USING AIRBORNE LASER SCANNING TO IDENTIFY FINE SCALE MOVEMENT PATTERNS OF GRIZZLY BEARS IN WEST-CENTRAL ALBERTA

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Abstract

Grizzly bears utilize large home ranges and move through many stages of forest succession. Research to date has confirmed bears display preference for habitats along forest edges, as well as certain landcover classes. However, the effect of fine-scale patterns and changes in forest structure on bear movement and habitat selection is less well understood. To date, habitat selection studies of grizzly bears have thoroughly examined the effects of various habitat characteristics such as anthropogenic disturbance, food availability, topographic variables, and plant communities, though there is more opportunity to leverage advanced remote sensing, threedimensional data to refine and enhance our understanding. To address this, I processed Airborne Laser Scanning data in the Yellowhead region of Alberta to characterize forest structure and used resource selection functions to determine whether ALS-derived descriptions of habitat could effectively model habitat selection by bears. I found:

- 1) ALS, when combined with a topographic index, provides enough structural information and context to reliably describe habitat selection.
- Canopy cover and vegetation height both influence selection as a function of distance from the forest edge.
- Outside a forest stand, cover > 2 m increases the probability of selection, while inside forested stands, higher canopy cover is negatively related to selection.

My final model cross-validation demonstrated selective use of forest edge habitat. Selective use of forest edges implies that the shape and spatial arrangement of forest cut blocks and associated retention patches left during harvesting operations may be optimized to minimize human-bear encounters and associated human-caused mortality of grizzly bears, in accordance with the "emulating natural disturbance" forest management philosophy.

Lay Summary

I examined the influence of forest edge and vegetation structural conditions (height, canopy cover, and others) on the movement of grizzly bears in west-central Alberta, Canada. Most studies of animal habitat use classifications such as "coniferous forest," "deciduous forest," "non-forest," and others to describe habitat types; while this approach is useful, it does not account for the diversity of conditions that exist within a single habitat type. I used a technology known as Airborne Laser Scanning (ALS, also called lidar) to characterize the three-dimensional structure of vegetation in my study area. I used grizzly bear GPS collar data to compare areas frequently used by bears with areas that were used less frequently to determine the critical variables influencing grizzly bear movement throughout the year. I found that the distance to forest edge is a strong predictor of habitat use by bears in this area.

Preface

My research was conceptually outlined by question 5 of the NSERC research grant, "Grizzly-PAW: Grizzly Population Assessment in yelloWhead," specifically "Can grizzly bear movements be related to fine scale changes in forest structure, such as openings, gaps, and vegetation patterns?" I approached the question by conducting a literature review, identified the methodology I would use, processed the lidar and GPS collar data, performed the statistical analyses, and interpreted the results. My research was overseen by Dr. Nicholas C. Coops (Principal Investigator, UBC), Dr. A. Cole Burton (committee member, UBC), and Dr. Scott E. Nielsen (committee member, University of Alberta), and Mr. Gordon Stenhouse, who provided insight and editorial comments on my work.

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List of Abbreviations

AIC	Akaike Information Criterion	
ALS	Airborne Laser Scanning	
BMA	Bear Management Area	
СНМ	Canopy Height Model	
COY	Cub-of-the-Year	
CREML	Conditional Restricted Maximum Likelihood	
CTI	Compound Topographic Index	
CV	Coefficient of Variation	
DAP	Digital Aerial Photogrammetry	
DBH	Diameter at Breast Height	
DEM	Digital Elevation Model	
DNA	Deoxyribonucleic Acid	
FWC	Female-with-Cubs	
GDEM	Global Digital Elevation Model	
GPS	Global Positioning System	
IMU	Inertial Measurement Unit	
iSSA	Integrated Step Selection Analysis	
i.i.d.	Independent and Identically Distributed	
Lidar	Light Detecting and Ranging	
LOS	Line-of-Sight	
NDVI	Normalized Differential Vegetation Index	
RSF	Resource Selection Function	

SAI	Slope-Aspect Index
SPH	Stems Per Hectare
SRTM	Shuttle Radar Topography Mission
SSF	Step Selection Function
TWI	Topographic Wetness Index

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Dedication

For Hillard Tommy Thomas Jr, "Paw Paw." You never squandered a teaching opportunity, you taught me more than you know.

"I wish for you all the good things of life. They are all available. Choose the ones you want, work hard and they're yours. I love you very much."

"Always strive to do the best in all things!"

"Always remember what I have told you about your education. The reason we go to school is to learn how to keep learning all of our lives."

"Keep 'Hard Work and Character' at the top of your priorities. Never say I can't!!"

"Love everyone, They are the things the world's made of. Love every day, They're the things your life is made of. Then love yourself, For he is the one you must please and approve of."

Thank you for everything, Paw Paw.

Chapter 1: Introduction

1.1 Grizzly Bear Overview

Brown bears (Ursus arctos), known in North America as grizzly bears, are the second largest extant species in the family Ursidae and are characterized by their circumpolar distribution and formidable appearance. They first appear in the fossil record approximately 500,000 years before present in China and appear to have spread to Europe and North Africa approximately 250,000 years ago. Their arrival in North America is much more recent with records indicating their presence in Alaska ca 100,000 years ago, dispersing into the rest of North America towards the end of the Wisconsin Glaciation (McLellan & Reiner, 1994). Since the end of the Wisconsin Glaciation, the species has seen range contractions at the subcontinental scale – their range extended as far south as Mexico and east into the Great Plains in the 1800s, but by 1970 had been reduced by more than 50% (David J. Mattson & Merrill, 2002). In the modern era, resource extraction activities and associated road construction are widely considered to be the greatest threats to grizzly bear conservation. Roads increase access for hunters, poachers, and recreational users, increasing the threat of conflict and associated mortality (Boulanger & Stenhouse, 2014; McLellan & Shackleton, 1988; McLellan, 1989; Northrup et al., 2012). Additionally, vehicle collisions become a cause of mortality as roads commonly follow drainage bottoms (riparian areas often used by bears) and create forest edge habitat, a known ecological attractor (Penteriani et al., 2018). Despite their relatively recent phylogenetic divergence, brown bears display a great deal of phenotypic diversity - in 1918 there were 86 North American subspecies proposed and described (Merriam, 1918). The 86 subspecies were classified based on differences in cranial or dental characteristics, the degree of sexual dimorphism displayed, and other morphological

criteria. Since then, their taxonomy has been revised to acknowledge nine North American subspecies (Hall, 1984 as cited by Pasitschniak-Arts, 1993).

Ferguson and McLoughlin (2000) used multivariate clustering to group populations by population density, adult female weight, primary productivity, and seasonality. They found that coastal grizzly populations are most different from the rest of the North American populations, but also that interior and barren-ground grizzly populations were distinctive enough to warrant their own clusters. The first canonical variable of the clustering algorithm was most closely related to density and female size at maturity, while the second canonical variable was correlated with primary productivity and inversely correlated with seasonality. They characterized the Pacific-coastal populations as having high densities, larger size, living in higher productivity ecosystems with lower seasonality. Conversely, interior and barren ground populations are characterized by their lower densities, smaller sizes at maturity, and lower ecosystem productivity dominated by higher seasonality. Similarly, Waits et al. (2008) and Leonard, Wayne, and Cooper (2000) used mitochondrial DNA of extant and ice-age bears revealed by permafrost melt, respectively, to delineate the phylogeography of North American bears and found genetically, the continent is represented by 4 clades, illustrated in Figure 1, taken from Waits et al. (2008).



Figure 1 Taken from Waits et al. (1998) with permission, displays the sampling locations of extant grizzly bears (letters) grouped cladistically using mtDNA. Shaded areas represent the current range of the grizzly bear.

McLellan (2011) examined the diet and body composition of grizzly bears in the Columbia and Flathead River basins in British Columbia (the same genetic clade as bears in west-central Alberta) where bears have no access to salmon and found terrestrial meat sources to be positively correlated with female adult mass and negatively correlated with density. The size of an adult bear has been shown to be related to the availability of animal protein (Hilderbrand et al., 1999; McLellan, 2011). Mowat and Heard (2006) used stable isotope analysis of grizzly bear guard hairs from 81 locations throughout North America to determine the relative proportions of major diet components (terrestrial meat, fish, and plants). Concordant with patterns noted by Rausch (1963) and Hilderbrand et al. (1999), they found that salmon dominates the diets of coastal bears. Barren-ground grizzlies had the highest proportion of terrestrial meat in their diets. They noted interior grizzly bears on the western side of the Rocky Mountains in British Columbia had the lowest percent of terrestrial meat consumption. In west-central Alberta, specifically in the Yellowhead region, the density of bears is relatively low (4.74 male bears/1000 km², and 4.53 females/1000 km²) (Stenhouse et al., 2015), as bears have no access to salmonids and are much more dependent on vegetation and vegetation phenology (Munro et al., 2006). Bears in this region have diets that are highly variable, both temporally and spatially. Figure 2 displays the dry matter content of grizzly bear scats collected in the study area between 2001 and 2003, grouped by food category as a function of season. Munro et al. (2006) found that after den emergence, before general bud-break, bears relied heavily on roots, especially alpine sweet vetch (Hedysarum alpinum). During June, ungulate feeding peaked, though the percent dry matter contrasted starkly depending on habitat. In west-central Alberta, bears occupy both subalpine/montane and boreal habitats in the foothills to the east. Percent dry matter varied between 20% (mountain) and 49% (foothills). Insect, grass, and forb feeding was most significant during summer, and frugivory of species like huckleberry (Vaccinium membranaceum) and buffaloberry (Sherpherdia canadensis) begins during late summer. Bears in the foothills region of westcentral Alberta consumed less root matter than the bears in the mountains.



Figure 2 Taken from Munro et al. (2006) with

permission, seasonal breakdown of percent dry matter by

food group (a, meat; b, forbs; c, fruits).

1.2 Threats and Pressures on Interior North American Grizzly Bear Populations

Grizzly bears are a highly resilient, generalist species who adapt their behaviors to suit their environment. However, they are vulnerable to anthropogenic pressures, as evidenced by the extreme range contraction described above. They face varying degrees of encroachment by humans, often in the context of natural resource extraction (Pigeon et al., 2016a) such as forestry operations, mining, recreation, oil and gas exploration and road construction associated with those activities (Boulanger & Stenhouse, 2014). Roads have a variety of effects on bears; specifically, bears typically avoid highly trafficked roads (Northrup et al., 2012) but are known to use low and medium traffic roads which typically increase their movement rates (Munro et al., 2006). As a result, construction of roads is likely a critical threat to bears, as they improve access for recreation and increase the chances of conflicts with humans. Boulanger & Stenhouse (2014) found that road density was an important predictor of grizzly bear mortality, concordant with the findings of Nielsen et al. (2004), who reported that in some areas of their study, 100% of known grizzly bear mortalities occurred within 500 m of roads or 200 m of high use trails. They demonstrated that increased access increases the frequency of human-bear encounters and associated mortality. Proctor et al. (2020) summarized the threats introduced by roads concisely through identification of 4 mechanisms of action. First, increased access is highly correlated to human caused mortality, especially of females (which is most directly related to population size) (Boulanger & Stenhouse, 2014). Second, through avoidance - termed habitat displacement bears lose access to certain habitats near roads. Third, bears are threatened by habitat fragmentation and associated impacts on dispersal and movement. The fourth mechanism is habitat loss through land cover/land use conversion.

In addition to anthropogenic pressures, natural disturbances have the potential to alter landscape configuration. Mountain pine beetle (*Dendroctonus ponderosae*) exists at endemic levels in lodgepole pine (*P. contorta ssp. latifolia*) stands, but in mature stands it is known to form epidemic-size (or phase) populations, driving mortality in association with blue stain fungus

(Ophiostoma spp.) (Safranyik & Wilson, 2007). Alberta is in the midst of a mountain pine beetle outbreak, and the government has coordinated with Forest Management Area lease-holders to adjust forest management plans to reduce the area of mature stands (Alberta Mountain Pine Beetle Management Strategy, accessed 10 August 2019). This accelerated harvest schedule may be associated with increased vegetation biomass suitable for grizzly bear diets; however, the amount of additional biomass declines with time, and post-harvest food resources may decline towards the end of 60-year harvest planning periods. Post-harvest, early seral species such as horsetail (Equisetum spp.), cow-parsnip (Heracleum lanatum), or red raspberry (Rubus idaeus) increase in abundance while ericaceous shrubs (*Vaccinium spp.*) take longer (up to 20 years) to establish in cut blocks due to their propagation by rhizomes. Overall, food availability is increased due to the accelerated harvest schedule, however species abundance is expected to decrease as stands mature, dropping below or even with pre-harvest levels (Larsen, 2012). This suggests that at the landscape level, vegetative food resources may decline as harvested stands mature in close succession towards the end of the current planning period. Climate change will also shift the fire regime: fires are expected to increase in intensity (Flannigan & Wagner, 1991) and the fire season is expected to get longer (Wotton & Flannigan, 1993). This may shift selection patterns as bears have been shown to be attracted to burned areas, possibly due to lower levels of canopy closure and associated availability of food resources compared with postharvest managed forest stands (Kearney et al., 2019). Superficially this may be a positive outcome for bear habitat; however, the spatial arrangement of future fires may serve as attractive sinks (Delibes et al., 2001) where human-bear conflict leads to increased mortality. Ultimately, grizzly bears are facing numerous pressures that may dramatically alter landscape configuration and the habitats upon which bears depend.

1.3 Change in Forest Structure through Time

The community composition of a forest stand changes through time and is generally predictable. Site history characteristics, including details of pedogenesis and disturbance, site conditions, and life-history traits, all interact to dictate the development of a forest stand post-disturbance. Collectively termed forest stand dynamics, Oliver and Larson (1996) described a framework in which the development of forest structure can be described within the context of available light, where development of woody vegetation occurs in four stages. In the simplest case, a disturbance, such as an intense wildfire, removes the vegetative community, possibly to bare mineral soil, and the first phase of stand initiation begins. The occlusion of light by tree canopies is delayed while they establish as seedlings, and during this time competition between regenerating trees and herbaceous forbs and graminoids is the fiercest. As trees grow into the available space, they begin competing for light as a resource; shaded foliage begins to die and microsite conditions and genetic variation begin to interact in the stem exclusion phase. Competition for light and resources characterizes this phase of stand development, resulting in suppression of growth and the death of individuals. Note that death occurs in the competition for growing space so canopy gaps do not form. The third phase – understory reinitiation – begins as isolated trees in the aging cohort are lost to disease, pests, or windthrow, and gaps in the canopy allow light to reach the forest floor. This begins the establishment of a new cohort of woody vegetation. The final stage – the old growth stage – is characterized by a complex, vertical arrangement of tree crowns that varies substantially between and within biomes.

Stand dynamics differ by species composition, disturbance regime, and climatic conditions, and consequently produce different mosaics of habitat conditions at the landscape level according to

those parameters (Fricker et al., 2006). Along the eastern slopes of the Rocky Mountains in western Alberta, lodgepole pine is the dominant forest tree and is a fire-adapted species known for its serotinous cones and propensity to develop in dense, "dog-hair" stands where stem densities in young stands reach 800,000 stems per hectare (sph) (Mitchell & Goudie, 1980) and may remain at or well above 5000 sph, even after 100 years of natural regeneration postdisturbance (Johnstone, 1971; Koch, 1996). It grows best on scarified sites in full sunlight. As crowns close, light is occluded and between 10 - 40% of solar irradiance reaches the forest floor compared to the top of canopy (Koch, 1996). This tendency can result in stands without diverse herbaceous understories (Stone & Wolfe, 1996). In the early 2000s, many stands in west-central Alberta were considered over-mature in seral stages, not providing appropriate food resources (Nielsen et al., 2004) for bears. These characteristics suggest that in terms of food resources, closed-canopy forests may be considered matrix habitat linking patches producing greater biomass of suitable foods such as meadows, forest clearcuts, riparian areas, and patches of lodgepole pine mortality (Fricker et al., 2006; Nielsen et al., 2004; Stewart et al., 2013), though they provide other resources such as cover (Munro et al., 2006). Quantifying grizzly bear use of the ecotones between these habitats at the fine scale may reveal actionable insights supporting conservation of this threatened species (Stenhouse et al., 2015).

1.4 Detecting and Describing Landscape Configuration

Forest succession is predictable at the stand level (the scale at which forests are managed), however within stands, it is stochastic, dynamic, and varies at a fine scale. The spatial and temporal variability of forest succession generates mosaics of habitats providing different resources related to their physiognomy (structure). The specific plant community composition

(floristics) of a specific habitat patch is important; however, habitat physiognomy may provide cues driving habitat selection at the patch and sub-patch scale (Kennedy et al., 2018). The dynamic nature of forest succession makes current, accurate, and reliable information about the physiognomy of forest/meadow mosaics difficult to maintain. Additionally, due to cost (time, money, and effort), extensive sampling of vegetation structure is frequently limited to data derived from multispectral remote sensing datasets such as landcover class or greenness spectral measures like the Normalized Difference Vegetation Index (NDVI) (Ciarniello et al., 2007; Kite et al., 2016; Nielsen et al., 2003; Nielsen, 2005). These passive indices or classifications from remote sensing limit interpretation of vegetation structure due to a range of factors, including spectral saturation at high levels of leaf area and canopy cover (low signal-noise ratio), issues with spectral reflectances of different tree species, illumination angle effects, and shading (Koukoulas & Blackburn, 2004). As a result, these two-dimensional datasets ultimately provide limited perspective of the habitat needs and requirements of grizzly bears, with the physiognomy or structure of vegetation being largely ignored (Bergen et al., 2009; Guo et al., 2018).

The growth in development and application of Airborne Laser Scanning (ALS), or Light Detection and Ranging (lidar) systems, which measure the three-dimensional distribution of vegetation within forest canopies, has seen its use in forest management rapidly adopted (Lefsky et al., 1999). Lidar data can provide highly detailed, three-dimensional point clouds through a combination laser-rangefinder and a highly accurate, GPS-enabled inertial measurement unit (IMU). The IMU tracks the specific orientation of the laser instrument, ensuring high spatial fidelity of recorded ranges (Lim et al., 2003). In the case of airborne lidar, an aircraft typically flies between altitudes of 500 – 3000 m and, depending on the beam divergence parameters of

the lidar system, the laser footprint at the ground typically ranges between 0.2 - 0.9 m. Vegetation that intersects the beam scatters energy back to the sensor and the relative location of returns is recorded in a point cloud (Hilker et al., 2012; Lim et al., 2003). The distribution of points in the point cloud has been shown to be related to the distribution of vegetation in the stand, allowing for estimation of forest structure metrics (Thomas et al., 2006). Coops et al. (2007) used discrete-return lidar to fit a Weibull probability density function to lidar returns in several pure and mixed Douglas-fir (*Pseudotsuga menziesii*) stands and found that Weibull parameters were significantly correlated with measures of stand density and mean DBH. Their methods were used by Hilker et al. (2011) in several lodgepole pine stands of mixed density and species distribution in west Alberta, where they found that airborne lidar data was significantly correlated with basal area and stand density across a range of stand densities. Lidar-based estimation of canopy height and cover is often more accurate, with less bias than traditional field-based measurements (Næsset and Økland 2002; Coops et al. 2007).

Beyond height and cover, the distribution of points relative to their position within the canopy can be used to infer additional information about structure, such as crown shape or presence of understory vegetation. Lidar-based assessments of height, cover, and other metrics such as volume have demonstrated accuracy in the literature (Lefsky et al., 1999; Lim et al., 2003; Næsset & Gobakken, 2008; Nelson et al., 2004). Lidar also provides fine-resolution elevation models that may be used to generate topographic morphological variables, such as slope, aspect, and topographic wetness (Nijland et al., 2015; White et al., 2012). Vierling et al. (2008) provided a review of the status of lidar remote sensing for wildlife habitat characterization and concluded that, although a growing number of studies had highlighted lidar advances, few studies had

actually used the data to quantitatively address relationships between habitat selection and vegetation structure. Table 1 summarises habitat related studies that have utilized lidar, as well as the commonly extracted metrics from lidar point clouds that have shown a significant response in habitat models.

 Table 1 Examples of studies that have utilized ALS data for habitat assessment, the forest attribute predicted,

 and the ALS metrics used to derive the selected attribute.

Author(s)	Dependent Variable	Estimators
Martinuzzi et al., 2009	Shrub distribution	Proportion of ground returns
		Proportion of returns between 1-2.5m
		Percent slope * cos(aspect)
	Snag distribution	Median absolute deviation of height
Guo et al., 2017	Structure class of stand	Canopy cover
		Stratified canopy height density
		Standard deviation of height
Loarie et al., 2013	Viewshed	Average LOS at 5° increments
Zhao et al., 2012	Fisher Denning Sites	10m: Maximum height, slope
		20m: Standard deviation of height, slope
		30m: Standard deviation of height, kurtosis of heights, slope
		40m: Standard deviation of height, slope
		50m: Mean height, transmittance at 10 th percentile heights, canopy cover
Coops et al., 2010	Winter mule deer habitat:	
	Overall stand structure model	DEM, 25th Percentile height, low cover, solar radiation, height
	Forest Cover Model	Overstory cover, DEM, coefficient of variation (CV) of heights, mid-story cover, slope
	Species number model	DEM, understory cover, solar radiation, slope, CV
	Slope model	Slope, solar radiation
	Aspect model	Solar radiation, slope

After structurally defining a forest using lidar, information on the forest edge can then be used to better characterise this important landscape feature for bears. Edge effects in particular are

known in ecology to influence community composition and corresponding ecosystem function (Andren & Angelstam, 1988; Matlack, 1994). In the Yellowhead, Larsen et al. (2019) examined the effects of forest type, environmental conditions, relative abundance of competing vegetation, and the distance from forest edge on abundance of grizzly bear foods, and found that edges significantly influenced the abundance of food resources, though the effect varied according to food species and landscape configuration. Nielsen et al. (2004) examined the use of clearcuts by grizzly bears and found that distance to edge and the edge to perimeter ratio of clearcuts both affected selection. Stewart et al. (2013) found that the type of edge was also important - females preferred anthropogenic edges while males preferred natural edges, though males used edges less overall. Though there was no proposed explanation for the reason, their results were consistent with other researchers proposed explanations (females avoiding males to reduce infanticide (McLellan & Shackleton, 1988), competitive exclusion by males (Mattson et al., 1987 as cited in Stewart et al., 2013), or simply selecting for different food resources (Graham et al., 2010; Munro et al., 2006, as cited in Stewart et al., 2013) Table 2 highlights North American studies that examined the effects of different types of edges on grizzly bear ecology.

Table 2 Summary of North American studies that have examined the effects of edges on grizzly bear,

Author(s)	Species of Interest	Years of Study	Type of Edge	Subject of Study
Mattson, 1997	Grizzly bear (U. arctos horribilis L.)	1987-1992	Unspecified	Grizzly bear preference for edge
Stewart et al., 2013	Grizzly bear (U. arctos L.)	2005-2009	Both natural and anthropogenic	Grizzly bear preference for edge
Nielsen et al., 2004	Grizzly bear	1999-2002	Anthropogenic (forest harvest)	Grizzly bear preference for edge
Ciarniello et al., 2015	Grizzly bear	1998-2003	Anthropogenic (forest harvest)	Grizzly bear preference for edge
Blanchard, 1983	Grizzly bear	1977-1979	Unspecified	Grizzly bear preference for edge
Cristescu et al., 2014	Grizzly bear	2008-2010	Unspecified	Grizzly bear preference for edge
Eckrich et al., 2020	Mule deer (<i>Odocoileus hemionus hemionus</i> R.)	2006-2012	Unspecified	Prey using forest edge habitat
Rowland et al., 2018	Elk (<i>Cervus canadensis</i> E.)	1988-2009	Unspecified	Prey using forest edge habitat
Guiden, 2017	White-tailed deer (<i>Odocoileus virginianus</i> Z.)	2013	Anthropogenic	Prey using forest edge habitat
Kremsater & Bunnell, 1992	Mule deer (<i>O. h. columbianus</i> R.)	1982-1986	Anthropogenic (forest harvest)	Prey using forest edge habitat
Larsen et al., 2019	Grizzly bear	2013	Anthropogenic (forest harvest)	Bear foods growing along forest edge
Roever et al., 2008	Grizzly bear	2005	Anthropogenic	Bear foods growing along forest edge

ungulate prey, or plant food ecology.

1.5 Analyzing Animal Location Data

Habitat selection is the process by which organisms select among available resources to satisfy energy, reproductive, or other life requirements (Borchers et al., 1994). For motile animals, movement is a critical component of their ecology; it is the intersection through time of the organism and its environment (Ims, 1995). In his discussion of the distribution of mammals, Dice (1931) noted that the reaction of an animal to its environment is equally important as the characteristics of the environment in enabling the animal to survive. Further, he asserted that habitat selection is an incredibly complex process which science had only begun to unravel. Since then, there have been many advances in the study of animal movement and habitat selection (Northrup et al., 2021). One major innovation is the recognition that the study of individual animal movement can be organized using a scale-based approach. Resources are not identically distributed across biomes and landscapes, and within an animal's home range, different habitats provide different critical resources such as cover, food, or reproductive opportunities. Within a specific habitat type each respective resource is distributed differentially, and characteristics such as density, arrangement, and colocation with other resources elicit choices from an animal based on some set of criteria. When a resource is selected disproportionately to its availability, the behavior is considered selective (Borchers et al., 1994).

Habitat selection is recognized by animal ecologists as a hierarchical process defined by scale, and the framework proposed by Johnson (1980) has been widely adopted. This framework defines the broadest scale, or first order of selection, as the combination of biotic and abiotic factors that control the distribution of a species. A second order selection can be defined as the home range of an animal, third order selections are classified by the variety of habitats within the home range, and finally, the fourth order selections are the finest scale decisions. By comparing used and unused, or used and available habitats, researchers can answer ecological questions at a variety of scales. For example, researchers interested in home range sizes or population densities may use coarse estimates of primary productivity generalized for a region or study area (Ferguson & McLoughlin, 2000), while researchers interested in habitat patch selection within a home range may be interested in variables such as distance to roads or landcover class of a specific patch (Fortin et al., 2005). At the finest, within-patch scale, researchers may be interested in characteristics such as density of food resources or accessibility of food resources (Eads et al., 2011). Therefore, it is possible to quantify selection by identifying a function that

produces an output proportionate to the probability of use – this is known as a resource selection function (RSF) (Manly et al., 2002). RSFs typically model available habitat from an independent, random sample of locations drawn from across the home range of an animal and compare those control locations to a movement trajectory that has been rarified to statistical independence (Manly et al., 2002).

1.6 Objectives and roadmap

Given the high spatial resolution and detailed 3D structural information afforded by lidar, which allows for improved characterization of canopy cover and height, as well as refined measures of forest edge and the buffers around those edges, this paper examines two key questions:

- Can I use lidar-derived height and cover metrics combined with edge information to effectively model habitat selection by grizzly bears?
- 2) Does perceived utility of forest stands vary according to their structure as a function of the distance to forest edge?

I expect to show that, as others have shown, forest edges are highly utilized by bears, since they offer access to both cover and openings containing food resources (Ciarniello et al., 2015; Nielsen et al., 2004). As a result, statistical models of bear movement that include information on forest edge will have higher predictive capacity compared to models with no edge information. More importantly, I expect that by adding an interaction term to forest edge distance that describes some facet of stand structure such as height or canopy cover, I will be able to discern higher value habitats both within and outside forest stands.

This thesis is arranged in 4 chapters. Chapter 1 contains a brief literature review, chapter 2 contains a description of the study area and data sources, chapter 3 includes methods and results, and the final chapter includes implications, limitations, and directions for future work.

Chapter 2: Study Area and Data

2.1 Conservation Framework

To address the threats facing Alberta grizzly bear populations, Nielsen et al., (2006) laid out a framework for assessing and managing grizzly bear populations in Alberta, in which they compared spatial occupancy models to records of human-caused mortality events, creating a source-sink habitat index to prioritize conservation action. Subsequently, conservation areas were designated (Nielsen et al., 2009), and Boulanger and Stenhouse (2014) continued within this framework, assessing the effect of road densities on survival and recruitment. Current conservation management has been informed by that work. The Alberta Grizzly Bear Recovery Plan identifies seven bear management areas based on distinct genetic groupings of grizzly bear populations. Figure 3 displays the broader context of habitat conservation areas relative to road development (Transport Networks in Canada - CanVec Series - Transport Features, 2017). Core conservation areas have been identified as having high value habitat with open road densities of less than 0.6km/km², while secondary conservation areas have an open road density threshold of 0.75km/km² and were established to buffer and increase connectivity between management areas and allow for population expansion and recovery.



Figure 3 Displays road densities for development context across the entirety of Alberta, with Bear Management Areas delineated. Road data from CanVec topographic data series, Natural Resources Canada.



Figure 4 The Yellowhead Study Area in west-central Alberta, Canada. Note that the lidar coverage does not extend into the mountains, where Jasper and Banff national parks are located.

The focus of this research is the Yellowhead BMA (Figure 4), which includes portions of the alpine, subalpine, and montane natural subregions of Alberta to the west and the upper and lower foothills subregions in the central and eastern parts of the study area.

In west-central Alberta, the front range of the Canadian Rocky Mountains and the upper foothills to the east are dominated by forests in pure stands of lodgepole pine (*Pinus contorta*) or mixed coniferous stands with associated black (*Picea mariana*) or white (*P. glauca*) spruce. At higher elevations, Engelmann spruce (*P. engelmannii*) and subalpine fir (*P. lasiocarpa*) are also found. On lower, mesic sites, mixed stands of aspen (*Populus temuloides*), balsam poplar (*P. balsamifera*), white spruce, and lodgepole pine are found. Hanging wetlands and muskegs exist at all elevations due to the geomorphology of the area (Natural Regions Committee, 2006; Tande, 1979). The dominant tree in these wetlands is black spruce (Dumanksi et al., 1972).

The western portion of the study area is composed of the protected areas of Jasper and Banff national parks (8,660 km²). Immediately east of those protected areas, the Coal Branch Public Land Use Zone occupies 27,072,700 km², which, combined with the protected areas, represents more than 57% of the recovery zone for bears in the Yellowhead BMA (Alberta Environment and Parks, 2016). To the east of the protected areas of Jasper National Park and provincial wildland areas, coal mining, energy development, and forestry operations dominate the disturbance regime for approximately 100-120 km, transitioning to agriculture at the eastern edge of the study area.

Historically, the disturbance regime is dominated by fire (Tande, 1979), though two distinct patterns can be resolved with available data. In the mountains where drought is more infrequent,
mean fire return interval was negatively correlated with elevation, and fires tended to be more severe stand-replacing events (Tande, 1979). Lower, in the foothills, low-to-moderate severity fires were more common and maintained a mosaic of complex, uneven-age structured stands (Amoroso et al., 2011). However, effective fire suppression began in 1913, and the dominant drivers of secondary succession have shifted to forest harvest and associated road construction, mining operations and energy sector development, and exploration, recreation and tourism (Hood & Parker, 2001; Pigeon et al., 2016; Roever et al., 2008; Nielsen et al., 2004). These altered disturbance patterns change vegetation structure and dramatically increase the proportion of forest edge, an attractive habitat type for bears (Nielsen, Boyce, & Stenhouse, 2004).

2.2 Deriving the Habitat Domain from Remotely Sensed Data

Broadly, I quantified habitat with two data types: topographic and ALS-derived vegetation structure metrics. I declined to include information about community composition such as land cover classes because my objective was to determine whether ALS-derived products could effectively model habitat selection. From an ecological perspective I assumed that when combined in a multiple regression, information such as terrain wetness, aspect, elevation, canopy cover, or height provided sufficient information to describe a habitat unit in a way analogous to land cover classes. That is, I assumed that the information provided by those metrics would reliably describe the fundamental conditions that determine a landcover class. For example, the information contained in an alpine landcover class would be described by the variables elevation (> 2000 m ASL), low TWI values, and canopy cover near 0%.

2.2.1 Elevation Products

Topographic metrics were derived from the Shuttle Radar Topography Mission (SRTM) Global Digital Elevation Model (GDEM), and vegetation structural metrics were ALS-derived. The SRTM produced an accurate (mean absolute height error in North America < 10 m), near-global elevation model at a 1 arc-second resolution (30 m pixels) (Farr et al., 2007). From the GDEM, I quantified fine-scale topography using the topographic wetness index (TWI, also known as compound topographic index (CTI)), a measurement of topography that is highly correlated with soil moisture content, depth to soil horizons, and presence of vegetation (Pei et al., 2010), defined as:

$$TWI = Ln(\frac{f}{\tan(slope)})$$
(1)

where f is the area of the upstream catchment and the slope is measured in radians. Upstream catchment area was calculated using the fill sinks, flow direction, and flow accumulation tools in ArcGIS (ArcGIS [GIS Software], 2010). To account for effects of aspect and slope, I calculated slope aspect index (SAI) as described by Nielsen et al. (2004), defined as:

$$SAI = \sin(aspect + 225) \times (\frac{slope}{45})$$
(2)

where aspect and slope are calculated from the GDEM and measured in degrees. TWI, slope, and aspect have been shown to be important variables for habitat selection in grizzly bears (Chetkiewicz & Boyce, 2009; S. E. Nielsen, Boyce, et al., 2004; Pigeon et al., 2014; Pollock et al., 2019). Both metrics were represented as 30 m resolution raster images.

2.2.2 Lidar/ALS Products

The Government of Alberta has acquired near wall-to-wall coverage of ALS data over provincially managed forested lands covering > 33 million ha that are available free to biodiversity researchers. Other Canadian provinces have since begun large-scale acquisition efforts to aid forest inventory projects, however Alberta was the first to acquire such a large dataset. Over the eastern 21,000 km² of our study area, ALS data were acquired between March and December across a range of years (2005, 2006, 2007, 2008, & 2012) with an average pulse density of 1.2 returns/m². The "ground" class was derived with standard processing routines (Axelsson, 1999) and used to normalize the point elevations to height above ground level.

I calculated two canopy metrics from the ALS data to represent the height and cover of stands. Point cloud distributions were summarized as a 20 m raster. I assessed vegetative cover as the percent of all returns > 2 m height. I characterized height using the 75th percentile of return height (P75). Forest edge was defined first by classifying the ALS point clouds into either "forest" or "non-forest"; cells with a 95th percentile of return height (P95) > 3 m and cover > 20% were classified as forest, and other cells were classified as non-forest. A 3x3 majority filter was applied using this binary forest/non-forest mask, and simple Euclidean distance rasters were generated with a minimum mapping unit of 20 m. The distance rasters were generated separately to calculate distance from forested pixels and distance from non-forested pixels. The raster denoting distance from forested pixels had positive values of distance to forest edge and non-forest pixels had negative values, with the minimum distance from edge being either -20 or 20 meters (the resolution of the raster).

2.3 Bear Location Data

For this research I used global positioning system (GPS) telemetry locations of grizzly bears collected through the fRI Research Grizzly Bear Program from 2007 – 2014 to coincide with broader time period of the structural conditions assessed by the ALS data, though individual years were often mismatched. This introduces a potential source of disturbance-related bias, where forest harvest may have occurred after the ALS acquisition date. If the mismatch between acquisition dates is severe and bias is introduced, I would expect increased selection for interior stands and decreased selection for forest edges. Additionally, I would expect the model to validate poorly due to the "noise" of harvested stands being represented in their pre-harvest states. A Landsat-derived disturbance layer or a record of logging activities could be used to clip the lidar dataset, however I assumed that the process of generating sample relocations would account for this potential bias.

The original, complete GPS dataset included location data for 123 bears spanning the years 1999-2017. Bear capture and handling procedures followed ethics standards outlined by the American Society of Mammalogists' Animal Care and Use Committee, the Canadian Council on Animal Care, the Animal Behavior Society, and the criteria identified by Powell and Proulx ('CCAC guidelines on: the care and use of wildlife', 2003; 'Guidelines for the treatment of animals in behavioural research and teaching', 2003; Powell and Proulx, 2003; Gannon, Sikes and Mammalogists, 2007, as cited in Cattet et al., 2008); the procedures were authorized by provincial permitting authorities (Alberta Department of Environment and Sustainable Resource Development, Alberta Tourism and Parks), as well as federal permitting authorities (Parks Canada) (Boulanger & Stenhouse, 2014). Bears were captured using leg-snaring (up to 2009),

aerial darting from helicopters, or culvert traps. They were anesthetized and fitted with either Followit AB (formerly Televilt, Lindesberg, Sweden) or an Advanced Telemetry Systems (Advanced Telemetry Systems, Inc., Isanti, Minnesota) GPS radiocollar (Cattet et al., 2008).

Location data were collected at a variety of sampling rates: from 15-minutes to every 4 hours, with the most common sampling rate being hourly. Previous analysis of these GPS data demonstrated a positional accuracy of 3-10 m (Stenhouse - unpublished data). Because I was interested in the fine-scale effects of habitat structure on movement, I opted to use a 1-hr sampling interval as a compromise between temporal resolution and sample size. The process of filtering GPS collar data collected at intervals greater than 1-hr and rarifying GPS trajectories collected at a finer temporal resolution ultimately eliminated ~98% of GPS locations from the dataset (501,341 to 12,177 points). This includes eliminating GPS data collected outside the interval of years 2006-2014, which was done to help ensure the ALS data represented conditions on the ground during the analysis. Although grizzly bears in the region are predominantly a crepuscular foraging species (Munro et al., 2006), I did not filter out diurnal and nocturnal movements due to the sample size restrictions that would have imposed. Data cleaning and structuring was done using the R tidyverse packages in association with amt (Signer et al., 2019; Wickham, 2017). Because bears are known to utilize food resources differentially according to their availability throughout the year (Nielsen et al., 2003; Nielsen et al., 2004), I specified a *priori* that I would stratify locations and analyses to seasonal periods of hypophagia (den emergence – 15 June), early hyperphagia (16 June -15 August), and late hyperphagia (16 August - den entry) (Nielsen, 2005). Hypophagia, the post-denning period, is characterized by scarcer food resources and caloric intake comparable to non-hibernating mammals. Hyperphagia is a

period of increasing caloric intake in preparation for hibernation and corresponds to greater food availability (Nelson et al., 1983). As bears are known to display different patterns of selection according to their sex, age, and reproductive status, I also stratified individual models according to sex-class: male (including sub-adult and adult), female (including sub-adult and adult), and females with cubs older than 1 year (FWC). I excluded females with cubs of the year (COY) because of the altered movement patterns displayed by females with COY (Stenhouse, personal communication). In the final filtering step, I removed all collar-seasons with fewer than 50 observations. This partitioning of the data created 9 independent datasets for which I estimated separate resource selection functions. Table 3 presents the final GPS location totals for each data partition. Finally, reliability of GPS collars is known to vary according to habitat type, and that locations within dense canopy forests or complex, steep terrain are less likely to be sampled. This introduces a potential source of type II bias, which may be adjusted for given a sample of collar fix probability across a range of habitat types for a given area, however given the age of the dataset I was unable to account for this, and acknowledge it as a caveat for future research (Frair et al., 2004).

	2008	2009	2010	2011	2012	2013
Males						
G110			0 259 51			
G112		0 84 0				
G114		121 0 0				
G115		0 141 0	0 251 354	63 54 0		
G120					0 0 116	238 169 0
G127						124 0 0
G128						0 0 138
G129						0 0 199
G150						0 161 223
G151						0 229 288
G152						0 169 362
Females						
G016					0 235 0	0 253 0
G023			0 217 0			
G037				0 172 0		
G111	0 0 325	275 230 0	212 131 203			
G113		197 251 445	245 109 0			
G117			94 88 0			
G118			0 106 116	0 162 188		
G119				0 236 406		335 253 359
G126						96 67 0
G153						0 0 263
FWC						
G016				0 263 0		
G023		135 218 333				
G037			0 241 0			
G111					148 264 0	213 0 299

Table 3 GPS location totals by individual, year, and season. For a given individual-year, 3 values are displayed corresponding to hypophagia, early hyperphagia, and late hyperphagia, respectively.

Chapter 3: Methods and Results

3.1 Lidar Processing

Alberta Environment and Parks provided a 925 GB lidar dataset comprised of 22,200 .las files covering 23,937.49 km² and containing 38.24 billion points (1.6 points/m²). Data were quality checked and then processed in 6 steps using LAStools software (Isenburg, 2016). First, the function lasvalidate was used to ensure files conformed to industry standards for accuracy (ASPRS, 2015). Second, tiles were buffered 25 m to facilitate a post-processing mosaic using the function lastile. Third, a 2 m resolution DEM was created for each tile using classified ground points and the function blast2dem. Fourth, point heights were normalized relative to ground elevation using the function lasheight. Fifth, the .las files were converted to a raster format canopy height model (CHM) representing the height of vegetation using lasgrid. Sixth, the function gridmetrics was used in the FUSION software package to summarize the configuration of points in an area-based approach, calculating descriptive metrics at a 20 m resolution (McGaughey, 2016).



Figure 5 Map of lidar tiles processed to describe habitat.

3.2 Step Selection Functions

For the analysis, I used integrated step selection functions/analyses (iSSF/iSSA) to model bear resource selection as described by Avgar et al. (2016). An extension of the RSF framework (Manly et al., 2002), the iSSF is a discrete choice model that compares used locations to a spatially explicit sample of available habitat. It differs from a step selection function (SSF) in that it accounts for the movement process in estimating regression coefficients. Forester et al. (2009) found that failure to account for the movement process leads to biased estimates of habitat selection. The iSSF makes several assumptions to account for this. First, it is assumed that movement is the product of two independent kernels: a habitat-independent movement kernel (representing the movement of an animal across a homogenous landscape) and a habitat selection kernel (essentially an RSF). Second, it assumes the movement kernel is generated via a distribution of step lengths from the exponential family and a normal distribution of turn angles (von Mises). The iSSF acknowledges that the domain of habitat available to an animal changes through time, and it can be assumed we can model the changing availability below Johnson's (1980) second order of selection – the home range.

To model changing availability, the iSSF pairs consecutively used "case" locations, or "used steps," with some number of randomly generated "control" relocations originating at the same starting location, or "unused steps." Figure 6 illustrates the general process for using an iSSF. Habitat domain characteristics can be summarized along the full length of the step, or only at the step endpoint. Here, I used the step endpoint to characterize habitat components because the path between the step start and step end were not observed. These paired steps are assigned a unique

step ID and can then be compared using matched case:control conditional logistic regression, which estimates an independent intercept variable β_0 for each step ID (Fortin et al., 2005; Thurfjell et al., 2014). Thus, the iSSF relaxes the independence assumption for paired steps, at the cost of an estimate of $\hat{\beta}_0$. For this work, I assume that animals select habitat with the greatest utility to them – that utility is proportional to an exponential function of a linear combination of our habitat descriptor variables such that our RSF value is:

$$\hat{w_t} = e^{\beta_1 x_{1t} + \beta_2 x_{2t} + \dots + \beta_k x_{kt}} \tag{3}$$

where x are our k habitat descriptors that describe the end point of step t. The data structure used in the conditional logistic regression is summarized in table 4, with a cluster indicating an individual, strata totals indicating the number of case locations, and total observations indicating the range of summed case:control clusters for a given data partition.



Figure 6 illustrates the general process I used for using integrated step selection analysis. The figure is

modified from figures presented in Avgar et al. (2015) and Thurfjell et al. (2014).

Table 4 GPS location data sample breakdown. Observations were clustered by individual; the range of strata totals indicates the range of observations for each individual. A cluster would be the set of locations for an individual for a given collar-season (observations for one year), and the stratum is the combination of used and unused locations for that cluster. Some individuals do not have clusters across all seasons.

Sex Season	# Clusters	Range of Strata Totals	Total Observations (1:10 Matching)
Male			
Hypophagia	4	50-190	4796
Early Hyperphagia	9	43-207	13343
Late Hyperphagia	8	41-290	15224
Female			
Hypophagia	7	75-268	12804
Early Hyperphagia	14	54-202	22099
Late Hyperphagia	8	93-356	20273
Female W/ Cubs (FWC)			
Hypophagia	3	108-170	4356
Early Hyperphagia	4	174-211	8668
Late Hyperphagia	2	239-266	5555

The iSSF is a type III resource selection study design that allows analysis of each individual in a population and requires that animals be randomly sampled from the population. Additionally, it is assumed that the distributions of the variables that characterize habitat do not change over the study period (Manly et al., 2002). I also assume that "animals have free and equal access to all available locations" (Manly et al., 2002, p. 14), which may be violated if the influence of spatial memory and navigational capacity on movement is considered. This assumption supported my decision to eliminate females with cubs-of-the-year, as they are known to utilize habitats with the objective of reducing infanticide by male grizzly bears.

To model the availability domain, I generated unused steps as an unbiased random walk, where step lengths were drawn from an empirically fit gamma distribution, and turn angles were drawn from an empirically fit von Mises distribution. Both distributions were fit from collar data aggregated at the sex-season level.

By using a gamma distribution to generate control steps, the properties of the estimator $\hat{\beta}_{Ln(step})$ length) in the conditional logistic regression allow estimation of the scale parameter governing the unobserved, selection-free distribution of step lengths, reducing bias of other estimators and allowing for hypothesis testing within a pseudo-mechanistic movement model framework (Avgar et al., 2016). $\hat{\beta}_{Ln(step length)}$ was not included in equation 3 as it is not relevant to the underlying habitat selection kernel. Including the cosine of the angular deviation from the previous step regression would allow estimation of the concentration parameter of the underlying von Mises distribution. However, I declined to include the estimate of this parameter in the iSSF due to a general lack-of-fit of the distribution to the observed turn angles.

Normally, residuals of conditional logistic regression are assumed independent and follow an extreme value distribution (Hosmer & Lemeshow, 2005). However, as individuals are known to display particular patterns of selection and spatial memory, it is known that movements of an individual are correlated. To handle this correlation structure, a mixed effects conditional logistic regression was used with a random effect added per individual per year to account for non-independence within individuals, and fixed effects of habitat at the step level, as demonstrated by Duchesne et al., (2010). The two-step estimation procedure developed by Craiu, Duchesne, Fortin, & Baillargeon (2011) and implemented in the *TwoStepCLogit* R package (Craiu et al.,

2016) was used to apply conditional restricted maximum likelihood (CREML) to the data. In this approach the authors describe the derivation of the likelihood for a utility function, similar to equation 1 above, to create a mixed effects conditional logistic regression modelling habitat utility for n = 1, ..., K individuals for the locations j = 1, ..., J. Thus, $x_{j1}, ..., x_{jm}$ are the values defining the *m*-dimensional habitat domain of location *j*.

Therefore, the final RSF value (*w*) is:

$$w_{nj} = e^{x'_{nj}\beta + x'_{nj}b} + \varepsilon_{nj} \tag{4}$$

where β is a vector of fixed effects, *b* is an i.i.d. vector of random effects for individual *n* from the multivariate normal distribution $N(0; \Sigma)$, and Σ is a diagonally structured between-cluster variance-covariance matrix. From here on, I will be referring to RSF scores (*w*) as utility, as it represents the potential utility a habitat unit may represent to an animal. Because the conditional logistic regression does not produce a probability of selection for a given habitat unit (there are no intercept estimates in the equation), I 0-centered predictions of habitat utility for plotting purposes.

3.3 Model Selection and Validation

A suite of 6 candidate models for each season per individual bear-year were developed, all of which were built around a "core" model that included only topographic variables: topographic wetness index (TWI), slope-aspect index (SAI), and elevation (DEM). The models represented hypothesized relationships between bear habitat selection and the vegetation structure metrics (with the core model representing the null hypothesis of no effect of vegetation structure). I

declined to use a forward selection procedure for model selection to avoid a data-mining approach that may have resulted in a model that was difficult to interpret from a pragmatic, implications-driven point of view. The correlation between variables was evaluated to minimize risk of collinearity between predictor variables (table 5).

	TWI	SAI	DEM	P75 Canopy Height	% Cover >2m	Forest Edge Distance
TWI	1.00	0.06	-0.29	-0.04	-0.04	0.02
SAI		1.00	-0.06	0.04	0.05	0.01
DEM			1.00	-0.34	-0.26	-0.36
P75 Canopy Height				1.00	0.87	0.65
% Cover >2m					1.00	0.69
Forest Edge Distance						1.00

Table 5 Pearson correlation between candidate predictor variables.

The first alternative model assumed an independent, linear relationship between selection and height and cover. Despite the correlation between height and cover, I included both in several candidate models due to their interpretability and relationship with forest succession. I expected that should the model be unable to determine the relative effects of each explanatory variable, the validation procedure would identify the problem and the model could be revised. The second assumed intermediate values of height and cover may be preferred, and it assumed independent, quadratic relationships between selection and height and cover. The third alternative assumed a quadratic relationship between height and selection, and an effect of cover that varied with distance from the forest edge. The fourth assumed a relationship between height and selection that varied with distance with forest edge. The final alternative assumed a linear relationship between height and selection and independent relationship between cover, the

distance to the forest edge, and selection. In addition, a seventh model was developed post-hoc using a reduced set of variables from the core and the forest variables, focused on parsimony with a terrain variable, edge distance and cover. It was cross-validated the same way. For the post-hoc model, TWI was used as the terrain variable, as it was not only correlated with riparian areas but contains information about local (or fine-scale) relative elevation. Edge distance and cover were selected as variables based on the strength of evidence indicating preference for forest edges (Table 2) and added interpretability of cover as an independent variable mediating selection over P75 canopy height – P75 height and cover are correlated, and the relationship between cover and sub-canopy vegetation is well established.

For model selection, an alternative model was fit for every collar-season and tallied the model with the lowest AIC (Akaike, 1973). Following the procedure of Prokopenko et al. (2017), The model with the highest tally of "support" across all models was selected, fit to individuals (fixed effects only) split by season, for a total of 59 tallies. This method is analogous to AIC weights. I randomly selected without replacement 80% of steps for each individual bear in each season and held the other 20% in reserve for validation. This process was repeated 10 times. The sample size for each of the 9 data partitions is summarized in Table 4.

To evaluate model fit, 10-fold cross-validation was used according to the procedure described by Boyce et al. (2002). Utility was calculated for each population-averaged sex-season class and then pixel-based decile breaks were estimated to divide RSF scores (utility) into 10 equal-area bins. The frequency of observations in each RSF bin from the validation dataset (described above) for each of the 10 replicates was evaluated to estimate robust area-adjusted frequencies

and used Spearman rank correlation to determine the strength ($\bar{\rho}$) of the relationship between RSF bins and area-adjusted frequency. A model that performed as well as a random guess would be expected to have approximately 10% of observations in each bin, and a Spearman's rho calculation of near 0, indicating no correlation. For ease of comparison in figures, I centered and scaled all independent variables prior to model fitting to allow for comparison of $\hat{\beta}$ between variables.

3.4 Results

The final tally indicated that overall, the model including core variables, height, edge distance, and the interaction between height and edge distance had the greatest support. Both classes of female had higher tallies for the model including cover instead of height; however, there were enough tallies indicating support (6 and 3 versus 8 and 4 for females and FWC, respectively) that the same model for all sex-season classes was used. The results of the AIC tally procedure are displayed in Table 6 below.

Table 6 AIC tally results summarized by sex class. Each sex class includes all tally results for each season.

Bold numbers ind	icate the highes	t tally for	that sex class.
-------------------------	------------------	-------------	-----------------

Model	k	Male	Female	FWC	Total Tally
Core	4	1	2	1	4
Core + Height + Cover	6	5	3	0	8
Core + Height ² + Cover ²	8	3	3	0	6
Core + Height ² + Cover + Edge Distance + Cover * Edge Distance	9	2	0	0	2
Core + Height + Edge Distance + Height * Edge Distance	7	7	6	3	16
Core + Cover + Edge Distance + Cover * Edge Distance	7	3	8	4	15
Core + Height + Cover + Edge Distance + Cover * Edge Distance	8	0	7	1	8
Sum of Individuals		21	29	9	59

3.4.1 Fully Specified Model



Population Averaged — Subject Specific

Figure 7 Cross-validation results. Purple lines indicate population averaged frequencies and green lines indicate subject-specific frequencies. Error bars denote minimum and maximum frequency values across all 10 folds. The dashed line marks 10% of observations – if model predictions were random a uniform distribution across all RSF bins would be expected.

Figure 7 displays the results of my validation procedure. In nearly all cases, the relationship between RSF bin and frequency of observations is non-monotonic, with peaks of observation frequencies in the middle range of RSF bins. This violates the assumption of a linear relationship between two variables in Spearman's rank correlation (Ruscio, 2008). There are two instances where this is not the case. For males during late hyperphagia, observations are monotonic and weakly positively correlated ($\bar{\rho} = 0.52$). However, p-values indicate that the relationship has a substantial probability of being due to random chance ($\bar{\rho} = 0.128$). The second instance, females with cubs during hypophagia, is strongly positively correlated ($\bar{\rho} = 0.93$), and p-values indicate the pattern is unlikely to be random (see Table 7 for a summary of Spearman's rank correlation for the 10 folds).

	Spearman's rho			p-value				
	Male	Female	FWC	Male	Female	FWC		
			Hypopl	nagia				
Minimum	-0.332	-0.146	0.838	0.533	0.0249	< 0.001		
Mean	-0.239	0.132	0.928	0.744	0.383	< 0.001		
Maximum	-0.0303	0.632	0.993	0.825	0.656	0.00120		
			Early Hype	erphagia				
Minimum	-0.430	-0.510	-0.361	0.631	0.559	0.353		
Mean	-0.280	-0.258	-0.115	0.782	0.752	0.617		
Maximum	-0.115	-0.0547	0.139	0.897	0.934	0.847		
	Late Hyperphagia							
Minimum	0.0909	-0.515	-0.706	< 0.001	0.0204	0.937		
Mean	0.521	-0.150	-0.566	0.127	0.659	0.953		
Maximum	0.975	0.652	-0.519	0.405	0.938	0.988		

 Table 7 10-fold cross-validation results. Spearman's rho describes the strength of a linear relationship

 between two variables, in this case the area-adjusted RSF bins and the frequency of observations in each.

Table 8 Mean parameter estimates (n = 10) for the fully specified model. Mean estimates are derived from the 10-fold model cross-validation procedure. 95% confidence interval is in parentheses. Asterisks in sexclass headings indicate models that performed well during the cross-validation prodedure. Asterisks following confidence intervals indicate the interval does not cross 0.

		Hypophagia					
	Males	Females	Females with Cubs*				
Edge Distance	-0.124 (-0.25 - 0.0015)	-0.213 (-0.2760.15)*	-0.377 (-0.5290.225)*				
Elevation	-1.16 (-1.790.528)*	-0.262 (-0.4130.111)*	0.112 (-0.0936 - 0.318)				
Height	0.137 (0.0631 - 0.211)*	0.259 (0.212 - 0.306)*	0.444 (0.356 - 0.532)*				
Edge Distance : Height	-0.255 (-0.3660.144)*	-0.68 (-0.7990.561)*	-0.841 (-0.9890.693)*				
Slope-Aspect Index	-0.0978 (-0.198 - 0.00252)	0.236 (0.182 - 0.29)*	0.0014 (-0.0727 - 0.0755)				
Topographic Wetness Index	-0.0175 (-0.0692 - 0.0342)	0.000546 (-0.0373 - 0.0383)	-0.18 (-0.2430.117)*				
Ln(Step Length)	0.0188 (0.000762 - 0.0368)*	0.0182 (0.0116 - 0.0248)*	0.0189 (-0.00327 - 0.0411)				
	Early Hyperphagia						
	Males	Females	Females with Cubs				
Edge Distance	-0.193 (-0.2390.147)*	-0.0887 (-0.1650.0123)*	-0.298 (-0.5160.0797)*				
Elevation	-0.565 (-0.6690.461)*	-0.238 (-0.3470.129)*	-0.25 (-0.3980.102)*				
Height	-0.0857 (-0.1390.032)*	0.025 (-0.0131 - 0.0631)	0.154 (0.0132 - 0.295)*				
Edge Distance : Height	-0.162 (-0.2450.0788)*	-0.358 (-0.4280.288)*	-0.738 (-0.9620.514)*				
Slope-Aspect Index	-0.179 (-0.2330.125)*	-0.136 (-0.1650.107)*	-0.183 (-0.2370.129)*				
Topographic Wetness Index	0.0836 (0.0505 - 0.117)*	0.0689 (0.0506 - 0.0872)*	0.0244 (-0.0202 - 0.069)				
Ln(Step Length)	0.0268 (0.0146 - 0.039)*	0.0195 (0.0126 - 0.0264)*	0.00963 (-0.0118 - 0.031)				
	Late Hyperphagia						
	Males*	Females	Females with Cubs				
Edge Distance	-0.07 (-0.149 - 0.00937)	-0.114 (-0.1650.0635)*	-0.958 (-1.170.751)*				
Elevation	-0.0206 (-0.152 - 0.111)	-0.108 (-0.241 - 0.0254)	-1.04 (-1.240.843)*				
Height	0.169 (0.123 - 0.215)*	0.13 (0.106 - 0.154)*	0.657 (0.466 - 0.848)*				
Edge Distance: Height	-0.276 (-0.4020.15)*	-0.338 (-0.3630.313)*	-0.726 (-0.9110.541)*				
Slope-Aspect Index	0.0677 (0.00685 - 0.129)*	0.0197 (-0.0183 - 0.0577)	0.0472 (-0.0659 - 0.16)				
Topographic Wetness Index	0.0138 (-0.0147 - 0.0423)	0.0114 (-0.0111 - 0.0339)	-0.0718 (-0.1210.0228)*				
Ln(Step Length)	0.0183 (0.00998 - 0.0266)*	0.0148 (0.0101 - 0.0195)*	0.0124 (-0.00277 - 0.0276)				

Table 8 shows the mean (n=10, the number of folds in the validation procedure) population averaged estimates of beta coefficients, with the 95% confidence interval of the estimates in parentheses. For both males in late hyperphagia and females with cubs in hypophagia, the coefficients with the highest relative effect sizes were edge distance, height of vegetation, and the interaction between the two. In addition, the beta value estimates for elevation were either positive (for females with cubs in hypophagia) or negative, but not significant (for males in late hyperphagia). This may explain the model's lack of explanatory power for the other sex-season classes, as they all had coefficients for elevation that were greater in magnitude.



Figure 8 Smoothed conditional mean RSF (with 95% CI) output values as a function of distance to forest edge.

Figure 8 illustrates the marked effect of forest edge on the RSF model. It displays the smoothed conditional mean of RSF values for each data partition, using the function geom_smooth from

the ggplot2 library in R (Wickham, 2016). This method of examining the effects of independent variables on RSFs was described in Avgar et al. (2017). Each sex class displays a strong forest edge attraction that varies with season. Mean utility is displayed without units because each curve represents a different conditional logistic regression, making the numeric utility estimates incomparable between regressions (Norton & Dowd, 2018). The shape of the resulting curve is the key result of interest. Overall, the effect is weakest during hypophagia for males and females, and weakest for females with cubs during late hyperphagia. Males are the only sex class for which the modeled relationship is completely parabolic in all seasons – females and females with cubs each have local maxima approximately 1000 meters outside of forest stands. However, this is likely an artifact of the correlations between the underlying habitat variables.



Figure 9 Smoothed conditional mean RSF output values as a function of P75 canopy height, stratified by distance from forest edge.

Figure 9 displays the modeled relationship between distance from forest edge, P75 canopy height, and utility. There are several trends of note. First, the relationship between utility and

height for males inside forest stands is only apparent during hypophagia. During both phases of hyperphagia, there is no modeled relationship between P75 canopy height and utility while inside forest stands, and the relationship is weak during hypophagia. For males outside forest stands, the modeled relationship is only moderately positive during hypophagia and early hyperphagia when near forest edges, where there is an increase in utility with increasing P75 canopy height.

For females, the modeled relationship is more clearly positive or negative during all seasons. During hypophagia and when inside forest stands but near the edge, there is an increase in utility with increasing canopy heights. However, further inside stands, utility is inversely related to canopy height, suggesting a preference for more complex forest structure with gaps bringing the 75th percentile of heights lower. Outside forest stands, there is a consistent, positive relationship between utility and canopy height, suggesting preference for cover while in the open.

For females with cubs, the relationship is generally the same as with females – preference for cover when in the open and preference for low canopy heights inside forest stands. However, during late hyperphagia the inverse relationship between utility and canopy height is reversed. For all sex-classes and seasons, the dominant pattern of selection as a function of the distance to forest edge appears to be a preference for some vegetative cover when outside the forest edge. The modeled relationship is approximately linear for all panels (sex-season groups) except males during hypophagia (Figure 9a). In this panel, when > 300 m from the edge, the relationship appears quadratic. The fully specified model validated poorly, suggesting that the conditional logistic regression is overfit and amplifying noise.

3.4.2 Minimally Specified Model

Following the poor performance of the fully specified model, I examined a simplified model form, using only 4 variables: natural log of step length, Topographic Wetness Index, forest edge distance, and forest edge distance multiplied by canopy cover over 2 meters. TWI served two purposes: first, as an indicator of potential habitat wetness correlated with food availability (Nielsen et al., 2004a), and second, as an indicator of local elevation. My rationale was that my core model included DEM and SAI, but those variables – while not broadly correlated with TWI - were both captured by TWI at the scale of third and fourth order habitat selection. For instance, DEM was generally associated with negative beta coefficients (indicating selection for lower elevations), and the calculation of TWI is maximized with larger upstream catchment areas (i.e. lower elevations at both the local and broader scales). Forest edge distance was included as the only main effect including information about vegetation structure because of the established relationship between grizzly bears and edge habitat (Nielsen et al., 2008) I also included percent cover over 2 m as an interaction term with forest edge distance to account for both differential food resource availability (Nielsen et al., 2004a) and availability of cover when outside forest stands. This minimally specified model was then included in a new AIC tally procedure, with the tally indicating this new model was marked improvement over the others. The results of the AIC tally procedure are displayed below (table 9).

Table 9 New AIC tally results summarized by sex class. Bold numbers indicate the highest tally for that sex

class.

Model	k	Male	Female	FWC	Total Tally
Core	4	1	1	1	3
Core + Height + Cover	6	3	3	0	6
$Core + Height^2 + Cover^2$	8	2	3	0	5
Core + Height ² + Cover + Edge Distance + Cover * Edge Distance	9	2	0	0	2
Core + Height + Edge Distance + Height * Edge Distance	7	4	4	2	10
Core + Cover + Edge Distance + Cover * Edge Distance	7	2	2	2	6
Core + Height + Cover + Edge Distance + Cover * Edge Distance	8	0	5	1	6
Ln(Step Length) + TWI + Edge Distance + Cover * Edge Distance	4	7	11	3	21
Sum of Individuals		21	29	9	59



Figure 10 Cross-validation results. Purple lines indicate population averaged frequencies and green lines indicate subject-specific frequencies. Error bars denote minimum and maximum frequency values across all 10 folds.

Figure 10 displays the validation results for the minimally specified model. The contrast between the validation results of the two models is stark. The frequency of a non-monotonic relationship between observation frequency and RSF bin is much lower, and in all non-monotonic cases the peak of the relationship occurs in RSF bins 7-8, much higher than with the fully specified model. Overall, the model performed well, with minimum $\bar{\rho}$ being moderately positively correlated ($\bar{\rho}_{Male-hypophagia} = 0.58$) and maximum $\bar{\rho}$ being strongly positively correlated ($\bar{\rho}_{Female-hypophagia} = 0.95$). *P*-values in all cases indicate the relationship between the RSF and habitat selection is non-random. Table 10 summarizes the results of the Spearman's rank correlation for the 10-fold cross-validation.

 Table 10 Cross-validation results. Spearman's rho indicates the strength of the relationship between RSF bin

 and observed frequency of occurrence.

	Spearman's rho				p-value			
	Male	Female	FWC	Male	Female	FWC		
				Hypophagia				
Minimum	0.221	0.830	0.498	< 0.001	< 0.001	< 0.001		
Mean	0.583	0.952	0.746	0.0790	< 0.001	0.0200		
Maximum	0.954	0.987	0.993	0.269	0.00277	0.0712		
			Ear	ly Hyperphag	ia			
Minimum	0.689	0.527	0.492	< 0.001	0.00582	< 0.001		
Mean	0.783	0.634	0.643	0.00477	0.0314	0.0390		
Maximum	0.878	0.781	0.917	0.0137	0.0614	0.0741		
	Late Hyperphagia							
Minimum	0.503	0.503	0.772	< 0.001	< 0.001	< 0.001		
Mean	0.688	0.757	0.922	0.0262	0.0146	< 0.001		
Maximum	0.966	0.951	0.984	0.0716	0.0716	0.00443		

Table 11 Mean parameter estimates (n = 10) and 95% confidence intervals for the minimally specified model.

	Hypophagia						
	Males	Females*	Females with Cubs*				
Edge Distance	-0.0879 (-0.19 - 0.0145)	0.0199 (-0.0466 - 0.0864)	0.0273 (-0.0918 - 0.146)				
Edge Distance : Cover	-0.287 (-0.3880.186)*	-0.407 (-0.4690.345)*	-0.455 (-0.5730.337)*				
Topographic Wetness Index	0.0127 (-0.0467 - 0.0721)	-0.0172 (-0.0495 - 0.0151)	-0.209 (-0.2640.154)*				
Ln(Step Length)	0.0141 (-0.00402 - 0.0322)	0.0108 (0.00543 - 0.0162)*	0.0172 (-0.00454 - 0.0389)				
_	Early Hyperphagia						
	Males*	Females*	Females with Cubs*				
Edge Distance	-0.144 (-0.20.0881)*	-0.0896 (-0.1510.0278)*	-0.107 (-0.1680.0455)*				
Edge Distance : Cover	-0.322 (-0.4030.241)*	-0.367 (-0.4190.315)*	-0.453 (-0.5050.401)*				
Topographic Wetness Index	0.0971 (0.0653 - 0.129)*	0.0682 (0.0473 - 0.0891)*	0.0273 (-0.0152 - 0.0698)				
Ln(Step Length)	0.0213 (0.00886 - 0.0337)*	0.0184 (0.0116 - 0.0252)*	0.011 (-0.00974 - 0.0317)				
	Late Hyperphagia						
	Males*	Females*	Females with Cubs*				
Edge Distance	0.0662 (0.000899 - 0.132)*	0.00665 (-0.0388 - 0.0521)	-0.187 (-0.30.0736)*				
Edge Distance : Cover	-0.151 (-0.2320.0702)*	-0.253 (-0.2850.221)*	-0.182 (-0.2870.077)*				
Topographic Wetness Index	0.0153 (-0.00806 - 0.0387)	0.0112 (-0.0102 - 0.0326)	-0.0253 (-0.0705 - 0.0199)				
Ln(Step Length)	0.00947 (0.00144 - 0.0175)*	0.0069 (0.0022 - 0.0116)*	-0.00218 (-0.0173 - 0.013)				

Sex-class headings that were validated successfully and significant parameter estimates denoted by *.

Table 11 displays the 10-fold mean estimates for each $\hat{\beta}$ of the minimally specified model. Note that the coefficients with the strongest relative effect size in all cases are the coefficients for edge distance or the interaction between edge distance and cover.



- Male - Female - FWC

Figure 11 Smoothed conditional mean RSF output values as a function of distance to forest edge for the minimally specified model.

Figure 11 displays essentially the same dramatic relationship between distance to forest edge and the RSF. The shapes of the curves are almost identical to those in Figure 8, except that the maxima are bounded by steeper slopes on either side. This is explained by the lack of other variables in the model, which I suspect were diluting the relative effect of edge distance on the RSF and amplifying noise such as elevation, slope, and aspect.



Figure 12 Smoothed conditional mean RSF output values as a function of canopy cover over 2 meters, stratified by distance to forest edge for the minimally specified model.

Figure 12 displays the modeled relationship between RSF values, distance from forest edge, and canopy cover. Patterns in the relationship are more easily discernable than in the fully specified

mode. Generally, when inside forest stands, all sex-classes in all seasons are modeled to have inverse relationships between RSF score and canopy cover, with the strength of that inverse relationship increasing with greater distance from forest edges (the slopes are steeper). Conversely, when outside forest stands, the relationship is strong and positively related, with slopes getting steeper the further from the forest edge. Note however, that being nearer to the edge generally produces a higher value for habitat utility than being further away, regardless of canopy cover conditions.

For males, during hypophagia and early hyperphagia, the greatest utility values occur outside forest stands within 300 m of the edge. This is consistent with Figure 9 (panels a and b). During late hyperphagia, the pattern flips, and the highest utility values are found beyond 300 m from forest edges, both inside and outside forest stands. Additionally, there is a large confidence interval around the curves representing locations more than 300 m outside forest stands during both phases of hyperphagia. This is likely due to a confounding effect of TWI.

For females, the modeled relationship is similar, with locations within 300 m of forest edges being assigned the greatest utility values. The highest utility values are outside forest stands during hypophagia and early hyperphagia, and inside forest stands during late hyperphagia. For females with cubs, the relationship is most dissimilar from the other two sex classes. The magnitude of all slopes across seasons is low, near 0 when within 300 m of forest edge. During hypophagia and when more than 300 m outside forest edges, confidence intervals are large and indicate a confounding effect with TWI. Overall, for all sex classes and seasons, the pattern

clearly demonstrates a preference for cover when outside forest stands, and preference for low cover or forest gaps when inside forest stands.

3.5 Discussion

I investigated in this research the role of fine-scale measures of forest structure on habitat selection of grizzly bears. I used an AIC tally procedure similar to AIC weights to identify the best fitting model and applied it to matched case-control data for 9 classes of grizzly bear. The cross-validation of the fully specified model indicated by AIC tally was poor, likely due to overfitting and amplification of noise in the movement signal. However, the addition of ALSderived structural information, together with terrain and wetness variables, identified a pattern of selection for forest edges. I did not test every combination of environmental variables during the AIC tally to avoid an exercise in data mining. Using the results of the first model and my own knowledge of grizzly bear ecology, I constructed a second, "minimally specified" model containing only environmental variables relating to forest edge distance, canopy cover, and terrain wetness. TWI served two purposes in the model: first, as an index of terrain wetness, and second, as a proxy for elevation at the local (1-hr movement) scale. Using the minimally specified model, I successfully modeled habitat selection in 8/9 sex-seasons (Figure 10, $\alpha = .05$). Despite the relatively poor model fit for males during hypophagia, I still consider the model a valuable tool to analyze movement patterns of males during hypophagia. An alpha level of 0.05 may be excessively conservative for this type of investigation.

AIC tally indicated the best model was discordant with my hypothesis that canopy cover influences selection as a function of distance from the forest edge. 75th percentile canopy height

produced the best fit; however, cross-validation of both models indicated the best performing model was the minimally specified model, using edge distance and canopy cover, concordant with my hypothesis. Outside a forest stand, cover > 2 m increases the probability of selection, while inside forested stands, higher canopy cover is negatively related to selection. Estimates of fixed effects parameters showed greater relative effect sizes due to forest structural conditions.

The highest modeled RSF scores for males during early hyperphagia do not appear consistent at first glance – Figure 11b indicates the strongest preference for forest edge conditions, while 12b suggests interior forest and areas more than 300 m outside forests are the preferred habitat. This may be an artifact of the mean canopy cover conditions within forest stands – higher complexity stands may be preferred (Figure 12b – the highest utility with narrow confidence intervals is for >100 m inside forest stands when canopy cover is < 20%). However, they do not represent the mean forest condition (Figure 11b). This suggests forest stands undergoing understory reinitiation may mediate the strong edge effect on selection.

Females showed a very consistent response throughout the year – in most cases, the highest preference was for high cover conditions > 100 m from forest stands. This has important implications for the structure of retention blocks (groups of trees left uncut during harvests); however, further work should attempt to disentangle the nature of the relationship. For example, questions such as "if there is differential selection of harvest blocks by bears, what characteristics drive that selection?" and "can variables such as size of retention block, distance from the harvest unit edge, or the ratio of areas of the harvest unit and retention patches illuminate patterns in differential selection?" Due to the influence of non-habitat related factors,
this is unlikely. However, these questions may be answered with high fidelity, fine scale mapping of habitat alone.

Forest edges are dynamic in space and time. There are natural edges on each landscape which correspond to topographic, moisture, soil parent material, and other geomorphic gradients; there are also induced edges - the results of natural or anthropogenic disturbances to forest succession. Each edge has specific characteristics to its physical structure (length, width, spatial configuration) as well as the biotic gradient created between heterogeneous communities (Thomas et al., 1979). In their review of edge influences within fragmented landscapes, Harper et al. (2005) use this framework (e.g. structural versus functional gradients, abiotic vs biotic gradients) to describe edges in terms of the magnitude of edge influence (contrast between biotic communities) and the distance of edge influence (physical dimensions of the ecotone) to describe the successional dynamics of forest edges. They describe a sub-class of induced edge of note in our study area: the "maintained" edge, such as forest edges near roads or oil well pads. At those edges, they note the common development of dense sidewalls of vegetation that occlude light and dramatically shorten the distance of edge influence on habitat characteristics, such as plant community composition. Characterizing edge development, they describe edges as "sealing" when the magnitude of the edge effect increases but the distance of the edge effect decreases, such as at maintained edges. Edge "softening" occurs when both the magnitude and distance of edge influence decreases through time at a regenerating forest edge, and "expansion" refers to increases in the distance of forest edge influence. The effect of different edge types on selection is a subject that may reveal much about population performance and relative hazards of different edge types to bears. Near roads especially, the structure of a forest edge may be related to the

magnitude of its function as an ecological trap. The models tested in this investigation made no attempt to classify edges; our expectation was that one of the strongest signals would be the effect of vertical canopy cover, especially during hyperphagia, as previous studies have indicated that open canopy stands, forest edges, and young forest cut-blocks produce substantial berry mast (Nielsen et al., 2004). The RSF differences noted above (between Figures 11 and 12) provide insight into the effects of forest edge on grizzly bear habitat selection. Grizzly bears are known as exceptional generalists and display a strong preference for edge habitat, concordant with our results (Larsen et al., 2019; Nielsen et al., 2006).

Often, in habitat selection studies, the driving question is "how is *this population* responding to management?" This perspective generally avoids *a priori* designation of parameters, such as scale of selection or the definition of "patch" habitat, and instead defines them *operationally* at the scale that works (Chetkiewicz & Boyce, 2009; Nams et al., 2006). I did not address the multi-scaled nature of habitat selection in this investigation, as my intent was to first investigate whether lidar-derived habitat descriptors could effectively model habitat selection at the fine scale.

One model used by landscape ecologists is the patch-corridor-matrix model, in which suitable habitat is considered a patch, the matrix is the "background" habitat that is not suitable, and linear features connecting patches are corridors (Antrop & Van Eetvelde, 2017). When considering that model in the context of habitat selection, I suggest that male and female bears without cubs may perceive forest edges as patch/corridor and that "matrix" habitat may be considered dense canopy forest interiors, as Figure 12 suggests that high canopy cover is a strong

deterrent of selection. For females with cubs, however, the shape of the curves in Figure 12 suggest that dense canopy forest interiors are not such a strong deterrent to selection, possibly due to the provision of greater cover which may be associated with reduced cub mortality. Due to the greater cover afforded by dense canopies, females with cubs may utilize those areas as corridors more commonly than the other sex classes.

Scharf et al. (2018) used movement to define corridors according to the definition proposed by LaPoint et al. (2013) in which the corridor is defined by efficient, repeated traversals through matrix, between habitat patches. They tested the hypothesis that corridor use is correlated with higher habitat suitability, as well as associations between home range heterogeneity and corridor use with and between species. Most generally, they found that the number of corridors detected for an individual is non-random, correlated with home range size and the observation period of an individual. For black bears (U. americanus), they found that patch heterogeneity at the home range level was different from patch heterogeneity within the 95% utilization distribution of an animal, but there was no evidence supporting the hypothesis that heterogeneity of patches within corridors is different than matrix habitat. Additionally, there was no evidence to suggest that habitat suitability was significantly different within corridors and matrix habitat (habitat was classified using an SSF where utility was estimated using the proportions within 30 m of 6 land cover classes, as well as distance to road, and distance to water). However, efficient traversals as defined above are rapid, directionally persistent parallel movements. This functional definition of corridors may be inconsistent with the 3rd order of habitat selection (Johnson, 1980), especially in the highly fragmented, overstocked forests of the upper foothills. Scharf et al. (2018) propose that in lieu of habitat suitability driving corridor selection, the structure of the environment may

trigger corridor behavior in animals. This is consistent with the hypothesis that females with cubs utilize different habitat types as corridors.

Ultimately, as movement is a multi-scalar process, a discrete-choice movement model based on vegetation structure will not reliably predict movement but can be used to distinguish local landscape features to which bears respond. The implications of this step selection analysis are that grizzly bears may perceive forested stands in terms of their edge, rather than the specific cover or height conditions within the stand.

Lidar can be easily used to quantitatively describe the structure of forest edges according to the framework described by Harper et al. (2005). Next steps include testing whether edge habitat may be the link between the 2nd and 4th orders of selection and testing the influence of structure of retention patches on habitat selection. Edges are dynamic in space and time, and associated communities change akin to seral development of a forest stand (Harper et al., 2005). Different plant community compositions are represented by the different classes and condition of edge structure and development, and edge structure may be related to whether they are perceived as patches or corridors. I hypothesize that these edges have a detectible, asymmetrical effect on selection and "inter-patch" movements.

Chapter 4: Key Results, Implications, and Directions for Future Work

4.1 Summary of Results

Grizzly bears move across large home ranges through many stages of forest development, as well as alpine ridges, meadows, and riparian corridors. While the lifetime home range of a grizzly bear contains the full complement of resources needed for survival, variation is a key characteristic of this species (LeFranc et al., 1987), and they are known to display preference for habitats along forest edges, as well as certain categorical landcover classes. The effects of finescale patterns in forest structure, such as the relative density of gaps, the spatial characteristics of gaps, physical structure of forest edges, and vertical distribution of vegetation, have not been explored to the same extent as variables such as landcover type or food abundance – to date there have been few habitat selection studies of grizzly bears where habitat structure is described by continuous measurements of vegetation physiognomy that capture the diversity of conditions within and between forest stands. In this research, I use integrated step selection analysis with mixed-effects conditional logistic regression to characterize habitat selection in the context of lidar-derived forest structure and topography, stratified by sex-class and season. I found that inclusion of forest structural information improved the likelihood for most models; canopy cover influenced selection as a function of distance from the forest edge, and models demonstrated selective use of forest edges by bears. From a management perspective, the results suggest that high canopy cover conditions are preferred when bears are beyond 300 m from cover provided by forest stands. This has implications for structure and form of retention patches created by the "emulating natural disturbance" philosophy driving harvest decisions in this region. Beyond retention patches, forest interiors could be managed to allow more open canopy conditions; mountain pine beetle is currently at epidemic population levels in the region and salvage logging

is rapidly (within 3-4 years) employed to reduce economic losses (Weyerhaeuser, personal communication, AGM 3). It may be worthwhile to leave standing dead timber in some stands to promote natural gap dynamics normally absent in lodgepole pine.

4.2 Limitations

The lidar data were collected under contract for the Government of Alberta across much of the foothills and the boreal shield, an enormous area, and was flown during both leaf-on and leaf-off conditions between 2007 and 2013. During that time, forest harvest proceeded as normal throughout the forest management areas, and those structural changes are not captured with a single lidar snapshot of the region. The age of the lidar also influences the quality, as the average point density across the study area is low, at 1.2 points/m².

Additionally, my approach to identifying forest edge was simplistic and did not capture the range of variability present in ecotones across this forested landscape. There have been several studies which classified or characterized edges with metrics such as canopy height diversity and distance of edge influence using both airborne laser scanning and terrestrial laser scanning (Hladnik et al., 2020; MacLean, 2017; Rees, 2007; Vepakomma et al., 2018; Vepakomma et al., 2008). Harper et al. (2005) describe a framework for classifying the physiognomy of forest edges, and Stewart et al. (2013) identified differential selection of edges by bears based on landcover type. In my work, all edges were based on simple dominant canopy height and cover metrics and were treated equally. This is because of the age of the lidar dataset and it not being possible to develop metrics describing forest edge complexity which could then be ground truth to verify its accuracy.

Finally, the high spatial and temporal resolutions of the GPS collar dataset contain an extraordinary wealth of information, outstripping both our understanding of bear behavior and the capacity of our statistical modeling approach to explain how underlying behavioural processes influence habitat selection beyond what is described by the results of a multiple regression.

4.3 Directions for Future Work

Digital aerial photogrammetry (DAP) has numerous advantages over lidar: it is cheap, has high fidelity, and can be rapidly acquired (Goodbody et al., 2017; J. White et al., 2015). One of the greatest challenges in working with DAP occurs in dense closed canopy forests (such as the Yellowhead study area), where key points cannot be resolved at the ground surface and a reliable DEM cannot be generated (Holopainen et al., 2015, as cited by Goodbody et al., 2017). Additionally, large-scale area-based DAP operations are vulnerable to the same issues as multispectral imagery: namely the light conditions during the time of acquisition (White et al., 2015). The Alberta lidar provides a high-resolution DEM that circumvents the first issue entirely. However, acquisition conditions and their effects on DAP models may be more difficult to mitigate. At a fine scale, DAP can be used to accurately assess canopy closure as well as edge conditions; a classification algorithm would allow for more complex analyses of edge selection by bears.

Classifying edges may prove to be a challenge. They exist in 4 dimensions: latitude, longitude, the vertical dimension, and the temporal. The magnitude of the effect of edge on plant community structure changes according to the distance from the edge (Harper *et al.*, 2005), and

multiple edge types such as maintained edges along roads, induced edges such as harvest blocks, and natural edges such as riparian edges may exist in close proximity and have interactive effects on community structure (Harper et al., 2007). Spatial and temporal landscape context also influence the characteristics of a developing or shifting forest-meadow ecotone or alpine timberline, limiting the feasibility of a "one size fits all" approach to classification (Haugo et al., 2011; Kaczka et al., 2015). Decades of research on forest ecotones are available; however, guidance on the use of fine-scale remote sensing to describe edge community structure is lacking. Borrowing from the discipline of surface metrology, characterizations of the landscape surface, such as rumple (the surface area ratio of the canopy height model to the underlying digital elevation model), may be useful (McGarigal et al., 2009). Spinsante et al. (2019) used an individual tree-based approach to characterize roughness parameters of the 2-dimensional leading edge of the alpine timberline, reinforcing the relevance of surface roughness metrics.

Finally, new movement modeling approaches are constantly being developed, such as that by Michelot et al. (2019), which allow for more robust estimation of space use and underlying movement parameters. As I demonstrated, ALS is a valuable tool in an ecologist's toolkit; it can be used in the absence of landcover classifications to effectively model habitat selection. An ALS dataset contemporary with the research being done would be an excellent dataset well suited to refine descriptions of forest edges, allowing new questions about the nature of the edge effect to be posited and answered.

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