University of Alberta

The potential influence of mountain pine beetle (*Dendroctonus ponderosae*) control harvesting on grizzly bear (*Ursus arctos*) food supply and habitat conditions in Alberta

by

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Abstract

In response to the mountain pine beetle (*Dendroctonus ponderosae*) threat in Alberta, forest companies plan to surge harvest 75% of susceptible (mature) lodgepole pine (*Pinus contorta*) stands over 20 years. To assess potential changes to grizzly bear (*Ursus arctos*) habitat, I projected food availability over 60 years in the Upper Foothills. I also examined grizzly bear response to pine age, and its interaction with elevation and edge proximity. Post surge, forbs were predicted to increase by 25% and fruits by 2%. After 60 years, forbs should remain above (13%) while fruits could decline below (10%) pre-harvest conditions. Less *Vaccinium membranaceum* shrubs above 1228m and reduced *Vaccinium myrtilloide*s fruit production below 1228m contributed to the decline. If the surge cut proceeds, efforts should be made to increase fruit production by enhancing shrubs at specific environmental conditions (age, elevation). Small cut-blocks near non-harvested pine seemed to be particularly beneficial for bears.

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CHAPTER 1: General Introduction

1.1 Background

After the last glacial retreat, the North American grizzly bear (*Ursus arctos*) had a near continuous distribution that spanned most of the continent (Schwartz *et al.*, 2003). Elevated human-caused mortality with European settlement and the advent of firearms reduced the range of the grizzly bear considerably (Mattson and Merrill, 2002; Ross, 2002). In the continental United States excluding Alaska, the grizzly bear was eliminated from approximately 98% of its historical range and today maintains a threatened status with only 1400 individuals estimated to occur between six recovery zones (Anonymous, 2011). In Canada, during the late 1800's, the Prairie grizzly bear population was extirpated. The Northwest population remains the most robust and is estimated to have over 26,000 bears that occupy portions of the Yukon Territory, the Northwest Territories, Nunavut, British Columbia and Alberta (Ross, 2002). However, habitat loss and degradation leading to unsuitable conditions for survival, reproduction, and dispersal are creating increased challenges for maintaining viable grizzly bear populations into the future (Doak, 1995; Proctor *et al.*, 2012). Habitat loss and degradation seem to be particularly problematic along the southern fringe of the distribution where bear densities are low and subpopulations are isolated from the current continuous distribution (McLellan, 1998; Proctor *et al.*, 2012).

Along the southern fringe of grizzly bear range in British Columbia and Alberta, bears are largely confined to forested and mountainous habitats that occur within protected, crown, or private lands. Density varies considerably and appears to be related to gradients in the anthropogenic footprint coupled with ecosystem productivity (Apps *et al.*, 2004; Mowat *et al.*, 2005; Nielsen *et al.*, 2010). Given the effects of anthropogenic footprint on grizzly bear habitat quality, strategic land-use planning at local and regional scales is required to maintain or enhance effective grizzly bear habitat (North Cascades Grizzly Bear Recovery Team, 2004; Alberta Grizzly Bear Recovery Plan 2008-2013, 2008). Models describing habitat conditions at local and regional scales that influence grizzly bear density, movement, and use of resources (food and cover) are fundamental to land-use planning efforts (Apps *et al.*, 2004; Nielsen *et al.*, 2010; Proctor *et al.*, 2012).

In Alberta's forested land base, the grizzly bear population is believed to have declined from historical levels, possibly because of increases in human access and activity associated with industrial development (oil and gas, mining, and forestry) (Nielsen *et al.*, 2009). Based on a recent status review, the species designation was changed to threatened, while a recovery plan was already in place to address factors influencing grizzly bear population viability (Alberta Grizzly Bear Recovery Plan 2008-2013, 2008; Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). To understand what factors influence grizzly bear distribution and abundance, population inventories using DNA hair-snag techniques, capture and collaring, remote sensing based habitat maps, bear mortality locations, and food studies have been undertaken (Nielsen *et al.*, 2004a; Nielsen *et al.*, 2004b; Nielsen *et al.*, 2004c; Nielsen *et al.*, 2006; Nielsen *et al.*, 2008; Nielsen *et al.*, 2009; Nielsen *et al.*, 2010). Spatial models describing these relationships have been developed and integrated into the land use planning process and form the basis for quantifying the past, present, and future impacts of industrial land-use activities on grizzly bear habitat.

Grizzly bear range in Alberta spans the western edge of the province and includes the Rocky Mountains, foothills, and portions of the Boreal forest from the British Columbia border eastward to the towns of High Level, Peace River, Red Earth, and Slave Lake (Alberta Grizzly Bear Recovery Plan 2008-2013, 2008). Seven population management units are delineated by Alberta's major highways (Figure 1.1). Population units are genetically distinct with males contributing mostly to gene flow between units as female interchange is rare (Proctor *et al.*, 2012). The majority of grizzly bear research to date has occurred within the 6 southern population units that encompass the eastern slopes of the Rocky Mountains (Figure 1.1). Within the 6 southern units, the probability of female grizzly bear occupancy is highest in the conifer-dominated forests of the Upper Foothills, Montane, and Sub-alpine Natural Subregions (Nielsen *et al.*, 2009) (Figure 1.1). Conversely, occupancy is lowest in the lower elevation sub-regions (Central mixed wood, Foothills Fescue, Foothills Parkland) where forests tend to be dominated by deciduous species (Nielsen *et al.*, 2009) (Figure 1.1). These findings are consistent with DNA surveys that suggest bear density is greater along the western boundary and higher elevation areas of the province where the anthropogenic footprint and human activity is lower (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). In support of recovery, grizzly bear conservation areas were delineated for each population unit whereby road density would be limited in an effort to maintain secure and productive habitat with linkages for dispersal (Nielsen *et al.*, 2009). Although restricting road development and access is fundamentally important to reduce mortality risk, it is not the only factor potentially limiting grizzly bear recovery. Tracking and enhancing suitable habitat (food and security) is also a key recommendation of the provincial grizzly bear recovery plan (Alberta Grizzly Bear Recovery Plan 2008-2013, 2008). While assessing the cumulative impact of land use activities (forestry, mining, oil and gas, and recreation) is essential to this goal, forest harvesting will largely determine the future suitability of grizzly bear habitat (Nielsen *et al*., 2004a, Alberta Grizzly Bear Recovery Plan 2008-2013, 2008). Therefore, understanding how harvesting in the short and long-term alters the availability of food resources and habitat used by grizzly bears is essential to recovery efforts.

1.2 Mountain Pine Beetle Management in Alberta

Mountain pine beetle (*Dendroctonus ponderosae*; hereafter MPB) is considered the most destructive biotic agent of mature pine (*Pinus* spp.) forests in western North America (Safranyik *et al.*, 2010). Populations occur at low background levels during most years but occasionally erupt into epidemic outbreaks causing landscape level tree mortality that can impact a variety of forest values such as timber and wildlife habitat supply (Safranyik *et al.*, 2010). An outbreak that began in the mid 1990’s in British Columbia had affected over 13 million ha of pine forest by 2008, an area ten times larger than any previously recorded outbreak (Safranyik *et al.*, 2010). Rapid expansion and persistence of MPB outside of their historic distribution is believed to be the result of an increase in their primary host, mature (>80 years) lodgepole pine (*Pinus contorta*), which has tripled in area with fire suppression over the last century (Wulder *et al.*, 2006). At the same time, changes in temperature seem to have made more areas climatically suitable for brood development and survival (Carroll *et al.*, 2003). During the extreme outbreak in 2006, a massive influx of dispersing beetles resulted in widespread infestations in areas of northern west-central Alberta and raised concern that MPB could spread across the eastern slopes and into the boreal forest of Canada (Anonymous, 2007).

In response to this threat, Alberta Environment and Sustainable Resource Development implemented a long-term pine management strategy as part of provincial mitigation efforts. The aim of the pine strategy was to change the age distribution of pine at the landscape level through strategic forest management planning (Anonymous, 2007). Along the eastern slopes, lodgepole pine is most concentrated within the Lower and Upper Foothills, Montane, and Sub-alpine Natural Subregions where mature stands are abundant (Wang *et al.*, 2004; Anonymous, 2007). The Foothills were of particular management concern since 70% of the forested area is lodgepole pine and most of these stands were thought to be susceptible to MPB attack (Anonymous, 2007). On public lands, Forest Management Agreement (FMA) holders were directed to harvest at an accelerated rate and reduce by area 75% of the most susceptible pine stands expected to occur within the operable land base over a twenty year period (Anonymous, 2007). Historically, Alberta forestry operations follow a two-pass system whereby a merchantable stand of timber within a larger management area (FMA) is harvested while the adjacent stand is left until the harvested area regenerates for a minimum of 15 years (green-up delay). The surge cut is a significant departure from even flow timber supply which raises concerns about how this might influence habitat for species of concern such as the grizzly bear (Anonymous, 2007).

1.3 Forest Harvesting and Grizzly Bear Habitat

Forest harvesting affects grizzly bear habitat by altering the spatial and temporal configuration of forest age class structure. It is generally thought that harvesting mature (>80 years) stands of forest may improve habitat conditions for grizzly bears because of increased food associated with young forests (<60 years) and habitat edge (Nielsen *et al.*, 2008). However, this belief is based on studies conducted in landscapes with traditional two-pass harvesting. Whether larger cut-blocks from natural disturbance based forestry or surge cutting are as valuable for grizzly bears is not well understood. It is plausible that a diversity of forest age classes within an animal's home range may be need to buffer populations against future uncertainty and allow access to all of the resources required throughout a bear's life cycle (Nielsen *et al.*, 2008). Relatively little is known about how the dramatic changes in age distribution of pine that would be caused by surge cutting could influence habitat conditions for grizzly bears over time. Initially the MPB strategy will result in a substantial amount of young (~20 years) cut-blocks, but as this large cohort of pine ages there will be much more intermediate-aged forests. How grizzly bears will react to changes in food resource availability when the MPB surge cuts regenerate and begin to dominate the landscape in the future needs to be considered.

Although forest harvesting may increase the availability of plant based food resources for grizzly bears post harvest (Nielsen *et al.*, 2004c), availability of food is not static and changes through time due to succession (Reynolds-Hogland *et al.*, 2006). Following timber harvest, early seral species that respond positively to disturbance such as forbs and certain fruits may increase given the availability of previously limited resources (light, moisture, and nutrients) associated with open canopy conditions (Zager *et al.*, 1983; Coxson and Marsh, 2001; Bainbridge and Strong, 2005; Reynolds-Hogland *et al.*, 2006; Visscher and Merrill, 2009). However, other food resources (e.g. *Vaccinium* spp.) may be negatively affected from mechanical disturbance during harvest or following post harvest site treatments such as scarification (Martin, 1983; Zager *et al.*, 1983). Through succession, early seral species are replaced by mid-to-late seral species as the canopy of the forest closes (Bainbridge and Strong, 2005), which generally leads to less biomass of herbaceous vegetation (Visscher and Merrill, 2009) and lower fruit production (Martin, 1983). However, whether a closed canopy results in food production equivalent to mid-to-late seral forests is not well understood (Ihalainen and Pukkala, 2001). Past studies of grizzly bear food in lodgepole pine forests according to age since disturbance have either been qualitative, based on presence/absence data (Nielsen *et al.*, 2004c), or limited to community level changes in vegetation (forbs vs. shrubs) (Bainbridge and Strong, 2005; Visscher and Merrill, 2009). Other research that investigated changes in food abundance at the species level restricted their sampling to shrubs (Seip and Jones, 2009) or had a limited sample of age classes (Munro *et al*. 2008). Thus, none accounted for spatial heterogeneity in abundance relative to environmental gradients that will be important in understanding future food supply for grizzly bears after surge cutting. Whereas shrub cover tends to increase following timber harvest (Bainbridge and Strong, 2005), Nielsen *et al*. (2004c) found no difference in the abundance of fruit between cut-blocks and mature forest. For many species, shrub cover may not accurately predict total fruit production (Noyce and Coy, 1990).

The behavioral response of grizzly bears to forest harvesting has been investigated numerous times using radio-telemetry data (Waller and Mace, 1997; Wielgus and Vernier, 2003; Nielsen *et al.*, 2004a; Nielsen *et al.*, 2008; Martin *et al.*, 2010). Three studies (Wielgus and Vernier, 2003; Nielsen *et al.*, 2004a; Nielsen *et al.*, 2008) have evaluated how bears react to different ages of cut-blocks but none were specific to lodgepole pine. Only two studies examined grizzly bear response to different age classes in lodgepole pine forests (Mattson, 1997; Munro *et al.*, 2008). It appears that where natural openings are prevalent in mountainous systems, cut-blocks are avoided (Zager *et al.*, 1983; McLellan and Hovey, 2001). Conversely, in forested systems that lack natural openings, grizzly bears select cut-blocks (Nielsen *et al.*, 2004a). However, this pattern seems to be seasonally dependent as grizzly bears select younger (<10 years) cut-blocks when food intake is high (hyperphagia), while older cut-blocks with greater canopy are selected when food intake is comparatively low (hypophagia) (Nielsen *et al.*, 2004a). Mature forests tend to be abundant in most areas where grizzly bear habitat use and selection has been studied. Although research suggests that mature forests are used less than they are available (avoided) by grizzly bears, mature forests are often the most used age class (McLellan and Hovey, 2001; Wielgus and Vernier, 2003). High use suggests that mature forests contain important resources that may be related to food but also could provide other important requirements such as shelter (Waller and Mace, 1997). Given that mature lodgepole pine stands are the most available habitat in the system and the focus of the surge cut for MPB mitigation, it is imperative to assess grizzly bear response to different pine age classes using measures of both habitat use and selection.

Elevation and edge proximity are factors that likely influence grizzly bear behavior (Zager *et al.*, 1983; Mace *et al.*, 1996). In the Foothills of Alberta, Nielsen *et al.* (2004a) only found a weak association with elevation for bears using cut-blocks. However, in mountainous environments, elevation was a key driver of seasonal bear distribution and was attributed to plant phenology and habitat productivity (Hamer and Herrero, 1987; McLellan and Hovey, 2001). Grizzly bears are assumed to use edge because food is more abundant and the distance to escape cover is shorter (Nielsen *et al.*, 2004a; Nielsen *et al.* 2008). Other studies have found similar patterns with grizzly bears utilizing edge habitat adjacent to small openings (Blanchard, 1983; Zager *et al.*, 1983). However, I am unaware of any studies that have examined grizzly bear use or selection of different forest age classes in the context of elevation or edge proximity.

1.4 Habitat Use and Selection

Habitat is where animals live and includes both the biotic and abiotic resources (food, cover, and water) necessary to support self-sustaining populations over space and through time (McComb, 2008). Animals face competing demands to acquire essential resources, find mates, rear offspring, and avoid predators when using habitat (Gaillard *et al.*, 2010). Because resources are heterogeneously distributed across the landscape, animals must balance these trades-offs by distributing themselves in habitat over space and time (Fretwell and Lucas, 1970; Wiens, 1989). Habitat selection or the disproportionate use of habitat relative to its availability (i.e. non random use), can be described as the behavioral consequence of where animals live (Boyce and McDonald 1999). Patterns of habitat selection reflect where animals acquire essential resources, which directly influences survival and reproduction, and consequently fitness (Southwood, 1977). Therefore, ecologists seek to understand how and why animals use habitat at appropriate scales, to unravel the patterns and processes that give rise to the behaviors, which influences individual performance (i.e. survival, reproduction) and ultimately fitness (Beyer *et al.*, 2010).

Models that combine animal locations from Global Position System (GPS) technology with spatial depictions of habitat using Geographical Information

System (GIS) maps have been utilized extensively to understand patterns of animal habitat selection. Studies often assess wildlife-habitat relationships following the hierarchical spatial scaling process of Johnson (1980). The general approach is to relate the proportion of used habitats (GPS locations) to a proportional representation of available habitats (Manly *et al.*, 2002) with the unit of replication being the individual animal rather than the location to avoid pseudoreplication (White and Garrott, 1980; Manly *et al.*, 2002). Several use-availability designs exist and a variety of analytical procedures can be used to generate predictive models from such designs (Aebischer *et al.*, 1993; Cooper and Millspaugh, 1999; Manly *et al.*, 2002; Gillies *et al.*, 2006; Lele and Keim, 2006; Thomas and Taylor, 2006). When habitats are categorical, resource selection by individual animals can be quantified using various indices (Alldredge *et al.*, 1998); however, more sophisticated multi-variable models (e.g. logistic regression) can accommodate continuous covariates with the inclusion of interaction terms or non-linear responses (Manly *et al*. 2002). Because of this flexibility, these resource selection function (RSF) models have gained popularity in conservation and management application. Under the assumption of a random sample, the population level response (selection or avoidance) for any defined habitat can be obtained by averaging coefficients from individual models (Manly *et al*. 2002). However, because the number of GPS locations may differ between animals and influence the precision of habitat selection estimates, meta-analytical procedures (Nielsen *et al.*, 2009) and random effect models (Gillies *et al.*, 2006) have been proposed to obtain population level estimates.

Habitat quality is often inferred from resource selection patterns of animals (Fretwell and Lucas, 1970) as estimated by RSF (Boyce and McDonald 1999), and has been utilized widely as a tool in conservation and management applications (Gaillard *et al*., 2010). However, it has been long recognized that selection is dependent on habitat availability (Jacobs, 1974; Johnson, 1980). Recently, Beyer *et al*. (2010) showed that an increase in habitat availability corresponds to a decrease in selection even though use does not change. The dichotomy between resource use and selection is important, yet both measures are rarely incorporated into wildlife-habitat studies. In a comparison of use and selection models, Long *et al*. (2009) showed that coefficients differed, meaning that the interpretation of one model vs. the other if used independently would lead to different management actions. Therefore, it is prudent when investigating habitat selection to also incorporate use in the interpretation as well.

1.5 Thesis Overview

My thesis research began following the provincial governments decision to surge cut mature stands of lodgepole pine across the eastern slopes of Alberta. Rapidly changing the age distribution of pine within grizzly bear range raised conservation and management concern. It is not well understood how harvesting mature pine will affect grizzly bear habitat over time. Previous research and models used in management are limited to food distribution and habitat selection and are not specific to pine forests. I aimed to fill this knowledge gap and determine if the surge cut will likely improve or deteriorate habitat conditions for grizzly bears both immediately and into the future. I conducted my study in the

Upper Foothills of Weyerhaeuser Grande Prairies Forest Management Agreement Area in north-west central Alberta (Figure 1.1) where female grizzly bears have been monitored using radio-telemetry and MPB management has been underway since 2007.

In Chapter 2, I developed spatially explicit models describing the abundance of plant based food resources in pine as a function of stand age and other environmental covariates. I then projected changes in food abundance according to a proposed spatial harvesting sequence. In Chapter 3, I assessed the extent female grizzly bears use and select areas proposed to be harvested (operable vs. inoperable) and in relation to pine and other forest types. I also determined grizzly bear response to different age classes of pine including age associated differences in elevation and edge proximity at the stand level. In Chapter 4, I summarized my results, provide recommendations regarding the surge cut and grizzly bear habitat, discuss some of the limitations of my study, and elaborate on future research needs.

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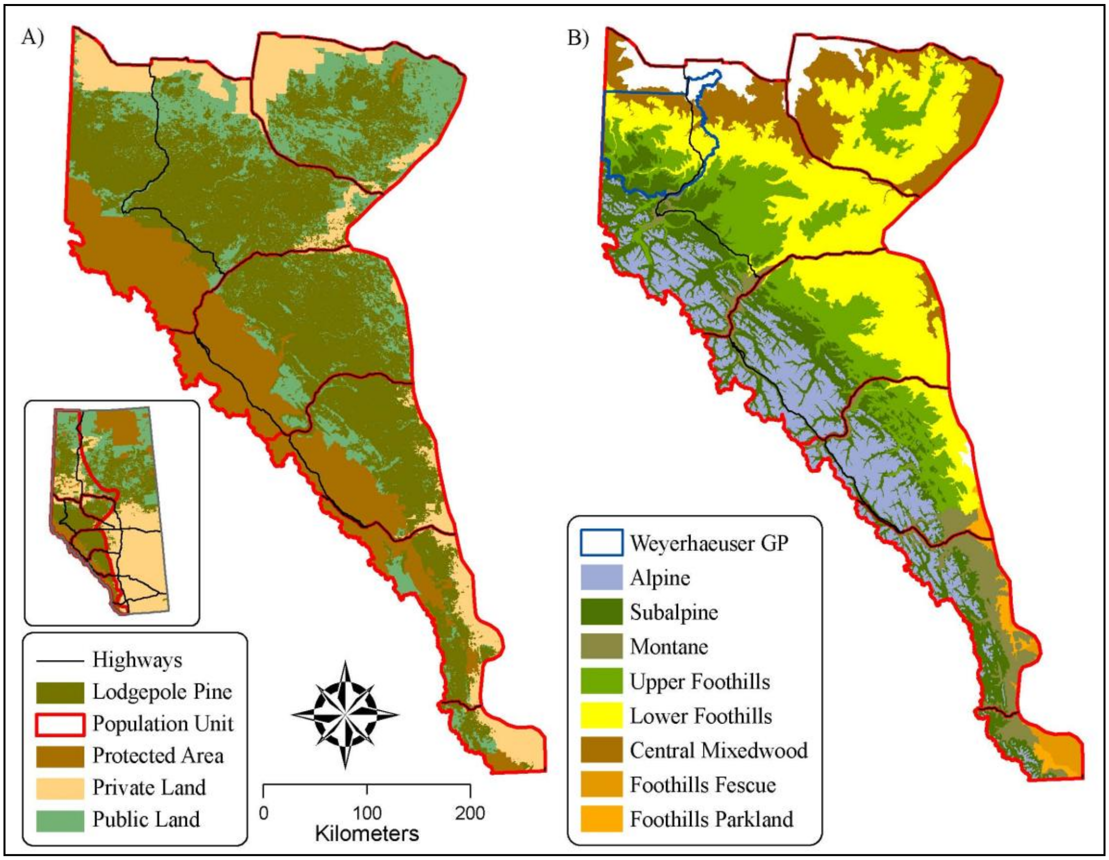

Figure 1.1 A) Distribution of lodgepole pine on public lands; and B) Natural Sub Regions and the southern boundary of Weyerhaeuser Grande Prairie Forest Management Agreement area within 6 grizzly bear population units separated by major highway divisions along the eastern slopes of Alberta.

CHAPTER 2: Forecasting food availability for grizzly bear: implications for mountain pine beetle control harvesting

2.1 Introduction

In western North America, the mountain pine beetle (*Dendroctonus ponderosae*: hereafter MPB) is considered the most destructive insect of mature pine (*Pinus* spp.) forests (Safranyik *et al.*, 2010). Since the mid 1990's, MPB have been at epidemic levels in British Columbia (Safranyik *et al.*, 2010). By 2008, beetle infestations had extended over 13 million hectares of mature pine forest causing a wide range of social and ecological impacts (Wulder *et al.*, 2006). Favourable climatic condition (temperature) across contiguous areas of mature pine forest at higher latitudes and elevations (Carroll *et al.*, 2003) is the hypothesized reason for this rapid expansion of MPB (Safranyik *et al.*, 2010). In 2006, MPB were found in many areas of northwest central Alberta, which raised concern the insect could spread throughout the eastern slopes of the Rocky Mountains and Canada's boreal forest (Anonymous, 2007b).

In response to the MPB threat, Alberta Environment and Sustainable Resources Development initiated a long-term pine management strategy on public lands where timber is commercially grown and harvested (Anonymous, 2007a). The intent of the pine management strategy is to rapidly change the age distribution of lodgepole pine (*Pinus contorta*), the beetles primary host, in an effort to reduce landscape-level susceptibility of pine forests to MPB attack today and in the future (Anonymous, 2007b). Within the Rocky Mountain Region of the eastern slopes, even-aged stands of mature pine are abundant in the Sub-alpine and Foothills Natural Sub-regions largely because of fire suppression efforts over the past century (Anonymous, 2007b). Because 70% of the Foothills area is comprised of pine and more climatically suitable for MPB to survive and reproduce, this is one of the areas of primary management concern (Anonymous 2007b). Following the pine strategy, Forest Management Agreement (FMA) holders were directed to surge harvest 75% of the most susceptible pine stands that were expected to occur over a 20 year period planning period (Anonymous 2007). The potential for a 125% increase in the annual allowable cut at the FMA level is a significant departure from standard even-flow timber supply management.

The implications of a surge cut of mature pine, both immediately and in the future, for a threatened species like the grizzly bear (*Ursus arctos*) is a key concern. Considerable research indicates that increased forest harvesting will negatively affect grizzly bear survival by creating new access roads that lead to bear-vehicle collisions, poaching, or animal-human conflict (Nielsen *et al.*, 2004a; Nielsen *et al.*, 2006; Nielsen *et al.*, 2008). While challenging to manage, the risks of roads to grizzly bears can be reduced by limiting road density and controlling human access (Nielsen *et al*., 2009). Less is known about how forest harvesting will alter food resource availability over time and how that might influence survival, reproduction, and population growth of bears (Nielsen *et al*., 2010a, Reynolds *et al*., 2007) as well as changes in their use of habitat and movement.

Cut-blocks are thought to contain a wider array of plant based food resources for grizzly bears than mature forests. However this may depend on local stand and environmental conditions (tree species composition, soil moisture, elevation) that influence plant occupancy and/or abundance (Nielsen *et al.*, 2004b; Visscher and Merrill, 2009). Past models of grizzly bear food supply as a function of forest age in pine forest have either been qualitative, based on presence/absence data, and/or limited to community level descriptions of vegetation form (herbaceous vs. shrub) with few studies accounting for spatial variation associated with environmental gradients within age classes (Nielsen *et al.*, 2004b; Bainbridge and Strong, 2005; Visscher and Merrill, 2009). Although logging generally results in increased graminoid, forb, and shrub cover, destruction of rhizomes can reduce shrub growth for certain species (Zager *et al.*, 1983; Bainbridge and Strong, 2005). Conversely, unimpeded tree growth after harvest may result in more shrubs but less fruit, as fruit production is influenced by fire in many plants (Minore and Smart, 1979; Martin, 1983; Hamer and Herrero, 1987). To my knowledge, no studies have quantified grizzly bear food abundance as a function of stand age in lodgepole pine forests and in relation to local environmental conditions. Given that shrub abundance and fruit production may not be that tightly linked (Noyce and Coy, 1990; Reynolds-Hogland *et al.*, 2006; Suring *et al.*, 2008), it is important to quantitatively evaluate how Alberta's MPB strategy may affect grizzly bear foods now and in the future.

I quantify changes in grizzly bear food supply based on forest age and other environmental covariates in an effort to forecast the consequences of surge harvesting mature stands of lodgepole pine in the Upper Foothills of north-west central Alberta, Canada. My specific objectives were to 1) determine what plant based foods resources are most common to the Upper Foothills; 2) determine what effect overstory pine composition, stand age, and environmental gradients had on the abundance of forbs, the abundance of shrubs, and the abundance of fruits; and 3) forecast total food biomass as a function of changes of pine forests over the proposed spatial harvesting sequence for MPB.

2.2 Methods

2.2.1 Study Area

The study area was the Upper Foothills Natural Subregion of the southern boundary of Weyerhaeuser Grande Prairie's Forest Management Agreement (FMA) area in northwest-central Alberta, Canada (119° 13'W and 54° 32'N; Figure 2.1). Alberta Vegetation Inventory (AVI) suggests the area is dominated by closed canopy conifer forests (95%) with few natural openings or burns (<1%). The remaining 4% is anthropogenic footprint including roads, pipelines, seismic lines, and well sites. Lodgepole pine is the dominant overstory tree species and occurs in pure and mixed stands often with black spruce (*Picea mariana*) and to a lesser extent white spruce (*Picea glauca*), balsam fir (*Abies balsamifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) (Natural Regions Committee, 2006). The majority of stands contain pine (91%) and of those, 61% is pine leading. Since the early 1970's, forests in this area have been intensively managed for commercial timber production creating a mosaic of seral stages, with an age distribution skewed towards mature (>80 years) and young (<35 years) age classes. Topographic relief is rolling and steeply sloping with elevations ranging from 950 to 1750m (Natural Regions Committee, 2006).

Climatic conditions fluctuate along a prominent elevation gradient that is orientated in a south west to north east direction. Average annual precipitation varies from 452.5 to 992.9 millimetres with average annual temperature from -1.6 to 2.5 °C (Natural Regions Committee, 2006). The short growing season is cool and wet, and winters are cold with substantial amounts of precipitation in the form of snow (Natural Regions Committee, 2006).

2.2.2 Grizzly Bear Food Resources

Grizzly bear diet in the Rocky Mountain Ecosystem of Canada is well documented from scat and isotope analysis (Hamer and Herrero, 1987; McLellan and Hovey, 1995; Hobson *et al.*, 2000; Larsen and Pigeon, 2006; Mowat and Heard, 2006; Munro *et al.*, 2006). These studies suggest that plant based food resources constitute a large proportion of grizzly bear diet (>50%). Grizzly bear diet and presumably the availability of specific plants, appears to differ by latitude and altitude. Thus, I quantified plants known to be used seasonally by grizzly bears in west and north-west central Alberta (Larsen and Pigeon, 2006; Munro *et al.*, 2006). Seasonal shifts in the diet of grizzly bear typically follow changes in food availability associated with plant phenology (Hamer and Herrero, 1987; Munro *et al.*, 2006). After den emergence and prior to green-up, grizzly bears dig sweet-vetch roots (*Hedysarum alpinium*, *Hedysarum boreale*). With the onset of green-up, grizzly bears forage on horsetails (*Equisetum* spp.), cow parsnip (*Heracleum lanatum*), clover (*Trifolium* spp.), dandelion (*Taraxacum officinale*), and clasping-leaved twisted stalk (*Streptopus amplexifolius*). When fruit ripens in July, grizzly bears consume buffaloberry (*Shepherdia canadensis*), black huckleberry (*Vaccinium membranaceum*), lingonberry (*Vaccinium vitis-idaea*), velvet-leaved blueberry (*Vaccinium myrtilloides*), dwarf blueberry (*Vaccinium caespitosum*), bearberry (*Arctostaphylos uva-ursi*), raspberry (*Rubus idaeus*), and crowberry (*Empetrum nigrum*). Grasses and sedges are often consumed by grizzly bears, but I did not consider these because no specific species have been identified in previous dietary studies.

2.2.3 Vegetation Sampling and Environmental Characteristics

I used a Geographic Information System (GIS) forest inventory database (net land base) provided by Weyerhaeuser to determine the extent of pine forests and to define my sampling area within the Upper Foothills. The net land base was the spatial input for the revised Timber Supply Analysis (TSA) for MPB management amended in 2009 (Anonymous, 2006a). I excluded stands (18%) where overstory composition and stand age were not known or classified as inoperable (land use, water buffer, steep slopes, non-merchantable). Remaining upland stands of pine were stratified according to age of origin using a 5 year interval for harvested (1-35 years) and 30 year interval for non-harvested (≥38 years). Because I expected greater variation in food abundance associated with post harvest site treatments (e.g. scarification) and since stands change more rapidly (canopy closure) during early regeneration, my goal was to sample more intensively in harvested areas over a shorter time scale. I used Hawth's Tools (Beyer, 2004) to generate random location coordinates within the stratified area, with the restriction that in uncut pine my sampling was within 1 km of roads to maximize accessibility.

I established 30x30m vegetation plots, orientated south to north, at random location coordinates in harvested (n=145) and non-harvested pine (n=104) from June 17 to September 1, 2008 (n=136) and from June 28 to October 1, 2009 (n=113). I chose a 30x30m (900 m^2) sampling area to match the scale of my GIS raster grids used as explanatory variables. Plot center was located as the nearest Universal Transverse Mercator (UTM) coordinate with the lowest GPS error that did not exceeded 10m. To avoid possible edge effects (Harper and Macdonald, 2002; Redding *et al.*, 2003; Lopez *et al.*, 2006), if any of the plot area fell within 30m of a harvested area boundary or anthropogenic land use feature (road, trail, seismic line, or well-site), the plot was moved in a random cardinal direction perpendicular to the edge or feature until there was no overlap. Plots were also moved 30m in a random cardinal direction if ten percent or greater of the plot area in harvest blocks contained overstory retention trees. Overstory tree species composition was determined by using an ocular estimate of percent cover values in classes (0, 1-5, 6-10, and 11-20...90-100) for each tree species that formed the canopy. Pine composition was determined by taking the median percent cover value for each tree species and averaged at the plot level. For ten plots that occurred in cut-blocks with no tree regeneration, overstory pine composition was determined from AVI.

Within the 30x30m sampling area, I established five 1x30m transects (south to north), evenly spaced along the southern plot boundary at 0.5, 7.5, 15, 22.5, and 29.5m. Using the same spacing, I placed five 1x1m quadrats along each transect. In quadrats, I counted individual stems of *T. officinale* and *Equisetum* spp. I also estimated percent cover and counted berries of *E. nigrum*, *V. membranaceum*, *V. myrtilloides*, *V. caespitosum*, *V. vitis-idaea*, *A. uva-ursi*, and *Trifolium* spp. Cover was estimated occularly using single percent values from 1 to 20 and in 5 percent increments above 20. In transects, I counted individual *Hedysarum* spp. plants, stems of *S. amplexifolius* and *H. lanatum*, and stems and berries of *S. canadensis*, *R. idaeus*, and *A. nudicaulis* that originated from ground level. In addition, I performed meander searches within the 30x30m area recording the presence/absence of forb and shrub species.

During the 2009 sampling season, I clipped the stems of forbs at ground level and collected ripe berries from a maximum of 5 random quadrats and 5 random transect sections (7.5m). Ripe fruit was weighed in the field using a 10g PESOLA® scale. Vegetation was collected, dried at room temperate, and weighed using an OHAUS® Adventurer SL digital scale. At the plot level, I calculated mean fresh weight of fruit (g/berry) and dry biomass of forbs (g/stem) for each of the species sampled. For each species, mean weight was converted to mean digestible dry matter (hereafter DDM) (Table 2.1). I used DDM rather than dry biomass because the digestibility of food types by bears can differ and since DDM is linearly related to digestible energy (KJ/g) in most plant species (Partridge *et al.* 2001, Pritchard and Robbins 1990, Welch *et al.* 1997). Because I did not dry forbs at a specific temperature and for a particular duration, biomass may be overestimated as additional moisture likely remained in samples.

2.2.4 Predictor variables

I used GIS raster grids to represent site specific environmental conditions at each plot and across the extent of pine stands within the Upper Foothills. From a 30m pixel digital elevation model (DMTI, 2003) I created aspect and slope grids using the Spatial Analyst Extension in ArcGIS 9.2 (ESRI® Redlands, CA). Aspect and slope grids were then used as inputs to calculate a Solar Radiation Index (SRI) (Keating *et al.*, 2007) and a Compound Topographic Index (CTI). The solar radiation index simultaneously combines aspect, slope, and latitude (Keating *et al.*, 2007). CTI is an index of wetness that considers the slope and uphill contributing area to flow direction and has been correlated with soil attributes such as horizon depth, percentage of silt, organic matter content, and phosphorous (Evans, 2004). I used elevation as a surrogate variable for climate because it was correlated (>0.7) with climate normals (Anon, 2003) including: annual moisture index, degree days below zero, length of the frost free period, growing season precipitation, mean annual temperature and precipitation, and summer moisture index .

A binary variable was used to represent leading (1) or non-leading (0) stands of pine and whether the sampling year was 2008 (0) or 2009 (1). Leading pine was defined as greater than or equal to 60 percent overstory canopy pine composition. From hemispherical canopy photos (1.5m above ground) averaged for each plot (n=5), canopy closure in pine stands younger than 20 years was 3% (range 0-40) with 63 of 78 sites having a value of zero. The average canopy cover for harvested stands between 21-35 years of age was 43% (range 0-68) and 53% (range 34-65) in non-harvested stands (Appendix A). I represented stand age by three variables: 1) a binary variable to distinguish between harvested (1) and non-harvested (0) (hereafter CutVsUncut); 2) a continuous 20 year interval (hereafter Age20); and 3) a categorical variable that split age into four levels: A) 1-20 years; B) 21-35 years; C) 38-80 years; and D) ≥80 years (hereafter AgeCat). AgeCat represents A) harvested stands and relative open canopy conditions; B) harvested stands and relative closed canopy conditions; C) non-harvested stands that were rare at the landscape level; and D) non-harvested stands that were abundant at landscape level and the target of MPB management. The categorical classification of age was similar to the seral stages used by Weyerhaeuser (Early 1-10; Intermediate 11-40; Mature 41-80; Late >80). My rationale for considering these different definitions was to test whether a specific age variable was a better predictor of plant distribution/abundance. From a sampling perspective, the 38-80 year age class was relatively uncommon, especially stands between 37-59 years. Of the 249 plots I sampled in 2008 (136) and 2009 (113), 188 were pine leading stands of which 108 were cut-blocks, 14 were 37-80 years of age, and 127 were mature.

2.2.5 Species Occurrence and Abundance

I calculated the occurrence probability of forbs and shrubs in pine, harvested, and non-harvested stands from meander searches of species presence/absence. I rank ordered bear foods by type (forbs or shrubs) according to the probability of occurrence in pine. I used logistic regression (StataCorp., 2009) to predict the effect of CutVsUncut on the probability of bear foods occurring.

At the plot level, I summed counts of forbs, shrubs, and fruits for each species. Low counts in 8 of the 16 bear foods precluded modelling abundance. Sampling variance was high for the other 8 species. To minimize the effect of outliers on model predictions, I visually inspected scatter plots of counts versus predictors, removing obvious outliers. In continuous form, environmental predictors (CTI, SRI, Elev) were highly variable with clear outliers. To minimize the impact of this high variability, predictors were transformed into equal frequency groups (Table 2.2).

I used zero-inflated negative binomial regression (StataCorp., 2009) with robust estimates of variance to quantify the effect of predictors on the mean relative abundance of the response variables (Table 2.2). Although expected given the excessive 0's and over-dispersion of counts, I used a Vuong test statistic (Vuong, 1989) and a model fitting procedure (Long and Freese, 2005) to confirm that ZINB was appropriate. The zero-inflated mixture model combines the probability distributions of two latent groups, a point mass at zero and a negative binomial distribution (Martin *et al.*, 2005; Nielsen *et al.*, 2005). Through a simultaneous process, the mean count is modelled with a proportion of 0's equivalent to a negative binomial distribution and the excessive 0's are modelled as a logistic function (Martin *et al.*, 2005). The model considers factors (covariates) influencing both distribution and abundance, while final predictions (abundance) are the product of the two (Martin *et al.*, 2005; Nielsen *et al.*, 2005). Because plants are sessile and sampling occurred during the growing season, I assumed that absences represent 'true zeros' and the result of ecological process rather than imperfect detection due to observer error or plant phenology (Martin *et al.*, 2005).

I used an Akaikie's information criteria model selection and inference, but corrected for small sample size (AIC_c) (Burnham and Anderson 2002). My approach had two steps, and in each step I retained the model with the lowest AIC_c score (best model) that was at least 2 AIC_c units smaller than a null (intercept only) model (Burnham and Anderson 2002). In my first step and beginning with the inflation group of response variables, I fit models with individual parameters for sampling year and each age variable including a non-linear effect for Age20 (squared term). In separate models I introduced year and each age variable including interactions between year and age. In my second step, I tested whether the top model from step 1 was better than individual models representing pine composition, environment (Elev, CTI, and SRI) or all possible combinations of these variables including non-linear effects for environment (squared term). I observed possible interaction effects between elevation and sampling year as well as pine composition and sampling year, thus, included these effects as separate models in my candidate set. I repeated these steps for the count group, but included the best model from the inflation group. Prior to model fitting, variance inflation factors (VIF) were used to assess multicollinearity for each combination of predictors excluding interaction effects. VIF was considered to be influential when values were greater than 10 or when the mean of all VIFs was greater than 1 (Nielsen *et al.*, 2005). Percent deviance (D^2) was calculated from the null and full models for each latent group to quantify model fit.

2.2.6 Spatial Harvesting Sequence

In a GIS, I used a spatial harvest sequence provided by Weyerhaeuser to determine the age of pine stands in period 1 (2006) and at each decadal time step from periods 2 through 12. Each harvesting period represents 5 years. I assumed that pine composition remained constant and that stands did not die (age=1) after 300 years for three reasons. First, conifer leading stands were assumed to transition without change within the TSA (Anonymous, 2006b). Second, deciduous leading stands that transition to conifer (Anonymous, 2006b) were rare and would have little influence on food abundance estimates unless a dramatic conversion to deciduous forest occurs. Third, my goal was to quantify potential changes in food abundance that was representative of harvesting rather than stand senescence. I consider the first 20 years of the projection to be a likely scenario since many of the blocks proposed for harvest were pre-selected. On the other hand, the next forty years is less likely because the TSA did not limit harvesting within caribou management zones, thus, my projections beyond 2018 and the end of the surge cut are more speculative. However, it does represent a change in the age distribution of pine and the legacy of MPB surge harvesting. GIS layers from each time step that described pine composition, stand age, and environmental conditions for each 30x30m pixel were used to predict total abundance (counts) of forbs, shrubs, and fruits from the best models.

Final model predictions for shrubs, fruits, and forbs were scaled to a $900m^2$ area by multiplying predicted counts by a factor of 36 for species collected in quadrats ($25\ m^2$) and 6 for those in transects ($150\ m^2$). I then converted count predictions of forbs and fruits to DDM (g/900m^2). Because of the difficulty of counting stems of *Vaccinium* spp. we used % cover estimates from the quadrats as my measure of abundance. Cover estimates were treated as counts to allow for the use of zero-inflated models. Unreported analyses using a logit link in a generalized linear model (StataCorp., 2009) provided similar predictions. *Vaccinium* spp. abundance was scaled by taking the mean predicted % cover and dividing by 90000 (100 units of cover/1m^2) to get abundance per 900m^2. Using this logic, I assumed one *R. idaeus* stem was equivalent to 1 unit of % cover and scaled abundance accordingly.

2.3 Results

2.3.1 Food Occurrence

The rank order occurrence probability of forbs was *Equisetum* spp. > *S. amplexifolius* > *H. lanatum* > *T. officinale* > *Trifolium* spp. > *Hedysarum* spp. (Table 2.3). For fruit producing shrub species, the rank probability of occurrence was *V. vitis-idaea* > *V. myrtilloides* > *V. membranaceum* > *R. idaeus* > *V. caespitosum* > *S. canadensis* > *A. nudicaulis* > *A. uva-ursi* > *E. nigrum* (Table 2.3). Based on logistic regression analysis, the forbs *H. lanatum* and *Trifolium* spp. were significantly more likely to occur in harvested pine, while *Equisetum* spp. and *S. amplexifolius* did not differ. Of the shrub species, *R. idaeus* and *A. uva-ursi* were significantly more likely to occur in harvested stands and *V. vitis-idaea*, *V. membranaceum*, *V. caespitosum*, and *E. nigrum* were more likely to occur in non-harvested stands (Table 2.3). CutVsUncut had no effect on *V. myrtilloides*, *S. canadensis*, or *A. nudicaulis* (Table 2.3).

2.3.2 Food Abundance

ZINB models describing the distribution and abundance of forbs, shrubs, and fruits explained between 1.4 and 11.8% of the total variance (Table 2.4). Appendix B provides species specific model predictions. Below I report on percent changes in shrub cover or mean DDM (g/900m^2) of forbs and fruits.

Pine composition was a predictor in 11 of 13 response variables but did not explain variation in *S. amplexifolius* or *V. caespitosum* shrubs. Compared to leading pine, Equisetum (120%), *H. lanatum* (234%), and *R. idaeus* shrub (83%) and fruit (128%) increased in non-leading stands. Conversely, *V. myrtilloides* shrub (46%) and fruit (46%), *V. membranaceum* shrub (61%) and fruit (82%), and *V. vitis-idaea* shrub (13%) and fruit (47%) decreased in non-leading stands. There was a significant interaction between pine composition and year in *V. caespitosum* as fruit was only abundant in pine leading stands in 2008.

Stand age was a predictor for 11 of 13 species but had no effect on *V. myrtilloides* or *V. caespitosum* shrubs. Compared to mature stands (>80 years), within the first 20 years post harvest (open canopy) *Equisetum* spp. (239%), *H. lanatum* (155%), *R. idaeus* shrub (983%) and fruit (700%), *V. myrtilloides* fruit (1172%), and *V. caespitosum* fruit (266%) increased (Figures 2.2 and 2.3). With succession over the next 20 years (closed canopy), *Equisetum* spp. (46%), *R. idaeus* shrub (72%), *V. myrtilloides* fruit (85%), and *V. caespitosum* fruit (22%) decreased, while *H. lanatum* increased by 137% (Figures 2.2 and 2.3). As stands continued to age, these species were predicted to decrease to below or at the level of pre-harvest abundance. *V. membranaceum* shrub (82%) and fruit (86%) and *V.*

vitis-idaea shrub (61%) and fruit (82%) decreased substantially after harvesting (Figures 2.3). Although shrubs and fruits were predicted to increase linearly with age, *V. membranaceum* fruit reached an asymptote in mature (>80 years) stands and *V. vitis-idaea* fruit peaked between 100-120 years, while shrubs continued to increase (Figures 2.3). In older cut-blocks (21-40 years), *V. membranaceum* and *V. vitis-idaea* fruit increased from young cut-blocks (1-20 years) to 68 and 61% less than the mean of mature stands and to 32 and 16% less in those from 41-80 years (Figures 2.3).

Elev, CTI, and SRI were predictors in 9, 11, and 2 of 13 response variables, respectively. In 4 of the 5 fruiting species, the relationship between abundance to Elev was consistent between shrub and fruit models. *V. myrtilloides* was most abundant at low and intermediate Elev (Figure 2.4). *R. idaeus* decreased with an increase in Elev, while *V. caespitosum* and *V. membranaceum* increased (Figure 2.4). *V. vitis-idaea* shrubs were most abundant at intermediate Elev, but this relationship was not consistent with the fruit model (Figure 2.4). Comparing the two most abundant fruiting species, dominance shifted from *V. myrtilloides* to *V. membranaceum* at an Elev of about 1204m based on the shrub (mean of 4th Elev interval) model or 1228m (upper limit of 4th Elev interval) according to the fruit model (Figure 2.4). There was a significant interaction between pine composition and Elev in *V. membranaceum* shrub and fruit models. In non-leading stands, the slope of the line was steeper as an increasing function of Elev. CTI consistently predicted patterns of shrub and fruit abundance in 4 of the 5 species. With an increase in CTI, *Equisetum* spp., *V. myrtilloides*, *V.*

caespitosum, and *V. vitis-idaea* increased. Conversely, *H. lanatum*, *S. amplexifolius*, and *R. idaeus* decreased. The relationship between *V. membranaceum* shrub abundance and CTI was non-linear and peaked at intermediate levels, while fruit showed no response. Both *Equisetum* spp. and *V. caespitosum* fruit decreased with an increase in SRI.

Sampling year was a predictor in 5 of 13 response variables, having no effect on *Equisetum* spp., *H. lanatum*, shrubs, or *R. idaeus* fruit. *Vaccinium* spp. fruit was most abundant in 2008 (Figure 2.3). In 2009, the mean dropped by 63, 47, 52, and 69% in *V. myrtilloides*, *V. caespitosum*, *V. membranaceum*, and *V. vitis-idaea*, respectively (Figure 2.3). For *V. myrtilloides*, the effect of year on abundance was more pronounced because of the interaction between year and AgeCat. From 2008 to 2009 in cut-blocks 1-20 years, the percent change in *V. myrtilloides* fruit was 96% (Figure 2.3). I also found a significant interaction between year and CutVsUncut in *S. amplexifolius*. *S. amplexifolius* was more abundant in harvested pine in 2008 and in 2009 this species was more abundant in non-harvested pine (Figure 2.2).

Based on model predictions in 2008, the rank order abundance of forbs was *Equisetum* spp. > *H. lanatum* (77%) > *S. amplexifolius* (98%); shrubs was *V. membranaceum* > *V. vitis-idaea* (50%) > *V. myrtilloides* (59%) > *R. idaeus* (87%) > *V. caespitosum* (91%); fruits in 2008 was *V. myrtilloides* > *V. membranaceum* (5%) > *V. vitis-idaea* (72%) > *R. idaeus* (78%) > *V. caespitosum* (92%); and fruits in 2009 was *V. membranaceum* > *R. idaeus* (53%) > *V. myrtilloides* (55%) > *V. vitis-idaea* (81%) > *V. caespitosum* (93%).

2.3.3 Food Supply

Stands of leading pine accounted for 68% of the simulation area. In period 1, leading pine was skewed towards mature (>80 years; 65%) and harvested (1-40 years; 28%) age classes (Figure 2.5). Taking the average between periods 2 and 4 to represent the end of the surge cut in period 3, mature decreased to 43% from period 1, while young cut-blocks (1-20 years) went from 17 to 33%, and older cut-blocks (21-40 years) from 11 to 16% (Figure 2.5). With the progression of harvesting and succession following the surge cut, in period 12 about 21% was mature, 17% was young cut-block, 18% was older cut-block, and 44% was between 41-80 years of age (Figure 2.5). Non-leading stands were also harvested in the spatial sequence and the change in the age distribution was similar but without any noticeable increase in any one age class.

At the landscape level in period 1, the rank order abundance of forbs was *Equisetum* spp. (930.4t). > *H. lanatum* (134.4t) > *S. amplexifolius* (2008=36.8t; 2009=41.0t) (Figure 2.5). Of the fruiting species, the rank order abundance of shrubs was *V. membranaceum* (0.029%) > *V. myrtilloides* (0.026%) > *V. vitis-idaea* (0.024%) > *V. caespitosum* (0.006%) > *R. idaeus* (0.001%); fruits in 2008 was *V. membranaceum* (59.0t) > *V. myrtilloides* (20.9t) > *V. vitis-idaea* (20.3t) > *R. idaeus* (6.4t) > *V. caespitosum* (3.1t); and fruits in 2009 was *V. membranaceum* (28.6t) > *R. idaeus* (6.4t) > *V. vitis-idaea* (6.3t) > *V. myrtilloides* (5.8t) > *V. caespitosum* (1.3t) (Figure 2.6).

At the end of the surge cut in period 3, *Equisetum* spp. (26%) and *H. lanatum* (15%) increased. Shrub cover increased in *R. idaeus* (62%), did not change in *V. myrtilloides* and *V. caespitosum*, and decreased in *V. membranaceum* (11%) and *V. vitis-idaea* (8%). Based on model estimates in 2008, *S. amplexifolius* (5%) and fruits of *R. idaeus* (42%), *V. myrtilloides* (67%), and *V. caespitosum* (21%) increased, while *V. membranaceum* (17%) and *V. vitis-idaea* (23%) decreased. In 2009, the percent change in abundance was nearly equivalent for each species with the exception that *S. amplexifolius* decreased by 5% and *V. myrtilloides* only increased by 25%.

Post surge and until the end of period 12, *Equisetum* spp. and *H. lanatum* both decreased but were 12 and 19% more abundant than in period 1. However, in periods 6 and 8 *H. lanatum* was exceedingly abundant compared to other harvesting periods. Shrub cover also decreased post surge, however, *R. idaeus* was 28% above, while *V. membranaceum* and *V. vitis-idaea* were 11 and 8% below pre-harvest estimates. Given conditions in 2008, *S. amplexifolius* decreased but was 3% more abundant than pre-harvest abundance. Fruit also decreased, but *R. idaeus* (32%), *V. myrtilloides* (30%), and *V. caespitosum* (27%) were more abundant than in period 1, whereas *V. membranaceum* (23%) and *V. vitis-idaea* (34%) were less abundant. Again, percent changes were similar for each species according to conditions in 2009 with the exception being that *S. amplexifolius* was 3% less abundant and *V. myrtilloides* fruit 4% more abundant compared to period 1.

Among the broad groups, forbs increased by 24% and shrub cover decreased by 5% at the end of the surge cut (Figure 2.6). Total fruit increased by 2% using model estimates for 2008 and decreased by 4% in 2009 (Figure 2.7).

After the surge harvest, forbs remained high in period 4 with a declining trend from periods 6 to 12, although there was a noticeable increase in period 8 (Figure 2.6). Shrub cover increased from period 3 to 4, but declined precipitously until the end of period 12 (Figure 2.7). Total fruit was similar in period 4, decreased sharply in period 5, and remained stable until the end of period 12 (Figure 2.7). After 12 harvesting periods – 60 years, forbs and shrubs were predicted to be 13% and 8% higher given conditions in 2008 and 2009, whereas fruit was expected to be 10 and 13% lower than what was available prior to MPB harvesting (Figure 2.6 and Figure 2.7).

2.4 Discussion

2.4.1 Food Occurrence in the Upper Foothills

Of the 15 bear foods I examined, 7 were relatively uncommon and associated with disturbance features or were outside common environmental conditions in the Upper Foothills. Similar to Nielsen *et al.* (2004b), the exotic species *T. officinale* and *Trifolium* spp. were more likely to occur in cut-blocks, but are even more common adjacent to roads where seeding is used for erosion control (Roever *et al.*, 2008). *Hedysarum* spp. appears to be limited to lower elevation disturbed sites or riparian areas that have high soil wetness and explains the lack of occurrence in operable forests of the Upper Foothills (Nielsen *et al.*, 2010a). The *Vaccinium* spp. were more common than the remaining fruit producing shrub species, yet associated with lodgepole pine forests under different climatic and edaphic conditions (La Roi and Hnatiuk, 1980; Strong, 2002). In a Montane environment, La Roi and Hnatiuk (1980) found that *S.*

canadensis was associated with xeric moisture regime, dominant below 1250m with cover peaking between 1100-1300m, and became rarer with increasing elevation. Nielsen *et al*. (2010b) found that *S. canadensis* was more abundant in the Lower than Upper Foothills. Similarly, *A. uva-ursi* was associated with xeric conditions and maximum cover was below 1150m where it occurs with *S. canadensis* (La Roi and Hnatiuk, 1980). *E. nigrum* was associated with higher elevation pine stands and appears to be a secondary species with other *Vaccinium* spp.

Although lodgepole pine is widely distributed across Alberta's Rocky Mountain region, using food models from different regions may be problematic since there appears to be distinct compositional changes in understory shrub dominance relative to other areas of the province (La Roi and Hnatiuk, 1980; Strong, 2002). I suspect that local and regional gradients in moisture, edaphic conditions, and productivity (Wang *et al.*, 2004) driven by elevation and latitude may explain variation in bear food distribution and abundance in lodgepole pine stands across the eastern slopes of Alberta (La Roi and Hnatiuk, 1980; Strong, 2002). Therefore, regional inventories of bear foods in lodgepole pine may be required to examine the consequences of MPB management at the provincial level.

2.4.2 Food Abundance in the Upper Foothills

My findings suggest that when the overstory composition was less dominated by pine, *Vaccinium* spp. shrub cover and fruit production decreased while there was an increase in *Equisetum* spp., *H. lanatum*, and *R. idaeus* shrubs and fruits. Other studies have also found *Vaccinium* spp. shrub cover and fruit production to decrease when other conifers and deciduous species are more prolific (Pelchat and Ruff, 1986; Ihalainen and Pukkala, 2001). Presumably, *Vaccinium* spp. will thrive in nutrient poor conditions with few competitors or where shading from other conifers is lacking (Kardell, 1980; Timoshok, 2000; Ihalainen and Pukkala, 2001; Bainbridge and Strong, 2005). Even in pure aspen, ericaceous shrubs occur where soil fertility is poor as they are outcompeted by other vascular plants when soil fertility is high (Chen *et al.*, 2004; Hart and Chen, 2006). An increase in site productivity associated with nutrient load, light, or tree density could explain the increase in *Equisetum* spp., *H. lanatum*, and *R. idaeus*, which are commonly associated with aspen or spruce (Kojima, 1996; Lautenschlager, 1999; Beaudry *et al.*, 2001).

Within the first 20 years post harvest, aggressive early seral pioneers (*Equisetum* spp., *H. lanatum*, and *R. idaeus*) that rapidly colonize available space via seeds, root suckers, or deep rhizomes were abundant (Beasleigh and Yarranton, 1974; Hendrix, 1984; Lautenschlager, 1999; Bainbridge and Strong, 2005). As the overstory canopy closed, *R. idaeus* shrubs decreased as expected (Kardell, 1980; Lautenschlager, 1999) yet fruit production remained high, which could be related to an investment into reproduction (Whitney, 1982). *Equisetum* spp. also decreased, but was more abundant than non-harvested stands, a trend that has been observed with other herbaceous species (Visscher and Merrill, 2009). An increase in *H. lanatum* suggested that slow establishment may preclude this species from being abundant initially post disturbance (Ellison, 1958). However, this species is better able to balance water demands and reduce the chance of frost damage given its large leaf area in closed canopy forest (Young, 1985). My data suggests that forb species will eventually decrease to pre-disturbance levels as pine continues to age since most understory growth occurs within the first 30 years of harvesting when resources (nutrients, light, moisture) are most available (Bainbridge and Strong, 2005).

Vaccinium spp. can be severely impacted by disturbance both from fire or harvesting because they propagate from rhizomes (Minore, 1984; Moola and Mallik, 1998; Haeussler *et al.*, 1999; Nielsen *et al.*, 2004b). However, following stand initiation post harvest, *V. myrtilloides* and *V. caespitosum* spp. had recovered to pre-disturbance levels within 20 years of succession in the study area. Because fruit production was high, shrubs appeared to be locally abundant and not suppressed by competing vegetation. As with most ericaceous shrubs, their performance likely depends on the duration and intensity of available light (Moola and Mallik, 1998). In a second-growth boreal mixedwood system, Moola and Mallik (1998) found that within 3 years post cutting aspen can overtop *V. myrtilloides* shrubs and suppress fruit production. Other studies have found negative effects of mechanical harvesting and site preparation on shrub cover in *V. myrtilloides* (Haeussler *et al.*, 1999; Nielsen *et al.*, 2004b). Although shrub cover may not be synonymous with fruit yield, less damage to rhizomes could enhance fruit production in *V. myrtilloides* and *V. caepsitosum* beyond what I predicted.

Harvesting severally reduced shrub cover and fruit production in *V. membranaceum* and *V. vitis-idaea* and post disturbance recovery tends to be slow (Minore and Smart, 1979; Coxson and Marsh, 2001; Bainbridge and Strong, 2005). However, I found a positive relationship with age, thus, recovery to pre-disturbance abundance is likely given that shading should not inhibit vegetative growth (Hall and Shay, 1981; Anzinger, 2002). My finding that *V. vitis-idaea* fruit production peaked in pine stands older than 80 years (50% canopy cover) was consistent with Kardell (1980), yet fruit yields can be ample in young managed stands as well (Ihalainen and Pukkala, 2001). In association with stand replacing wildfire and recurrent surface fire, *V. membranaceum* fruit production tends to be highest under an open canopy (Minore and Smart, 1979; Minore, 1984; Anzinger, 2002). However, fruit production can be relatively abundant in mature stands in certain years (Kerns *et al.*, 2004). In a similar species, *V. globulare*, Martin (1983) found that shrub cover and fruit was very low to non-existent in scarified cut-blocks less than 25 years old. Conversely, in stands burned by wildfire 25-60 years ago with 3% canopy closure, fruit production can be considerably higher compared to stands older than 60 years with 30% canopy closure and similar shrub cover (Martin, 1983). With mechanical harvesting, fruit production tends to be higher than mature forests when stands are partially cut or broadcast burned (Martin, 1983; Anzinger, 2002). Alternatively, canopy removal without mechanical damage to shrubs appears to be better for *V. membranaceum* fruit production (Minore, 1984).

I found elevation to be an important factor that influenced shrub cover and fruit production at the species level. Considering the two most abundant fruiting species, at about 1228m there was a shift in dominance from low elevation (≤1228m) *V. myrtilloides* to higher elevation (>1228m) *V. membranaceum*. This corresponds with patterns found in other studies (La Roi and Hnatiuk, 1980; Strong, 2002). I had little evidence to support an effect of elevation on *V. vitis-idaea* which might be expected given its wide distribution across North American (Ritchie, 1955; Timoshok, 2000). Elevation was a particularly important driver of *V. membranaceum* abundance, a pattern that also appears along the eastern slopes and areas of the USA. In Oregon, Anzinger (2002) found that a 450m increase in elevation (1200-1600m) corresponded to a one unit increase in *V. membranaceum* fruit production class, while in Montana, *V. globular*e fruit was limited at the extremes of a wide elevation (820-2120m) gradient, but production was pronounced between 1300-1850m (Martin, 1983). Strong (2002) identified *V. membranaceum* as a dominant understory component in a lodgepole pine community type that occurs between 1050 and 1600m elevation along the eastern slopes. Plausible mechanisms controlling this phenomenon could be related to deeper winter snow packs and more growing season precipitation that could minimize spring frost damage (Minore and Smart, 1978), promote plant growth (Anzinger, 2002), or reduce interspecific competition (Martin, 1983).

Drought may influence plant phenology and is often implicated in a lack of berry production (Hamer and Herrero, 1987; Krebs *et al.*, 2009). I observed less precipitation during the growing season (June and July) of 2008 that appeared to impact the abundance of *S. amplexifolius* and fruit production in the *Vaccinium* spp. Although *S. amplexifolius* has an affinity for low soil moisture, its abundance shifted from harvested to non-harvested stands and reflected the strong contrast in soil moisture between habitats (Hart and Chen 2006, Redding *et al*. 2003). Annual precipitation maps showed that summer precipitation levels were between 90-130% from normal in 2008 (wet) and 70-90% from normal in 2009 (dry) (Alberta Environment, 2012). Although simultaneous fruit failures are rare (McLellan and Hovey, 1995), differences in annual fruit yield are well known in the *Vaccinium* spp. (Minore and Dubrasich, 1978; Kardell, 1980; Martin, 1983; Ihalainen and Pukkala, 2001). Variation in *R. idaeus* fruit occurs (Noyce and Coy, 1990) but crops may be more consistent from year to year (Kardell, 1980; Noyce and Coy, 1990; Costello and Sage, 1994). The specific mechanisms controlling fruit production are poorly understood, yet temporal fluctuations in temperature and precipitation including atmospheric conditions (cloud cover) during and prior to the growing season may alter plant bud growth and phenology (Ericksson and Ehrlen, 1981; Selas, 2000; Bokhorst *et al.*, 2008; Krebs *et al.*, 2009; Holden *et al.*, 2012). For many species, meteorological factors affect berry production in similar ways (Wallenius, 1999). Spring frost, cold summer and winter temperatures, insufficient snow and rainfall, and windy conditions during pollination can influence crop yields (Howatt, 2005).

2.4.3 Food Supply in the Upper Foothills

Under better conditions for fruit production (2008), I predicted an overall negative change in food supply based on proposed plans to surge harvest mature

(>80 years) stands of lodgepole pine. At the end of the surge cut in 2018, lodgepole pine habitats became increasingly more productive with a 25% increase in forbs and 2% gain in fruit production largely because of increases in *Equisetum* spp., *H. lanatum*, *R. idaeus*, *V. myrtilloides* that were associated with young and old cut-blocks. However, this will be a short term gain as habitat productivity will decline near the end of the 60 year planning period with the progression of harvesting and succession of the large cohort of young pine. Although forbs will be more abundant than pre-harvest conditions, fruit production will decline by 10% based on my model predictions. The initial increase in *R. idaeus* and *V. myrtilloides* temporarily offset the decline of *V. membranaceum* and *V. vitis-idaea* post surge cut. Over the long-term, the gain in *V. myrtilloides* alone would be enough to compensate for the loss of *V. vitis-idaea*, but it would not make up for the reduction in *V. membranaceum*. The benefits of the surge cut and increase in food supply for grizzly bear occurred mainly below 1228m of elevation. This was because *V. myrtilloides* was abundant below whereas *V. membranaceum* was abundant above this point. Because recovery of shrubs to a reproductive phase is slow with secondary succession following timber harvest (Kardell, 1980; Martin, 1983; Anzinger, 2002), logging primarily above 1228m will likely lead to a decline in *V. membranaceum* over time. Overall, an increase in habitat productivity associated with forbs does not outweigh the potential negative effects of reduced fruit availability that may be linked to reproduction and density of interior grizzly bear populations (McLellan, 2011).

The negative effect of harvesting pine was more pronounced when conditions were dry (2009). I predicted a 4% decrease in fruit after the surge harvest that declined to 13% at the end of 60 years. The percent change was proportional for most species at each harvesting period for model estimates in 2008 and 2009. However, because *R. idaeus* was unaffected by sampling year and *V. myrtilloides* fruit increased slightly in older harvested stands in 2009, the pattern of change differed. *R. idaeus* alone could not offset the decline of *V. membranaceum* and *V. vitis-idaea* because of the tremendous decrease in *V. myrtilloides* (96%) fruit. Within a short distance (<15m) from the edge boundary, soil moisture and temperature increase in cut-blocks compared to adjacent forest (Redding *et al.*, 2003). During a drought year, sustained periods of solar radiation and higher evaporation rates (Redding *et al.*, 2003) in cut-blocks may explain this variation. At the species level, annual variation in berry production is common and may occur at local and regional scales (Nilsen, 2002). In years when preferred berry species are less available, bears may switch to less preferred species (Nilsen, 2002), thus, managing for multiple foods is important.

The year in which data was collected impacted inference regarding changes in food supply. Although I detected a simultaneous fruit failure in 2009, this could be a rare event that only occurs in severe drought. Multiple years of data that span a wide range of climatic conditions (e.g. precipitation) and age classes is necessary to fully understand variation in fruit production between species and at the landscape level. Because climate is expected to change in the lodgepole pine ecosystem of Alberta (Coops and Waring, 2011) the ability to integrate climate scenarios into food supply model predictions will be important. According to general circulation models (2039-2069) for the study area, mean precipitation is expected to increase by 1.2% (Anonymous, 2012b), however, average precipitation may be less important compared to annual fluctuations above or below normal. It is expected that with changes in air temperature there will be enhancement of the hydrologic cycle globally, meaning that extreme events such as drought could be more frequent in the study area (Ryan MacDonald pers. comm; Anonymous, 2012a). This is important because variation in fruit yield between species over several years may influence average productivity of habitats. Therefore, to effectively manage grizzly bear habitat, long-term monitoring of fruit production may be necessary to fully understand how productive habitats are and to better predict future food supply in the face of climate change (Holden *et al*. 2012).

My conclusions diverged based on models of shrub cover since the pattern of change clearly deviated from fruit models. After the MPB surge cut, I predicted a 5% decrease in shrubs that increased to 8% at the end of period 12. This was because *V. myrtilloides* was unaffected by age and *R. idaeus* was considerably less abundant than the two shrubs, *V. membranaceum* and *V. vitis-idaea*, that drove the relationship. For these species, shrub models based on forest age predicted a decline with harvesting, however, they over predicted the abundance of food in older stands compared to fruit models. For the most part, changes in shrub cover approximated fruit abundance considering variables such as pine composition, elevation, and soil moisture. However, in most cases shrub cover failed to capture the relationship to age as it pertained to fruit and perhaps more importantly did not adequately describe the relative differences in abundance between species. Quantifying the actual resource, fruit, is required to accurately project changes in food supply for grizzly bears.

MPB harvesting is in its infancy, thus, there is the potential to mitigate potential negative effects to grizzly bear food supply in the future. Because an increase in forbs is imminent with harvesting, more emphasis should be placed on managing habitat to enhance fruit production. The availability of energy dense (carbohydrates) fruit is hypothesized to be particularly important for females to gain body fat that may influence reproduction, cub survival, and have a disproportionate effect on population processes that influence density (Rogers, 1976; Farley and Robbins, 1995; Felicetti *et al.*, 2003; Robbins *et al.*, 2007; McLellan, 2011). Recently, Robbins *et al*. (2012) found that female grizzly bears with a body fat content ≤ 20% did not produce cubs even though breeding occurred. From my perspective, the ideal MPB management scenario and mitigation measure would be to limit harvesting mature stands above 1228m. In doing so, the two dominant *Vaccinium* spp., *V. membranaceum* and *V. myrtilloides*, that can be major dietary components of grizzly bear would be maximized and at the same time promote *V. vitis-idaea* (McLellan and Hovey, 1995; Larsen and Pigeon, 2006; Munro *et al.*, 2006). Although less abundant, *V. vitis-idaea* may be important to grizzly bears when berry crops fail of more preferred species or at other times of the year (late fall or spring) (Nilsen, 2002; Munro *et al.*, 2006). Not only would retaining mature stands above 1228m benefit grizzly bears, managers would also have the opportunity to enhance *V. membranaceum* fruit production by creating canopy openings (Minore, 1984) through harvesting practices that minimize disturbance to the shrub layer or prescribed fire (Trusler and Johnson, 2008). If high elevation mature pine stands were retained and an epidemic outbreak of MPB occurred without salvage harvesting, evidence suggests that understory forbs and shrubs may respond positively. Following tree mortality and the subsequent increase in moisture and light from needle shed (2-3 years) and tree fall (15-25 years) with no disturbance to the understory layer (Bunnell *et al*. 2011), vascular plants are likely to increase along with fruit production (Kovacic *et al*. 1985, Stone and Wolfe 1996). Siep and Jones (2009) found that dwarf shrub cover increased substantially over a relatively short period of time (~3 years) in pine stands attacked by MPB.

Given the threat of MPB in the study area, retaining large areas of mature pine may not be feasible. Alternatively, ‘good’ patches within stands could be identified and retained in the pre-block layout prior to harvesting. However, from an operational perspective this may not be realistic. Therefore, if harvesting continues as projected, broadcast burning higher elevation (>1228m) cut-blocks where *V. membranaceum* shrubs are most abundant may be necessary to increase fruit production (Martin, 1983; Anzinger, 2002), although this technique may not be that effective (Minore and Smart, 1979). Maintaining more young (open) cut-blocks below 1228m by thinning or harvesting the 21-80 age class on an annual basis may be an alternative solution. Not only would this preclude the need for future surge cutting, but it would also mitigate the decline in forbs and fruiting species associated with an increase in the 41-80 year age class. My model predictions suggested that this age class was most deficient in food resources. Spatially and temporally optimizing total potential fruit producing habitat may be prudent given the uncertainty of annual weather events that could impact *Vaccinium* spp. fruit yields.

2.5 Conclusion

Lodgepole pine dominant stands are associated with seasonally important fruit producing *Vaccinium* spp. The surge harvest and reduction of mature pine for MPB management lead to a substantial increase in available forbs and fruits. However, the boost in habitat productivity and possible benefit to grizzly bear was short lived and merely offset the larger problem of a decline in fruit producing habitat at the landscape level. Because elevation spatially separated the two dominant fruit producing *Vaccinium* spp. in the system, not only is there an opportunity to maintain a seasonally critical bear food (*V. membranaceum*) in mature pine, but also maximize fruit production given the predicted increase in *V. myrtilloides* associated with young cut-blocks. If these same shrub species dominate the Upper Foothills across the eastern slopes of Alberta as evidence suggests, a provincial wide decline in fruit producing habitat may occur with the surge cut. Because pine stands are associated with other fruiting producing shrub species that may be locally important to grizzly bear in other regions, provincial inventories are likely necessary to fully assess the impacts of MPB management in Alberta to grizzly bear habitat supply.

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Table 2.1. Mean dry weight of forbs (g/stem) and fresh weight of fruits (g/berry), sample size and standard error (S.E.), percent dry matter (D.M.) per berry, and percent dry matter digestible. Means and standard errors were derived from the plot level average weight (g/stem or g/berry) of each species.

Type	Common name	n	Weight (g)	S.E.	% D.M.	% D.M. Digestible
Fruit	*V. membranaceum*	13	0.38	0.07	14.6	72.5
	V. myrtilloides	13	0.07	0.01	12.2	72.2
	V. caespitosum	13	0.07	0.01	12.2	72.2
	V. vitis-idaea	10	0.13	0.01	12.2	72.2
	R. idaeus	14	0.49	0.05	15.1	34.4
Forb	*Equisetum spp.*	83	0.57	0.07	-	23.0
	H. lanatum	39	1.30	0.15	-	40.9
	S. amplexifolius	34	1.83	0.26	-	40.9

Percent dry matter and dry matter digestibility of fruits were taken from Welch *et al*. (1997) and percent dry matter digestibility of forbs (averaged over seasons) from Partridge *et al*. (2001). Percent dry digestible matter of *H. lanatum* was used for *S. amplexifolius*.

Table 2.2. Environmental variables used to predict the distribution and abundance of grizzly bear foods in pine forest of the Upper Foothills Natural Subregion within Weyerhaeuser Grande Prairie Forest Management Agreement in north-west central Alberta, Canada.

Variable Code	Description	Source	Type	Value	Data Range
YR	Year of data collection	Plot	Binomial	0 - 1	2008 - 2009
Block	Stand age according to harvested and non harvested	SHS	Binomial	0 - 1	1-35; 37-208
Age20	Stand age as a 20 year continuous interval	SHS	Interval	1 - 8	1-20...101-120; 140-208
AgeS	Stand age by seral stage	SHS	Categorical	1 - 4	1-20; 21-35; 38-80; 80-208
PineC	Leading pine (>=60%) by overstory canopy composition	Plot	Binomial	0 - 1	5-59; 60-100
CTI	Compound Topographic Index (CTI)	DMTI 2003	Interval	1	5.7 - 6.8
				2	6.8 - 7.2
				3	7.2 - 7.6
				4	7.6 - 8.0
				5	8.0 - 8.5
				6	8.5 - 10.1
SRI	Solar Radiation Index (SRI)	DMTI 2003	Interval	1	-0.99 - -0.65
				2	-0.65 - -0.25
				3	-0.25 - 0.21
				4	0.22 - 0.57
				5	0.57 - 0.78
				6	0.78 - 0.99
Elev	Elevation (meters)	DMTI 2003	Interval	1	950 - 1100
				2	1101 - 1138
				3	1140 - 1175
				4	1176 - 1228
				5	1229 - 1280
				6	1281 - 1428

Table 2.3. Grizzly bear food occurrence probabilities in pine, harvested (cut), and non-harvested (uncut) including odds ratios (OR), likelihood ratio test tests (LR χ^2), model significance (p), and pseudo R^2 from logistic regression analysis. The presence of bear foods was determined from meander searches within a 30x30m sampling area at 147 cut and 142 uncut field plots in pine.

Type	Common name	Species	Pine	Cut	Uncut	OR	LR χ^2	Prob.	R^2
Forbs	Sweet-vetch	*Hedysarum spp.*	0.02	0.01	0.04	0.17	-	-	-
	Clover	*Trifolium spp.*	0.11	0.18	0.01	21.70	22.50	0.00	0.13
	Dandelion	*Taraxacum officinalis*	0.23	0.39	-	-	-	-	-
	Cow parsnip	*Heracleum lanatum*	0.45	0.53	0.34	2.16	8.63	0.00	0.03
	Twisted stalk	*Steptopus amplexifolius*	0.63	0.63	0.62	1.07	0.06	0.81	0.00
	Horsetails	*Equisetum spp.*	0.91	0.93	0.89	1.49	0.80	0.37	0.01
Shrubs	Crowberry	*Empetrum nigrum*	0.06	0.03	0.12	0.21	8.17	0.00	0.07
	Bearberry	*Arctostaphylos uva-ursi*	0.07	0.10	0.03	3.47	4.55	0.03	0.04
	Sarasparilla	*Aralia nudicaulis*	0.08	0.09	0.06	1.55	0.77	0.38	0.01
	Buffaloberry	*Shepherdia canadensis*	0.20	0.18	0.23	0.74	0.89	0.34	0.00
	Dwarf blueberry	*Vaccinium caespitosum*	0.49	0.44	0.58	0.56	4.95	0.03	0.01
	Raspberry	*Rubus idaeus*	0.52	0.73	0.22	10.07	68.25	0.00	0.20
	Black Huckleberry	*Vaccinium membranaceum*	0.63	0.53	0.76	0.35	14.54	0.00	0.04
	Velvet-leaf blueberry	*Vaccinium myrtilloides*	0.63	0.63	0.63	1.02	0.00	0.97	0.00
	Ligonberry	*Vaccinium vitis-idaea*	0.71	0.64	0.82	0.38	10.42	0.00	0.04

Hedysarum spp. includes Hedysarum alpinum and Hedysarum boreale. *Equisetum* spp. represents *Equisetum arvense*, *Equisetum pratense*, and *Equisetum sylvaticum*.

Table 2.4. Sample size (n), null and final model AIC_c scores, number of model parameters (k), and percent deviance explained (D^2) from zero-inflated negative binomial regression models describing the distribution (inflate) and abundance (count) of shrubs, fruits, and forbs. Inflate represents the model fit prior to adding covariates to the count portion of the model.

			Inflate				Count			
Type	Species	n	null AIC_c	k	AIC_c	D^2	k	AIC_c	D^2	Total D^2
Shrub	*V. membranaceum*	249	2095.6	9	2049.7	2.8	13	2004.4	2.7	5.5
	V. myrtilloides	249	1996.1	7	1978.6	1.3	9	1964.3	0.9	2.2
	V. caespitosum	244	1393.3	5	1377.9	1.4				1.4
	V. vitis-idaea	249	2131.3	6	2108.2	1.4	9	2097.0	0.8	2.2
	R. idaeus	249	1601.0	6	1531.8	5.0	11	1510.6	2.1	7.0
Fruit	*V. membranaceum*	240	973.7	4	909.8	7.3	8	878.9	4.5	11.8
	V. myrtilloides	240	1182.7	4	1176.4	0.7	14	1138.5	5.2	5.9
	V. caespitosum	238	658.3	5	653.1	1.4	10	644.6	3.0	4.4
	V. vitis-idea	236	895.1	6	867.5	3.9	9	859.6	1.6	5.6
	R. idaeus	238	876.9	7	830.8	6.6	9	830.2	0.6	7.2
Forb	*Equisetum spp.*	249	2765.6				10	2727.4	1.9	1.9
	H. lanatum	249	1395.4	7	1367.6	2.6	11	1355.4	1.5	4.2
	S. amplexifolius	247	1109.3	7	1092.2	2.3	8	1080.9	1.2	3.6

Percent deviance (D^2) for the inflate model was represented as the reduction in the log likelihood from the intercept only (null) model (k=3). D^2 for the count model was determined by the reduction in the log likelihood from the 'best' inflate model.

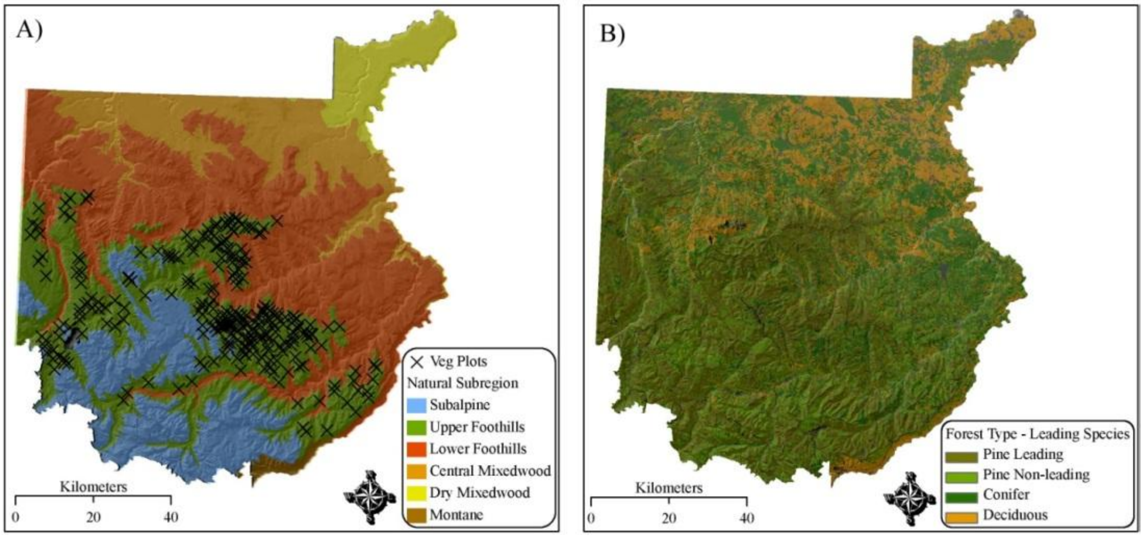

Figure 2.1. A) Location of vegetation plots in lodgepole pine (*Pinus contorta*) forests and Natural Subregions; and B) forested stand classified by leading species within Weyerhaeuser Grande Prairie Forest Management Agreement Area in north-west central, Alberta, Canada.

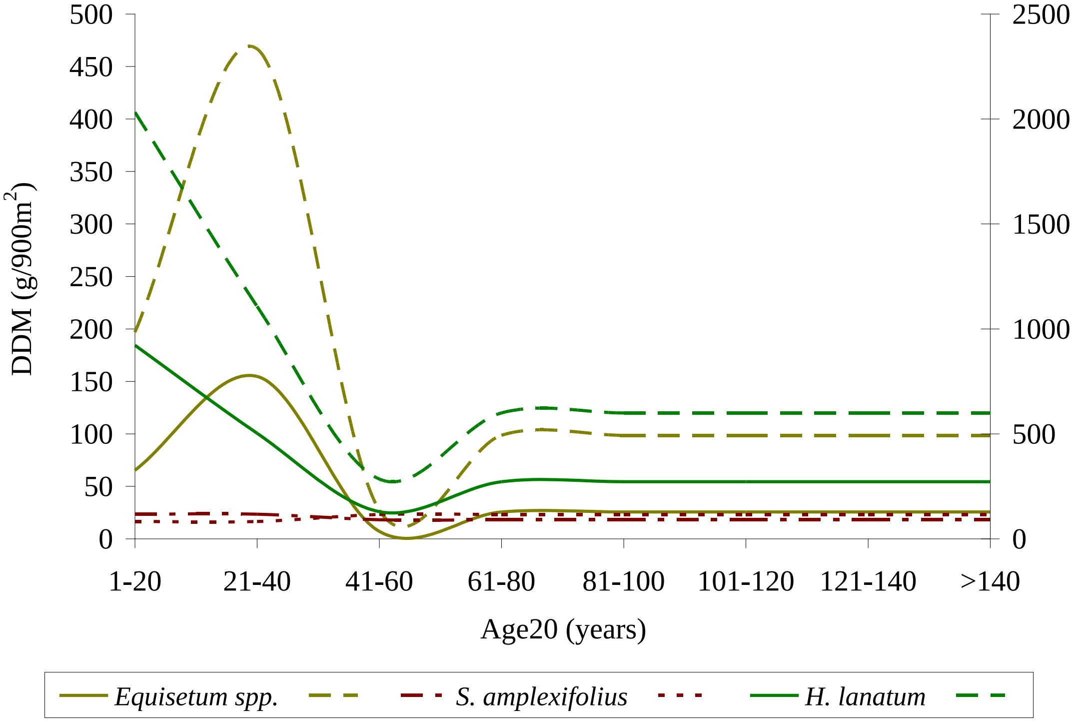

Figure 2.2. Relationship between mean dry digestible matter (g/900m^2) and stand age (Age20) for *Equisetum* spp. and *H. lanatum* in leading (solid) and non-leading (long dash) stands of lodgepole pine and in 2008 (long dash - dot) and 2009 (dot) for *S. amplexifolius*. Refer to the secondary y-axis for *Equisetum* spp.

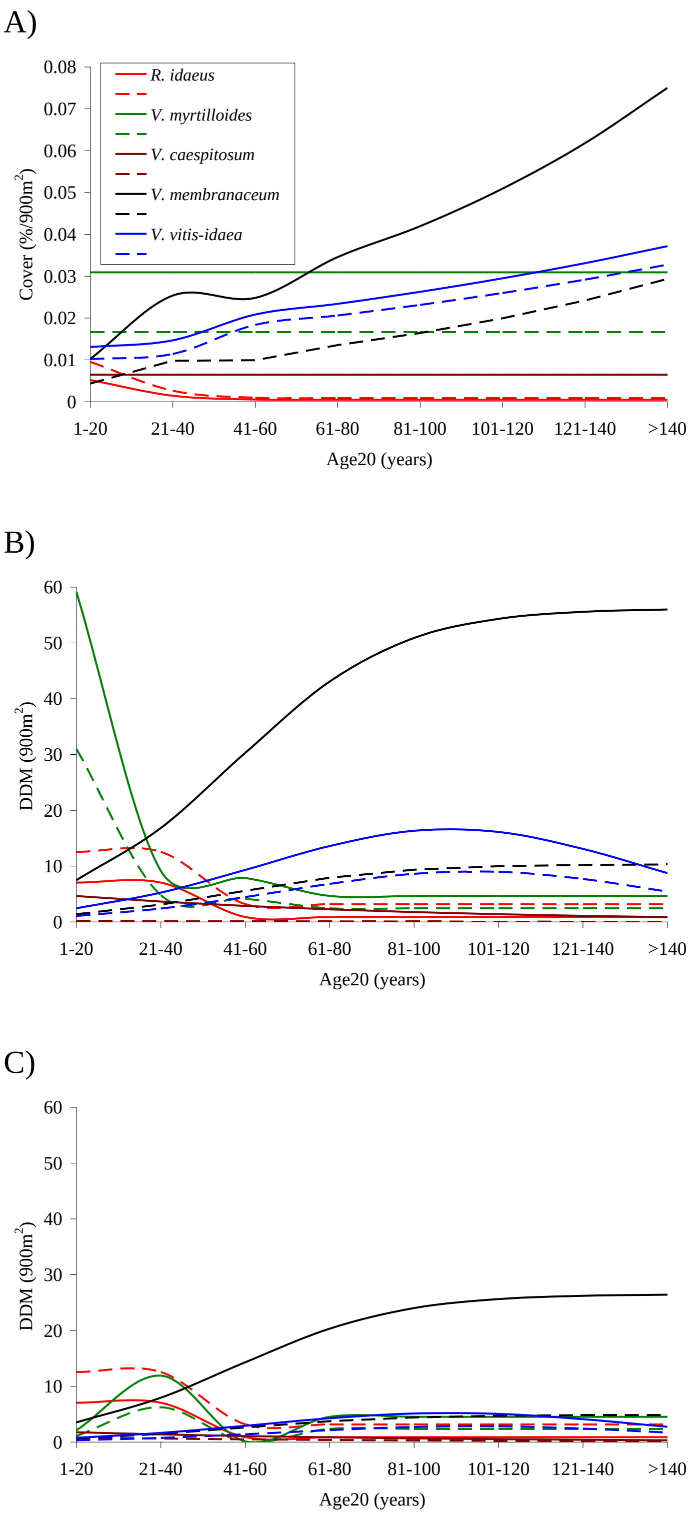

Figure 2.3. A) Relationship between mean cover (% cover/900m^2); B) mean dry digestible matter (g/900m^2) of fruit in 2008; C) mean dry digestible matter (g/900m^2) of fruit in 2009 and stand age (Age20) for five fruit producing shrub species in leading (solid) and non-leading lodgepole pine (long dash).

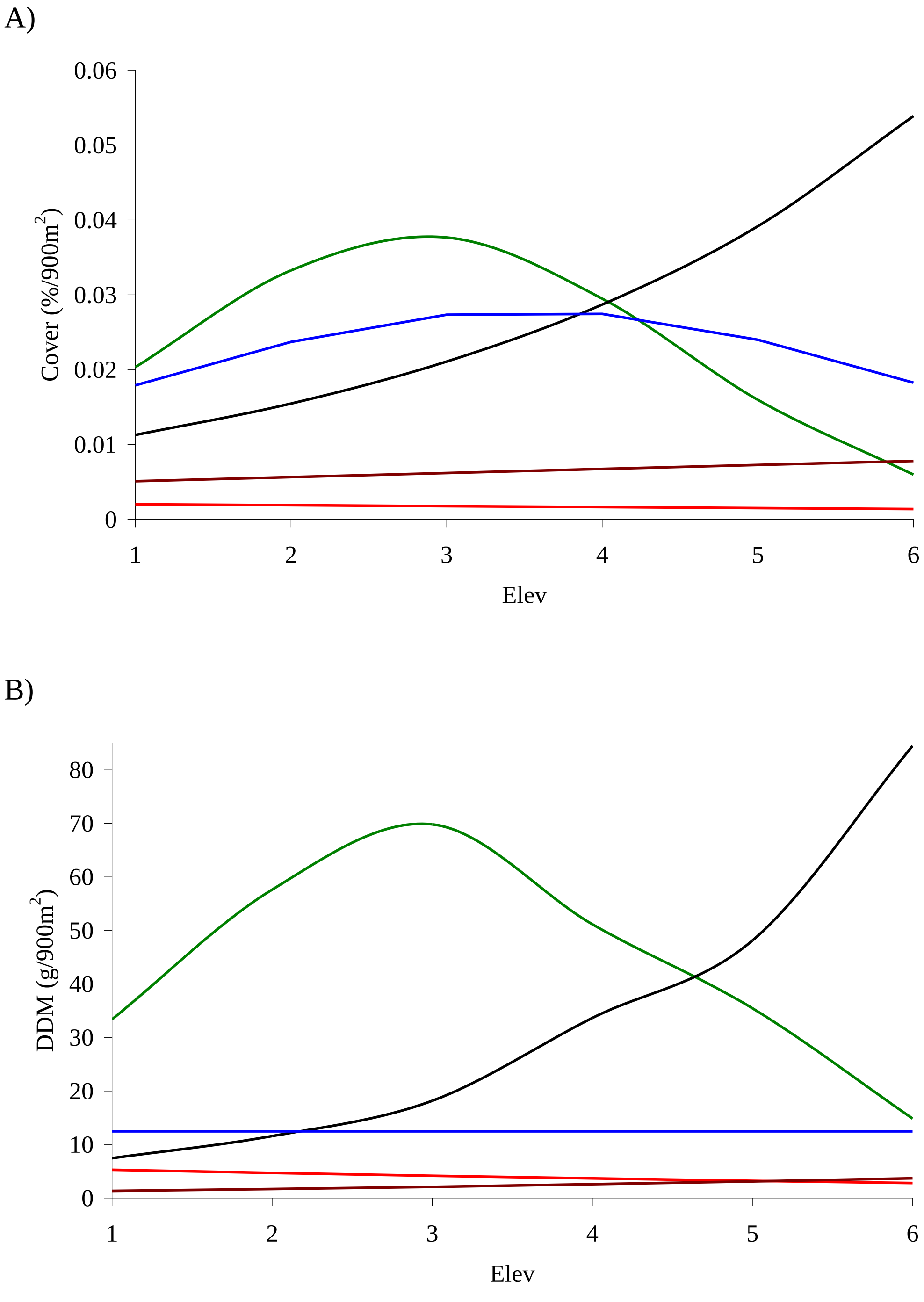

Figure 2.4. A) Relationship between mean shrub cover (%/900m^2); and B) dry digestible matter (g/900m^2) of fruit as a function of elevation (Elev) for five fruit producing shrub species in lodgepole pine.

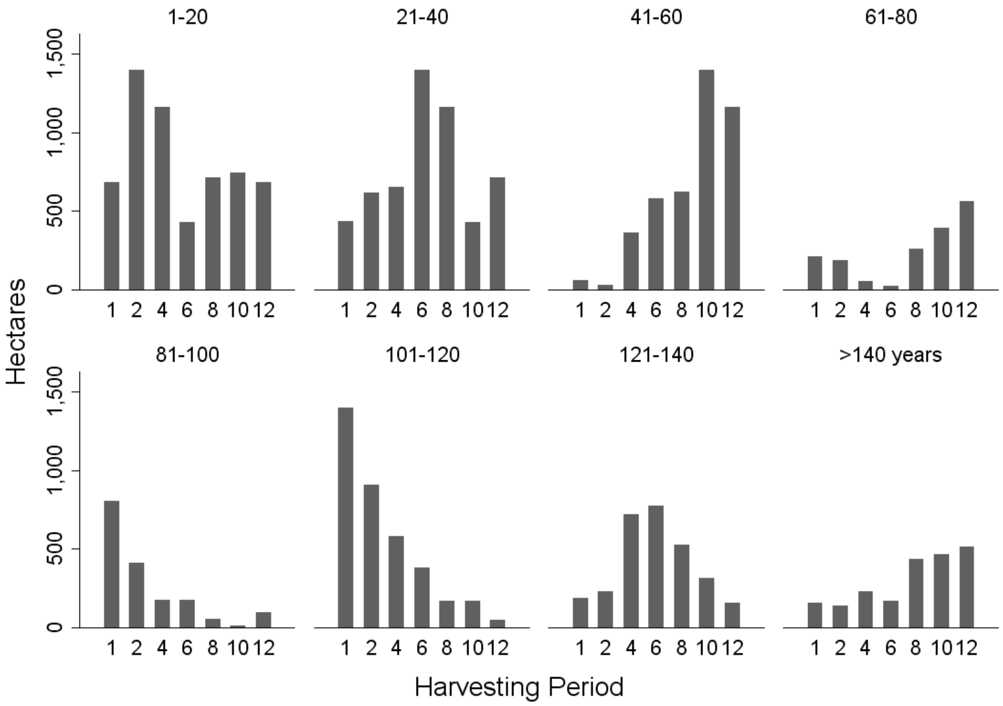

Figure 2.5. Total harvested area (hectares) of leading lodgepole pine over twelve harvesting periods by stand age (Age20) within the Upper Foothills of Weyerhaeuser Grande Prairie Forest Management Agreement in north-west central Alberta, Canada.

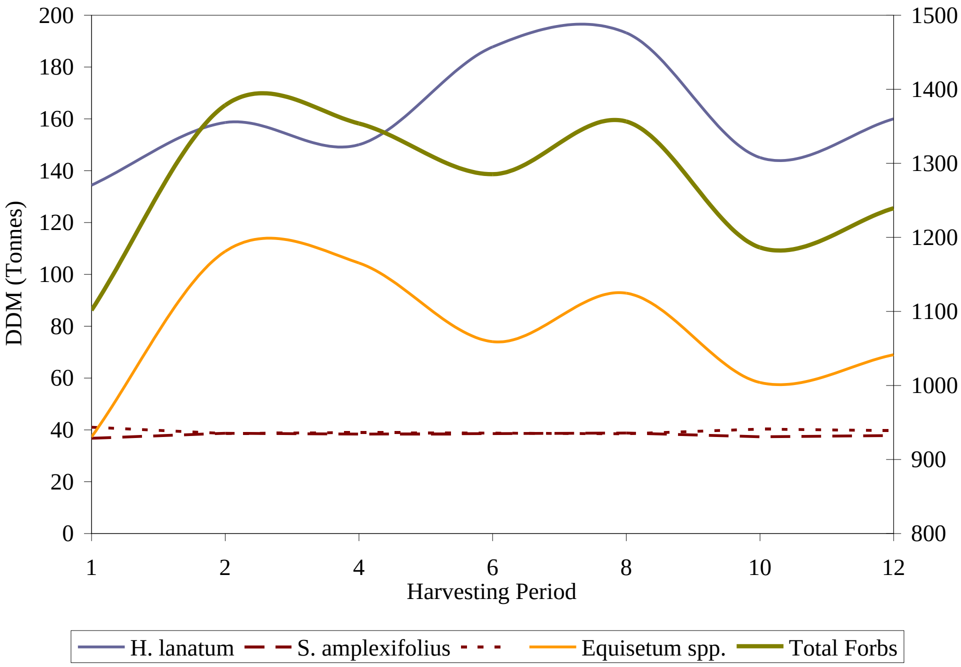

Figure 2.6. Changes in dry digestible matter (DDM; Tonnes) of *Equisetum* spp., *H. lanatum*, *S. amplexifolius* (2008 long dash; 2009 dot), and total forbs over 12 harvesting periods within the Upper Foothills. Refer to the secondary y-axis for *Equisetum* spp. and total forbs

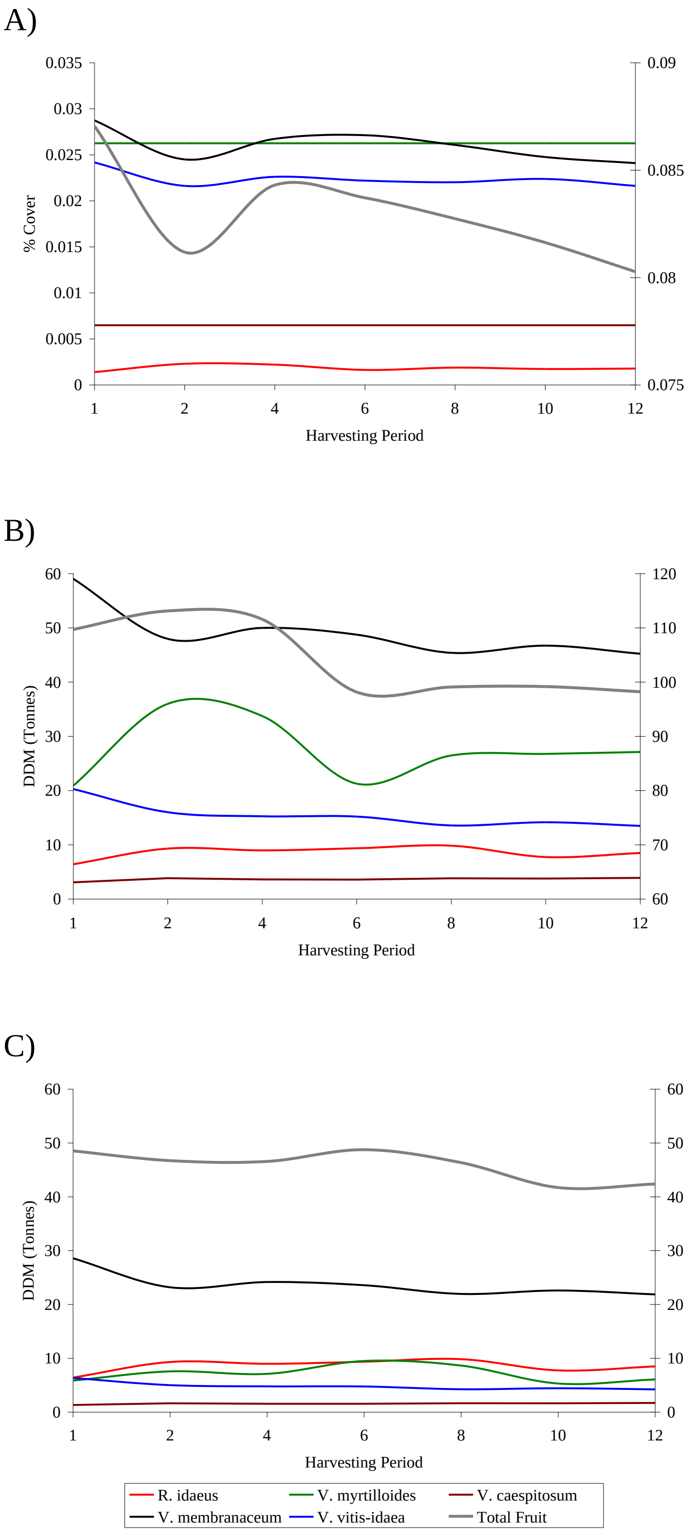

Figure 2.7. Changes in A) % cover of shrubs; dry digestible matter (DDM; Tonnes) of B) fruit in 2008; C) fruit in 2009 over 12 harvesting periods for five shrub species in the Upper Foothills. Refer to the secondary y-axis for total fruit.

CHAPTER 3: Grizzly Bear Response to Harvesting Mature Stands of Lodgepole Pine for Mountain Pine Beetle Management in North-West Central Alberta

3.1 Introduction

Mountain pine beetle (*Dendroctonus ponderosae*; hereafter, MPB) is widely distributed across the southern extent of their primary host, lodgepole pine (*Pinus contorta*), in the western portions of Canada, United States, and Mexico (Carroll *et al.*, 2003; Safranyik *et al.*, 2010). Historically, MPB populations have occurred at innocuous levels, however, landscape-level outbreaks can arise causing mortality of millions of mature pine trees impacting economic, social, and ecological systems (Safranyik *et al.*, 2010). Most notably, the epidemic that began in central British Columbia in the mid 1990's had by 2008 affected over 13 million hectares of mature pine forest, and an area ten times larger than any previously recorded outbreak (Wulder *et al.*, 2006; Safranyik *et al.*, 2010). Rapid expansion of MPB beyond their historic range is believed to be the direct result of climate change as vast and contiguous areas of mature pine have become suitable (temperature) for MPB to survive and reproduce (Carroll *et al.*, 2003). In 2006, MPB infestations were detected across large areas of north-central Alberta, which raised federal and provincial concern that populations could spread through the Rocky Mountain eastern slopes and boreal forest of Canada (Anonymous, 2007a).

In response to the threat of a MPB epidemic along the eastern slopes, Alberta Environment and Sustainable Resource Development implemented a long-term pine management strategy as part of provincial mitigation efforts (Anonymous, 2007b). The strategy aimed to change the age class structure of lodgepole pine and thereby reduce landscape level susceptibility of forests to MPB infestation on public lands (Anonymous, 2007b). Although stands of mature pine were concentrated in the Sub-alpine, Upper and Lower Foothills, and Montane Natural Sub-regions (Horton, 1956) the Foothills were of particular management concern. About seventy percent of the forested area in the Foothills is pine and because of favourable climatic conditions and proximity to local infestations, mature stands were deemed highly susceptible to MPB attack (Anonymous, 2007b). Under the direction of the provincial government, Forest Management Agreement holders developed plans to harvest mature pine at an accelerated rate (~125%) with a goal of reducing the amount of susceptible stands by 75% over a 20 year period within their respective operable land base (Anonymous, 2007b). The surge cut deviates considerably from Alberta's traditional two-pass harvesting that is based on even-flow timber supply.

A rapid change in the age distribution of pine occurring within habitats considered essential to the recovery and conservation of the grizzly bear (*Ursus arctos*) (Nielsen *et al.*, 2009) is of management concern (Anonymous, 2007b). It is well established that roads associated with timber harvest operations can negatively impact grizzly bear populations because of the increased chance of human-bear interactions and concurrent higher risk of bear mortality (Nielsen *et al.*, 2004b; Nielsen *et al.*, 2008). Limiting road development and human use of roads are fundamental components of managing grizzly bear habitat in support of population recovery (Nielsen *et al*. 2009) and will be important as MPB harvesting moves forward in Alberta. However, it is not as well understood how changing the age class structure of pine might influence habitat conditions for grizzly bears.

In forested environments that lack natural openings (fire, avalanche chutes) due mainly to aggressive fire suppression, grizzly bears often select regenerating cut-blocks and the forest-cut-block interface (edge) over mature forest (Nielsen *et al.*, 2004a). Selection of cut-blocks by grizzly bears, however, may vary according to time of year (season), age since harvest, site preparation treatment, local environmental gradients such as elevation as well as structural attributes of the patch (edge proximity) (Nielsen *et al.*, 2004a). While the specific mechanisms are not well understood, the availability (presence, abundance, calories, and phenology) and accessibility (security) of preferred foods are believed to be key drivers influencing grizzly bear behaviour (Blanchard, 1983; Mattson, 1997; Nielsen *et al.*, 2004a; Nielsen *et al.*, 2004c). For female grizzly bears, abundant plant food such as forbs and especially seasonal fruits may influence body condition (fat) that ultimately influences reproduction and the survival of cubs (Rogers, 1976; Farley and Robbins, 1995; Schwartz *et al.*, 2006; Robbins *et al.*, 2007; McLellan, 2011; Robbins *et al.*, 2012). As such, research highlights the value of cut-blocks and associated edge habitat with management recommendations emphasizing the need for site preparation techniques and harvesting designs (size and shape) that might augment use of cut-blocks by bears (Nielsen *et al.*, 2004a).

A recent study that quantified changes in food abundance along an age and elevation gradient of existing pine forests in Alberta found that forbs and certain fruits were projected to increase in abundance at low elevations (≤1228m) immediately following the proposed surge cut for MPB management. Although food abundance declined post harvest as older cut-blocks (>20 years) with closed canopies became more available, they remained more abundant than initial (pre-harvest) conditions and suggested a net benefit to grizzly bears. However, a reduction in shrubs associated with mature pine, was observed at higher elevations (>1228m) and resulted in the decline of available fruit at the landscape level (Chapter 2). This research also showed that pine dominant stands were associated with important fruit producing dwarf shrubs (*Vaccinium* spp.) while other stand types contained more forbs.

The seasonal response of grizzly bears to variation in forest age, elevation, and/or edge proximity has been investigated (Blanchard, 1983; Zager *et al.*, 1983; Aune, 1994; Mattson, 1997; Waller and Mace, 1997; Mace *et al.*, 1999; McLellan and Hovey, 2001; Wielgus and Vernier, 2003; Nielsen *et al.*, 2004a; May *et al.*, 2008; Martin *et al.*, 2010). However, relatively few studies have considered these factors explicitly in pine dominant forests. Moreover, none of these studies considered that there may be forest age associated differences in selection as a function of elevation and that edge use may also depend on the difference in forest age on either side of the edge. Thus, there is a need to determine grizzly bear responses to these factors in the current landscape to better understand and mitigate the potential consequences of harvesting mature stands of pine for MPB management in Alberta.

Habitat resources (food, cover, and water) are essential for animals to acquire in order to support self-sustaining populations over space and through time (McComb, 2008). Because resources are heterogeneously distributed, animals distribute themselves in habitat over space and time (Fretwell and Lucas, 1970; Wiens, 1989). The disproportionate use of habitat (use >availability), which reflects where animals live (Boyce and McDonald, 1999), is a consequence of animals actively selecting for essential resources that directly influences survival and reproduction, and consequently fitness (Southwood, 1977). However, the magnitude and direction of selection is dependent on the availability of habitat (Beyer *et al.*, 2010). Even when use is high habitats may be avoided, while rare habitats can be selected when use is comparatively low (Beyer *et al.*, 2010). This is problematic as mature forests are often the most available habitat for North American grizzly bear populations and although bears may avoid this age class relative to what is available they may also be used the most (McLellan and Hovey, 2001; Wielgus and Vernier, 2003). Therefore, independent measures of use and selection are both essential to assessing the population level response of grizzly bears to MPB management.

I examine population level use and selection of habitats by female grizzly bears in a conifer (pine) dominant landscape of north-west central Alberta where MPB control harvesting is underway within the operable land base. My specific objectives were to describe the seasonal use and selection of 1) operable vs. inoperable forested habitats; 2) leading pine vs. other forest types within the operable land base; 3) different age classes of leading pine within the operable land base; and 4) different age classes of leading pine relative to elevation and edge proximity.

3.2 Methods

3.2.1 Study Area

The study area encompassed the southern boundary of Weyerhaeuser Grande Prairie Forest Management Agreement (FMA) in northwest-central Alberta, Canada (119° 13’W and 54° 32’N; Figure 1.1). Variation in climate, topography, and vegetation follow a prominent elevation gradient from the south-west to the north-east. The higher elevation and more rugged conifer dominated forests of the Subalpine and Upper Foothills transitions to lower elevation gently rolling terrain characteristic of the Lower Foothills and Central Mixedwood Natural Sub Regions. The Subalpine is a mixture of lodgepole pine (*Pinus contorta*), engelmann spruce (*Picea engelmanni*), and subalpine fir (*Abies lasiocarpa*) (Natural Regions Committee 2006). Lodgepole pine dominates the Upper Foothills often with black spruce (*Picea marianna*), while white spruce (*Picea glauca*) occurs along river valleys (Natural Regions Committee 2006). Mixed and deciduous stands are confined to south and west aspects at the lowest elevations (Natural Regions Committee 2006). The Lower Foothills are diverse with pure and mixed stands of trembling aspen (*Populous tremuloides*), poplar (*Populous balsamifera*), white birch *(Betula papyrifera*), lodgepole pine, black and white spruce, balsam fir (*Abies balsamifera*), and tamarack (*Larix laricina*) (Natural Regions Committee 2006). The Central Mixedwood is largely dominated by aspen and mixed with white spruce and jack pine (*Pinus banksiana*) among poorly drained fens (Natural Regions Committee 2006). Summers are relatively short in duration with long and snowy winters. Average annual temperature (-5.1 – 3.1°C) and precipitation (333 – 1474mm) levels fluctuate substantially with elevation (Natural Regions Committee 2006). Forest harvesting has created a mosaic of seral stages that is currently dominated by young (<35 years) and older (80-120 years) age classes.

3.2.2 Grizzly Bear Locations and Home Range Delineation

Female grizzly bears (n=12) were captured between 2007 and 2010 by the Foothills Research Institute's Grizzly Bear Program using helicopter darting, leg hold snares, or culvert traps. Because snares are more likely to cause severe muscle injury compared to the other capture methods (Cattet *et al*., 2008), in 2009 and 2010 bears were captured using either a helicopter or culvert trap. Bears were fit with a Televilt Tellus 2D brand GPS radio-collar (Televilt® TVP Positioning AB, Lindesberg, Sweden) programmed to collect locations at an hourly interval. For each year and individual bear, I grouped GPS locations by seasonal period that corresponds to major dietary changes determined from scat analysis (Munro *et al.*, 2006). The spring (May 1 until June 15) represented hypophagia (low food intake), whereas the summer (June 16 to 31 July) and the fall (August 1 to October 15) characterize early and late hyperphagia (high food intake) (Nielsen *et al.*, 2009). Hyperphagia is the time of the year when energy intake, growth, and fat deposition is maximized (Robbins *et al.*, 2007). My limited sample size precluded assessing differences in the use/selection of habitat between females with or without cubs.

Using 47,809 GPS locations from the 12 bears (min=154, max=1244, median=828, mean=887), I calculated a utilization distribution (UD) for each grizzly bear by year and season using fixed kernel analysis (Worton, 1989). A UD is a relative probability surface that sums to 1 and describes both the spatial boundary (x-y axis) and intensity of use (z-axis) of GPS locations. I used the plug-in method to select the appropriate bandwidth (smoothing parameter) for each UD (Gitzen *et al.*, 2006; Duong, 2012). Smoothing parameter values and UD's were calculated using the KS package (Duong, 2012) and the statistical software R (R Development Core Team 2012) following the methods of Robinson *et al*. (2010). I use the Percent Volume Contour tool available in Hawth's Tools (Beyer, 2004) for ArcGIS 9.2 (ESRI® Redlands, CA) to extract the 95% volume from UD raster grids (30m pixel) for each home range, which corresponds to an area where on average 95% of GPS locations are found. The home range area (mean=163km^2, SD=121.6) defined potentially available habitat for each grizzly bear by year and season.

3.2.3 Habitat Stratification

I used a GIS forest inventory polygon database (net land base) provided by Weyerhaeuser Canada to stratify habitat within the home range area of female grizzly bears (Figure 1.2). I removed polygons where overstory tree species composition and age were not known (2%) including those classified as anthropogenic (4%; roads, well sites, pipelines, seismic lines and other land use dispositions) or non-forested (2%). The remaining forested stands were classified as operable (82%) or inoperable with the latter distinguished as either water buffers (7%) or steep slopes (5%). Because stand age and overstory composition were based on updated forest inventory data for 2009, I back-casted harvested stand attributes to pre-harvest values for home ranges circa 2007 and 2008. I further stratified forested stands into leading pine (>60% overstory composition) versus other forest types and by age class: A) 1-20 years; B) 21-37 years; C) 38-80 years; D) >80 years. The age classes represent A) young cut-blocks with open canopies; B) old cut-blocks with closed canopies; C) non-harvested immature closed canopy forest; and D) non-harvested mature to old-growth forests that are the focus of MPB management (Chapter 2).

For each grizzly bear home range, I defined the forest edge interface as the polygon line that separated harvested from adjacent non-harvested or harvested stands that differed by age class. Edges were buffered by 70m to classify edge from interior habitat. This cut-off point roughly corresponds to edge effects related to forest understory composition and structure (up to 60m) (Harper and Macdonald, 2002) and the lower end of GPS error (10-28m) commonly reported (Frair *et al.*, 2010). Finally, elevation was obtained from a 30m pixel digital elevation model (DMTI, 2003) and used to classify the area of forested stands as being above 1228m or not. This was the change point in dominance of the two most abundant *Vaccinium* spp. (Chapter 2).

3.2.4 Population Level Selection and Use of Habitat

Of the 47,892 GPS locations used to define grizzly bear home ranges, 8815 (18%) overlapped with polygons classified as anthropogenic and 1113 (2%) with non-vegetated. I intersected the remaining 37,879 locations (80%) that fell within forested grizzly bear habitat. About 68 and 13% of bear locations occurred within the Upper and Lower Foothills with the remaining 19% in the Sub-alpine Natural Sub Region. Grizzly bear locations and habitat strata were sub-divided into five datasets: 1) operable and inoperable stands; 2) operable stands only that were either leading pine or other forested stand types; 3) operable stands of leading pine by age class; 4) operable stands of leading pine by age and interior vs. edge classes; and 5) operable stands of leading pine by age and elevation classes. Using Hawth's Tools (Beyer, 2004), I calculated the habitat area for each of the five datasets by home range (year, bear, and season) and generated 5 random locations per km^2 of home range to define available habitat. Because the 37-80 year age class, which will become more common in future, was quite rare and contained relatively few bear locations, I created a single non-harvested age class (≥ 37 years) for the 4th and 5th habitat datasets. The area of each unique habitat combination within overlapping home ranges (2007-2010) of female grizzly bears is included (Table 1.1).

To determine the use and selection of habitat by female grizzly bears at the population level, I used a two stage analysis similar to Nielsen *et al.* (2009) to account for potential differences among individuals and ensure that the unit of replication was the animal rather than the telemetry location (Aebischer *et al.*, 1993). First, I estimated selection (electivity) (Ivlev, 1961) of habitat for each combination of year, bear, and season among the five datasets. Electivity ([$E_i = (o_i - pi_i) / (o_i + pi_i)$]; where $_i$ indicates the i^{th} habitat, o_i is the proportion of used (GPS locations) habitat i, and pi_i is the proportion of available habitat. The electivity index is similar to the selection ratio ($w_i = o_i / pi_i$) (Manly *et al.*, 2002), however, they differ in that E_i is constrained between -1 and +1 and w_i is bound between - / + infinity when taking the log of the numerator and denominator of the ratio (Jacobs, 1974). Electivity offers a distinct advantage when averaging across individuals of a population because the mean selection coefficient will be less sensitive to high and low values (Jacobs, 1974). Interpretation of E_i follows that when a habitat is selected values are positive, negative denotes habitat avoidance, and zero represents random use of habitat (Strauss, 1979). For datasets 3-5, I only considered observations where habitat availability was greater than 5% by home range in an attempt to minimize the effect of rare habitats. In addition, for the 4th and 5th datasets, I only considered observations (year, bear, and season) where edge/interior and elevation classes were matched (available) for each respective age class.

I used a weighed random effects linear model (xtregre2) within the statistical software Stata (StataCorp 2009) to predict the mean and 95% confidence intervals of my two dependent variables (use and electivity) by season and habitat. To meet the assumption of normality, I performed the logit transformation on the use proportion and then back transformed the model predictions post estimation. Bear identity was specified as the random effect in each model to account for the repeated observations (years) among individual animals. Analytical weights for each observation were estimated as the inverse variance weights from standard errors to account for precision of habitat use and selection estimates among individuals (Nielsen *et al.*, 2009). Because not all habitats were available and/or used by bears and multiple comparison tests were inappropriate given the unit sum constraint (Aebischer *et al.*, 1993), I limited my inference to describing differences between the mean and variance among habitats. At the population level, habitat use was considered proportional to availability when confidence intervals overlapped zero.

In a separate analysis, I found that daily female grizzly bear movement (step length) conformed to the circadian pattern observed by Heard *et al*. (2007) (Appendix C). At the population level, bears travelled less (inactive) between 24:00-04:00 hours and corresponded to when bears rested more and foraged less (Appendix C). However, in unreported analysis where I removed inactive locations, the patterns reported here did not change. Thus, I retained all GPS data in my analysis. Grizzly bears are known to spend most of their time foraging and resting and these activities tend to occur in relatively close proximity (Herrero *et al.*, 1986).

3.3 Results

The operable land base accounted for 85% of the forested stands encompassing female grizzly bears overlapping home range area (Table 1.1). At the population level, I found little evidence of major seasonal changes in the use and selection of the operable vs. inoperable land base by female grizzly bears. However, variation within seasons was most pronounced during the spring and even more so in the fall, when bears used operable habitat less compared to the summer (Table 1.3). In the spring and fall, females used operable forests about 6 and 8% less and avoided this habitat (Table 1.3). Across seasons, female grizzly bears spent about 80% of their time within the operable land base.

Pine leading stands made up 55% of female grizzly bear habitat (home range area) within the forested land based where timber harvest may occur (Table 1.1). When females used the operable land base, they showed little seasonal difference in use and selection of leading pine vs. other forest types (Table 1.3). However, use and selection of leading pine was slightly lower in the spring and fall when compared to the summer (Table 1.3). In the spring, females avoided leading pine, while use was proportional to availability in the summer and fall (Table 1.3). Overall, female grizzly bears spent 57% of their time in leading pine habitat.

The age class distribution of leading pine within operable grizzly bear habitat was largely comprised of regenerating (≤37 years) cut-blocks and mature (>80 years) stands (Table 1.2). In each season, females used mature pine more than any other age class, but from the spring use slightly decreased in the summer and again in the fall (Figure 1.2). Although use of mature stands was consistently high, grizzly bears showed neutral (use=available) selection in the spring and avoidance during the summer and fall (Figure 1.2). Conversely, non-harvested intermediate (38-80 years) age pine stands were the least used age class in every season and females avoided this age class in the spring, while use was proportional to availability in the summer and fall (Figure 1.2). Seasonal variation in the use and selection of pine age classes by females was associated with young (≤20 years) and older cut-blocks (21-37 years). The general pattern was that females used young cut-blocks less than older ones in the spring with the opposite occurring in the summer and fall seasons. Young cut-blocks were used the least in the spring (neutral selection) with a trend of increased use in the summer (selected) and fall (selected) (Figure 1.2). Selection of this age class was particularly high during the fall with the mean being about 2.4 times greater than the summer. Conversely, use of older cut-blocks by female bears was highest in the spring (selected) and summer (neutral) and substantially lower in the fall (avoidance) (Figure 1.2).

Approximately half of the operable pine leading stands within the home range area of female grizzly bears occurred above 1228m of elevation (Table 1.1). Although the age distribution above and below 1228m was similar, above this point there was about half as many older cut-blocks than below (Table 1.1). The use of young and older cut-blocks was similar above and below 1228m in each season. Although differences were negligible, young cut-blocks appeared to be used the least above 1228m in the spring, while older cut-blocks were used the least in the fall (Figure 1.2). However, non-harvested stands were used the most below 1228m in the spring and above 1228m in the summer and fall (Figure 1.2). Young cut-blocks were selected in the fall below 1228m (Figure 1.2). Non-harvested stands were avoided at higher elevations in the spring and at lower elevation in the summer (Figure 1.2). Although confidence intervals overlapped zero for all other age class and elevation combinations, positive electivity values were associated with young cut-blocks both at low and high elevations in each season (Figure 1.2). The exception being that electivity was negative for young cut-blocks above 1228m in the spring (Figure 1.2). For older cut-blocks, electivity values were positive in the spring and summer and negative in the fall for both elevations categories (Figure 1.2). In mature stands, electivity values were consistently negative (Figure 1.2).

The interior of cut-blocks and edge made up a relatively small proportion of grizzly bear habitat compared to the interior non-harvested stands (Table 1.1). Female grizzly bears spent more time on the edge compared to interior of young cut-blocks, but the opposite was true of older cut-blocks and non-harvested stands (Figure 1.3). As the use of young cut-blocks increased in the summer and fall, so did the use of the interior and edge habitat (Figure 1.3). However, the use of non-harvested interior and edge were consistent across seasons (Figure 1.3). Although females avoided the interior of young cut-blocks in the spring, bears showed neutral selection in summer, and selection in the fall. Young cut-block edge was used in proportion to availability in the spring and selected in the summer and fall (Figure 1.3). The interior of older cut-blocks were selected in the spring and avoided in the fall (Figure 1.3). Although bears showed neutral selection to the edge of older harvested stands in all seasons, electivity values were positive in the spring and summer, but negative in the fall (Figure 1.3). The interior of non-harvested were avoided in every season, but the edge was selected during the spring and summer and used in proportion to availability in the fall (Figure 1.3).

3.4 Discussion

Female grizzly bears used operable forests considerably more in every season than inoperable stands distinguished primarily by riparian buffer zones and steep slopes. For the most part, habitats were used at availability; however, females avoided operable areas in the spring and fall that only corresponded to 6 and 8% less use on average. Riparian areas in particular are often viewed as important seasonal habitats for grizzly bears associated with *Hedysarum* spp. roots and forbs (Zager *et al.*, 1983; McLellan and Hovey, 2001; Nielsen *et al.*, 2002). Compared to upland habitats they are often used substantially less, yet bears do show positive selection (Zager *et al.*, 1983; McLellan and Hovey, 2001). I suspect that greater variation and use of operable habitats during the spring may be related to the local availability of *Hedysarum* spp. for individuals, while variation in the fall may be related to annual pulses of *Vaccinium* spp. fruit that have been documented in the study area (Chapter 2). In years when fruit production is low, roots tend to constitute a greater proportion of the fall diet in grizzly bears (Hamer and Herrero, 1987a). Field observations confirm that grizzly bears may dig roots in certain inoperable areas (T. A. Larsen, unpublished data) as roots tend to be rare in operable forests (Chapter 2). Other shrubs such as *Shepherdia canadensis* and *Arctostaphylos uva-ursi* also are rare in operable areas but often associated with dry and/or steep terrain features and thus could be more common on steep slopes. I do not dispute the importance of riparian areas, but on an annual basis grizzly bear meet the vast majority of their life history requirements within the operable land base where timber harvesting has or is planned to occur.

Lodgepole pine dominant stands comprised the majority of the operable forested land base available to female grizzly bears. My results indicate that female grizzly bears spent more time in pine during early and late hyperphagia (summer/fall) when food availability and intake is maximized (Nielsen *et al.*, 2009). Previous studies have not investigated seasonal variation in selection and use of pine versus other forests types specifically. In general, pine forests tend to be used proportional to availability, but in most studies pine has been a fairly common habitat (Mattson, 1997; Ciarniello *et al.*, 2007). Grenfell and Brody (1986) found that black bears selected lodgepole pine in the summer/fall, but compared to other habitat selection studies of bears, availability was substantially less in their study area. I found evidence of pine avoidance during the spring when grizzly bears are known to forage on *Equisetum* spp. (McLellan and Hovey, 1995; Larsen and Pigeon, 2006; Munro *et al.*, 2006). Avoidance of pine could be related to *Equisetum* spp. being more abundant when pine is not the dominant overstory tree (Chapter 2). Herrero *et al.* (1986) found grizzly bears foraged on *Equisetum arvense* in mature spruce forests. *H. lanatum* was also more abundant in non-pine forest (Chapter 2), but females spent more time in pine during the summer when bears typically forage on this food resource (McLellan and Hovey, 1995; Larsen and Pigeon, 2006; Munro *et al.*, 2006). Bear use of pine during the fall was consistent with *Vaccinium* spp. fruit (Chapter 2) being more abundant at this time (Pelchat and Ruff, 1986). However, the similarity in use of pine during early and late hyperphagia may partly be caused by the fact that bears were using cut-blocks which are often planted to pine.

The spatial and temporal availability of food resources associated with canopy closure is often related to patterns of habitat use by grizzly bears (Hamer and Herrero, 1987b; Wielgus and Vernier, 2003; Nielsen *et al.*, 2004a). Following harvest of pine stands, my results suggest that seasonal patterns of use/selection reflected age associated differences in canopy closure and plant based food resource abundance (Chapter 2). Females used young (1-20 years) open canopy cut-blocks less in the spring, but use increased as the year progressed. Grizzly bears selected this age class in summer which could be related to numerous foods becoming more available (forbs, graminoids, ants, or ungulates) (Nielsen *et al.*, 2004c; Martin *et al.*, 2010). Selection was even stronger in the fall when fruiting resources were most likely to be available (Chapter 2), but at the same time variation among bears was higher than other seasons which could be related to annual pulses in *Vaccinium* spp. fruit (Chapter 2). Even when fruit crops fail (Chapter 2), young cut-blocks provide alternative foods for grizzly bears (Nielsen *et al.*, 2004c; Martin *et al.*, 2010). Older (21-37 years) cut-blocks were used the most during the spring/summer likely because forbs were abundant (Chapter 2). In the fall, use decreased considerably when females avoided this age class presumably because fruit production declined with canopy closure, a pattern that has been observed in other studies (Wielgus and Vernier, 2003; Brodeur *et al.*, 2008; Mosnier *et al.*, 2008). The observed patterns of selection are consistent those observed among bears in west-central Alberta (Nielsen *et al.*, 2004a) even though the foods (i.e. *Hedysarum* spp. and *S. canadensis*) associated with these age classes appear to differ to some degree from the study area (Nielsen *et al.*, 2004c; Chapter 2). Regardless of the specific foods found, cut-blocks seem to be seasonally productive habitats and bears respond positively to their availability especially in landscapes where natural disturbances are lacking (Mace *et al.*, 1996; Wielgus and Vernier, 2003; Nielsen *et al.*, 2004a; Brodeur *et al.*, 2008; Martin *et al.*, 2010).

The MPB surge cut will result in substantially more harvested habitat in the very near future. Perhaps more importantly, in the next 60 years stands between 38 and 80 years of age will be far more abundant. Because this age class was the least used and also least available habitat in the study area, my ability to assess grizzly bear response to this age category was quite limited. Given that food resources appear to be less abundant than in mature stands (Chapter 2), my assumption is that more of this age class will not benefit grizzly bears (Chapter2). Nielsen *et al.* (2004a) found that grizzly bears selected harvested stands between 36 and 45 years of age during hyperphagia and associated this with *S. canadensis*, a shrub that was quite rare in portions of the study area. Thus, it remains somewhat unclear what the outcome could be as this age class becomes more available. If managers continue with the MPB surge cut, there may become a future need to harvest or burn this age class earlier than expected in a traditional two-pass harvesting scenario if bears truly require the edge and open habitat that they currently select.

Although female grizzly bears used mature pine leading stands more in every season than any other age class, they also avoided these stands during early and late hyperphagia. Thus, my supposition is that harvesting from MPB will be beneficial to bears given the increase in forage (Chapter 2) albeit dependent on season. Mature forests are commonly avoided by bears but in many cases are the most common and used habitat (Blanchard, 1983; Zager *et al.*, 1983; McLellan and Hovey, 2001). Given this predicament, a modeling approach that links GPS locations to bear behaviour (foraging vs. resting vs. movement) to determine the proportion of calories ingested in each habitat would be ideal (Marsh, 2012). Overall, open habitats are more often associated with foraging whereas mature stands tend to be associated with resting (Blanchard, 1983; Hamer and Herrero, 1987b; Mattson and Merrill, 2002; Munro *et al.*, 2006). However, mature pine does offer foraging opportunities for grizzly bears that depending on moisture regime and elevation food may be relatively abundant (Hamer and Herrero, 1987a; Mattson, 1997). Furthermore, the strong moisture contrasts in cut-blocks versus forested habitat (Redding *et al.*, 2003) means that in years with moisture deficits, mature stands may be more important as plant phenology and fruit production can be more negatively affected in cut-blocks with open canopies (Meiners and Smith, 1984). Mature stands are also probably used as cover for thermal regulation, resting, and/or security in proximity to foraging sites and could even facilitate movement through the landscape (Blanchard, 1983; Zager *et al.*, 1983; Hamer and Herrero, 1987b; Waller and Mace, 1997; Mace *et al.*, 1999; Brodeur *et al.*, 2008).

Most importantly, increased food supply with the MPB surge cut may be a short term gain. As Chapter 2 demonstrated, fruit production is predicted to decline at the landscape level caused by harvesting mature pine above 1228m in the Upper Foothills. Below 1228m, harvesting pine may be most beneficial since females used and selected older cut-blocks during the spring and summer, while young cut-blocks became increasingly important as the growing season progressed. Above 1228m, female grizzly bears responded positively (increased use and selection) to young cut-blocks during early and late hyperphagia suggesting harvesting at this elevation would also be positive for bears. However, the substantial decrease in use (avoidance) of older cut-blocks during the fall (fruit) season, considering that mature stands were used more often than young cut-blocks even though they were avoided, suggests over the long-term an increase in this age class above 1228m may be detrimental.

Although grizzly bears tend to be found at lower elevations in the spring and then move to higher elevations with the progression of the seasons because snow cover is less and succulent vegetation is first available, not all individuals conform to this pattern (Hamer and Herrero, 1987a; Waller and Mace, 1997; Mace *et al.*, 1999; McLellan and Hovey, 2001). The consistent use and selection of harvested habitat at lower elevation from spring to fall and increased use and selection of young cut-blocks and mature stands at higher elevations suggests that plant phenology and habitat productivity (Mace *et al.*, 1999), may explain temporal patterns in bear use of pine forest. Certain individuals may switch between food resources as they become available, while others may track the phenological changes of specific food items (i.e. *Equisetum arvense*) such that foraging could extend late into the summer (Hamer and Herrero, 1987a). Females are better able to capitalize on plants when they are in an immature stage of development and of higher nutritive value (Hamer and Herrero, 1987a; McLellan and Hovey, 1995). On the other hand, fruits tend to occur at distinct bands of elevation and can be unrelated to plant phenology (Hamer and Herrero, 1987b; Raine and Kansas, 1990). Collectively, retaining certain mature stands above 1228m may benefit bears both in the short and long-term (Chapter 2). Particularly if mature stands contained abundant *Vaccinium membranceum* (Chapter 2) and other food resources like *Empetrum nigrum, Vaccinium scoparium* or *Lupinus* spp., which may occur at these higher elevations (Raine and Kansas, 1990; Strong, 2002).

Edge is often viewed as an important habitat feature for grizzly bears either because there is hiding cover, more food, or a combination of these factors (Blanchard, 1983; Zager *et al.*, 1983; Nielsen *et al.*, 2004a). My results support the management recommendation to create smaller cut-blocks (Nielsen *et al.*, 2004a) since bears spent more time and selected the edge of young cut-blocks during hyperphagia even though they showed no sign of avoidance during spring/summer. Although use did not appear to be higher on average, females selected non-harvested edge during hyperphagia. Whether edge versus interior use by bears is related to more food or the perceived risk of open habitats is unknown, yet it is probable that both influence behaviour. Grizzly bears have been found to use cut-blocks during nocturnal and crepuscular periods (Nielsen *et al.*, 2004a). Roever *et al*. (2008) found that certain foods (*Equisetum* spp., *Taraxacum officinale, and* sedges) were more likely to occur on the edge versus the interior, while others were not (Graminoids, *S. canadensis, Arctostaphylos uva-ursi, Vaccinium myrtilloides, V. vitis-idaea*). Other studies found that *V. myrtilloides* shrub cover to be highest on the forested side of the edge compared to the adjacent harvested area (Harper and MacDonald, 2001; Harper *et al.*, 2004). Bears may also kill ungulates more frequently near forested edge (May *et al.*, 2008). MPB harvesting may be a concern since many of the mature stands being harvested will be removed as the second pass in the study area. In addition, cut-blocks could be larger in areas where first pass timber harvest has yet to occur in order to meet pine reduction goals in the study area. Thus, the juxtaposition of young/mature edge and favoured by grizzly bears and created through traditional two-pass harvesting may be reduced. Even though food is predicted to increase in young cut-blocks, accessibility may be a concern and its value (food or security) may be reduced when adjacent to young or older cut-blocks. Structural retention within cut-blocks could be a potential solution to the problem (Zager *et al.*, 1983) but its effectiveness has yet to be tested for bears.

Population measures of use and selection provided complimentary information that aided in my interpretation of seasonal habitat associations and response of female grizzly bear to forest harvesting for MPB. The dichotomy of resource use and selection is important, yet habitat selection remains a common means by which to determine animal habitat requirements. I strongly believe that selection alone clouds our understanding of wildlife-habitat relationships that ultimately influences inference and management actions, and advocate that both measures should be integrated into all habitat analyses. Understanding grizzly bear habitat use/selection is important and can help guide management action. However, it should be cautioned that high use or selection may not be indicative of vital habitat and low use or avoidance may not signify unsuitable or unimportant habitat for bears (Grenfell and Brody, 1986; Craighead, 1998). These are assumptions that always should be tested (Pendleton *et al.*, 1998).

3.5 Conclusion

Managing habitat for grizzly bears is complex and requires considering not only stand age, but age in the context of elevation and the configuration of habitat patches. MPB surge harvesting creates a fundamentally new problem about how to best create a landscape that allows an appropriate spatial and temporal availability of food that will benefit grizzly bears. Although measures of habitat use and selection did not always correspond, both provided complimentary information in assessing grizzly bear response to habitat. This was particularly important as female grizzly bears generally avoided mature pine stands, but used this age class more than cut-blocks during the critical foraging period (hyperphagia). Collectively, some level of harvesting appears to be beneficial depending on what impact it may have on understory vegetation and food resources for grizzly bears (Chapter 2). Ultimately, to maintain or enhance grizzly bear habitat as the surge cut proceeds, it is necessary to understand how use and selection of habitat links to animal health, reproduction, and the demographic response of the population so that appropriate management actions can be taken in a timely manner.

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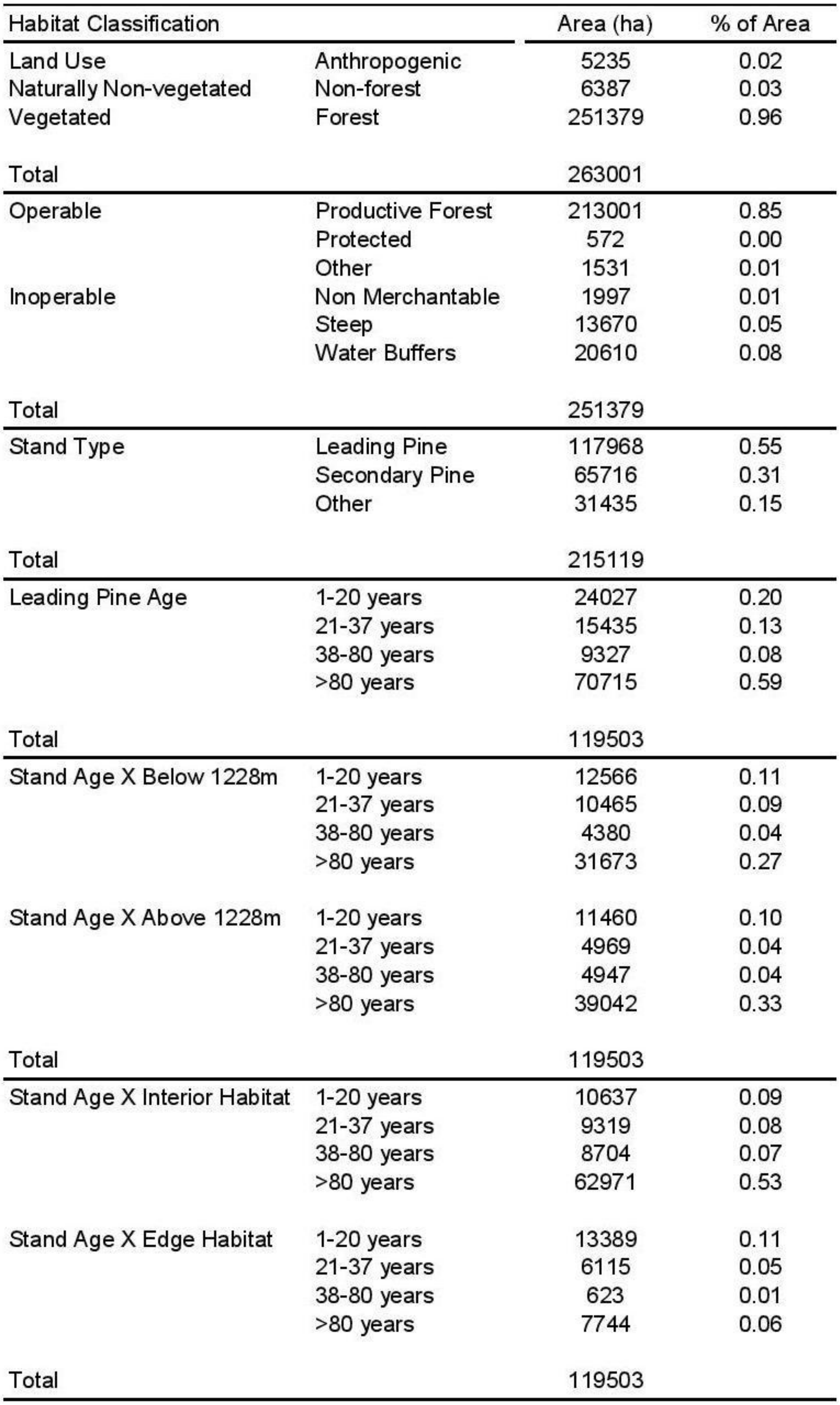
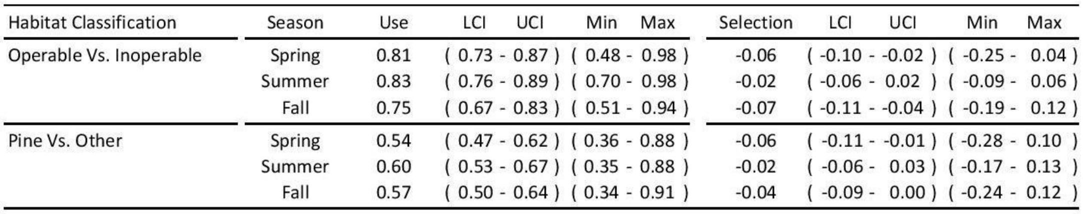
Table 3.1. Classification of habitat encompassing grizzly bear home ranges between 2007 and 2010.



Habitat Classification		Area (ha)	% of Area
Land Use	Anthropogenic	5235	0.02
Naturally Non-vegetated	Non-forest	6387	0.03
Vegetated	Forest	251379	0.96
Total		263001	
Operable	Productive Forest	213001	0.85
	Protected	572	0.00
	Other	1531	0.01
Inoperable	Non Merchantable	1997	0.01
	Steep	13670	0.05
	Water Buffers	20610	0.08
Total		251379	
Stand Type	Leading Pine	117968	0.55
	Secondary Pine	65716	0.31
	Other	31435	0.15
Total		215119	
Leading Pine Age	1-20 years	24027	0.20
	21-37 years	15435	0.13
	38-80 years	9327	0.08
	>80 years	70715	0.59
Total		119503	
Stand Age X Below 1228m	1-20 years	12566	0.11
	21-37 years	10465	0.09
	38-80 years	4380	0.04
	>80 years	31673	0.27
Stand Age X Above 1228m	1-20 years	11460	0.10
	21-37 years	4969	0.04
	38-80 years	4947	0.04
	>80 years	39042	0.33
Total		119503	
Stand Age X Interior Habitat	1-20 years	10637	0.09
	21-37 years	9319	0.08
	38-80 years	8704	0.07
	>80 years	62971	0.53
Stand Age X Edge Habitat	1-20 years	13389	0.11
	21-37 years	6115	0.05
	38-80 years	623	0.01
	>80 years	7744	0.06
Total		119503	

Table 3.2. Population level use and selection of habitat by female grizzly bears over three seasonal periods. Predicted means, 95% confidence intervals, and raw min and max values are shown.



Habitat Classification	Season	Use	LCI	UCI	Min	Max	Selection	LCI	UCI	Min	Max
Operable Vs. Inoperable	Spring	0.81	0.73	0.87	0.48	0.98	-0.06	-0.10	-0.02	-0.25	0.04
	Summer	0.83	0.76	0.89	0.70	0.98	-0.02	-0.06	0.02	-0.09	0.06
	Fall	0.75	0.67	0.83	0.51	0.94	-0.07	-0.11	-0.04	-0.19	0.12
Pine Vs. Other	Spring	0.54	0.47	0.62	0.36	0.88	-0.06	-0.11	-0.01	-0.28	0.10
	Summer	0.60	0.53	0.67	0.35	0.88	-0.02	-0.06	0.03	-0.17	0.13
	Fall	0.57	0.50	0.64	0.34	0.91	-0.04	-0.09	0.00	-0.24	0.12

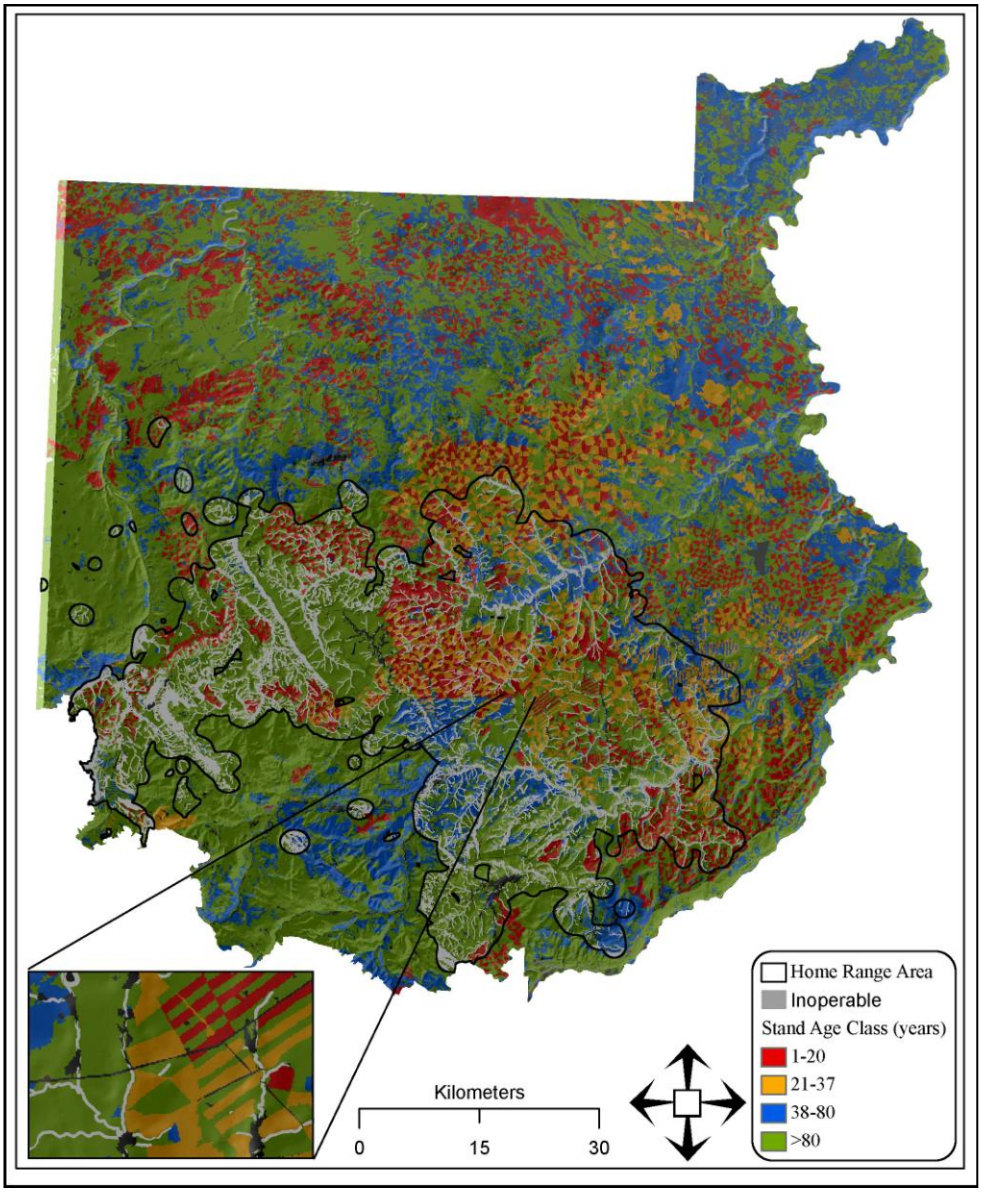


Figure 3.1. Stand age classes, and inoperable forests among overlapping (2007-2010) 95% Kernel Home Ranges of female grizzly bears within Weyerhaeuser Grande Prairie Forest Management Agreement Area in north-west central, Alberta, Canada.

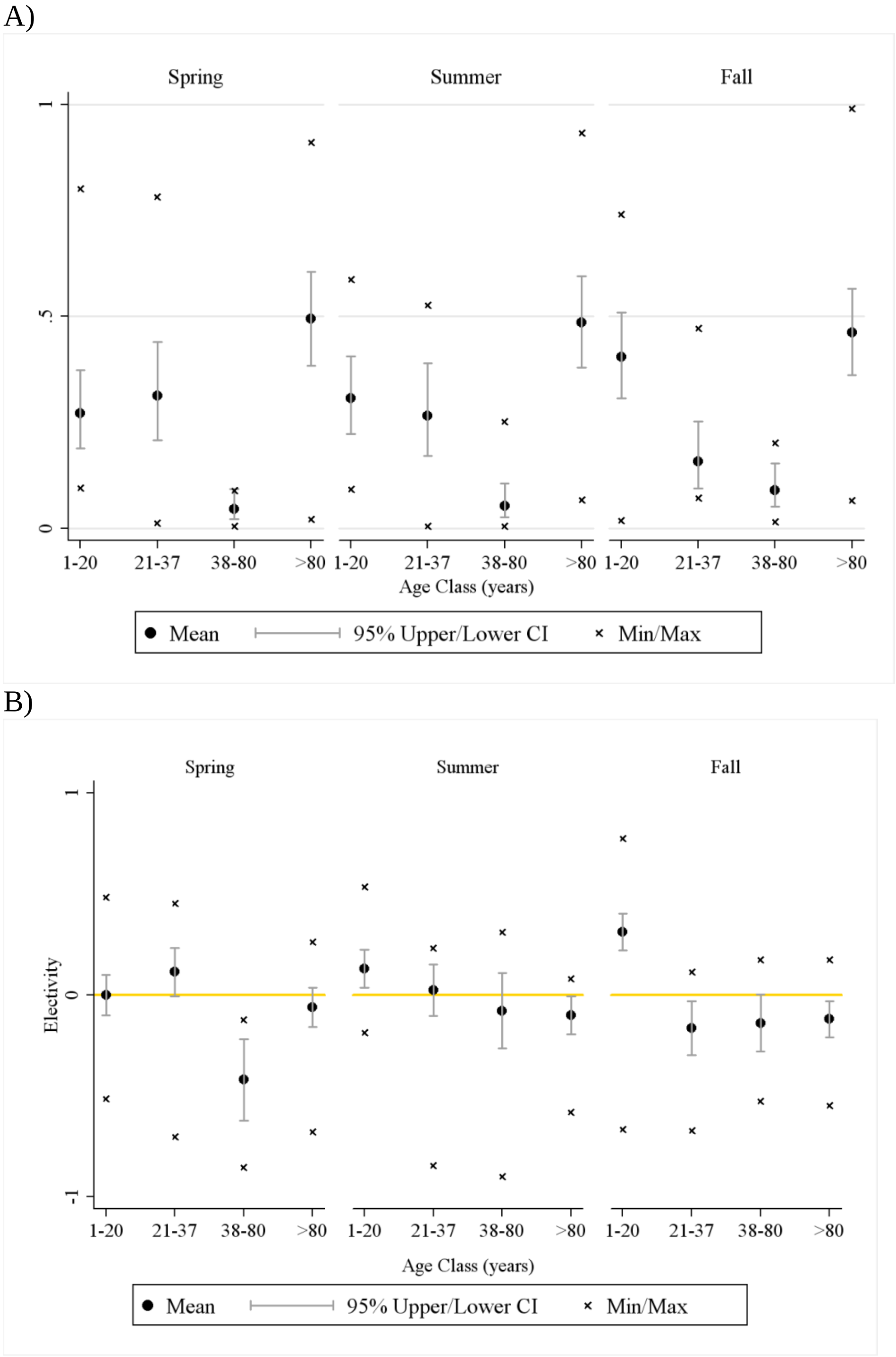
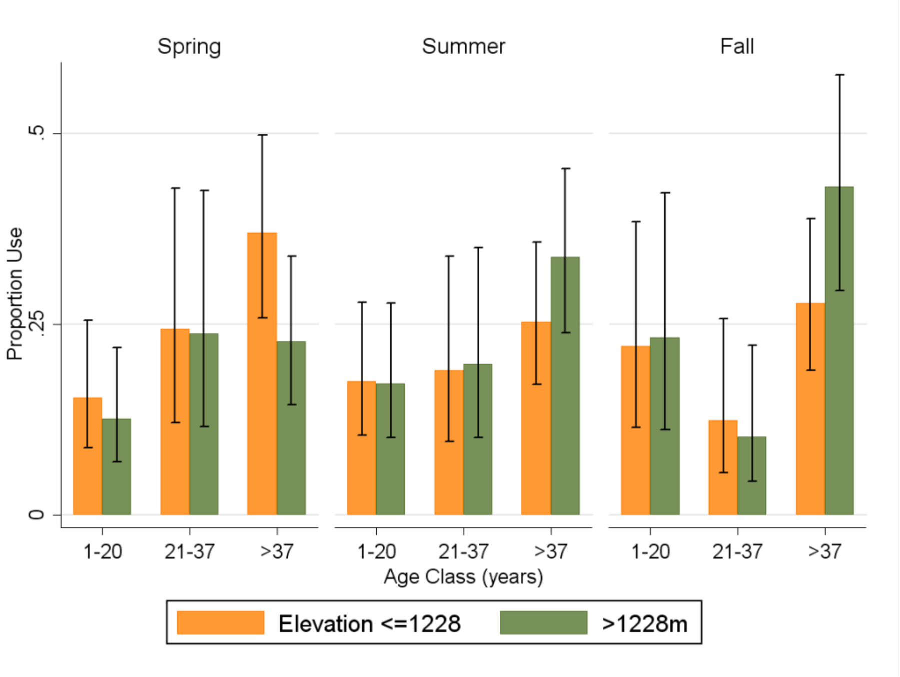


Figure 3.2. Population level A) use and B) selection of age classes by female grizzly bears (n=12) over three seasonal periods. The predicted means and associated 95% confidence intervals including minimum and maximum raw values are shown.

A)



B)

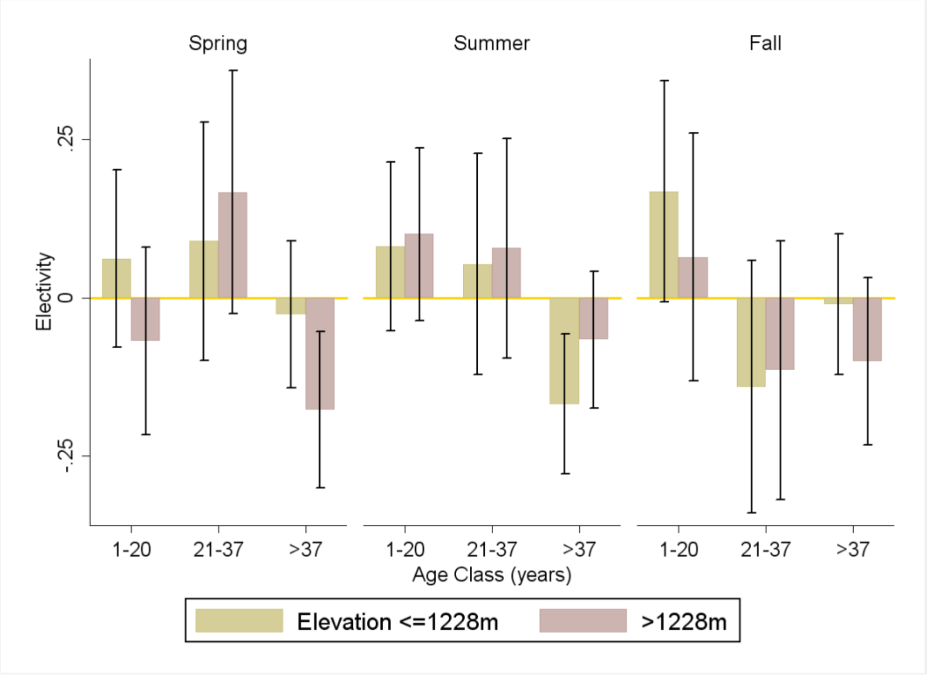


Figure 3.3. Population level A) use and B) selection of low and high elevation habitat according to age class by female grizzly bears (n=11) over three seasonal periods. The predicted means and associated 95% confidence intervals are shown.

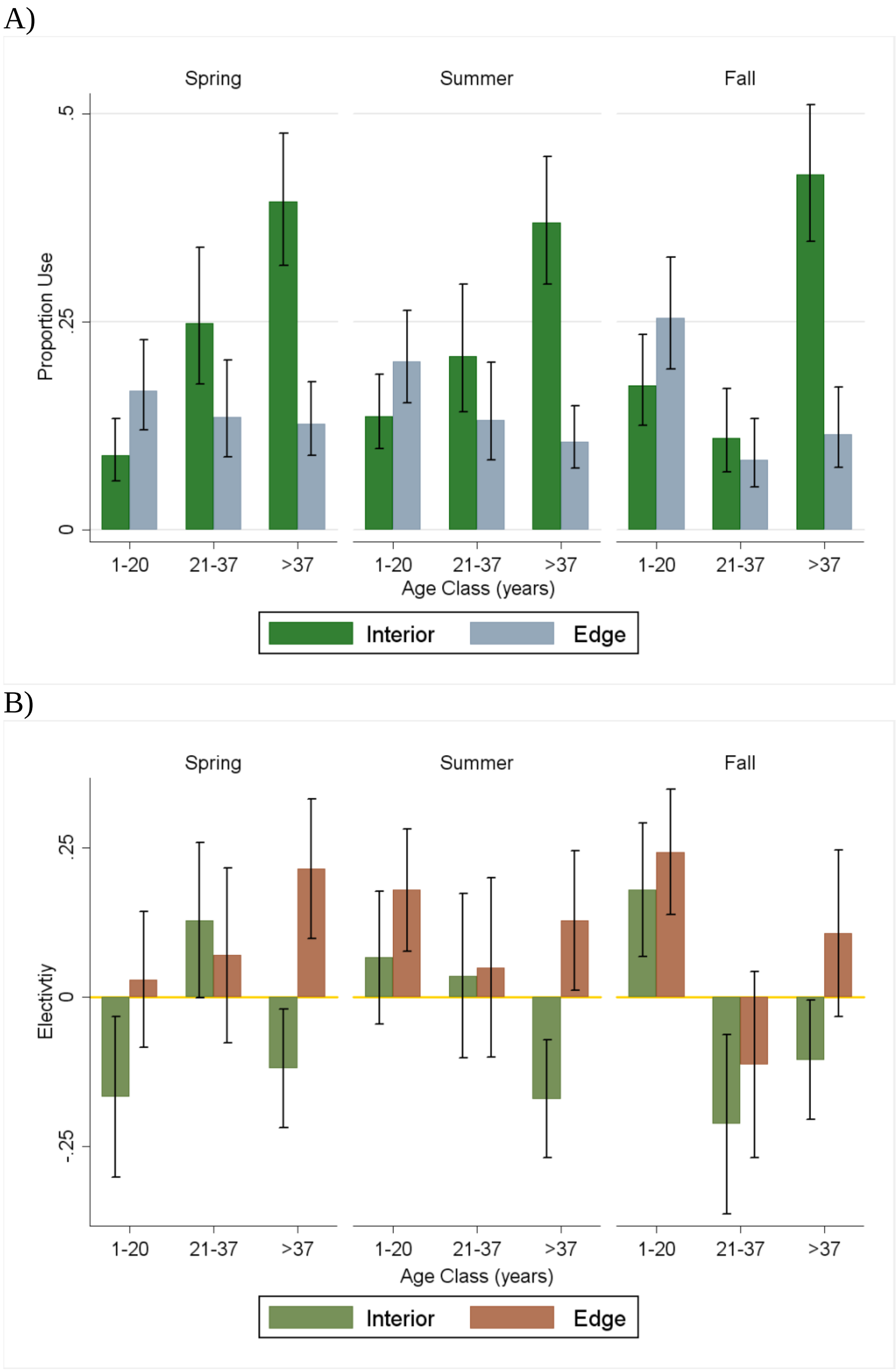


Figure 3.4. Population level A) use and B) selection of interior and edge habitat according to age class by female grizzly bears (n=11) over three seasonal periods. The predicted means and associated 95% confidence intervals are shown.

CHAPTER 4: General Conclusions, Synthesis, and Recommendations

4.1 Research Summary

The purpose of my research was to determine whether the surge harvesting of mature (>80 years) stands of lodgepole pine (*Pinus contorta*) for mountain pine beetle (*Dendroctonus ponderosae*; hereafter MPB) management, would have a positive or negative effect on habitat conditions for grizzly bear (*Ursus arctos*) both immediately and into the future. I conducted my study within the Upper Foothills Natural Sub Region of Weyerhaeuser Grande Prairies Forest Management Agreement (FMA) area in north-west central Alberta for three reasons: 1) lodgepole pine was most abundant within the Upper Foothills, meaning, that harvesting would have the greatest impact on important grizzly bear habitat (Nielsen *et al.*, 2009); 2) the Grande Prairie region was at the forefront of MPB mitigation; and 3) the Weyerhaeuser FMA was the northern study site of the Foothills Research Institutes Grizzly Bear Program. I used two approaches to assess changes to grizzly bear habitat conditions associated with MPB control harvesting, which builds on previous research conducted in west-central Alberta (Nielsen *et al.*, 2004a; Nielsen *et al.*, 2004b).

In Chapter 2, using spatial models of food abundance (forbs, shrubs, and fruits) as a function of stand age and other environmental covariates, I predicted changes in food supply according to a proposed 60 year harvesting sequence for MPB management. My analysis revealed that 1) certain fruiting shrub species (i.e. *Vaccinium* spp.) appeared to be associated with climatic and environmental conditions of the Upper Foothills; 2) pine leading stands (≥60% composition) were associated with important fruit producing *Vaccinium* spp., while forbs tended to be more abundant in non-leading stands; 3) exotic species (i.e. *Taraxacum officinale* and *Trifolium* spp.) were associated with cut-blocks, however, low counts precluded modeling their abundance; 4) species specific quantitative models were necessary to understand what foods were most abundant in the system and assess changes in food supply; 5) fruit production was not synonymous with shrub abundance and can vary markedly between years; 6) stand characteristics (overstory pine composition, age) including site specific environmental gradients related to soil moisture and climate (elevation) were important predictors at the microsite (30x30m) level; and 7) forbs were in general abundant in cut-blocks, while fruit production was highest in young cut-blocks (1-20) and mature stands (>80 years).

My study showed that with an increase in young cut-blocks (open canopy) immediately post surge cut, forbs increased by 24% but fruit only increased by 2% based on a better year (2008) of fruit production. The large gain in fruit (*Rubus idaeus* and *Vaccinium myrtilloides*) immediately after the surge cut only temporarily offset the decline in fruiting species (*Vaccinium vitis-idaea* and *Vaccinium membranceum*) associated with mature stands at the landscape-level. As the large cohort of regenerating pine aged, my models suggest that fruit production will drop suddenly when canopy closure is achieved and will decline to 10% below what was predicted prior to MPB harvesting. This was because the availability of young cut-blocks in the Upper Foothills only increased slightly overall compared to older (21-40) harvested stands and the non-harvested intermediate age class (41-80). Because forbs were abundant in both young and older cut-blocks, forbs remained relatively high for about 40 years after which abundance decreased to 13% above pre-harvest conditions when intermediate aged stands became more common. While age was fundamental to understand changes in food supply, it was not the only contributing factor. The two most abundant *Vaccinium* spp. in the system shifted in dominance at about 1228m and were associated with different age classes. Harvesting mature stands below 1228m lead to the tremendous increase in *V. myrtilloides* fruit, while harvesting above this point reduced *V. membranceum.* The reduction in *V. myrtilloides* across the elevation gradient was compensated by the overall increase in fruit, but reduction in *V. membranaceum* resulted in the decline in fruit production at the landscape level. *V. membranaceum* shrubs in particular may respond negatively to disturbance and not fully recover (no fruit) during the open canopy period.

In Chapter 3, using a GPS locations dataset from female grizzly bears (2007-2010) that spent the majority (68%) of their time within the Upper Foothills, I examined the population level response of bears to forested habitat. More specifically, using measures of use and selection (Ivlev, 1961), I examined the seasonal response of bears to 1) forested stands classified as operable vs. inoperable; 2) pine leadings stands vs. other forest types within the operable land base; 3) different age classes of pine leading stands within the operable land base; and 4) pine age in the context of elevation and edge proximity.

My analysis revealed that females spent 80% of their time in operable habitat where MPB surge harvest will occur. Seasonal variation was more apparent in the spring and summer when operable habitat was avoided. This suggested that inoperable (riparian buffer zones, steep slopes) habitats were important, yet females meet the vast majority of their life history requirements in the operable land base. When females used the operable land base, they spent less time in pine leading stands during the spring (avoidance) and more time during the critical summer (use=availability) and fall (use=availability) foraging periods. Overall, females spent 57% of their time in pine leading stands and responded seasonally to age associated differences in canopy closure. Young cut-blocks were used the least in the spring (use=availability), but use increased in the summer (selected) and again in the fall (selected) coinciding with the availability of forbs and fruits. Older (21-37 year) cut-blocks characteristic of closed canopy conditions were used the most in the spring (selected) when foods were scarce and summer (use=availability) when forbs were most available. However, use decreased substantially in the fall (avoidance) when fruits were most likely to be available. Non-harvested intermediate aged stands (38-80), the most deficient of food resources were also the least used and available habitat in all seasons. Mature stands were almost always avoided by females particularly in the fall, yet use exceeded cut-blocks in every season with the fall being relative high.

My findings suggest that the seasonal availability (abundance, plant phenology) of plant food as well as the perceived risk of open habitats (security) likely influenced observed patterns of grizzly bear habitat use surrounding different age classes associated with elevation and edge proximity. Females displayed consistent use of young and older cut-blocks irrespective of elevation in each season, while mature stands were used more below 1228m in the spring and above this point in the summer and fall. Young cut-block interiors were used less than the edge in all seasons, however, use increased in the summer (use=available) and fall (selected). Conversely, the interior of older cut-blocks and non-harvested stands were used more than the edge across seasons, and use was comparably low relative to young cut-blocks. Although non-harvested edge use did not exceed that of young or older cut-blocks, females showed strong selection of non-harvested edge particularly in the spring and summer. The interior of non-harvested stands were used more than any other interior or edge age class, yet avoided in every season. The apparent disconnect between use and selection shows the importance of incorporating both measures because common habitats (i.e. mature pine) tended to be used the most and either avoided or used at random. Female grizzly bears did not always spend more time or select habitat where food was supposedly more abundant. Meaning, that females could either be excluded from these habitats or that other factors unrelated to food may also be important.

4.2 Management Implications

Lodgepole pine is abundant within the operable forested land base of the Upper Foothills and encompasses a substantial amount of habitat used by female grizzly bears to meet life history requirements. Lodgepole pine occurs across a wide range of edaphic, moisture, and climatic conditions that influence site productivity (i.e. tree growth) (Wang *et al.*, 2004). Variation in these environmental gradients, thus, can have a strong influence on understory plant communities (occupancy/abundance) in pine forests (Chapter 2; Heringa and Cormack, 1963; La Roi and Hnatiuk, 1980; Strong, 2002) and as a consequence impact the availability of food resources for grizzly bears. How pine forests are managed now and into the future will be important for the conservation and recovery of the grizzly bear in Alberta, and maintaining the availability of essential resources especially used by female grizzly bears is fundamental to this goal.

Lodgepole pine dominant stands are associated with important fruit producing shrub species (*Vaccinium* spp.). As the canopy composition of pine shifts towards a greater amount of coniferous/deciduous trees, *Vaccinium* spp. shrub and fruit abundance decreases, while forbs (*Equisetum* spp. and *Heracelum lanatum*) and other shrub (*Rubus idaeus*) increase. The positive association between *Vaccinium* spp. fruit production and pine forests is consistent with other studies (Pelchat and Ruff, 1986; Ihalainen and Pukkala, 2001) and highlights the importance of nutrient poor habitats because they contain seasonally important food resources for grizzly bears. Although pine is most often planted following timber harvest in Alberta (Coops and Waring, 2011), since mineral soil is regularly exposed to promote pine regeneration, cut-blocks tend to have an aspen component (Landhausser *et al*., 2010) while spruce can be planted or retained in the understory during harvest. For grizzly bears, diversifying the composition of the canopy may be ideal by providing an array of foods with different seasonal availabilities, and at the same time may reduce landscape level susceptibility of forests to MPB infestation (Amoroso *et al.*, 2011). However, carbohydrate rich fruits may have a disproportionate effect on population level processes that influence density (McLellan, 2011), thus, maintaining pine dominance may be critical.

In the short and long-term following the surge cut for MPB management, forbs increase beyond what was predicted at pre-harvest conditions. Given the increase in forbs and positive response of female grizzly bears during the spring when food is scarce and in the summer when food is abundant, MPB harvesting appears to be beneficial from the perspective of food resources. However, changes in fruiting resources over the course of the proposed 60 year harvesting sequence suggests that production drops to 10% below pre-harvest conditions. Because seasonal fruits are believed to be essential for female grizzly bears to gain the fat reserves necessary for reproduction and hibernation, especially when they have young of year. Steps should be taken to ensure no net loss of fruit at the landscape-level occurs since a decline in habitat productivity may hinder ongoing grizzly bear recovery efforts.

Following the surge cut and open canopy conditions, there is a large increase in fruiting resources, but due mainly to *V. myrtilloides* below 1228m where shrubs are most abundant. At the same time, harvesting mature stands above this point leads to a decline in *V. membranaceum* and *V. vitis-idaea*, but the latter is compensated for by the increase in other fruiting species. Harvesting these mature stands coupled with succession of the large cohort of young pine forest (canopy closure), fruit production declines at the landscape-level. Although grizzly bears showed a positive response to young cut-blocks irrespective of elevation, females used mature stands above 1228m more in the fall than any other time of the year where *V. membranaceum* fruit was most abundant. The most effective means to maintain *V. membranaceum* fruit production would be to retain patches of mature timber where this shrub occurs locally and is abundant (>1228m). In addition, retaining mature patches along the elevation gradient where *V. vitis-idaea* occurs and is abundant could be important in years when other fruits are not available (Nilsen, 2002). Augmenting fruits would be beneficial and could be possible through harvesting practices that limited destruction of rhizomes (Martin, 1983; Haeussler *et al.*, 1999). This appears to be particularly important for *V. membranaceum* as this species is slow to recover post harvest (Minore, 1984). Prescribed fire could be used to augment *V. membranaceum* fruit in cut-blocks (Trusler and Johnson, 2008), however, limiting disturbance of the shrub layer would be most effective (Minore, 1984). In addition to limiting mechanical disturbance, silvicultural (i.e. thinning, fire) prescriptions could be focused where *V. myrtilloides* is likely to be abundant in older cut-blocks below 1228m, to open the canopy and stimulate fruit production. Through these combined efforts, fruit production could be enhanced in the system and over the proposed harvesting period.

Managing grizzly bear habitat according to forest age and in relation to elevation creates a complex situation, which is further complicated by cut-block design. As previous research suggests small cut-blocks would be beneficial to bears given that females spend more time on the edge compared to the interior of this age class. Although food availability (i.e. abundance, energy) may play a role in this response, security cover coinciding with a more open canopy appears to be important. Furthermore, young cut-block edges associated with adjacent non-harvested stands may offer habitat conditions that enhance food resources and use by grizzly bears. Large cut-blocks in areas where harvesting has yet to take place or will be removed in the second pass to meet the pine reduction goal associated with the surge cut, may reduce the potential benefits of young cut-blocks to female grizzly bears. Overall, it is important to consider that mature stands were used more than any other age class in every season, meaning there is potential value to this age class beyond what was considered in this study. However, the use-available design (selection) failed to capture the importance of mature stands. Although harvesting appears to be beneficial given that female grizzly bears showed avoidance or random use of the mature, this age class may contain important fruiting resources and influence the phenological stage of plants during drought conditions, thus, energy available to bears. Therefore, future modeling of grizzly bear habitat supply should not rely solely on measures of habitat selection as I argue selection and use are both important components of understanding seasonal habitat use by grizzly bears.

To maximize economic benefit to Alberta’s forest industry, the goal of the mountain pine beetle (hereafter MPB) surge cut is to change the age distribution of pine within a relatively short timeframe (~20 years). Managing the age structure of pine is the most viable means to mitigate future impacts of MPB by reducing landscape level susceptibility of forests to beetle attack (Safranyik and Carroll, 2006). However, the proposed harvesting regime in Alberta will create a similar landscape in 80 years that is also highly susceptible to MPB attack, thus, efforts should be made to manage this future risk accordingly. Because host susceptibility (tree age, diameter, and density) (Whitehead *et al.*, 2006) and weather patterns largely dictate establishment and spread of MPB (Safranyik and Carroll, 2006), managers should attempt to create stand conditions over space and time that has the greatest potential to reduce opportunities for MPB to establish and spread. This might require that some forests cut now are recut, thinned, or burned (Coops *et al.*, 2008) prior to rotation age (i.e. within next 30-40 years) to allow more diversity in age classes across the landscape to exist in the future. However, mitigating MPB risk and enhancing grizzly bear habitat (food) into the future presents a considerable management challenge, and will likely require trading-off the economic and habitat values of pine forests.

4.3 Limitations and Recommended Research

My research fills important knowledge gaps regarding grizzly bear habitat and MPB surge harvesting by assessing changes in food supply and determining seasonal patterns of habitat use in lodgepole pine forests. However, this research occurred within a relatively small area of north-west central Alberta. Lodgepole pine is widely distributed across the eastern slopes and there appears to be distinct compositional changes in understory shrub distribution and dominance relative to other areas of the province. I suspect that gradients in moisture, edaphic conditions, and productivity driven by elevation and latitude likely explain variation in bear food distribution and abundance in lodgepole pine forests along the eastern slopes (Strong, 2002; Wang *et al.*, 2004). Even though vegetation and climate in the Upper Foothills is distinct, I caution extrapolation beyond the study area. Developing regional food abundance and habitat use/selection models may be necessary given the potential for novel conditions in other population management units.

I intensively sampled vegetation within a 30x30m area to quantify food in lodgepole pine stands. Although the data yielded average model predictions that were robust, exceptionally high sample variance appeared to limit predictive capability. As environmental variables tend to be better predictors of species distribution rather than abundance, more sophisticated models that consider life history, competition, and site history may be necessary to improve model fit (Nielsen *et al.*, 2005). My method was very time consuming and limited the number of plots that could be collected. Techniques to rapidly quantify food (Nielsen *et al.*, 2010) and that minimize sample variance would be invaluable and necessary given the diverse lodgepole pine understories that occur across the eastern slopes. Because fruit production can vary tremendously over space and time, repeated sampling and/or permanent plots may also be necessary to quantify fruit availability.

In an attempt to quantify grizzly bear food at the landscape level, I relied on a limited number of spatial environmental predictors. Elevation influenced abundance at the regional level because of a strong climatic effect, whereas soil moisture influenced finer scale processes. One could argue that more spatial predictors would allow for a more accurate assessment of abundance across the landscape. With fewer predictors, abundance could be overestimated, particularly if a key variable is missing. For example, *V. membranaceum* was most abundant in mature pine leading stands above 1228m and therefore the most abundant fruit in the system. Other spatial covariates related to the frequency and intensity of fire, topographic position, soils and parent material (Nielsen *et al.*, 2010), which may influence site productivity may be useful in explaining additional variation and could influence food supply predictions. In addition to making better predictive food models, other spatial covariates could also be useful in better understanding grizzly bear response to habitat conditions given that lodgepole pine is widely distributed in Alberta and occurs across a wide range of soil, moisture, and climatic conditions (Lotan *et al.*, 1985). Furthermore, edge proximity appears to be a key factor influencing grizzly bear behavior and a study to more fully explore whether food is more abundant on the edge versus the interior is warranted.

To determine changes in food supply relative to the surge cut, I limited inference to plant based food resources. Determining changes in plants, particularly for females, is considered a reliable means of assessing the ecological value of habitat for grizzly bears (Craighead 1998). Because females are typically half the size of adult males (Schwartz *et al.*, 2003), they have the physiological capacity to gain body mass in lean tissues (protein) and fat (carbohydrates) with a diet that is almost entirely plant based (Rode *et al.*, 2001; Robbins *et al.*, 2007; McLellan, 2011). However, grizzly bears are generalist omnivores that utilize a variety of other seasonal foods such as insects (wasps, ants) and ungulates (neonates, carrion) (Munro *et al.*, 2006). During the summer, grizzly bears forage on ants in regenerating cut-blocks often associated with coarse woody material (Munro *et al.*, 2006). Ungulates can occur in the diet of grizzly bears throughout the year but typically peaks in June and July coinciding with neonate availability (Munro *et al.*, 2006) and can be a major dietary component in the fall (McLellan and Hovey, 1995). Munro *et al*. (2008) postulated that lower reproduction and cub survival in the Flathead area of British Columbia was related to a drop in ungulate numbers and fruit production because the availability of other foods in the system remained consistent. However, there is evidence that fruits rather than meat may have a disproportionate effect on population processes (McLellan, 2011). Depending on local availability of fruiting species and the frequency with which fruit production is ‘good’ or ‘bad’, it is plausible that other foods such as forbs, ants and ungulates are more consistent from year to year, and therefore could contribute more to individual animal performance and population productivity over the long-term.

I emphasize that using a stand level description of leading pine may not adequately represent grizzly bear’s use and selection of pine dominant habitats at the third-order (Johnson, 1980). Given that overstory canopy composition influenced food abundance at the microsite (30x30m) level, quantifying grizzly bear use/selection of pine at the third-order (Johnson, 1980) using remote sensing products that estimate the proportion of pine at this scale may be more appropriate. Moreover, investigating use/selection at the fourth-order (Johnson,

1980) could provide a more mechanistic and perhaps meaningful means of determining the contribution of foods in lodgepole pine to the foraging ecology of female grizzly bears. One approach might be to use a case-control design whereby grizzly bear locations in pine forests would be visited randomly over the growing season, stratified by different classifications of age, to quantify the availability (abundance, energy) of food resources at use locations to a paired random sample.

Spatial models of food abundance are powerful tools to predict the consequences of forest harvesting relative to grizzly bear habitat. I showed the potential short term benefits and long-term consequences of proposed MPB harvesting plans. Based on this information, strategies can be implemented on the ground to optimize food resources for grizzly bears, but this requires that some mature stands are retained. Trading off wildlife habitat and socio-economic values may not be realistic given the urgency of MPB management in Alberta. For this reason, optimizing food resources in cut-blocks should be emphasized, particularly fruiting shrubs as they have the greatest potential to be impacted and since forbs increase regardless. There are other factors that could limit fruit production in cut-blocks and should be investigated such as the timing of mechanical harvesting (summer vs. winter) (Coxson and Marsh, 2001) and site preparation (Haeussler *et al.*, 1999). However, wildfire appears to be a key factor influencing the productivity of *V. membranaceum* shrubs. Historically, surface fires were used by first nations to enhance berry crops (Trusler and Johnson, 2008). Broadcast burning of cut-blocks has also successful in achieving similar objectives (Martin, 1983). However, prescribed fire can have positive and negative outcomes depending on burn frequency, intensity, and depth (Carter and Foster, 2004; Duchesne and Wetzel, 2004). Optimizing the benefits will require an understanding of the short and long-term consequences to soils and other ecosystem processes (Carter and Foster, 2004). If enhancements are successful, it may be possible to offset the 10% loss in fruit producing habitat caused by MPB harvesting over the long-term.

Understanding how forest management influences food resource supply and the subsequent behavioral response of grizzly bears are objective ways to investigate the consequences of MPB harvesting in Alberta. This is especially true since long-term information on individual performance, and its affect on population demographics is difficult to obtain (Gaillard *et al*., 2010). Because female grizzly bears did not always spend more time in habitats where food resources were expected to be more abundant nor did they select for them, spatial and temporal differences in plant phenology (energy) may be more important than abundance, particularly with forbs (Hamer and Herrero, 1987; Davis *et al.*, 2006; Coogan *et al*., 2011), and should be considered in future studies. Ultimately, until the links between behavior (i.e. food acquisition and/or habitat use and selection), the performance of individuals, and the vital rates of populations can be made, we are limited in our ability to effectively manage the forested landscape for grizzly bears if we rely on food and/or habitat models alone.

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Appendix A – Canopy Cover by Stand Age in Lodgepole Pine

At 247 field plots (Chapter 2), we took 5 hemispherical canopy photos at 1.5m above ground in a level position with a Nikon® Coolpix 8700 digital camera with Nikon® Fisheye FC-08 (10.5mm) lens. The top of the camera was orientated to the north. Photos were taken at plot center and at four locations from plot center approximately 7.5m at bearings of 45, 135, 225, 270 degrees. The software WinSCANOPY® was used to analyze hemispherical photos and calculate percent canopy cover from gap fraction.

I used a zero-inflated negative binomial regression model to predict mean canopy cover as a function of a continuous 20 year age interval (Age20 Figure A-1). The 8th interval encompasses all field plots older than 140 years. Age20 was also used as the inflation variable because there were a large number of zeros (63 of 78) within the first age interval.

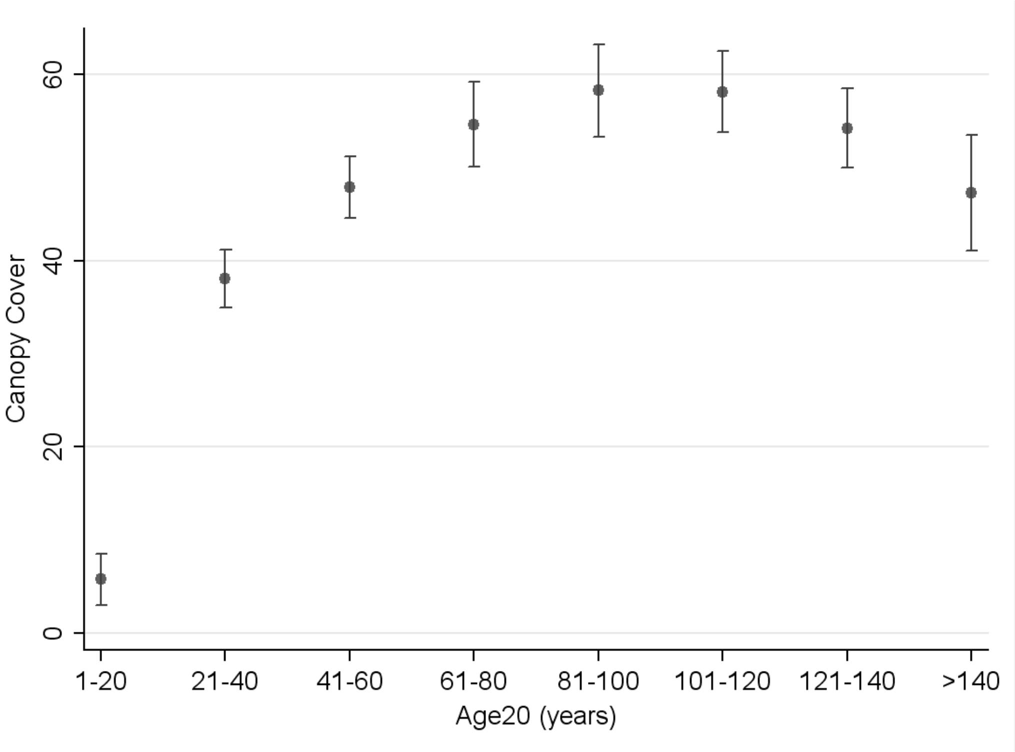

Figure A-1. Predicted mean percent canopy cover (95% confidence intervals) as a function of stand age using a zero-inflated negative binomial regression model. Age20 represents a 20 year continuous interval with stands older than 140 years grouped in the final interval. Stand age was used as an inflation variable because of the large number of zeros (63 of 78 plots) in the 1st age interval.

Appendix B – Zero-Inflated Negative Binomial Model Estimates

Table B-1. Forb distribution (inflate) and abundance (count) model variables including coefficients, statistical significance (p), z-score (z), and 95% confidence intervals (CI) from zero-inflated negative binomial regression models.

Model	*Equisetum. spp.*					*H. lanatum*					*S. amplexifolius*				
Variable	Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI	
Count															
AgeS2	-0.61	0.01	-2.46	-1.09	-0.12	0.86	0.01	2.70	0.24	1.49					
AgeS3	-1.97	0.00	-5.93	-2.62	-1.32	-1.70	0.00	-4.56	-2.44	-0.97					
AgeS4	-1.22	0.00	-5.99	-1.62	-0.82	-0.41	0.21	-1.26	-1.06	0.23					
PineC	-0.79	0.00	-3.66	-1.21	-0.37	-0.52	0.04	-2.03	-1.03	-0.02					
CTI	0.56	0.06	1.85	-0.03	1.15						-0.28	0.00	-3.56	-0.44	-0.13
CTI^2	-0.06	0.12	-1.54	-0.14	0.02										
SRI	-0.19	0.00	-3.74	-0.29	-0.09										
Constant	5.66	0.00	10.65	4.62	6.70	4.44	0.00	15.67	3.89	5.00	2.73	0.00	9.71	2.18	3.29
Inflate															
YR											-0.93	0.22	-1.22	-2.43	0.57
YR*Block											2.17	0.04	2.10	0.15	4.20
Block						-0.80	0.01	-2.65	-1.39	-0.21	-1.00	0.09	-1.68	-2.16	0.17
PineC						1.40	0.00	4.11	0.73	2.07					
CTI						0.18	0.04	2.10	0.01	0.34	0.31	0.04	2.01	0.01	0.60
SRI						0.18	0.05	2.00	0.00	0.35					
Constant	-3.52	0.00	-3.57	-5.46	-1.59	-1.44	0.01	-2.61	-2.51	-0.36	-1.38	0.05	-1.95	-2.77	0.01

* Interaction effect

Table B-2. Shrub distribution (inflate) and abundance (count) model variables including coefficients, statistical significance (p), z-score (z), and 95% confidence intervals (CI) from zero-inflated negative binomial regression models.

Model	*V. membranaceum*					*V. myrtilloides*					*V. caespitosum*					*V. vitis-idaea*					*R. idaeus*				
Variable	Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI	
Count																									
Age20	0.19	0.00	4.4	0.11	0.28											0.12	0.00	3.9	0.06	0.17					
AgeS2																					-1.29	0.00	-3.8	-1.95	-0.63
AgeS3																					-1.41	0.02	-2.3	-2.63	-0.18
AgeS4																					-1.49	0.00	-3.5	-2.34	-0.65
PineC	2.27	0.00	3.3	0.92	3.62	0.62	0.03	2.2	0.07	1.17											-0.61	0.05	-2.0	-1.21	0.00
Elev	0.47	0.01	2.8	0.14	0.80	1.09	0.00	3.6	0.49	1.68						0.49	0.03	2.2	0.05	0.93					
Elev^2						-0.18	0.00	-4.1	-0.27	-0.09						-0.07	0.03	-2.2	-0.13	-0.01					
Elev*PineC	-0.30	0.09	-1.7	-0.64	0.05																				
CTI																					-0.24	0.02	-2.4	-0.43	-0.05
Constant	0.95	0.13	1.5	-0.26	2.16	2.95	0.00	5.4	1.88	4.02	3.41	0.00	28.89	3.18	3.64	3.09	0.00	8.6	2.39	3.80	5.80	0.00	12.8	4.91	6.68
Inflate																									
AgeS2	-2.57	0.00	-3.4	-4.07	-1.07																				
AgeS3	-1.33	0.04	-2.0	-2.61	-0.04																				
AgeS4	-1.99	0.00	-4.7	-2.82	-1.15																				
Block																1.08	0.00	3.3	0.44	1.72	-3.48	0.01	-2.5	-6.24	-0.72
PineC																-0.68	0.05	-1.9	-1.36	0.01					
Elev	-0.33	0.02	-2.4	-0.60	-0.06	0.21	0.04	2.0	0.01	0.42	-0.20	0.03	-2.16	-0.38	-0.02						0.36	0.06	1.9	-0.01	0.73
CTI	-1.11	0.06	-1.9	-2.27	0.05	-0.30	0.00	-3.2	-0.48	-0.12	-0.38	0.00	-4.16	-0.55	-0.20	-0.35	0.00	-3.8	-0.53	-0.17	0.50	0.04	2.0	0.02	0.98
CTI^2	0.18	0.03	2.2	0.02	0.34																				
Constant	2.80	0.02	2.3	0.42	5.18	-0.34	0.53	-0.6	-1.40	0.71	1.86	0.00	3.39	0.79	2.94	0.03	0.95	0.1	-0.95	1.01	-2.06	0.16	-1.4	-4.95	0.84

* Interaction effect

Table B-3. Fruit distribution (inflate) and abundance (count) model variables including coefficients, statistical significance (p), z-score (z), and 95% confidence intervals (CI) from zero-inflated negative binomial regression models.

Model	*V. membranaceum*					*V. myrtilloides*					*V. caespitosum*					*V. vitis-idaea*					*R. idaeus*				
Variable	Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI		Coef.	p	z	95% CI	
Count																									
YR	-0.73	0.04	-2.0	-1.42	-0.03	-3.33	0.00	-8.9	-4.07	-2.60	1.47	0.05	2.0	0.02	2.93	-1.16	0.00	-3.6	-1.80	-0.52					
YR*AgeS2						3.60	0.00	5.4	2.28	4.92															
YR*AgeS3						-0.84	0.22	-1.2	-2.18	0.51															
YR*AgeS4						3.31	0.00	5.0	2.01	4.60															
YR*PineC											-2.45	0.00	-2.9	-4.11	-0.78										
Age20											-0.24	0.00	-3.8	-0.37	-0.12	0.88	0.00	3.4	0.37	1.39					
$Age20^2$																-0.09	0.00	-3.2	-0.15	-0.03					
AgeS2						-1.87	0.00	-4.3	-2.73	-1.01															
AgeS3						-2.02	0.00	-6.9	-2.59	-1.44															
AgeS4						-2.54	0.00	-6.2	-3.35	-1.74															
PineC	5.26	0.00	4.1	2.76	7.75	0.65	0.03	2.2	0.06	1.23	3.24	0.00	4.6	1.87	4.61										
Elev	1.12	0.00	5.0	0.68	1.56	1.08	0.01	2.5	0.25	1.91															
$Elev^2$						-0.18	0.00	-2.9	-0.30	-0.06															
Elev*PineC	-0.69	0.01	-2.7	-1.20	-0.18																				
SRI											-0.25	0.04	-2.0	-0.49	-0.01										
Constant	-3.37	0.00	-2.9	-5.61	-1.12	4.76	0.00	7.2	3.47	6.05	2.29	0.01	2.6	0.58	4.01	2.35	0.00	5.0	1.42	3.27	4.77	0.00	14.4	4.12	5.42
Inflate																									
Age20	-1.07	0.01	-2.5	-1.92	-0.22											-0.25	0.00	-3.3	-0.39	-0.10					
Block																					-2.74	0.00	-3.8	-4.16	-1.32
CTI						-0.25	0.00	-2.9	-0.42	-0.08	-0.22	0.06	-1.9	-0.44	0.01	-0.35	0.00	-3.2	-0.56	-0.13	0.48	0.00	3.1	0.17	0.78
Elev											-0.27	0.01	-2.5	-0.50	-0.05						0.28	0.07	1.9	-0.02	0.58
PineC																-1.05	0.02	-2.4	-1.91	-0.20	1.47	0.04	2.1	0.08	2.86
Constant	2.97	0.00	4.1	1.56	4.38	1.54	0.00	4.4	0.85	2.23	2.94	0.00	3.8	1.44	4.43	3.67	0.00	5.4	2.34	5.00	-0.77	0.54	-0.6	-3.24	1.70

* Interaction effect

Appendix C – Grizzly Bear Movement and Activity by Time of the Day

I used Global Positioning System (GPS) locations from collared female grizzly bears (n=12) programmed to collect locations at an hourly fix interval between May and October 15 over four years (2007-2010) in the following analysis. My objective was to determine how much female grizzly bears move as a function of the time of the day. At the population level, I predicted the mean distance travelled for each hour of the day by season using successive (t-1) locations where 1 hr had elapsed using a generalised linear model and the statistical software Stata (StataCorp., 2009) (Figure C-1). Grizzly bears appeared to follow a daily circadian pattern whereby they moved significantly less between 24:00 and 4:00 compared to between 5:00 and 23:00 in both the spring (May 1 – June 16) and summer seasons (June 16 – July 31). This changed slightly in the fall season (August 1 – October 15) when bears moved significantly less between 23:00 and 5:00 hours and more between 6:00 and 22:00. I defined when bears were moving the least as the inactive period (23:00-4:00; Figure C-1). During the active period when bears were moving the most, there was an obvious decrease in the average distance travelled between about 11:00 and 16:00 hours (Figure C-1). Because of this finding, I stratified the active period into three groups each about 6 hours each in duration and using Stata (StataCorp., 2009), estimated at the population level mean distance travelled during active and inactive time periods (Table C-1). I accepted statistical significance when alpha was less than 0.05.

Between June 4 and August 19, 2009, I visited 355 GPS locations in the field where female grizzly bears (n=6) spent time. My objective was to determine the proportion of time grizzly bears spent foraging and resting based on the time of the day. GPS locations were acquired from collared study animals via monthly downloads using aircraft primarily. Because grizzly bears are known to bed during nocturnal time periods, I stratified locations by day (diurnal/crepuscular) and nocturnal according to sunrise, sunset, and civil twilight tables (Anonymous, 1999) relative to the centre of the study area (119° 13’W and 54° 32’N) and a Mountain Time Zone (Munro *et al.*, 2006). I randomly selected one location per bear and strata for each 24 hour period (0:00-23:00) and navigated to the nearest UTM coordinate of pre-selected GPS locations in the field using a hand held GPS. Within a 30x30m area, I searched for sign (activity) of a foraging or resting grizzly bear including ripped open logs, digging, carcasses (neonates or adults), clipped vegetation (assumed to be foraging), and bed sites (Munro *et al.*, 2006). The foods I considered included: ants, *Hedysarum* spp., *Heracleum lanatum*, *Equisetum* spp., *Streptopus amplexifolius*, *Lupinus* spp., and ungulate carcasses. Grazing activity is often difficult to detect with any certainty, thus, my judgement of bears foraging on *Equisetum* spp. was not as stringent as other activities (Mattson, 1997). Bed sites were shallow depressions usually dug out to some extent and contain grizzly bear hair (Munro *et al.*, 2006). I determined the amount of grizzly bear activity by time of day as the proportion of GPS locations with no sign, beds only, foraging only, beds and foraging, or no beds and foraging only (Table C-1).

Table C-1. Mean distance travelled (m) with 95% confidence intervals (CI) and the proportion of each grizzly bear activity by time of day across three seasons.

Time of Day	Mean	95% CI		No Sign	Bed	Foraging	Bed & Foraging	No Bed & Foraging
23:00 - 4:00	149.7	74.1	225.2	0.18	0.54	0.23	0.48	0.13
5:00 - 10:00	451.7	314.4	589.0	0.23	0.13	0.22	0.07	0.29
11:00 - 16:00	434.7	328.7	540.8	0.26	0.21	0.32	0.27	0.34
17:00 - 22:00	504.2	372.7	635.7	0.34	0.13	0.23	0.18	0.25

Means and confidence intervals were estimated at the population level using a generalised linear model (StataCorp 2009) and bear as a cluster variable (n=12). The proportion of each activity by time of day was calculated from 355 field investigations at grizzly bear use locations.

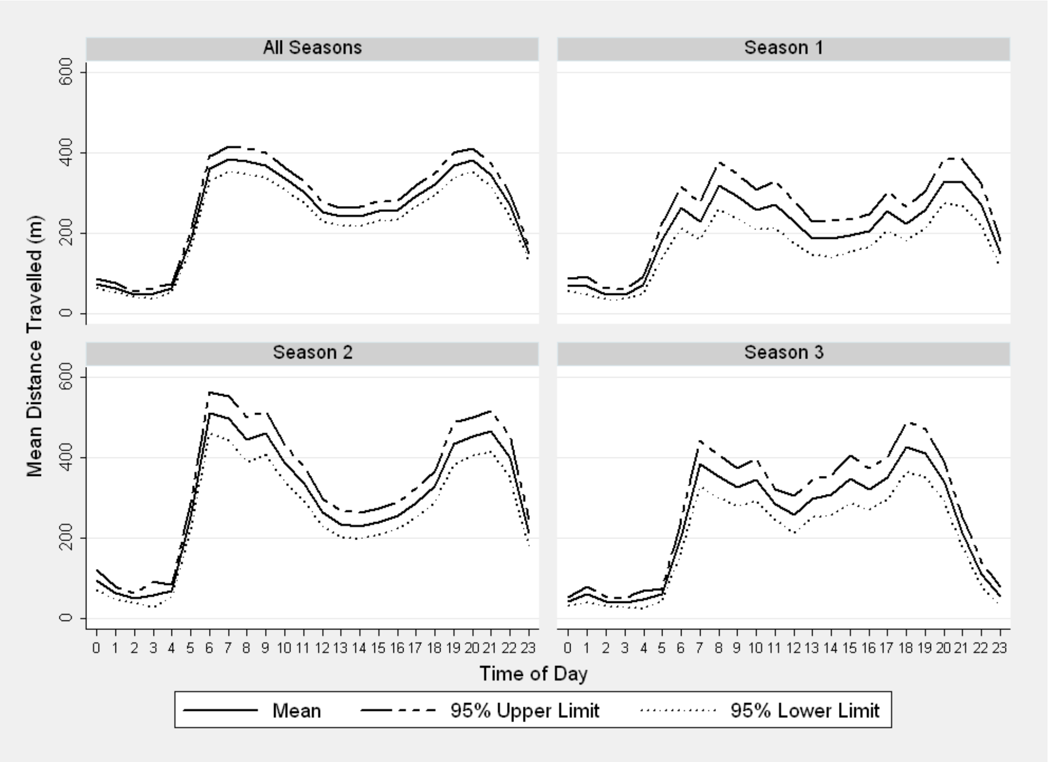

Figure C-1. Predicted mean distance travelled and 95% confidence intervals for each hour of the day (Time of Day) both across seasons and by season using successive hourly GPS locations from female grizzly bears (n=12) between 2007 and 2010.

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