E. C. (1975). *Ecological diversity* (p. 165). New York: John Wiley & Sons.

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed effects models in S and S-PLUS*. Springer.

Polziehn, R. O. (2000). *Genetic studies of north american wapiti subspecies.* University of Alberta, Edmonton, Alberta.

Post, E., & Stenseth, N. C. (1999). Climatic variability, plant phenology, and northern ungulates. *Ecology*, *80*(4), 1322–1339.

Preisler, H. K., Ager, A. A., & Wisdom, M. J. (2006). Statistical methods for analysing responses of wildlife to human disturbance. *Journal of Applied Ecology*, *43*(1), 164–172.

Prescott, C. E. (1997). Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. *Forest Ecology and Management*, *95*(3), 253–260.

Prescott, C. E., Maynard, D. G., & Laiho, R. (2000). Humus in northern forests: friend or foe? *Forest Ecology and Management*, *133*(1-2), 23–36.

Proctor, M. F., McLellan, B. N., Strobeck, C., & Barclay, R. M. R. (2005). Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1579), 2409–2416.

Proffitt, K. M., Grigg, J. L., Garrott, R. A., Hamlin, K. L., Cunningham, J., Gude, J. A., & Jourdonnais, C. (2010). Changes in Elk Resource Selection and Distributions Associated With a Late-Season Elk Hunt. *The Journal of Wildlife Management*, *74*(2), 210–218.

R Core Team. (2012). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Rabb, D., Rooney, R., & Bayley, S. (2013). A visual obstruction method to estimate wet meadow aboveground biomass in marshes of the Boreal Plains, Canada. *Journal of the Society of Wetland Scientists*, *34*(2), 363–367.

Ramovs, B. V, & Roberts, M. R. (2003). Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. *Ecological Applications*, *13*(6), 1682–1700.

Regier, H. A. (1993). The notion of natural and cultural integrity. *Ecological Integrity and the Management of Ecosystems*, *1*, 3–18.

Rhemtulla, J. M. (1999). *Eighty years of change: the montane vegetation of Jasper National Park*. University of Alberta.

Rhemtulla, J. M., Hall, R. J., Higgs, E. S., & Macdonald, S. E. (2002). Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, Alberta, Canada. *Canadian Journal of Forest Research*, *32*(11), 2010–2021.

Richardson, E., Stirling, I., & Hik, D. S. (2005). Polar bear (Ursus maritimus) maternity denning habitat in western Hudson Bay: a bottom-up approach to resource selection functions. *Canadian Journal of Zoology*, *83*(6), 860–870.

Risbrudt, C. (1995). Ecosystem management: a framework for management of our National Forests. *Natural Resources and Environmental Issues*, *5*(1), 1-15.

Robel, R. J., Briggs, J. N., Dayton, A. D., & Hulbert, L. C. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management*, 295–297.

Roberts, M. R., & Gilliam, F. S. (1995). Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. *Ecological Applications*, *5*(4), 969–977.

Roberts, M. R., & Zhu, L. (2002). Early response of the herbaceous layer to harvesting in a mixed coniferous–deciduous forest in New Brunswick, Canada. *Forest Ecology and Management*, *155*, 17–31.

Robinson, B., Hebblewhite, M., & Merrill, E. H. (2010). Are migrant and resident elk (Cervus elaphus) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia*, *164*(1), 265–275.

Robinson, H., Hebblewhite, M., Musiani, M., DeCesare, N., Peters, W., Weckworth, B., & McDevitt, A. (2010). Modeling relationships between fire, caribou, wolves, elk and moose to aid recovery of Southern Mountain Woodland Caribou in the Canadian Rocky Mountain National Parks. Final Report submitted to Parks Canada, Banff and Jasper National Parks, Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., & Musiani, M. (2011). Human Activity Differentially Redistributes Large Mammals in the Canadian Rockies National Parks. *Ecology and Society*, *16*(3).

Roloff, G. J. (1998). Habitat potential model for Rocky Mountain elk. In *Proceedings of the 1997 elk/deer workshop. Phoenix, AZ: Arizona Game and Fish Department* (pp. 158–175).

Rost, G. R., & Bailey, J. A. (1979). Distribution of mule deer and elk in relation to roads. *The Journal of Wildlife Management*, 634–641.

Rowland, M. M., Wisdom, M. J., Johnson, B. K., & Kie, J. G. (2000). Elk distribution and modeling in relation to roads. *The Journal of Wildlife Management*, 672–684.

Rowland, M. M., Wisdom, M. J., Johnson, B. K., & Penninger, M. A. (2005). Effects of Roads on Elk: Implications for Management in Forested Ecosystems, 42–52.

Sachro, L. L., Strong, W. L., & Gates, C. C. (2005). Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada. *Journal of Environmental Management*, *77*(3), 183–193.

Sawyer, H., Kauffman, M. J., Nielson, R. M., & Horne, J. S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, *19*(8), 2016–2025.

Schimmel, J., & Granström, A. (1996). Fire severity and vegetation response in the boreal Swedish forest. *Ecology*, 1436–1450.

Schooley, R. L. (1994). Annual variation in habitat selection: patterns concealed by pooled data. *The Journal of Wildlife Management*, *58*(2), 367–374.

Scott, J. H., & Reinhardt, E. D. (2001). Assessing crown fire potential by linking models of surface and crown fire behavior.

Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, *77*(7), 2075–2085.

Shepherd, B., & Whittington, J. (2006). Response of wolves to corridor restoration and human use management. *Ecology & Society*, *11*(2).

Simpson, E. H. (1949). Measurement of diversity. *Nature*, *163*.

Singh, N. J., Grachev, I. A., Bekenov, A. B., & Milner-Gulland, E. J. (2010). Tracking greenery across a latitudinal gradient in central Asia–the migration of the saiga antelope. *Diversity and Distributions*, *16*(4), 663–675.

Skovlin, J. M., Zager, P., & Johnson, B. K. (2002). Elk habitat selection and evaluation. *Elk of North America: Ecology and Management. Smithsonian Institution Press, Washington, DC*, 531–555.

Skrondal, A., & Rabe-Hesketh, S. (2004). *Generalized latent variable modeling: Multilevel, longitudinal, and structural equation models*. CRC Press.

Soper, J. D. (1970). *The mammals of Jasper National Park, Alberta.*

Stelfox, J. B. (1995). *Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forest in Alberta. Project No. 001A* (p. 308). Edmonton, Alberta.

Stocks, B. J. (1991). The extent and impact of forest fires in northern circumpolar countries. In *Global biomass burning - Atmospheric, climatic, and biospheric implications* (pp. 197–202).

Stocks, B. J., Mason, J. A., Todd, J. B., Bosch, E. M., Wotton, B. M., Amiro, B. D., … Skinner, W. R. (2002). Large forest fires in Canada , 1959 – 1997. *Journal of Geophysical Research: Atmospheres (1984–2012)*, *108*(D1), FFR 5–1–FFR 5–12.

Sweeney, J. M., & Sweeney, J. R. (1984). Snow depths influencing winter movements of elk. *American Society of Mammalogists*, *65*(3), 524–526.

Swetnam, T. W., Allen, C. D., & Betancourt, J. L. (1999). Applied historical ecology: using the past to manage for the future. *Ecological Applications*, *9*(4), 1189–1206.

Tande, D. (1979). Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. *Canadian Journal of Botany*, *57*(18), 1912–1931.

Taper, M. L., & Gogan, P. J. P. (2002). The northern Yellowstone elk: density dependence and climatic conditions. *The Journal of Wildlife Management*, 106–122.

Thomas, J. W. (1979). *Wildlife habitats in managed forests the Blue Mountains of Oregon and Washington* (p. 512). Agriculture Handbook No. 553. U.S. Department of Agriculture, Forest Service.

Thomas, J. W., & Toweill, D. E. (1982). Elk of North America: ecology and management. *Elk of North America: Ecology and Management.*

Thompson, M. J., & Henderson, R. E. (1998). Elk habituation as a credibility challenge for wildlife professionals. *Wildlife Society Bulletin*, 477–483.

Troxel, T. R., & White, L. D. (1989). Balancing forage demand with forage supply.

Unsworth, J. W., Kuck, L., Garton, E. O., & Butterfield, B. R. (1998). Elk habitat selection on the Clearwater national forest, Idaho. *The Journal of Wildlife Management*, *62*(4), 1255–1263.

Van Dyke, F., Fox, A., Harju, S. M., Dzialak, M. R., Hayden-Wing, L. D., & Winstead, J. B. (2012). Response of elk to habitat modification near natural gas development. *Environmental Management*, *50*(5), 942–955.

Visscher, D. R., & Merrill, E. H. (2009). Temporal dynamics of forage succession for elk at two scales: Implications of forest management. *Forest Ecology and Management*, *257*(1), 96–106.

Volney, W. J. A., & Hirsch, K. G. (2005). Disturbing forest disturbances. *The Forestry Chronicle*, *81*(5), 662–668.

Wagner, C. E. Van, Finney, M. A., & Heathcott, M. (2006). Historical fire cycles in the Canadian Rocky Mountain Parks. *Forest Science*, *52*(6), 704–717.

Wagner, C. E. Van. (1995). *Analysis of fire history for Banff, Jasper, and Kootenay National Parks*. Ottawa, ON, Canada.

Walker, P. A. (1990). Modelling wildlife distributions using a geographic information system: kangaroos in relation to climate. *Journal of Biogeography*, 279–289.

Weatherspoon, C. P., & McIver, J. (2000). A national study of the consequences of fire and fire surrogate treatments. *USDA Forest Service Pacific Southwest Research Station, Redding, California, USA*.

Weber, M. G., & Stocks, B. J. (1998). Forest fire and sustainability in the boreal forest of Canada. *Ambio*, *27*(7), 545–550.

Westhaver, A. L. (2003). Environmental Screening Report: FireSmart - ForestWise community protection and forest restoration project. Jasper National Park.

Westhaver, A. L. (2006). *FireSmart - ForestWise: Managing Wildlife and Wildfire Risk in the Wildland/Urban Interface*. University of Calgary, Calgary, Alberta.

White, C. A., Feller, M. C., & Bayley, S. (2003). Predation risk and the functional response of elk–aspen herbivory. *Forest Ecology and Management*, *181*(1), 77–97.

White, C. A., Olmsted, C. E., & Kay, C. E. (1998). Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin*, 449–462.

White, C.A. (2001). Aspen, elk, and fire in the Canadian Rocky Mountains.

White, P. J., Proffitt, K. M., Mech, L. D., Evans, S. B., Cunningham, J. A., & Hamlin, K. L. (2010). Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy*, *91*(4), 827–837.

Whittington, J., St. Clair, C. C., & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications*, *15*(2), 543–553.

Wicklum, D., & Davies, R. W. (1995). Ecosystem health and integrity? *Canadian Journal of Botany*, *73*(7), 997–1000.

Wierzchowski, J., Heathcott, M., & Flannigan, M. D. (2002). Lightning and lightning fire, central cordillera, Canada. *International Journal of Wildland Fire*, *11*(1), 41–51.

Williams, R. L. (1992). *A guide to Rocky Mountain plants* (p. 452). Roberts Rinehart Publishers.

Wilmshurst, J. F., Fryxell, J. M., & Hudson, R. J. (1995). Forage quality and patch choice by wapiti (Cervus elaphus). *Behavioral Ecology*, *6*(2), 209–217.

Winnie Jr, J., Christianson, D., Creel, S., & Maxwell, B. (2006). Elk decision-making rules are simplified in the presence of wolves. *Behavioral Ecology and Sociobiology*, *61*(2), 277–289.

Wolfe, M. L., Kimball Jr, J. F., & Schildwachter, G. T. M. (2002). North American elk: ecology and management. Smithsonian Institution Press, Washington, DC, USA, 583–616.

Woodley, S. J. (1994). *Assessing and monitoring ecological integrity in parks and protected areas*. University of Waterloo.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*(1), 164–168.

Wright, E. F., Canham, C. D., & Coates, K. D. (2000). Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research*, *30*(10), 1571–1580.

Yarie, J. (1993). Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research*, *23*, 1001–1014.

Appendices A: Data sheets for FireSmart monitoring program

Grid # __ Grid Pt. __
Plot # __ Treatment ______
Treatment Date:
Habitat Type:

FIRESMART – FORESTWISE STAND DESCRIPTION

Observer:__________ Date:__________
Location:______________________
Ecoregion:________ Ecosite:__________
UTM: 11U - x
Elevation:________ m Slope:________
Aspect:__________
Topographic Position:__________
Relief shape:__________________
Hygrotope:____________________

DBH range (cm)
DBH mean (cm)
Canopy Ht mean (m)
Ht to Crown Base (m)
Ht of Live Crown (m)

AGE STRUCTURE

LAYER	SPECIES	AGE1	AGE2

General description and remarks

(disturbances, erosion, fire history, wildlife use, etc.)

Vegetation structure:

Stratum		Cover %	Height	Total %
Tree:	A_1	____	(- m)	
	A_2	____	(5 - m)	____
Shrub:	B_1	____	(2 - 5 m)	
	B_2	____	(0.5 - 2 m)	____
Herb:	C_h	____	(herbaceous)	
	C_w	____	(dwarf shrub) <0.5 m	____
Moss: Bryoid	D_b	____	(mosses)	
	D_1	____	(lichens)	____

Ground cover % other than vegetation
L-H:_____ Rocks & stones:_____
Exposed min. soil:_____ Deadfall:_____
Water:_____ Others:______________

DENSITY

LAYER	COUNT	# / Ha.
A1 Overstory		
A2 Understory		
B1 Sapling		
B2 Regeneration		

Figure A-1: Data collection form for monitoring grid characteristics, vegetation composition and tree density for the FireSmart program in Jasper National Park, 2003-2012.

FireSmart-ForestWise Horizontal Sight Distance Form

Grid: _____ Study Area: ________________________ Observers: ____________________

Center GP # ______

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

Center GP # ______

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

Center GP # ______

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

_____	BOTTOM (white)		TOP
Bearing/GP#	V		
_____%	H		
Canopy	LEFT (white)		RIGHT

Site Sketch and Notes:

FireSmart-ForestWise

Figure A-2: Data collection form for horizontal site distance (i.e., vegetation structure) for the FireSmart program in Jasper National Park, 2003-2012.

Appendices B: FireSmart data analysis results

Table B-1: Means and summary of physical characteristics of treatment sites prior to tree removal among stand types in FireSmart experiment in Jasper National Park, Alberta. Krustkal-Wallis tests used to compare stand type characteristics. Letters donate the results of post hoc Mann-Whiney U-tests, the same letter indicates that the means are not significantly different.

Variables	Open Pine	Douglas Fir	Closed Pine	*H*	*P*
Site Conditions					
Mean slope (percent)	3.33 (0.35)a	5.00 (2.52)a	3.89 (1.18)a	0.2369	0.883
Mean moisture regime*	4.39 (0.22)a	3.67 (0.67)a	4.00 (0.33)a	1.9976	0.368
Mean elevation (m)	1037.56 (3.73)a	1029.00 (5.13)a	1058.33 (2.63)	13.1901	0.001
Typical aspect (degrees)	245.67 (18.07)a	223.67 (39.67)a	211.22 (27.41)a	3.2954	0.193
Relief Shape	5.44 (0.44)a	3.33 (0.88)a	3.78 (0.62)a	5.7146	0.057
*based on 1-5 scale (Beckingham et al. 1996, p16-12 and 16-13) 1, very xeric; 2, xeric, 3, subxeric, 4, submesic, and 5, mesic					
Ground Cover (percent cover)					
Deadfall	1.92(0.21)a	3.33 (1.33)a	3.89 (1.05)a	3.7287	0.155
Litter and Humus	67.67 (3.18)a	45.00 (10.07)ab	24.62 (2.95)b	18.15	<0.001
Exposed Mineral Soil	1.67 (0.30)a	3.33 (2.33)a	1.12 (0.36)a	1.9	0.386
Rocks and stones	1.12 (0.16)a	0.00 (0.00)a	2.43 (0.68)a	1.7788	0.411
Stand Density					
Overstory Trees	306.17 (26.25)a	214.81 (47.89)a	644.44 (73.83)	18.87	<0.001
Understory Trees	190.12 (16.95)a	185.19 (37.04)a	160.49 (35.23)a	1.7019	0.427
Sampling Trees	382.72 (58.68)a	303.70 (40.44)a	320.99 (64.93)a	0.3702	0.831
Regeneration Trees	748.15 (119.74)a	3474.07 (1169.62)	350.62 (42.80)a	14.3296	<0.001
Tree Characteristics					
DBH minimum (cm)	24.83 (2.96)a	16.67 (1.33)a	18.33 (2.57)a	1.9213	0.383
DBH maximum (cm)	30.69 (4.89)a	54.67 (10.49)a	32.78 (2.63)a	5.7676	0.056
DBH mean (cm)	24.58 (0.78)a	27.67 (2.19)a	21.56 (0.60)	8.1918	0.017
Mean Canopy height (m)	20.51 (0.48)	27.00 (2.00)	22.50 (0.58)	9.8718	0.007
Mean height of live crown (m)	14.44 (0.69)a	20.25 (2.75)a	14.06 (0.85)a	4.8266	0.09
Height (m)	15.46 (0.56)	19.74 (0.93)a	17.41 (0.46)a	13.5775	0.001
Overstory tree age	110.97 (8.97)	196.67(20.88)	112.00(2.72)	10.9531	0.004
Understory tree age	63.00(13.04)	85.00(NA)	NA	0.5	0.479
Vegetation Cover (percent)					
Tree Cover	51.56 (2.69)a	45.00 (5.77)a	65.89 (3.41)	9.461	0.009
Shrub Cover	33.50 (3.23)a	45.67 (16.19)a	49.22 (4.78)a	5.8171	0.055
Grass and Forb Cover	44.39 (4.65)a	16.00 (2.65)	38.11 (3.89)a	7.396	0.025
Bryoid Cover	28.50 (3.21)a	48.33 (12.02)a	72.56 (3.95)	18.3298	<0.001
Species Richness					
Total Trees	2.61 (0.13)a	2.17 (0.17)ab	1.89 (0.21)b	8.0051	0.018
Overstory Trees	2.39 (0.18)a	2.00 (0.00)ab	1.56 (0.24)b	6.6235	0.036

Understory Trees	2.83 (0.19)a	2.33 (0.33)a	2.22 (0.32)a	3.043	0.218
Total Shrubs	3.40 (0.37)a	1.89 (0.45)a	2.30 (0.35)a	4.9633	0.084
Shrubs (2-5m) and samplings	2.28 (0.18)a	1.33 (0.33)ab	1.22 (0.15)b	11.4918	0.003
Shrubs (0.5-2m) and regeneration trees	6.78 (0.37)	3.33 (0.88)b	4.67 (0.37)b	13.1387	0.001
Dwarf Shrubs	1.00 (0.00)a	1.00 (0.00)a	1.00 (0.00)a	NA	NA
Grass and Forbs	8.28 (0.57)a	3.5 (0.5)	6.67 (0.53)a	8.0029	0.018
Total Byroids	1.19 (0.10)a	1.33 (0.33)ab	1.86 (0.18)b	8.9644	0.011
Moss	1.2 (0.13)a	1.5 (0.5)ab	2.25 (0.16)b	11.4811	0.003
Lichen	1.17 (0.17)a	NA	1.33 (0.21)a	0.7333	0.693
Biodiversity					
Total trees	0.37 (0.03)a	0.34 (0.06)a	0.21 (0.06)a	5.4543	0.065
Overstory trees	0.33 (0.05)a	0.26 (0.08)ab	0.10 (0.04)b	7.0861	0.029
Understory trees	0.42 (0.05)a	0.43 (0.05)a	0.32 (0.09)a	0.2646	0.876
Total Shrubs	0.40 (0.05)a	0.19 (0.11)ab	0.18 (0.05)b	7.2576	0.027
Shrubs (2-5m) and samplings	0.59 (0.09)a	0.33 (0.33)ab	0.02 (0.02)b	10.1921	0.006
Shrubs (0.5-2m) and regeneration trees	0.58 (0.04)a	0.23 (0.12)a	0.51 (0.06)a	5.8516	0.053
Dwarf Shrub	0.00 (0.00)a	0.00 (0.00)a	0.00 (0.00)a	NA	NA
Grass and Forb	0.39 (0.04)a	0.41 (0.19)ab	0.62 (0.01)b	10.1448	0.006
Bryoid	0.05 (0.03)a	0.16 (0.16)ab	0.20 (0.05)b	7.5507	0.023
Moss	0.04 (0.03)a	0.24 (0.24)ab	0.29 (0.04)b	10.3636	0.006
Lichen	0.05 (0.05)a	0.00 (NA)a	0.10 (0.07)a	0.7482	0.688
Biomass					
Grass	35.17 (2.07)a *	29.30 (7.83)b *^{2}	30.39 (3.62)ab *	18.14	<0.001
Forb	4.88 (0.55) *	3.25 (0.71)a *^{2}	3.09 (0.48)a *	13.23	0.001
Used post-treatment plots, not pre-treatment ,* 5 years since treatment, *^{2} 3 years since treatment					
Mean no. Elk pellet groups/transect					
Elk	1.18 (0.07)a	1.32 (0.09)a	1.34 (0.11)a	0.9563	0.62
Elk (pellets per ha)	65.66 (3.79)a	73.38 (5.14)a	74.71 (6.33)a	0.9563	0.62
Deer	1.12 (0.12)a	1.25 (0.18)a	1.15 (0.10)a	0.2877	0.866
Deer (Pellets per ha)	62.50 (6.94)a	69.44 (10.17)a	64.10 (5.79)a	0.2877	0.866
Forage Cover/Structure					
Foliage Cover *	43.00 (2.43)a	52.51 (5.23)a	52.11 (3.48)a	4.999	0.082
Minimum vegetation height (cm)*^{2}	61.32 (3.79)	NA (NA)	112.5 (5.3)	84.9839	<0.001
*percent that can be seen within a 2 m vertical rod 15 away from observer, *^{2} 30 cm is zero					

Table B-2: Physical and vegetation characteristics (mean (SE)) of treatment sites before and after timber removal in FireSmart experiment in Jasper National Park, Alberta, 2003-2012. Mann-Whitney U-tests used for pair-wise comparisons.

	Treatment Phase				
Variables	Before	After	Effect	*U*	*P*
Ground Cover (percent cover)					
Deadfall	2.65 (0.38)	4.49 (0.55)	+69.43	632	0.056
Litter and Humus	53.45 (4.25)	26.87 (2.86)	-49.73	1330	<0.001
Exposed Mineral Soil	1.73 (0.32)	1.72 (0.23)	-0.58	588	1.000
Other (not enough plots with this type)	2.5 (1.5)	2.40 (0.41)	-4.00	31.5	0.174
Rocks and stones	1.55 (0.27)	2.40 (0.41)	+54.84	389	0.529
Stand Density (stems/ha)					
Overstory Trees	398.52 (34.46)	147.27 (11.38)	-63.04	5898.5	<0.001
Understory Trees	180.74 (14.97)	111.11 (10.49)	-38.52	4915.5	<0.001
Sampling Trees	356.30 (40.28)	543.88 (129.67)	+52.65	4368.5	0.011
Regeneration Trees	901.48 (172.78)	1320.15 (189.09)	+46.44	3458.5	0.803
Tree Characteristics					
DBH minimum (cm)	22.07 (2.01)	26.95 (1.63)	+22.11	623	0.030
DBH maximum (cm)	33.72 (3.39)	35.69 (1.48)	+5.84	766	0.362
DBH mean (cm)	23.98 (0.63)	28.41 (0.74)	+18.47	415.5	<0.001
Mean Canopy height (m)	21.58 (0.48)	20.02 (0.45)	-7.23	1083.5	0.028
Mean height of live crown (m)	14.72 (0.59)	12.93 (0.43)	-12.16	1044.5	0.031
Tree Height (m)	22.12 (0.04)	17.56 (0.33)	-20.61	1207.5	0.006
Overstory tree age	116.37 (6.12)	96.93 (3.86)	-16.71	2193	<0.001
Understory tree age	67.4 (11.02)	59.25 (3.39)	-12.09	97.5	0.450
Vegetation Cover					
Tree Cover	55.20 (2.35)	29.30 (2.15)	-46.92	1555.5	< 0.001
Shrub	39.43 (3.04)	41.03 (3.17)	+4.04	925.5	0.728
Grass and Forb	39.67 (3.36)	59.64 (3.02)	+50.34	446.5	<0.001
Byroid	43.70 (4.40)	26.21 (2.16)	-40.02	1255.5	0.001
Species Richness					
Total Trees	2.35 (0.11)	1.88 (0.08)	-20.00	4488.5	<0.001
Overstory Trees	2.10 (0.15)	1.56 (0.09)	-25.71	1172	0.002
Understory Trees	2.60 (0.16)	2.19 (0.11)	-15.77	1106.5	0.028
Total Shrubs	2.91 (0.26)	3.33 (0.22)	+14.43	7469	0.567
Shrubs (2-5m) and samplings	1.87 (0.15)	1.79 (0.11)	-4.28	906	0.629
Shrubs (0.5-2m) and regeneration trees	5.80 (0.34)	7.10 (0.22)	+22.41	553	0.004
Dwarf Shrubs	1.00 (0.00)	1.05 (0.03)	+5.00	812	0.225
Grass and Forbs	7.45 (0.46)	15.06 (0.53)	+102.15	106	<0.001
Total Byroids	1.48 (0.11)	2.15 (0.12)	+45.27	889	0.002

Moss	1.65 (0.15)	2.53 (0.14)	+53.33	283.5	<0.001
Lichen	1.23 (0.12)	1.37 (0.12)	+11.38	161	0.604
Biodiversity					
Total Trees	0.32 (0.03)	0.26 (0.02)	-18.75	4035.5	0.078
Overstory Trees	0.25 (0.04)	0.18 (0.03)	-28	1067	0.071
Understory Trees	0.39 (0.04)	0.34 (0.03)	-12.82	978	0.342
Total Shrubs	0.31 (0.04)	0.36 (0.03)	16.13	7215	0.380
Shrubs (2-5m) and samplings	0.39 (0.08)	0.38 (0.05)	-2.56	903.5	0.653
Shrubs (0.5-2m) and regeneration trees	0.52 (0.04)	0.66 (0.02)	+26.92	475	<0.001
Dwarf Shrubs	0.0 (0.00)	0.03 (0.02)	0	797.5	0.220
Grass and Forbs	0.46 (0.03)	0.69 (0.02)	+50	200	< 0.001
Total Byroids	0.12 (0.03)	0.25 (0.02)	+108.33	1325.5	0.002
Moss	0.16 (0.04)	0.33 (0.03)	+106.25	300	0.003
Lichen	0.07 (0.04)	0.16 (0.03)	+128.57	345	0.126
Biomass					
Grass	7.53 (1.57)	32.61 (2.26)	+333.33	1749.5	<0.001
Forb	0.59 (0.15)	4.05 (0.35)	+584.18	2153.5	<0.001
Ungulate Usage					
Elk	1.29 (0.05)	1.83 (0.10)	+41.86	7494.5	<0.001
Elk (pellets per Ha)	71.50 (3.05)	101.63 (5.45)	+42.14	7494.5	<0.001
Deer	1.20 (0.10)	1.57 (0.09)	+30.84	1596.5	0.002
Deer (pellets per Ha)	66.67 (5.75)	87.13 (5.43)	+30.69	1596.5	0.002
Forage Cover/Structure					
Foliage Cover *	47.52 (1.98)	48.61 (2.25)	+2.29	8768	0.745
Minimum vegetation height (cm)*²	52.55 (4.0)	78.35 (3.22)	+49.01	82357	<0.001
*percent that can be seen within a 2 m vertical rod 15 away from observer, *² 30 cm is zero					