USE AND SELECTION AT TWO SPATIAL SCALES BY FEMALE MOOSE (*ALCES ALCES*) ACROSS CENTRAL BRITISH COLUMBIA FOLLOWING A MOUNTAIN PINE BEETLE OUTBREAK

by

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B.Sc., University of Northern British Columbia, 2014

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES
(BIOLOGY)

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

July 2018

Abstract

Moose are a keystone species and play a substantive role in predator-prey systems, nutrient cycling, and forest succession. Following a mountain pine beetle (MPB) spread across British Columbia, I quantified seasonal home-range selection, home-range size and daily movements, and within home-range selection of GPS-collared female moose in three study areas. I used case-matched logistic regressions with individual seasonal home ranges, and mixed-effects logistic regressions for seasonal locations of female moose to determine habitat selection at two spatial scales. Individual variation was evident at both home-range and within-home-range scales. Female moose selected lodgepole pine-leading stands at both spatial scales regardless of mass die-off due to MPB. Clear-cuts following the MPB outbreak were avoided in drier locations, and trade-offs between cover and browse were evident where disturbance due to salvage logging was highest. My findings indicate that MPB salvage-logging reduced moose habitat, and thereby, influenced selection by female moose.

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Acknowledgements

This thesis was completed in partnership with the University of Northern British Columbia (UNBC) and British Columbia Ministry of Forests, Lands, and Natural Resource Operations and Rural Development. Funding for this project was provided by the British Columbia Ministry of Forests, Lands, and Natural Resource Operations and Rural Development. The research design was developed by the Provincial Moose Management Team.

I am grateful to have had the opportunity to learn and work with my supervisory committee: Dr. Michael Gillingham, Dr. Katherine Parker, and Doug Heard.

I am most humbled and honored to have Dr. Michael Gillingham as a supervisor. Mike constantly went above and beyond to ensure my work was done with precision, and most importantly, he ensured that I understood what I was doing. Over the past few years, Mike has treated me with unwavering respect, and genuinely cared about my personal well-being and life inside and outside of his lab. Mike's previous students have described him as the "man of a million macros," which is hard to argue with, but I also know him as the "man with a million puns" who can make anyone laugh, given enough time to understand his quick wit. I know looking back on my time being Mike's student, I will always remember to double and triple check my data entries, keep extremely detailed notes, and never lose sight of the big picture.

Thank you to my committee members, Dr. Katherine Parker and Doug Heard. Kathy is one of kindest and most humble individuals one could ever meet. Her passion for wildlife is contagious, and the incredible ability for her to understand how spatial data translates to biological relevance has increased my understanding tremendously. Doug's passion for wildlife biology, his drive to understand biological processes at the finest scale, and

investigating techniques are infections. Before my master's began, Doug had begun mentoring me and his ability to teach meaningful concepts that can be scaled up to the big picture always leaves me fascinated. Thank you, Kathy and Doug, you have made this degree an incredible learning experience far beyond the scope of my research.

I am very thankful for Dr. Roy Rea who mentored me throughout my undergraduate degree and beyond! Roy taught me the way of the moose, and I'll never forget our annual Bull trout fishing trips!

Dr. Matt Mumma was always there to discuss concepts and methods for moving forward. He was also there to vent to when my presentations never went as planned. Matt's ability to teach statistical concepts to anyone, including myself, should be an indication of how talented he is. Thanks for all the help buddy!

Many thanks to the Government biologists who got me out into the field and away from the computer: Doug Heard, Shelley Marshall, Mike Klaczek, Adrian Batho, Becky Cadsand, Heidi Schindler, Michael Bridger, and Morgan Anderson.

I would like to thank West Fraser Mills-Quesnel Woodlands for generously supplying me with spatial data within TFL 52 that filled in missing spatial data crucial for this research.

Lastly, I could not have had the opportunity to complete this Master's without the support from my family and friends, even if they all still think I am a 'Fish Cop'. I would like to specifically thank my brothers (John and Mike), my sister (Skylar), my parents (Craig and Charlotte), and my grandparents (Owen and Agnes) for their extraordinary support, even from afar.

I look forward to the future, to see what life has in store for me, and what kind of adventures I can get myself into!

Chapter 1 : Introduction

BACKGROUND

Originating in 1999, a mass die off of lodgepole pine (*Pinus contorta* var. *latifolia*) caused by an unprecedented outbreak of mountain pine beetle (*Dendroctonus ponderosae;* MPB) spread across western North America (Taylor and Carroll 2003), including British Columbia's (BC) central interior (Kurz et al. 2008). In many regions, forest harvesting increased to historical levels to salvage lumber before loss of marketability. Many regions in BC experienced moose (*Alces alces*) population declines concurrent with the MPB outbreak. Due to concern for moose population numbers, and to understand the mechanisms of their survival, the province of BC began a 5-year study on female moose fitted with global positioning satellite (GPS) collars across five study areas. Using GPS collar data from female moose in three study areas in central BC, my thesis investigates the mechanism of the landscape-change hypothesis (*sensu* Kuzyk and Heard 2014) post MPB outbreak. The landscape change hypothesis predicts negative effects on moose population growth rate resulting from increases in hunting and predation, because of changes in forest age structure (from heterogeneous to a relatively early seral stage) and increases in road density associated with salvage logging.

SPECIES OVERVIEW

Moose are a keystone species, and play a substantive role in predator-prey systems, nutrient cycling, and forest succession (Molvar et al. 1993, McLaren and Peterson 1994). Moose are the second largest species of Artiodactyla in North America, smaller only than the two subspecies of bison (*Bison bison bison, B.b. athabascae*), and the largest extant species of true deer (Cervidae family) in the world. The nomenclature of moose has been widely debated since Linnaeus first named the species *Cervus alces* in 1758. As recently as 2005, Eurasian Elk (*Alces alces*) and North American moose (*Alces americanus*) were recognized as distinct species (Wilson and Reeder 2005), but there is still debate surrounding whether North American moose is its own species (Groves and Grubb 1987) or a subspecies based on chromosomal numbers (Boeskorov 1997), geographical ranges, and physical characteristics (Hundertmark and Bowyer 2004). Within BC, physical characteristics historically separated three subspecies of moose: Northwestern moose (*A. a. andersoni*; Peterson 1955), Alaskan moose (*A. a. gigas*; Miller 1899), and Shiras' moose (*A. a. shirasi*; Peterson 1955). The Northwestern moose (hereafter moose) have the largest distribution in BC (Shackleton 1999) and is the subspecies of focus for my thesis.

Moose are considered an iconic species of the north, being culturally important and having subsistence, recreational, and economic values (Santomauro et al. 2012). Prior to 1860, there were no known records of moose in BC's interior landscape (Franzmann and Schwartz 1998). During the 'invasion' of the interior in the late 19th century (Peterson 1955, Hatter 1970, Telfer 1984, Spalding 1990) and the coastal rainforests in the mid 1900's (Darimont et al. 2005), moose range expanded throughout much of BC and their populations grew considerably. Moose populations across BC, however, have been on a slow decline since the 1960's (Karns 1998).

Moose populations in the central interior of BC have not always remained constant and yearly variations due to natural causes are expected (Telfer 1984, Karns 1998). Recently, however, moose numbers in BC have been a cause for concern in some areas of the central interior where populations have experienced 50 – 70 % declines, in contrast to other areas in the province that have remained stable or have increasing numbers (Kuzyk and

Heard 2014). As of 2014 (the last available province-wide estimate), there were between 120,000 – 205,000 moose in BC (FLNRO 2015). This estimate is ~27,500 moose lower than the 2011 estimate and is consistent with the observed moose declines in the central interior (FLNRO 2015). Some believe that the variation in moose population growth throughout the province is related to disturbance and changes to intact forests (Karns 1998, Kuzyk and Heard 2014). The drastic increased rate of forest harvesting and subsequent decline of intact forests in recent years is worrisome, and is the focus of this project (Karns 1998, Kuzyk and Heard 2014, FLNRO 2015).

COMMERCIAL LOGGING

Logging in BC has a long history, but logging in the central interior began only in the mid-19th century and large-scale commercial logging began only in the late 1960's. Today, commercial logging is one of the main employers and grossing industries in the province. Historically, logging was more selection-based, where the best-quality trees were felled for lumber for housing, steamships, and mining purposes (Drushka 1998). This trend first changed with the development of the railroad in the late 19th century, when timber was needed in much higher volumes and selectivity decreased. Until the early 1900's, the interior was believed to be an untouched resource where the quantity of trees was endless and could be harvested on a one-time basis. Early conservation movements altered this paradigm so that the lands harvested were replanted for future harvesting. Once the interior was accessible by railroad, however, logging was not constrained to river systems, and road networks were eventually established. Technology has continually advanced in the logging industry, as has the distance at which timber is harvested from mills — as extracted volumes increased, tree species selectivity decreased. Logging in BC has continued for over 100 years, but BC forests are now in a transition between a natural and a managed state in which natural disturbances are suppressed to improve forest harvesting as the main disturbance agent (Taylor and Carroll 2003).

Forest pests and pathogens have undergone well-documented outbreaks (Martinat et al. 1987, Peltonen et al. 2002, Taylor and Carroll 2003, Romme et al. 2006) in BC. Most recently, a mass die off of lodgepole pine caused by an unprecedented outbreak of MPB spread across western North America, including BC's central interior (Kurz et al. 2008). Tree death and subsequent needle cast generally spans 3 – 5 years post MPB infestation (Mitchell and Preisler 1998), and tree blowdown increases after 15 – 20 years (Ritchie 2008). As of 2011, the MPB outbreak spread into 50 % of the total provincial merchantable pine volume (Walton 2012). Subsequently, logging rates have increased to over 15 million m^3 annually (~30%) above what was previously harvested in 2000 to salvage wood before it degrades to a point it cannot be used for profit (Parfitt 2007).

Salvage logging of pine-beetle infected stands is a cost-effective method for harvesting these stands of dead pine, but many salvage-logging operations have also removed spruce (*Picea* spp.), fir (*Abies lasiocarpa*, and *Abies balsamea*) and Douglas fir (*Pseudotsuga menziesii* var. *glauca*) in great quantities (Parfitt 2007). Although cutblocks attempt to mimic natural stand-replacing fire events (Delong and Tanner 1996), they produce access roads where forest fires do not (McRae et al. 2001). Roads fragment mature forest, allow predators linear corridors to follow in search of food, and allow hunters into areas otherwise unavailable with the use of motorized transportation. Thus, the MPB outbreak, and associated salvage logging, has had unknown consequences to moose and other wildlife values.

Spatial and temporal use of harvested blocks by moose

Disturbances to forest communities can be caused by natural or anthropogenic events. The anthropogenic events in BC associated with disturbances to climax forests are primarily due to commercial logging activities. Regardless of the cause of disturbance, changes to climax forests allow for competitive replacement of early seral species (White 1979), known as secondary succession. Many secondary-succession plant species, which generally grow after a disturbance, are palatable deciduous species preferred by moose (Bunnell et al. 2004). Moose numbers and other generalist herbivores are expected to increase from the creation of early (5 – 40 years post-logging) seral vegetation (Bunnell et al. 2004, Janz 2006), but there have been few long-term studies on the effects of post-harvest silviculture on moose (Thompson et al. 2003).

A young cutblock contains an array of coniferous tops and branches, felled un-merchantable timber, slash piles, and a variety of understory brush. The degree of use a new cutblock receives by moose is dependent on multiple factors including the browse and remaining uncut timber available post-harvest and post-treatments (Rempel et al. 1997). Many researchers suggest moose survival is reduced following forest harvesting due to predators and hunters utilizing disturbed forests (Dalton 1989, Eason 1989, Rempel et al. 1997). Other researchers argue that cutblocks of specific ages, configurations, and sizes may increase moose populations through the production of deciduous forage (Bunnell et al. 2004, Janz 2006). Although new cutblocks may produce deciduous forage, researchers have observed moose to avoid non-vegetated and recently disturbed areas (Gillingham and Parker 2008*a*, Street et al. 2015*b*).

Moose forage on many plant species with seasonal variations (generally due to growing seasons), but seral stage preference and preferred browse species differ across moose ranges. Biomass of aspen (*Populus tremuloides*), a main food source for moose (Schwartz et al. 1988), and other understory species peaks 5 years after disturbance, although increased production of browse available to moose may continue for an additional 15 years (Lemke 1998). In Newfoundland, moose selected cutblocks between 8 – 10 years old (Parker and Morton 1978). Courtois et al. (2002) grouped all cutblocks ≤11 years old as a cut vegetation class that could potentially provide summer and winter forage, clearings >11 years old where young stands provide forage and summer cover, and mature forest stands >60 years old providing primarily cover. Stands with >10,000 stems•ha^{-1} of deciduous browse such as aspen, willow (*Salix* sp.), or paper birch (*Betula papyrifera*) provide the highest food abundance, whereas stands with 3,000 – 5,500 stems•ha^{-1} provide moderate food abundance (Dussault et al. 2005*b*). Coniferous species in plantations are not readily browsed by moose in North America, although subalpine fir (*Abies lasiocarpa*) is an exception (Crête and Courtois 1997). Subalpine fir made up 42% and 45% of moose winter pellets at two study sites (Aleza Lake Research Forest and John Prince Research Forest, respectively) in north-central BC (Hodder et al. 2013, Rea 2014). It is evident that trends in seral stage preference are variable across North America potentially due to regeneration rates and stand-tending practices. However, moose prefer early seral stage for foraging a few years post-harvest, allowing for sufficient time for vegetation to become available to moose.

Spatially, the size of the cutblock may not be as important as is the matrix extent and configuration of the surrounding un-cut forest for moose (Potvin et al. 1999). Moose select different-sized cutblocks with reserve uncut zones between them. In north-central BC, "moose habitat can be conserved or improved with 4-ha clear-cuts", whereas small openings with sufficient forage surrounded by mature timber were highly selected for (Schwab 1985). Lemke (1998) recommended that block sizes be limited to 10 ha to minimize distance to adjacent coniferous stands for cover. Moose in western Alberta selected cutblocks of 16.6 – 32.4 ha, and blocks that were buffered from adjoining forest openings by 220 – 400 m (Tomm et al. 1981). A Newfoundland study observed that the greatest winter browsing occurred in 40 – 50-ha cutblocks (Parker 1978).

Moose are generally not considered an edge species; under high harassment, however, moose tend to stay near edges for escape cover and under low harassment, moose utilize browse further from an edge (Tomm et al. 1981). In Sweden, where predation abundance is low, moose presence in cutblocks during the winter was significantly higher than within the forest or stand edge (Hansson 1994).

Linear features

Roads modify the landscape by bisecting forests, resulting in fragmentation, loss of cover, increases in edge, and often increased human-wildlife interactions (Forman and Alexander 1998, Gillingham and Parker 2008*b*, Laurian et al. 2008). At the same time, the use of roads by moose, particularly highways, is well studied (Yost and Wright 2001, Laurian et al. 2008, Beyer et al. 2013, Bartzke et al. 2015) and variation in behaviour is likely a result of seasonality, predation risk, habitat (Beyer et al. 2013), and limiting factors such as sodium or other mineral deficiencies (Laurian et al. 2008). Moose avoid crossing some roads and other linear features (Bartzke et al. 2015), but the size and amount of traffic on roads affects crossing rates (Laurian et al. 2008, Eldegard et al. 2012). While feeding alongside highways, moose can be more vigilant (Yost and Wright 2001), but behaviour of moose feeding alongside industry roads (generally not paved, with seasonally different traffic patterns, and differences in roadside vegetation management) is not well studied. Research on road density has shown that crossing rates vary seasonally: moose cross roads more often during the summer than winter, likely a result of greater movement rates (Beyer et al. 2013). Roads offer moose unobstructed travel corridors, easily accessible forage, and sources of sodium (where the application of road salts persist); however, they may reduce moose survival as higher encounter rates of roads may result in a greater likelihood of injury or mortality (James and Stuart-Smith 2000, Eriksen et al. 2009).

Moose using linear features such as roads, transmission lines, pipeline corridors, or seismic lines (cleared land for the exploration of oil and gas, generally 5 – 10 m wide) are likely more visible to predators and hunters (Janz 2006). Generally, the effects of these linear features persist longer than do young cutblocks in which visibility decreases as the seral stage advances. Although roads are not the only landscape feature that offers high visibility, predators of moose such as wolves (*Canis lupus*) may be more efficient near linear features due to higher search rates (James and Stuart-Smith 2000, Dickie et al. 2017). Hunter success can be much greater with the use of vehicles (Schmidt et al. 2005) and roads allow the public (including hunters) access into areas otherwise inaccessible to them. Singular roads may not have a great net effect on moose populations (unless the road is localized to small drainages, with steep slopes, etc.); however, moose have been shown to avoid areas with high road densities (Beyer et al. 2013). Road density of $0.6 \text{ km}\bullet\text{km}^{-2}$ have been suggested as a threshold for large mammal declines (Beazley et al. 2004), in part because access to wildlife by humans has become increasingly easier (McLellan and Shackleton 1988).

Concurrently, roads and other linear features offer easier movement pathways for moose to follow, and generally provide plentiful seral vegetation for browse (Rea 2003). Use of linear features depends on size and level of harassment (e.g., noise, accessibility, traffic level, visibility). Small-width openings provide escape cover for moose, which are selected in high harassment areas and wider openings may be selected when mortality risk and harassment are low (Tomm et al. 1981). Secondary resource roads may not be the leading cause of mortality; however, road networks increase landscape fragmentation, and allow hunters and predators unobstructed access to landscapes otherwise inaccessible.

Use of mature timber by moose

Moose use mature coniferous stands for concealment cover, snow interception, and thermal refuge (Belovsky 1981). Mature timber has been recognized as a cover type required for moose range in all seasons in central BC (Schwab 1985). Lemke (1998) suggested moose require a minimum of 50 % conifer crown closure during winter, and an even greater crown closure if the escape terrain is adjacent to a forest opening.

Moose may require both vertical and horizontal cover to be sheltered from the environment and to provide concealment cover from predators and other stress factors in all seasons, and specifically when snow depths exceed 90 cm (Schwab 1985). Stands of mixed forests (during the growing season) and coniferous stands >30 years old (80 – 85 % cover) provide the highest degree of concealment cover (Dussault et al. 2005*b*). Horizontal cover is achieved when vegetation exceeds 2.5 m, but little is reported about the amount of lateral cover needed to avoid predation and provide concealment cover (Dussault et al. 2005*b*).

Moose utilize mature mixed forests and coniferous cover during all seasons for thermoregulation (Schwab and Pitt 1991). During the snow-free period, moose avoid heat by selecting wet and shaded areas (Melin et al. 2014). Cold temperatures are believed to have little effect on moose metabolism during the winter, as their lower critical temperature is reported to be <-40°C (Renecker and Hudson 1986). Moose are intolerant of heat, however, especially during the winter (Karns 1998). Metabolic rates have been observed to increase when ambient temperatures exceed -5.1°C in winter and 14°C during summer (Renecker and Hudson 1986). Areas with large salvage-logging operations, where mature cover patches have been removed, could therefore negatively affect moose by causing heat stress (Ritchie 2008, Melin et al. 2014).

During winter, moose movements can be impeded when snow depths are >60 cm (Franzmann and Schwartz 1998), above which the snowpack substantially increases energetic demands (Karns 1998). Mature timber provides snow interception, allowing moose to avoid deep snow during the winter months (Timmermann and McNicol 1988). At a landscape scale, moose may avoid areas that receive the least snowfall due to predator avoidance (Dussault et al. 2005*b*).

MOVEMENTS AND HOME RANGES

Movement rates of moose differ seasonally: they are generally highest during the summer and lowest during early winter and late winter (Phillips et al. 1973, Gillingham and Parker 2008*b*). Aside from the rut, when male moose travel greater distances than females, movement rates of males and females are similar throughout the year. Average daily movement rates for female moose during the summer and winter in northern Minnesota were 1.9 and 1.3 km per day, respectively (Phillips et al. 1973). In BC's northern mountains, average daily movement rates were approximately 2.4 km per day during the summer, and 960 m during the winter (Gillingham and Parker 2008*b*).

A home range is defined as an area that an animal traverses for its normal daily activities for a given amount of time (Burt 1943, Jewell 1966). Over the last several decades, techniques for estimating home ranges have evolved from direct observation to live-trapping individuals over large areas, and now radio-collaring with GPS units to acquire real time location data (Seton 1909, Hayne 1949, Losier et al. 2015). Home-range estimators vary from simple minimum convex polygons (MPC; Hayne 1949, Sanderson 1966) surrounding location data to density-distribution functions (Dixon and Chapman 1980, Anderson 1982, Worton 1989, Getz and Wilmers 2004), and home-range sizes vary considerably depending on which estimator is used (Boulanger and White 1990, Worton 1995, Seaman and Powell 1996), the number of location points (Harris et al. 1990, Seaman et al. 1999, Powell 2000), and the computer software program used for analysis (Lawson and Rodgers 1997). Consequently, there is no single appropriate home-range estimator for all species, individuals, age classes, or time of year.

Estimating home range is problematic as intraspecific variation affects home-range size depending on factors or variables measured (VanBeest et al. 2011): spatial and temporal variables such as habitat, topography, season, weather, reproductive status, sex, body mass, etc., all influence home-range size. Previous studies that all used 100% MCP (Jennrich and Turner 1969, Eddy 1977) annual home ranges for female moose reported variable estimates between 8.9 – 19.3 km^2 in low topography areas in Sweden (Cederlund and Okarma 1988, Cederlund and Sand 1994), 53.9 ±4.3 (SE) km^2 in southern Quebec (Laurian et al. 2008), 56 km^2 in western Quebec (Potvin et al. 1999), 73.7 ±10.9 (SE) km^2 in northwestern Quebec

(Courtois et al. 2002), 142 – 2,025 km^2 in south-central Yukon (McCulley 2015), 11 – 235 km^2 in south central BC (Lemke 1998), and 39 – 899 km^2 in BC's northern mountainous terrain (Gillingham and Parker 2008*b*). Courtois et al. (2002) demonstrated that home-range size was positively correlated with the proportion of clear-cut landscapes within the home ranges. McCulley et al. (2017) reported that female moose had the smallest home ranges (100% MCP) during the Summer, 72 ±15 (SE) km^2, and the largest during Early Winter, 172 ±34 (SE) km^2. Lemke (1998) also noted that by using 100% MCP home-range estimators, female moose home ranges were smallest during the Summer and largest during the Winter (8.6 and 29.5 km^2, respectively), regardless of moose travelling the furthest distance daily during the Summer (Lemke 1998, McCulley 2015).

HABITAT SELECTION

Ecologists assume that wildlife select the highest-quality resources available to meet life requirements, unless other factors influence the animal's opportunities to do so. Because resource quality is not uniform (e.g., landcover types are not all equal), an animal's use changes with availability (Manly et al. 2007). Resource selection, however, is viewed at a hierarchical scale ranging from a species' geographic range (first-order selection), selection of landscape features (including vegetation cover) specific to home ranges (second-order), selection of characteristics within a habitat (third-order), and selection of general features (feeding or bedding sites; fourth-order selection; see Johnson 1980). Animals make decisions at different spatial scales (Johnson 1980), which are believed to be primarily driven by limiting factors (Dussault et al. 2005*b*) and motivations such as finding food, rearing offspring, mate selection, and predator avoidance (Beyer et al. 2010).

Habitat-selection analysis is used to understand animal-habitat relationships, predict space-use by animals, and assess important features used by animals (Beyer et al. 2010). Use indicates an association with, or consumption of a habitat or food resource. Selection occurs when an animal chooses a specific vegetation or food type if given alternatives, and preference is the likelihood of a single resource being selected if an alternative is available in equal amounts (Johnson 1980). Resource selection can be for or against a resource; here, selection refers to the use of a vegetation cover class more than it is available, and avoidance is the alternative. Selection is estimated primarily through use-availability models, but a concurrent qualitative assessment of use and availability (e.g., Gillingham and Parker 2008*a*) helps in understanding the importance of 'selecting' rare resources or 'avoiding' abundant resources (Stewart et al. 2002). Many types of selection models have been employed to estimate selection, but the appropriate model depends on the sampling design and the research question (Keating and Cherry 2004, Manly et al. 2007). Frequently, logistic regression software is used to estimate the coefficients in resource selection probability functions (RSPF), which are used to compare used and unused samples (Manly et al. 2007).

There are challenges when estimating both use and availability in resource-selection studies. Use is generally taken to be the presence of an individual at a location (e.g., GPS location) or consumption of a food item, but a GPS location may represent simply an animal moving through a habitat, over or underestimating use (Serrouya et al. 2017). Concurrently, complications arise when determining availability both because the researcher must make assumptions about the animal's perception of availability and because resource abundance may not be directly related to availability. Availability of a food resource suggests it is both accessible and usable to the animal during the time of the study, and independent of weather

(McDonald et al. 2012) and other covariates often not considered during the analyses. Used locations or space can be determined by GPS or very high frequency (VHF) telemetry, or visual identification where the area is defined as a surrogate for predicted resources (e.g., riparian represents food). Availability, however, is more generally assumed, either being calculated across an area or assessed individually with random replicates identified to represent what resources were available to an individual.

CONTEXT

In response to moose population declines in north-central BC that coincided temporally with increased salvage logging following a broad-scale MPB epidemic, my thesis investigates the mechanism of the landscape-change hypothesis to determine how large-scale landscape change contributes to habitat selection by female moose. This hypothesis states that moose population declines have occurred from timber harvesting over very large areas, resulting in a loss of cover (creation of greater proportions of early seral vegetation), increased road density, and therefore greater risk from hunting, predation, and natural disease. This hypothesis is based on moose being more vulnerable because of where they live following a large disturbance, and I looked at where moose live to see if they were vulnerable. I tested this mechanism by using ~30 GPS collared female moose in each of three study areas differing in the amount of MPB salvage logging in north-central BC over a period of 3 years. Although extensive salvage logging post MPB may benefit moose by providing forage over a very large area (Bunnell et al. 2004, Janz 2006), it also may have negative effects on moose due to reduced cover (Belovsky 1981, Schwab 1985, Lemke 1998) and increased vulnerability to predators and hunters (Dalton 1989, Eason 1989, Rempel et al. 1997, Ritchie 2008). I used vegetation attributes (e.g., early seral stage cutblocks, which both create food, and represent an increased risk from mortality), and moose movements and behaviour (selection) to assess hypotheses related to landscape change. I hypothesized that moose would avoid areas with the greatest proportion of landscape change (given the population decline) and select vegetation cover unassociated with MPB salvage logging.

GOALS AND OBJECTIVES

The goals of this study were to determine: 1) what the differences in habitat selection by female moose across three study areas altered by MPB salvage logging in central BC were to predict the potential limiting factors; and 2) if the intensity of logging in these areas changed movement behaviour and home-range selection of female moose. My specific objectives were to:

- document home-range size and movement rates of female moose in relation to the intensity of forest harvesting;
- determine if selection of home ranges (2nd-order) by female moose differ in relation to the intensity of forest harvesting;
- assess habitat selection (3rd-order) by female moose over a range of landscapes altered by intensive forest harvesting; and
- examine potential limiting factors for moose in north-central BC.

THESIS ORGANISATION

My thesis is organized into four chapters: an introductory chapter, two stand-alone chapters to be submitted for peer-reviewed publication, and a project synthesis chapter containing study limitations, future research, and management objectives for central BC.

Chapters 1 and 4 are written in first person singular; Chapters 2 and 3 are written in first person plural to recognize the contributions of co-authors.

In Chapter 1, “Introduction”, I present an overview of moose and logging in BC, as well as relevant background information on moose habitat selection and home ranges. In this chapter, I also present my objectives and goals.

In Chapter 2, “Does salvage logging of beetle-killed coniferous forests affect home-range selection by female moose?”, I examined selection of home ranges by female moose in relation to the intensity of MPB salvage logging and associated logging operations, and whether movement rates and seasonal home ranges differ by study area. I used home ranges and ‘available’ areas of identical size to examine selection by collared female moose at the home-range scale. I compared vegetation cover classes and road density between five seasonal used and available home ranges and three study areas using case-matched logistic regression.

In Chapter 3, “Habitat and space use of female moose in central BC following a mountain pine beetle outbreak”, I evaluated whether female moose were using specific vegetation cover classes that were selected during 2nd-order selection, and whether escapement cover (distance to cover given the animal is in the open), or distance to mature cover edge (reflective of a food-cover boundary) was more important to determine risk trade-offs. To do this, I generated five random locations (available) for every used location point and compared used and available location points with attributes such as vegetation cover, distance to road, and elevation. I examined use and availability by study area and season to look at “important” vegetation cover classes that may not be inherently obvious in logistic regressions. I then used mixed-effects logistic regression analyses for each season and study area to determine which *a priori* model sets best estimated habitat selection by female moose in central BC.

In Chapter 4, “Overview of habitat selection by female moose in a clear-cut world”, I provide a synthesis of my results at both the home-range and within-home-range scales relative to the landscape-change hypothesis within north-central BC. In that chapter, I include a discussion of the study limitations and recommendations for future research, along with several management recommendations that could benefit moose habitat across my study areas.

Chapter 2 : Does salvage logging of beetle-killed coniferous forests affect home-range selection by female moose?

ABSTRACT

Progressive landscape change resulting from forest harvesting can alter ecosystems from a heterogeneous state to a more homogenous one, potentially changing habitat suitability for wildlife species. Following a large-scale mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreak and subsequent salvage logging, we studied home-range selection by female moose (*Alces alces*) over 3 years in central British Columbia (BC). Female moose were equipped with GPS-radio collars in three different study areas and we investigated seasonal home-range selection by individual animals. Daily movements of moose were longest during the Summer, and shortest during Late Winter. At the home-range scale, collared female moose had shorter daily movements and smaller home ranges in areas with greater proportions of clear-cutting. Home-range size for female moose did not increase with road density or with the proportion of cutblocks on the landscape. Further, selection of individual seasonal home ranges did not avoid recent forest harvesting, although areas with higher road densities were avoided in most seasons and study areas. More homogenous landscapes were also avoided because moose selected more complex habitats. Our findings indicate that broad-scale salvage logging in lodgepole pine (*Pinus contorta* var. *latifolia*) forests following a MPB outbreak influenced home-range selection by female moose. This habitat selection likely resulted from a trade-off between the avoidance of risky areas with high densities of roads and clearcut areas with potentially high browse quantity.

INTRODUCTION

Anthropogenic disturbance can have negative impacts on wildlife (Gill et al. 1996, Arlettaz et al. 2015, Wilson 2016, Stewart and Komers 2017) and is a contributing factor for species decline worldwide (Vors and Boyce 2009). Frequently, habitat for wildlife is reduced with expansion of forest clearing and other resource-extraction industries (MacNearney et al. 2016). Progressive landscape change due to forest harvesting (occurring year after year) can alter ecosystems from a heterogenous state to a more homogenous one (Scheffer et al. 2001). Functionally, movements, home-range size and fidelity, distribution, and behaviour are among the strategies that wildlife use to cope with a changing landscape (Berger 2007, Roever et al. 2010, Semeniuk et al. 2012, Ehlers et al. 2014, Latham and Boutin 2015).

Habitat selection is a hierarchical process with animals making decisions at different spatial and temporal scales (Johnson 1980) — limiting factors can be potential drivers of selection at any scale. At a course scale (i.e., landscape or home-range scale; termed 2nd-order selection by Johnson 1980), selection of seasonal home ranges may attempt to reduce the most important limiting factors to populations such as predation (Rettie and Messier 2000); other limiting factors such as food availability, snow depth, calving sites, and specific browse items would be associated with selection by individuals at finer scales (Dussault et al. 2005*b*). Although selection within a home range (see Chapter 3) affects the resources and risks encountered by an animal on a daily basis, selection at the home-range (HR) scale can directly impact animal fitness (Leblond et al. 2013).

We examined home-range (HR) selection of female moose (*Alces alces*) in three landscapes differing in disturbance intensities 15 years after a mountain pine beetle

(*Dendroctonus ponderosae*; MPB) outbreak in central British Columbia (BC; Alfaro et al. 2015). Our objectives were to test a landscape-change hypothesis (Kuzyk and Heard 2014) by: determining if selection of HRs by female moose differed in relation to the intensity of MPB salvage and associated logging operations; and determining if movement rates and seasonal HR size differed by study area. We predicted that HR size would be positively related to daily movement distance as seen for moose in northern BC (Gillingham and Parker 2008*b*). We expected that daily movement rates and HR size of female moose would be largest during the Summer when movement is least restricted and smallest during the Winter due to increased snow depths that restrict movements (Cederlund and Okarma 1988, Lemke 1998, McCulley 2015), thereby reducing energetic expenditures (Parker et al. 1984) when food quality is poorest (Moen et al. 1997). We predicted that HR size would increase with the amount of salvage logging because of fragmentation of mature cover, increased browse searching time, and predator avoidance (Courtois et al. 2002, Laurian et al. 2008). We also expected daily distances moved by female moose to be greater in all seasons for study areas with the greatest proportion of recent forest harvesting because they would move greater distances to acquire food and cover. Further, we predicted that female moose would: avoid areas with high proportions of new cutblocks and high road density (little to no remaining cover), and utilize mature forests on the periphery of forest harvesting for predator and human avoidance (Stankowich 2008, Eldegard et al. 2012). We expected those responses to vary due to severity of MPB salvage logging. Such a strategy would minimize risk from predators (James and Stuart-Smith 2000, Kunkel and Pletscher 2000, Dickie et al. 2017), increase thermal protection (Timmermann and McNicol 1988), and increase food-cover boundary selection (Courtois et al. 2002).

METHODS

Female moose were fitted with a GPS Plus Vertex Survey collar (VECTRONIC Aerospace, Berlin, Germany (Vectronic)) or an ATS Iridium GPS G2110E collar (Advanced Telemetry Systems Inc., Insanti, MN (ATS)) by the BC Ministry of Forests Lands and Natural Resource Operations and Rural Development (FLNRORD) staff as part of a larger moose survival study (BC Provincial Animal Care Permit CB17-277227) ongoing since December 2013. Vectronic collars were set for only one fix per day (0900 during the Summer, and 1000 during the Winter) to conserve battery life. ATS collars, however, received four fixes a day (0300, 0900, 1500, 2100), but we used only 0900 fixes in our analyses so that collar manufacturer did not influence our results. Fix time of collars was chosen to represent a time when not all individuals were likely to be active or inactive (Belovsky 1981). Collared animals were monitored between January 15, 2014 – September 12, 2016.

Study areas

Our study was conducted in three areas in central BC (Figure 2.1, Table 2.1), Canada; Prince George (PG) South (53° N, -123° W), Entiako (53° N, -125° W), and Big Creek (51° N, -123° W). Each study area had substantial lodgepole pine (*Pinus contorta* var. *latifolia*) die-offs (generally all pine >30 years old) due to BC's most severe MPB outbreak on record (British Columbia Ministry of Forests 2007) and subsequent intensive forest harvesting between early 2000 – 2016 to salvage wood before loss of marketability in wood product. Most of the forest harvesting was completed prior to the commencement of our study, although small-scale logging activities continued throughout the study period in each study area. Differences in study areas were primarily tree species composition, elevation, and

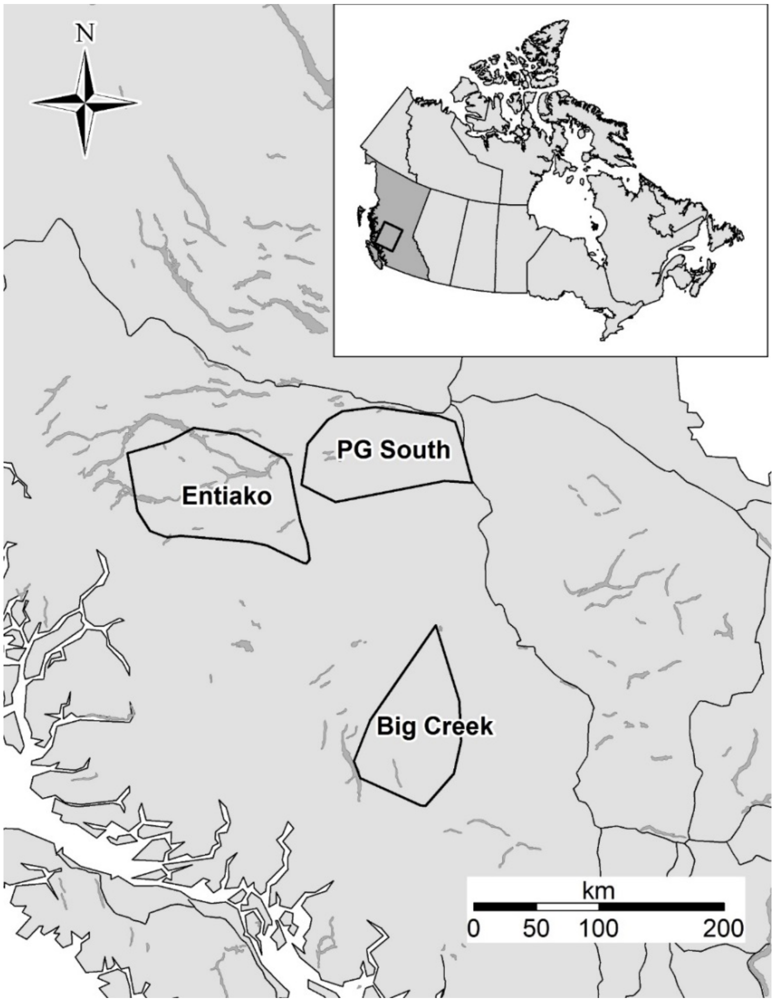

Figure 2.1. Boundaries encompassing all collared female moose location points of three study areas in central British Columbia used to evaluate home-range selection by female moose. Major lakes are depicted with darker grey shading and major highways are show as black lines.

Table 2.1. Numbers of GPS collars deployed on female moose with their associated fix success in three study areas in central British Columbia between January 15, 2014 – September 12, 2016. Note: if an animal died and its collar was recovered, extra 'downloaded' data associated with missing fixes were included in the analysis.

Study Area	# Moose	# of Seasonal Home Ranges	# of Fixes	Fix Success Percent	Fix Success SE
Entiako	51	386	22,366	75.7	1.93
Big Creek	58	490	32,724	86.7	1.26
PG South	48	289	18,611	72.7	2.04

gradient of disturbance associated with salvage logging, but the major agents of moose mortality also differed somewhat among the study areas (see Kuzyk et al. 2016).

The PG South study area (~7,610 km^2), defined by a minimum convex polygon surrounding all animal locations, had the greatest proportion of recent commercial forest harvesting, with an average road density of 1.9 km•km^{-2}, and was located closest to a populated center (Prince George). Elevations ranged from 550 – 1,400 m above sea level (ASL). Vegetation was primarily mixed species coniferous stands with small patches of mixed deciduous stands, except for regenerating clear-cuts where extensive silvicultural treatments reduce herbaceous species. Mature spruce (*Picea engelmannii* x *glauca*), subalpine fir (*Abies lasiocarpa*) and Douglas fir (*Pseutosuga menziesii* var. *glauca*) stands were historically removed, and later replaced primarily with plantations of lodgepole pine.

Portions (~42%) of the Entiako study area (~10,340 km^2) were within two provincial parks (Tweedsmuir Provincial Park and Entiako Provincial Park) where minimal forest harvesting and road building occurred; the remaining area was available for commercial forest harvesting activities, resulting in an average road density across the whole study area of 0.6 km•km^{-2}. Elevations ranged from 850 – 1900 m ASL. Vegetation was primarily lodgepole pine on the upper plateaus with mixed forests occurring in drainages. A wildfire (~1,330 km^2) burned ~13 % of the study area, primarily dead pine trees in 2014.

The Big Creek study area (almost 7,300 km^2) encompassed portions of Big Creek Provincial Park and Ts’yl-os Provincial Park in the southern extents, whereas the northern extents contained forest harvesting, range land, and agricultural operations. Average road density across the study area was 1.2 km•km^{-2}. Elevations ranged from 1100 – 2450 m ASL, including high-elevation swamps, where the climate is arid and regeneration in cutblocks is slow. The study area was primarily coniferous forests with moderate levels of forest harvesting activities; however, the southern portions included meadow and wetland complexes with preferred herbaceous forage species for moose (B. Cadsand, pers. comm.).

The original Provincial study design (see Kuzyk and Heard 2014) covered a range of intensities of MPB salvage logging, but the three study areas differed in many additional ways (e.g., topography, main causes of mortality, hunting pressure, etc.). Therefore, our analyses were done separately for each study area to avoid concluding the main effects were study area and to allow us to better examine more subtle differences among study areas that could not be adequately addressed with additional covariates.

Seasonal movements and home-range calculation

Location points of female moose were divided into five biologically relevant seasons (Table 2.2) adapted from Gillingham and Parker (2008*a*), trends observed in the three study areas, and from local and expert knowledge. Individual, consecutive (no missed fixes) daily movement distances were calculated for each season-study area combination to determine if movement distances differed by season and study area.

We constructed individual seasonal HRs by buffering location points (Arthur et al. 1996, Walker et al. 2007). To build individual seasonal HRs, a minimum of 30 locations for each season was required (Seaman et al. 1999) because of lower than expected fix rates (Table 2.1). In addition, using a minimum of 30 locations for home-range selection models minimized the effects of fix bias on HR estimates because missed fixes were unlikely to consistently be outside the area covered by existing points. To increase number of fixes,

Table 2.2. Seasons defined by date for analysis of home-range selection and movements of female moose in central British Columbia.

Season	Date Range	Number of Days
Late Winter	Jan 15 – Apr 25	101
Calving	Apr 26 – Jun 20	56
Summer	June 21 – Sept 12	84
Fall	Sept 13 – Nov 20	69
Early Winter	Nov 21 – Jan 14	55

collars were directly downloaded whenever collars could be recovered (i.e., if an animal died or slipped its collar during the study; see Appendix A). We undertook several initial steps to determine an appropriate buffer size for home-range estimates. Preliminary work using Gillingham and Parker's (2008a) method of buffering location points by the 95th longest seasonal daily movement resulted in large non-biologically relevant HRs for our study — Gillingham and Parker's (2008a) study used more daily fixes (*n* = 4). We did, however, have both ATS (four fixes a day) and Vectronic (one fix per day) collars deployed in the Entiako study area. Therefore, we examined individual, seasonal HRs for ATS-collared moose with potentially four times more fixes per day using the 95th longest (animal-specific) seasonal movement and then examined what centile was needed to get comparable animal-specific home ranges using only one fix per day. We determined that the 70th longest seasonal consecutive movement had the fewest outliers — therefore, we used a 70th-centile buffer on each location point in all our subsequent analyses for consistency across collar types.

Each buffered HR represents the maximum area an individual female moose would likely use during a season, excluding rare excursions between consecutive GPS locations (Gillingham and Parker 2008*b*). With individual-specific seasonal HRs calculated, we then created circular replicates (i.e., available HRs) of the same area for each used seasonal HR (*n* = 5), randomly distributed on the landscape. Each random HR was constrained to be 2 – 5 radii from the centroid of the used HR to avoid substantial overlap between individual used and available HRs. Used and available HRs were then compared (see below) to assess selection among vegetation cover classes and road densities by individual moose for each study area and season. For comparison with other studies, we also constructed seasonal 100% minimum convex polygon (MCP) HRs (Eddy 1977) for each animal.

Due to lower than anticipated fix rates (Table 2.1), we were concerned about bias associated with missed fixes (Frair et al. 2004, 2010). Using location data downloaded directly from recovered collars (e.g., moose that died during the study), we examined whether our estimates of vegetation cover were biased by the missing fixes. We regressed the proportion of vegetation cover (by animal) from the downloaded data on the proportion of used locations from the upload (satellite) data. We concluded that while there were differences between uploads and direct downloads, vegetation cover appeared to affect the satellite uploading of collar data and not the acquisition of GPS locations by the collar, and we observed that there was a ~15 % chance of missing fixes in any given cover class (Appendix B). Although we do not believe that our data are biased with respect to vegetation cover, we have no way of assessing potential bias with continuous 'distance-to' parameters.

Spatial data

We obtained forest-cover information (Vegetation Resource Inventory,VRI, veg_comp_lyr_r1_poly) and data for wetlands (fwa_wetlands_poly), lakes (fwa_lakes_poly), roads (dra_digital_road_atlas_line_sp, abr_road_section_line, resultsroads, ften_road_section_lines_svw, trim_transportation_lines, og_petrlm_dev_rds_pre06_pub_sp, og_petrlm_dev_roads_pub_sp, og_petrlm_access_roads_pub_sp), wildfires (prot_historical_fire_polys_sp) and cutblocks (rslt_opening_svw) from 1:20,000 map sheets (DataBC Distribution Service 2015). An additional VRI layer from TFL52 (South-East portion of PG South) was generously provided by West Fraser Mills (Quesnel, BC). The most recent VRI layer used was from 2016, and the most current wetland, lake, road, wildfire, and cutblock layers were from 2015. A non-overlapping map sheet was generated in ArcGIS 10.2.2 (ESRI Corp. 2014) by year to accommodate changes in landcover from logging and wildfire activity over study years; seasonal HRs were queried with their respective year of spatial vegetation cover classes. With this technique, all seasonal HRs for 2014 were queried on a spatial map without the disturbance that occurred after 2014; the 2015 and 2016 seasonal HRs were queried with all changes to the vegetation cover map.

We then used broad categories to designate forest types by leading species and age (hereafter "vegetation cover classes"; Table 2.3) to intersect with used and available HRs in ArcGIS 10.2.2 (ESRI Corp. 2014). These leading species cover classes represent our best assessment of how moose might utilize areas differentially. Coniferous species were separated into 'Conifer' and 'Pine' to test the hypothesis that a reduced canopy cover may differ between the leading species following the MPB, as both classes should represent concealment cover throughout the year with reduced browse prior to MPB. Generally, pine beetles did not kill all stems in a stand but rather stems >30 years old. Therefore, as of 2015, Pine could represent trees aged 1 – 45 years old, but because of the included dead stems, uncut stands typically had a reduced canopy closure and potentially greater browse that Conifer. Deciduous cover represents high-biomass browse areas, although cover may be greatly reduced from the summer to the winter due to leaf senescence. Wetted classes include all annually permanent wet areas (riparian areas, emergent and submergent vegetation, and open water) and indicate a potential forage source for moose year-round, although submergent vegetation would only be accessible during the frost-free season. New Cuts and Old Cuts are representative of early seral vegetation and potentially high foraging potential, but also represent risky areas due to road proximities and openness/visibility (primarily for New Cuts). Although New Cuts and Old Cuts could be selected by moose, we used density calculations for 2nd-order selection models to represent selection or avoidance

Table 2.3. Vegetation cover class, anthropogenic, and habitat richness variables used in analysis of home-range (2nd-order) selection by female moose in central British Columbia. Note: leading forests stands were categorized as ≥50% leading at the time of analysis.

Variables		
C	Conifer	All coniferous-leading forest stands except for *Pinus* spp.
P	Pine	All *Pinus* spp.-leading forest stands
D	Deciduous	All deciduous-leading forest stands. Includes tall shrub-leading
W	Wetted	All water features and annually permanent wet areas
NC	New Cut	All areas logged since the year 2000
OC	Old Cut	All areas logged between 1975 – 2000
FP	Pine Fire	Wildfires since the year 2000 in *Pinus* spp.-leading forest stands
FO	Other Fire	Wildfires since the year 2000 in any species-leading forest stand except for *Pinus* spp.
OF	Old Fire	All wildfires between 1975 – 2000 in any forest stand
RD	Road Density	Length of road divided by area (km•km^{-2})
Hab. Rich.	Habitat Richness	Number of distinct vegetation cover classes except for Road Density and Mature Forest
MF	Mature Forest (C+P+D)	The addition of three vegetation cover classes representing older seral stages of Conifer, Pine, and Deciduous

from what was available on the landscape. Fire classes represent potential high-value habitat to moose because forage regeneration, forest structure complexity, and reduced human access (compared to cutblocks). Fires were separated by the year 2000 to represent a contrast between natural and anthropogenic seral advancement. Pine Fires were separated from Other Fires because ground-truthing areas where MPB-burned stands existed had a much hotter fire, leaving primarily exposed mineral soil, and therefore a stark difference between seral stages within the two vegetation cover classes.

We calculated the proportions of area within each HR for all cover classes and road density. We described habitat richness as the number of vegetation cover classes (proportion ≥0.01) within a given HR. Although the age of cutblocks and fires increased throughout the study, the vegetation cover classes remained the same if they occurred before or after the year 2000 because we were interested in the effects and differences post MPB, not necessarily the exact age of cutblocks that moose selected (see Chapter 3).

Use and availability

We used seasonal HRs instead of annual HRs to address home-range selection because we believe that seasonal limiting factors are important, and moose select seasonally different habitats. One of the potential challenges with interpreting selection (or avoidance) with resource selection models is that abundant resources frequently used by an individual may be ‘avoided’ (because that resource is used less than its abundance), and rare resources may be highly selected even though that resource is encountered very infrequently. Consequently, selection and avoidance of resources need to be placed in the context of actual use and availability (Stewart et al. 2002). Therefore, for descriptive purposes only, we examined the seasonal, relative use and availability of vegetation cover classes and road density — no statistical analyses were used to compare use and availability, per se, because resource selection models were used for that purpose. To examine relative use and availability, we calculated the proportion of use and availability of vegetation cover classes and road density within each individual's used and available (average of the five random HRs) seasonal HR area. We then averaged across individuals, study area and season to compare use and availability seasonally.

Statistical analysis

To test both the landscape-change hypothesis as well as to examine potential limiting factors for seasonal HRs of female moose (i.e., 2nd-order selection), we developed 12 *a priori* competing models (Table 2.4). Those models were based on avoidance of factors related to perceived risk (Anthropogenic, Accessibility, Access, Openness, Vulnerability), forage potential (Water and Natural Browse, Water and All Browse, Water), or a combination of both reduced risk and increased forage (Water Browse and Pine, Water Browse and Conifer); specific hypotheses associated with each candidate model are presented in Table 2.4.

We assessed competing models using an Information Theoretic framework (Burnham and Anderson 2002). Each competing model was fit with case-matched logistic regression using clogit in Stata 14 (StataCorp 2015) such that attributes from individual seasonal HRs compared to that animal's corresponding available HRs. Each study area (n = 3) and season (n = 5) combination had separate model sets (n = 15 model sets for each competing model) so that we could examine differences among areas and time of year while addressing differences among study areas that could not be accounted for in the models. Competing models were ranked using Akaike's Information Criterion (Akaike 1973) corrected (AIC_c) for small sample sizes (Burnham and Anderson 2002). To prevent collinearity and avoid

Table 2.4. Competing models used for analyzing selection of home ranges (HR) during five seasons by female moose with case-matched logistic regression (clogit in Stata 14) in three study areas within central British Columbia. See Table 2.3 for variable descriptions.

Model Name	Model Structure	Hypothesis
Anthropogenic Disturbance	NC + RD + Hab. Rich.	Moose avoid recent disturbance and high road densities due to stress factors and utilize more cover classes than what is available on the landscape.
Accessibility	NC + FP + FO + RD	Moose avoid recent disturbance due to stress factors and low amount of cover.
Openness	NC + OC + FP	Moose avoid harvested lands and pine fires at the home-range scale.
Access	RD	Access negatively affects HR selection due to vehicles, and predator travel corridors.
Vulnerability	MF + RD	Moose select for "mature" forest with limited access to reduce vulnerability of harvest and predation.
Habitat Richness	Hab. Rich.	Selection of habitat richness is an indication of less common cover classes being utilized, and the need for a diverse landscape.
Water and Natural Browse	W + D + FO + OF	Moose select for the greatest quantity of natural browse instead of anthropogenic additive browse.
Water and All Browse	W + D + NC + OC + FO + OF	All major browse categories imply food as an approximate driving factor for HR selection.
Water	W	Water and browse provided within the riparian area are intrinsically linked to moose, especially in warm seasons.
Water, browse, and pine	W + D + P	Dead standing pine still retains horizontal and vertical cover to be selected as cover.
Water, browse, and conifer	W + D + C	Natural browse and cover provide food, water, and shelter.
Saturated	C + P + D + W + NC + OC + FP + FO+ OF + RD + Hab. Rich.	Saturated/ Full model.

inflated coefficients, covariates were not included in the same model if tolerance scores were >0.20 (Menard 2002). Supported models had the lowest AIC_c, or were within a ΔAIC_c of 2 from the top (lowest AIC_c) model (Burnham and Anderson 2002). Individual models within a ΔAIC_c of the best model were excluded if the model contained uninformed parameters — parameters that did not explain sufficient additional variation to justify including the model in a top model set (Burnham and Anderson 2002, Arnold 2010). Akaike's weights (w_i) were calculated for interpretation as the conditional probabilities for each model.

Using an Information Theoretic framework to rank candidate models always identifies the 'best' model, but it doesn't determine how good the best model is (see Mac Nally et al. 2018). There are several ways of assessing model fit depending on the way data were collected. The area under the receiver-operating characteristic curve (ROC; DeLeo 1993) is a preferred measure used to assess the predictive accuracy of logistic models, when presence and true absence data are available (Fielding and Bell 1997, Pearce and Ferrier 2000). In our case, we know that random home ranges were not used by the same animal in the same season, but they could have been used by other moose, thus confusing true presence and absence. Resultant ROC values between 0.5 – 0.7 are considered to have low discrimination ability, 0.7 – 0.9 are considered to be good, and >0.9 have excellent discrimination ability (Manel et al. 2001).

When there is the potential for 'cross-contamination' between presence (used) and absence (available), k-fold partitioning (Boyce et al. 2002) is appropriate for determining model fit. In our case-matched design (a used home range is paired with the random available home ranges), the k-fold approach holds back a 5th of the animals, and predicts the values for those animals from the rest of the data. After the process is repeated five times (each with a 5th of the animals), a Spearman's rank correlation coefficient (r_s) is calculated between the ranks of the observed and fitted model predictions based on 10 bins of data. Models with significant r_s values ($r_{s\_critical,\ 10} = 0.648$, Zar 1999) are considered valid models. Because of potential issues with separating true presence from absence data, and for consistency with Chapter 3, we used both ROC and k-fold measures for all top models. The ROC values estimate how well all the data predict the result, while the k-fold tests suggest how consistent the results are across animals.

Because k-fold results for seasonal home-range models suggested that selection was highly variable among individual moose, we assessed seasonal HR site fidelity within individual moose for which we had data for three consecutive years for each season. For those animals, we determined the area overlap between consecutive years (e.g., proportion of the 2015 HR that was also covered by the 2014 HR). For each animal and year, we then divided the amount of area overlapped by the previous year's (same season) HR and then divided that area by the size of the following year's HR. The two-consecutive individual seasonal overlapping HR's were averaged, and this value was used as a measure of home-range site fidelity.

RESULTS

Home-range size

We used data from 51, 58, and 48 female moose in Entiako, Big Creek and PG South study areas, respectively (Table 2.1). The sizes of seasonal HRs for collared female moose showed similar trends across study areas: smallest in Late Winter and largest during the Summer (Figure 2.2). On average, Big Creek consistently had the largest HRs, and PG South had the smallest, with the exceptions being Late Winter and Calving. The same trend

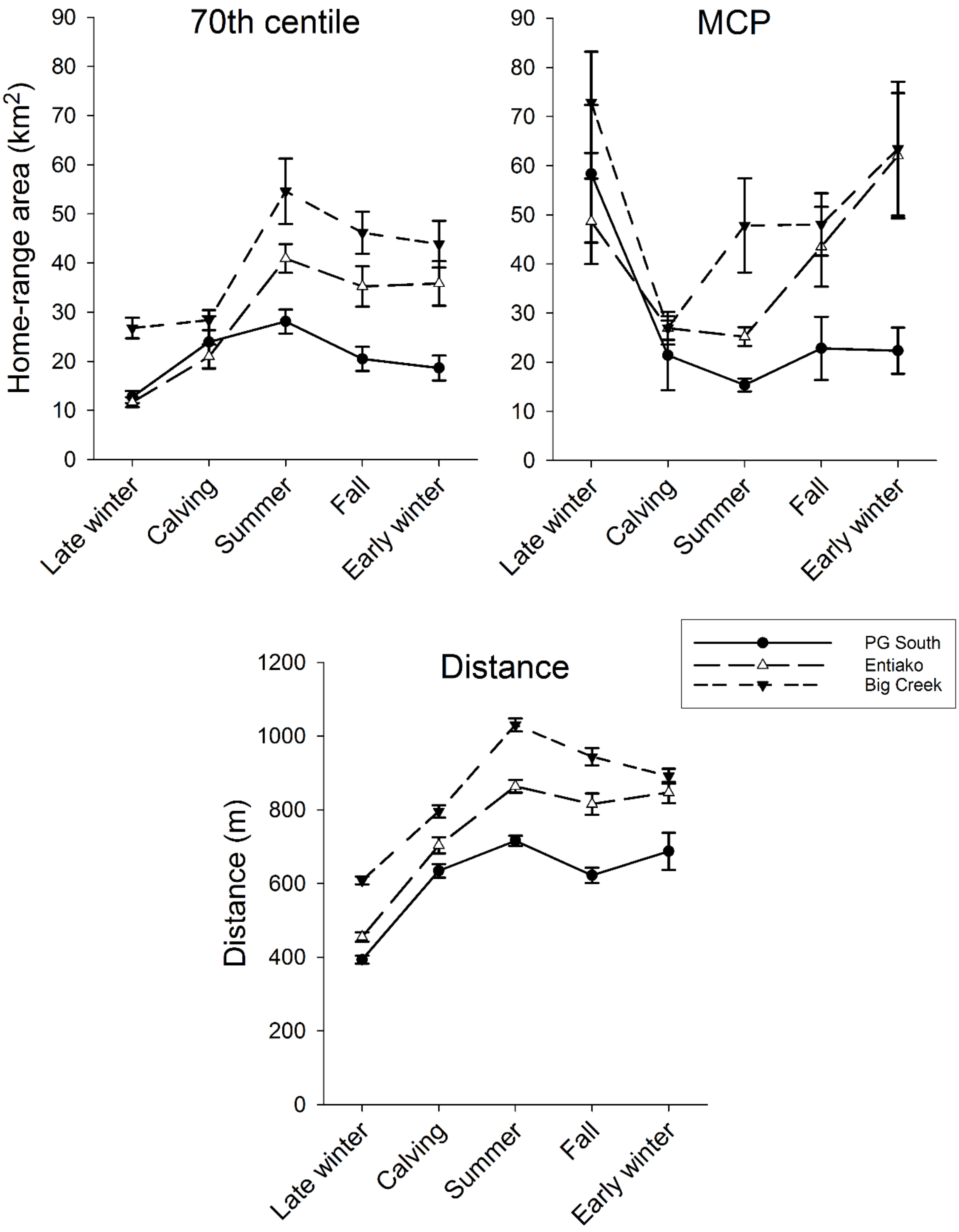

Figure 2.2. Comparison of home-range size ($\bar{x}$ and SE) for collared female moose using two methods (70th centile and 100% minimum convex polygon [MCP]), along with daily distances moved by collared female moose (based on consecutive days) by study area and season in central British Columbia.

with regards to seasonality and study area was observed with consecutive daily movement distances (Figure 2.2), which is expected because the 70th longest seasonal daily distance was used to construct HRs. Using the buffered HR method, the smallest individual seasonal HR was 0.4 km^2 in PG South during Calving, and the largest was 678.1 km^2 in Big Creek during Summer. Minimum convex polygon HRs had similar study area differences, although they did not follow the same trend by season (Figure 2.2). Early and Late Winter had the largest seasonal HRs (100% MCP), except for PG South in Early Winter when it was comparable in size to the 70th centile-buffered HRs. In Calving and Fall, HRs were similar in size using both methods, whereas the 70th centile-buffered HRs were slightly larger during the Summer than the 100% MCP's. The smallest individual seasonal 100% MCP was 0.8 km^2 in Entiako during Early Winter and the largest was 963.7 km^2 in Big Creek during Summer. Interestingly, HR sizes estimated by MCP and by the 70th centile buffers were not correlated when comparing mean HR sizes by both HR estimators for study area and season ($r = 0.219$, df = 13, $P = 0.433$).

Home-range size for collared female moose was correlated with proportion of cutblocks in only one of the 15 study area-season combinations (Big Creek during Calving ($r = 0.353$, df = 116, $P < 0.001$)). Road density and HR size were significantly correlated in three of 15 study area-season combinations, but both positive and negative correlations occurred (Appendix C).

Use and availability

Attributes within seasonal HRs used by collared female moose were variable among study areas, but similarities also existed across study areas (Figures 2.3 – 2.5). Mature forest cover (generally mostly Pine) made up the highest proportion of vegetation in HRs for all

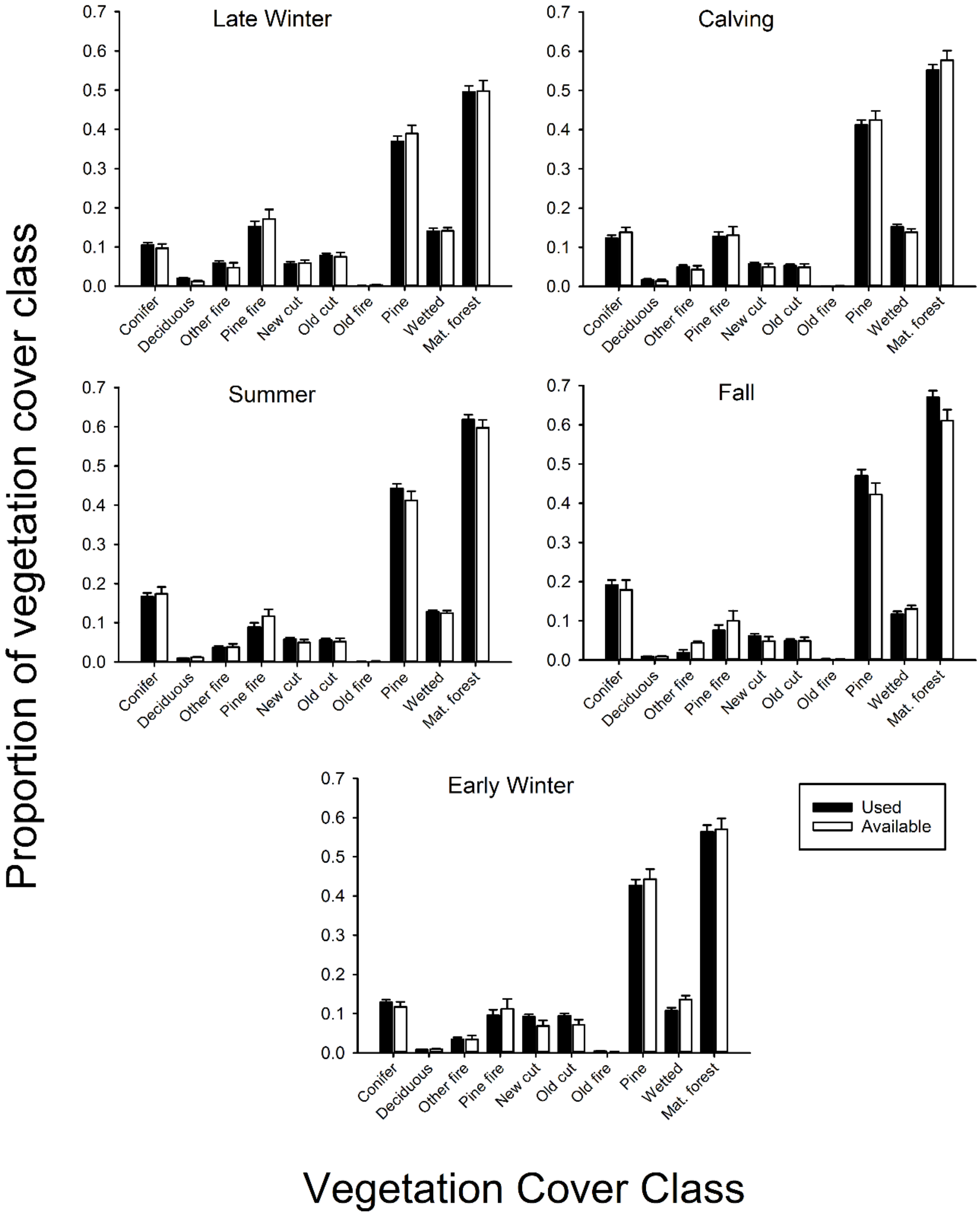

Figure 2.3. Vegetation cover classes used by and available to ($\bar{x}$ + SE) GPS-collared female moose in home ranges in Entiako study area in British Columbia between January 15 – September 12, 2016 during five seasons. Mat. Forest includes Conifer, Pine, and Deciduous.

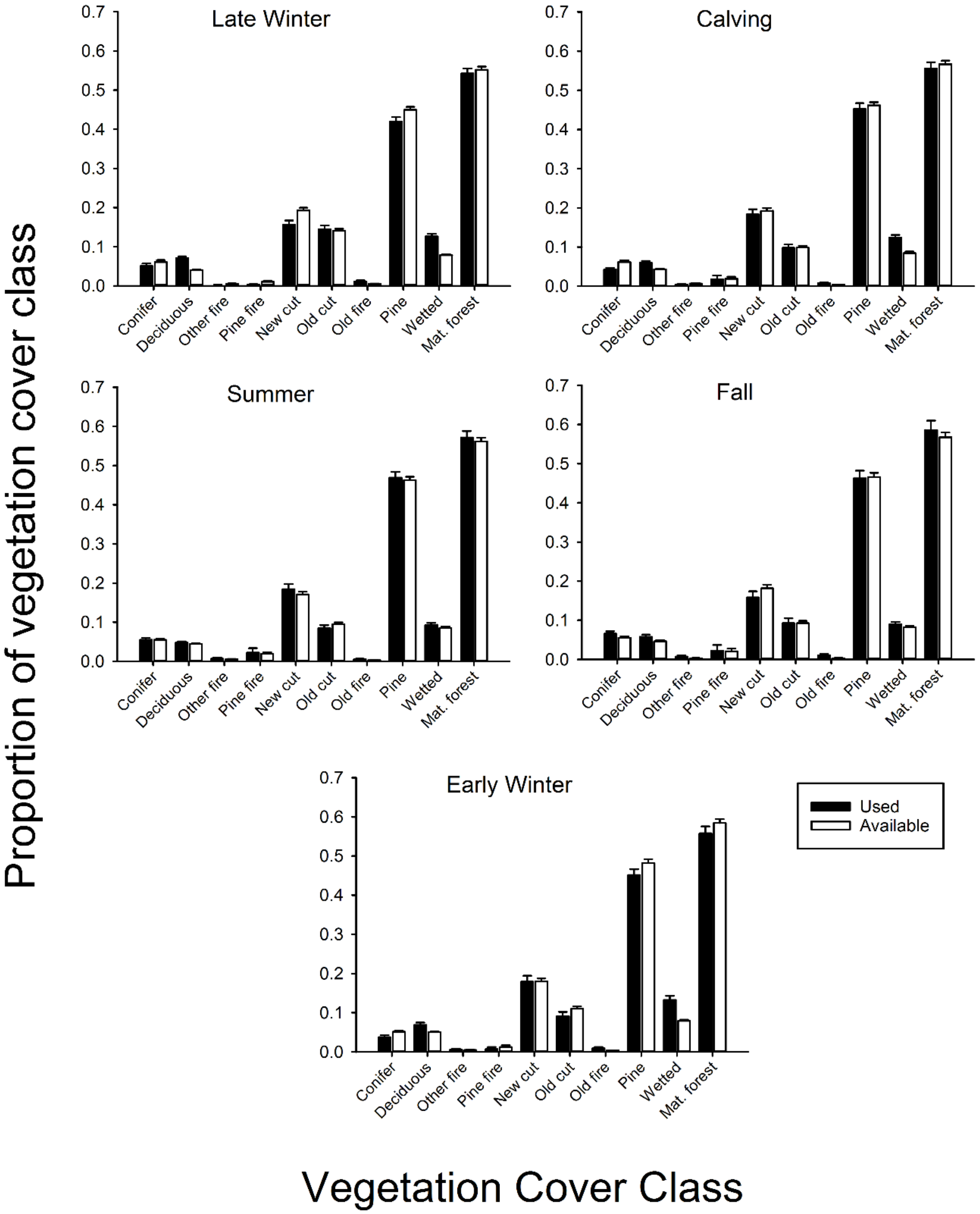

Figure 2.4. Vegetation cover classes used by and available to ($\bar{x}$ + SE) GPS-collared female moose in home ranges in Big Creek study area in British Columbia between January 15 – September 12, 2016 during five seasons. Mat. Forest includes Conifer, Pine, and Deciduous.

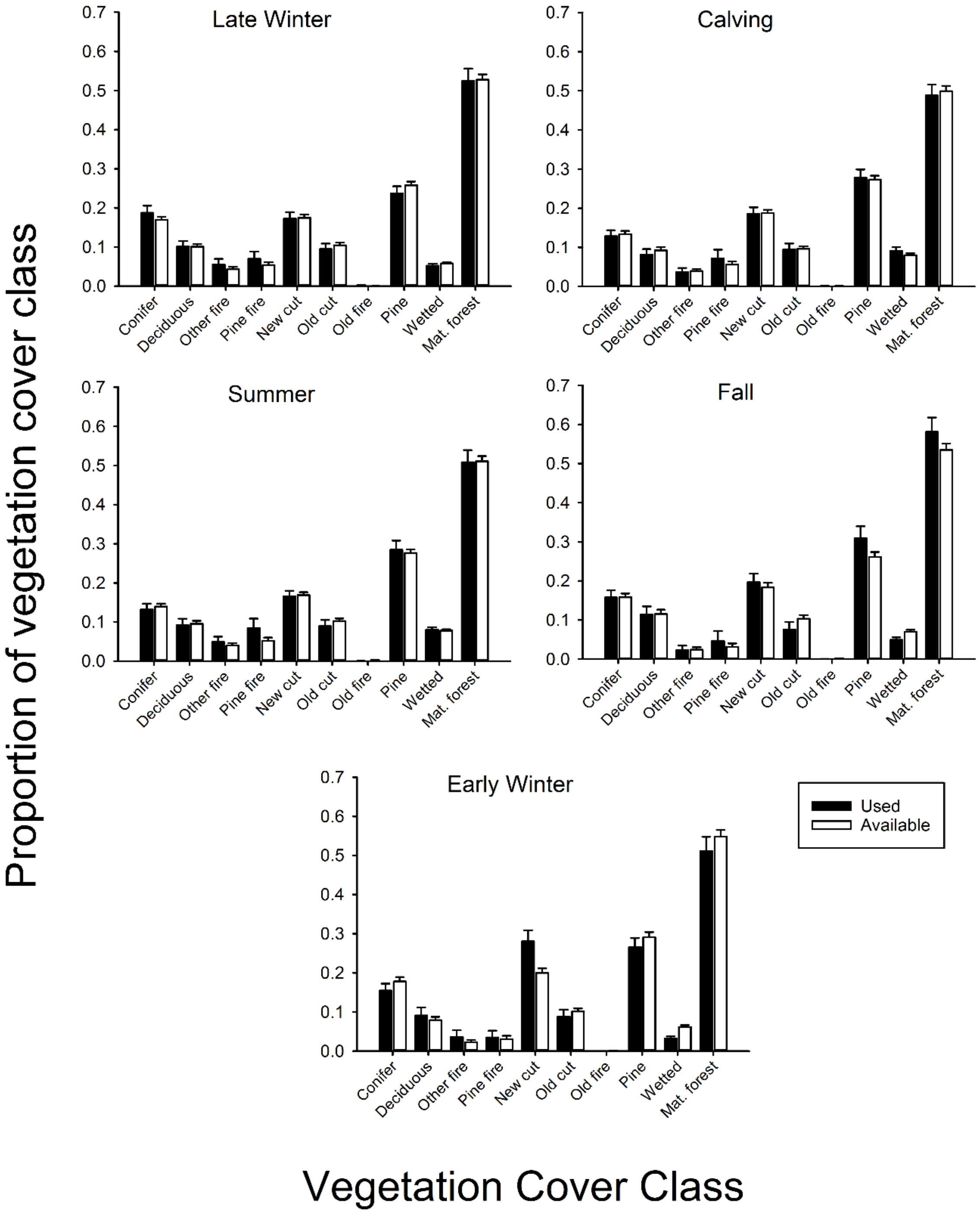

Figure 2.5. Vegetation cover classes used by and available to ($\bar{x}$ + SE) GPS-collared female moose in home ranges in PG South study area in British Columbia between January 15 – September 12, 2016 during five seasons. Mat. Forest includes Conifer, Pine, and Deciduous.

seasons in each study area. No vegetation cover class was completely absent in used HRs in any study area.

In Entiako (Figure 2.3), the Pine cover class was the predominant vegetation in HRs used by collared moose during all seasons, and it was also the most prevalent individual species-leading cover class available (Mature forest includes Conifer, Pine, and Deciduous). Pine Fires occurred at lower proportions in used HRs than available HRs in all seasons. The greatest proportion of Mature Forest cover in HRs occurred in the Fall, and the least was in Late Winter (Figure 2.3).

In Big Creek (Figure 2.4), Pine cover within HRs occurred in higher proportions than any other cover class, making up nearly 50%, followed by New Cutblocks (16 – 18%), in all seasons. Collared moose used the Wetted cover class more than available during Late Winter, Calving, and Early Winter (Figure 2.4).

Use of vegetation cover classes by collared moose in the PG South (Figure 2.5) did not have the same trend in use as Entiako or Big Creek. Pine comprised the highest proportion of vegetation cover in HRs in all seasons except for Early winter, when the proportion of New Cutblocks was greater than Pine, and much greater than what was available. The Conifer cover class was the third most used and available cover class (Figure 2.5).

Road density was variable across the three study areas depending on degree of forest harvesting and was not distributed consistently within each study area. Entiako had the lowest road density, and moose used HRs with higher road densities than what was available. Collared moose in Big Creek used areas with lower road density for their HRs in all seasons.

Collared moose in PG South area also used lower road densities than what was available, except during Early Winter.

Home-range selection

Selection of HRs by collared female moose differed by study area and season (Table 2.5). Within the Entiako study area, the Habitat Richness model was the most parsimonious model during Late Winter, Calving, and Summer (Table 2.6) when female moose selected to have more distinct vegetation cover classes within their HRs (Appendix D) than what was available on the landscape. Anthropogenic Disturbance and the Saturated models were both supported during Fall (Table 2.6), and New Cutblocks and Habitat Richness were selected in both models (Appendix D). Anthropogenic Disturbance and Saturated models also were supported during Early Winter (Table 2.6) — in those models there was selection by collared moose for New Cutblocks and Habitat Richness, and avoidance of high road density (Appendix D).

In Big Creek, the most parsimonious model during both Late Winter and Calving was the Saturated model (Table 2.6), in which female moose selected Habitat Richness and parameters associated with cover in areas with high road abundance (Appendix D). Anthropogenic Disturbance and Habitat Richness models were supported during the Summer (Table 2.6) when moose were selecting for New Cutblocks and Habitat Richness while avoiding high road density (Appendix C). The Saturated and Water and Natural Browse models were both supported during the Fall (Table 2.6) when moose appeared to select for Old Fires, New Cutblocks and Habitat Richness (Appendix D). The Water and All Browse and the Saturated models were both supported during Early Winter (Table 2.6) when high-

Table 2.5. Visual representation of supported models in home-range selection by female moose during five seasons (LW: Late Winter, C: Calving, S: Summer, F: Fall, EW: Early Winter) in three study areas in central British Columbia using case-matched logistic regression.

Model Name	Entiako					Big Creek					PG South				
	LW	C	S	F	EW	LW	C	S	F	EW	LW	C	S	F	EW
Anthropogenic				x	x			x			x				
Accessibility												x	x		
Openness															
Access												x	x	x	
Vulnerability												x	x		
Habitat Richness	x	x	x		x			x			x	x			
Water & Natural Browse									x						
Water & All Browse										x					x
Water												x			
Water, Browse, Pine															
Water, Browse, Conifer															
Saturated				x		x	x		x	x	x			x	

Table 2.6. Supported models for home-range selection by female moose in three study areas during five seasons (LW: Late Winter, C: Calving, S: Summer, F: Fall, EW: Early Winter) in central British Columbia using case-matched logistic regression indicating the chi squared goodness of fit test statistic (P), the log likelihood (LL), number of parameters (k), number of home ranges (n), Akaike information Criterion corrected for small sample size (AIC_c), change in AIC from top model ($\Delta\text{AIC}_\text{c}$), Akaike weight ($w_\text{i}$), the average k-fold returned from all iterations ($n = 5$), the maximum k-fold returned (to show variability in k-folds), and area under the receiver-operating characteristic curve (ROC). Variables and Models are described in Tables 2.3 and 2.4.

Season	Model	Study Area	P	LL	k	n	AIC_c	$\Delta\text{AIC}_\text{c}$	w_i	Avg. k-fold	Max. k-fold	ROC
LW	Hab. Rich.	Entiako	<0.001	-131.89	1	546	265.78	–	0.83	-0.20	0.06	0.63
	Saturated	Big Creek	<0.001	-132.02	11	756	286.34	–	1.00	0.52	0.76	0.61
	Hab. Rich.	PG South	<0.001	-132.82	1	480	267.64	–	0.50	0.20	0.40	0.64
	Saturated	PG South	<0.001	-123.05	11	480	268.57	0.93	0.31	0.31	0.73	0.60
	NC+RD+Hab. Rich.[a]	PG South	<0.001	-131.79	3	480	269.61	1.97	0.19	0.27	0.81	0.64
C	Hab. Rich.	Entiako	<0.001	-148.71	1	570	299.43	–	0.85	-0.13	0.53	0.64
	Saturated	Big Creek	<0.001	-178.72	11	708	379.75	–	0.91	0.46	0.79	0.62
	RD	PG South	0.13	-120.68	1	408	243.37	–	0.25	0.04	0.53	0.50
	MF+RD [b]	PG South	0.13	-119.79	2	408	243.59	0.22	0.23	0.01	0.54	0.52
	W	PG South	0.26	-121.19	1	408	244.39	1.02	0.15	0.09	0.44	0.58
	Hab. Rich.	PG South	0.29	-121.27	1	408	244.54	1.17	0.14	0.20	0.38	0.63
S	Hab. Rich.	Entiako	0.01	-162.88	1	558	327.75	–	0.67	-0.03	0.19	0.63
	NC+RD+Hab. Rich.[a]	Big Creek	0.01	-185.44	3	642	376.90	–	0.45	0.20	0.74	0.63
	Hab. Rich.	Big Creek	0.01	-188.22	1	642	378.44	1.54	0.21	-0.37	0.04	0.63
	NC+RD+FP+FO [c]	PG South	0.02	-112.43	4	396	232.92	–	0.31	0.18	0.83	0.51
	RD	PG South	0.02	-115.61	1	396	233.23	0.30	0.27	0.10	0.75	0.50
	MF+RD [b]	PG South	0.03	-114.78	2	396	233.57	0.65	0.22	0.00	0.85	0.51

Table 2.6. Continued.

Season	Model	Study Area	P	LL	k	n	AIC$_c$	ΔAIC$_c$	w_i	Avg. k-fold	Max. k-fold	ROC
F	NC+RD+Hab. Rich.[a]	Entiako	<0.001	-85.73	3	312	177.50	–	0.45	0.41	0.60	0.60
	Saturated	Entiako	<0.001	-77.58	11	312	177.89	0.39	0.37	0.18	0.89	0.55
	Saturated	Big Creek	<0.001	-99.32	11	402	221.20	–	0.46	0.37	0.85	0.62
	W+D+FO+OF [d]	Big Creek	<0.001	-106.67	4	402	221.39	0.19	0.42	0.36	0.71	0.57
	Saturated	PG South	<0.001	-48.46	11	210	120.04	–	0.34	0.44	0.65	0.49
	RD	PG South	0.01	-59.59	1	210	121.18	1.15	0.19	0.06	0.74	0.50
EW	NC+RD+Hab. Rich.[a]	Entiako	<0.001	-82.68	3	330	171.41	–	0.59	0.14	0.87	0.61
	Hab. Rich.	Entiako	<0.001	-85.23	1	330	172.45	1.04	0.35	0.07	0.44	0.64
	W+D+NC+OC+FO+OF [e]	Big Creek	<0.001	-99.48	6	432	211.11	–	0.53	0.34	0.77	0.59
	Saturated	Big Creek	<0.001	-95.02	11	432	212.56	1.45	0.26	0.40	0.69	0.62
	W+D+NC+OC+FO+OF [e]	PG South	<0.001	-56.92	6	240	126.11	–	0.79	0.45	0.79	0.44

[a] Anthropogenic Disturbance model
[b] Vulnerability model
[c] Access model
[d] Water and Natural Browse model
[e] Water and All Browse model

biomass browse cover classes and Habitat Richness were selected while avoiding high road density areas (Appendix D).

Female moose in the PG South study area showed the most variability in selection models across seasons. During Late Winter, they selected for Habitat Richness and New Cutblocks, and avoided high density road areas (Appendix D) as supported by Anthropogenic, Habitat Richness, and Saturated models (Table 2.6). Avoiding high road density and selecting mature forests and Wetted areas were important during the Calving season. During the Summer, female moose avoided high road density and Mature Forests, and selected for New Cutblocks and Pine Fires in their HRs compared to the available landscape (Appendix D). Saturated and Access models were both supported during the Fall (Table 2.6) when high road densities were avoided, and Habitat Richness, high vegetation cover, and areas with high browse biomass potential were all selected. During Early Winter, high-biomass herbaceous browse was selected, whereas Wetted areas and Old Fires were avoided (Appendix D).

The Habitat Richness parameter was important in HR selection by collared female moose and had a strong positive relationship for many of the study area-season combinations (Appendix D) when it appeared in supported models. Therefore, we looked at habitat selection as a distribution from used and available cover classes in all HRs. In all study area-season combinations (except for PG South in Summer), HRs of female moose contained greater numbers of distinct vegetation cover classes than what was available to them. Habitat Richness was also positively correlated with HR size in eight of 15 study area-season combinations (Appendix C). Because of the strong support for this parameter, we tested to see if there was a single vegetation cover class present on the landscape that showed up only in an individual's home-range and was not present in any of the five available home ranges. No cover class was present in used HRs and absent in available HRs in all study area-season combinations, although some were evident within study areas (Table 2.7). Deciduous stands were rare cover classes in HRs and were not present in available HRs in Entiako. The three fire classes, (i.e., Pine Fires, Other Fires, and Old Fires) occurred in used HRs, but were not available to all individuals in Entiako and Big Creek HRs more frequently than any other cover class (see Appendix D).

Model validation using k-folds suggested that there was high variation among individuals or within year (Table 2.6). For some iterations of the k-fold, model fit appeared good (max r_s values ≥0.70 in Table 2.6) indicating that for some groups of individuals the model fit quite well, but generally models had a poor fit (Table 2.6). The average r_s returned for all k-folds was unsatisfactory (df = 9, $\alpha = 0.05$, critical threshold $r_s = 0.648$). Results from ROC scores indicate low (0.5 – 0.7) or poor (<0.5) predictive accuracy (Manel et al. 2001) for all supported models (Table 2.6). Because a subset for the k-folds held back individual moose HRs and the corresponding random areas, our interpretation is that there was considerable variability among moose in their home-range selection. Although these results represent our best descriptions for moose HR selection in general, individual moose appeared to select HRs quite differently.

Individual HR fidelity could be tested only on a sample of the study animals due to some only being present for part of the study or unsatisfactory collar transmissions during some seasons. For those animals that lived for the entire study and had enough location data for us to estimate seasonal HRs, Late Winter showed the least amount of home-range fidelity,

Table 2.7. Number of individual seasonal home ranges (HR) of female moose for which the vegetation cover class was present (≥1% HR area) and which was not present in any of the associated five available home ranges in three study areas in central British Columbia. Seasons were Late Winter (LW), Calving (C), Summer (S), Fall (F), and Early Winter (EW). Cover classes defined in Table 2.3.

Cover	Entiako					Big Creek					PG South				
Class	LW	C	S	F	EW	LW	C	S	F	EW	LW	C	S	F	EW
Conifer	3	1	2	1	1	0	0	0	0	1	0	0	0	0	0
Deciduous	10	8	8	2	2	3	2	0	0	0	0	1	1	0	0
Other Fire	2	4	1	2	2	4	2	2	1	2	6	1	0	0	0
Pine Fire	4	3	1	2	1	4	2	2	1	2	3	1	0	0	0
New Cut	0	4	4	3	0	1	1	0	0	0	0	0	0	0	1
Old Cut	1	1	3	0	0	1	1	1	0	0	0	2	1	0	0
Old Fire	0	0	2	2	1	8	5	8	3	3	0	2	0	0	0
Pine	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Wetted	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

and Summer had the most (Table 2.8). Although collared female moose had overlapping seasonal HRs year after year, they did not completely overlap (Table 2.8). There may be an inherent bias to this method of defining HR fidelity — if the following consecutive year is much larger than the previous, the HR fidelity output could be greater than realized.

DISCUSSION

Because selection is hierarchical (Johnson 1980), course-scale habitat selection is expected to influence the most important limiting factors. We tested whether HR selection by female moose varied depending on the degree of salvage logging in central BC as expected with the landscape-change hypothesis. Contrary to our expectations, daily movements and HR sizes of female moose were lowest in the study area with the greatest proportion of new cutblocks. Home ranges included mature forest cover (primarily Pine) more than any other vegetation cover class and avoided the highest proportion of disturbance on the landscape. Avoidance of New Cutblocks as the proportion of clearings on the landscape increased did not occur as we expected. Collared female moose, however, did avoid the highest level of disturbance and selected for heterogenous HRs. In addition, female moose showed a wide variety of individual variation within the three study areas, and between seasons. Areas with the highest road densities were avoided in certain seasons among study areas, likely due to the lack of adequate cover. Home-range selection by female moose in central BC is presumably influenced by a trade-off between escapement cover for temperature and predator avoidance and feeding areas with high biomass potential.

Home range and movements

Home-range estimates can vary widely depending on the technique used to estimate them (Boulanger and White 1990, Powell 2000). Different HR estimators may have

Table 2.8. Seasonal home-range fidelity for female moose with three consecutive seasonal home-ranges for Late Winter (LW), Calving (C), and Summer (S) in central British Columbia.

Season	*n*	Fidelity (%)	SE	Min	Max
LW	18	41.1	8.86	8.8	100
C	18	50.9	9.95	12.3	96.7
S	18	60.7	8.17	4.3	92.5

provided smaller or larger estimates, but our technique (Gillingham and Parker 2008*b*) was most appropriate to examine individual moose differences, whereas the MCP estimators were useful for comparisons to existing literature. Movement rates and seasonal HR size differed by study area, but they did not correspond to the proportion of forest harvesting in each study area (correlations between HR size and proportion of cutblocks were significant in only one of 15 study area-seasonal combinations, HR size and road density were correlated in only three of 15 study area-seasonal combinations). Home-range size using the buffered HR estimates was greatest during the Summer and smallest during the Winter, consistent with other literature (Cederlund and Okarma 1988, McCulley 2015). Our MCP estimates of HRs were consistent with the seasonal HR sizes documented elsewhere in western Canada (Lemke 1998, McCulley 2015), being greatest during the Winter and smallest during Cavling. The difference between these HR estimates is likely due to individual daily movements. For example, during Late Winter when moose move the least, a 'rare' long excursion away from their core HR may significantly inflate the size of an MCP HR but could result in a small 70th percentile buffered HR estimate if the animal was consistently using a small area during the rest of that season. Conversely, during the summer when female moose move the greatest distances, the buffered HR estimate becomes increasingly large regardless of how close the used locations are away from one another due to the buffering of location points. Similarly, during Calving when movements are reduced spatially possibly due to neonate development, both HR estimates are similar in size.

The greatest difference between the two HR estimators was during Late Winter for all study areas, when the 100% MCP was over twice the size of the buffered HRs. This was due to female moose making short daily movements during the winter to conserve energy, but not staying in one localized spot for the entire season, presumably roaming larger areas in search of adequate forage plots or avoiding predators with a few long-distance movements (inflating the MCP HR estimate). Late Winter represents a season when the forage has the lowest quality and when it takes more time for a moose to acquire the same quantity of forage (Risenhoover 1986). During this season, female moose in high-biomass browse areas would benefit from staying in those areas instead of roaming. As body stores decrease throughout the winter, the challenge of balancing intake and movements can affect the animal's daily and annual energy balance (Moen et al. 1997). If, however, the browse provided is not in high quantity, moose must travel between food sources and search further from a central location, which is likely what occurred in Big Creek during Late Winter.

Daily movements by female moose differed by study area. We hypothesized that female moose living in study areas with the greatest amount of forest harvesting activities would have the highest daily movements. We also expected that HR size would increase as forest harvesting increased in a study area. Courtois et al. (2002) reported that (100% MCP) HR size was positively correlated with proportion of cutblocks. Prince George South had the greatest proportion of New and Old Cutblocks (Appendix E), but daily movement distances and HRs were smaller than in the other two study areas. In contrast, moose in Big Creek with fewer new cutblocks (Appendix E) and the southern portion of the study area completely cutblock-free had the largest daily movement distances and HRs. During Calving, study-area differences relative to forest practices did not influence daily movement distances. Concurrently, HR sizes during Calving were similar regardless of forest practices, perhaps because biological constraints during this season override environmental constraints. Cederlund and Sand (1994) observed that female moose with calves had larger HRs than those without calves. Although we could not use the presence of a calf as a coefficient in any model, we expected that the cow:calf (female to young of the year) ratio was similar within the three study areas (Kuzyk and Heard 2014) and, therefore, should not have made a difference in our observations of HR sizes.

Use, availability and selection

Overall, the proportions of vegetation classes in used and available seasonal HRs were more similar than expected. Female moose were selective at the HR scale, but due to the study site selection of three similar landscapes with varying degrees of logging, inferences could only be made to the attributes of each study area. Mature forest cover in all study areas and seasons made up at least ~50% of used HRs, approximating what was available. Cutblocks appeared in the same proportions in used and available HRs and were included in 14 of the 28 supported models for selection — inconsistent with our hypothesis that female moose would avoid areas with high concentrations of new cutblocks. In the study area with the highest road density (PG South: average road density 1.93 $km \cdot km^{-2}$), collared female moose selected HRs with lower road densities in all supported models including that covariate, whereas in the other two study areas high road densities were neither selected nor avoided consistently.

Female moose selected HRs with Mature cover (specifically lodgepole pine) regardless of the proportion of new cutblocks. Other researchers have shown that selection for cover by moose changes relative to abundance (Osko et al. 2004). Indeed, there are moose populations that thrive in areas where there is very little to no mature conifer cover such as on the Seward Peninsula or north slope of Alaska (Machida 1995), whereas moose populations living in other geographic areas seem to require this habitat type to provide cover for predator avoidance, buffer extreme temperatures, and provide a refuge from deep snow accumulations (Balsom et al. 1996). Our results for all seasonal HRs, having ~50 – 60 % mature forest cover, may reflect a critical proportion required for suitable moose habitat in central BC. The risk of having HRs with low proportions of mature cover and increased proportions of forest openings could negatively affect moose by causing heat stress (Renecker and Hudson 1986, Ritchie 2008), and an increased risk of predation (James and Stuart-Smith 2000, Stotyn et al. 2005, Janz 2006). Balsom et al. (1996) hypothesized that the removal of mature cover would lead to lower moose densities because of lower forage availability and malnutrition. In our study, moose selection for the Pine cover class did not decrease as cover quality declined (in response to canopy die-off after MPB), perhaps because blowdown provided lateral cover and restricted access by hunters and predators, and there was more preferred regenerating browse (Timmermann and McNicol 1988, Rempel et al. 1997, Alfaro et al. 2015). Salvage logging in central BC removed the Pine cover class, which may be important for moose as a source of cover and forage, and therefore could leave moose more vulnerable by creating large forest clearings.

The creation of roads is inevitable with inland logging operations, as they are essential for both access and log extraction for wood products to get to a mill. Therefore, areas with the greatest proportion of logging often have the highest road densities. Forman et al. (1997) suggested a threshold road density (0.6 $km•km^{-2}$) for a “naturally functioning landscape containing sustained populations” of large mammals. Other large mammals have been shown to have road density thresholds ranging from 0.25 –1.9 $km•km^{-2}$, but thresholds for moose have not been reported (Beazley et al. 2004). All three of our study areas had an average road density that surpassed the suggested threshold (Forman et al. 1997). Beyer et al. (2013) observed a functional response of moose HRs when road density reached 0.2 – 0.4 km•km^{-2}, whereas PG South collared moose HRs had road densities that were five to ten-fold greater. These moose in PG South avoided high road densities in every supported model that included this covariate. Prince George South in the mid 1990's had high moose densities, and surpassed Forman et al. (1997) recommended threshold of disturbance; a tipping point likely occurs where road density surpasses the equilibrium for a landscape to have high moose densities.

Our results suggest that female moose select a mid-level of road density, with animals in the most disturbed areas selecting for lower road densities, and female moose in study areas with lower road densities showing neither selection nor avoidance of road density. This result, however, may be an artifact of the study design, which focused on changes at differing scales of MPB salvage logging. Courtois et al. (2002) showed that only three of their 47 study moose shifted their home ranges following progression of clear-cuts. It is possible that our moose were collared in areas with existing clear-cuts and already established home ranges. The proportion of new clear-cuts and road densities within their HRs would be more similar to what was available if the moose that had been collared were more spatially separated across the landscape.

Habitat selection at the HR scale by female moose differed among study areas and seasons in areas subject to differing levels of forest harvesting, suggesting that moose selection is not fixed and individual variation exists. The study area with the greatest proportion of logging activity (PG South) had multiple competing selection models for all seasons. Concurrently, the study area with the least logging (Entiako) had a single supported model for Late Winter, Calving, and Summer, and two supported models for Fall and Early

Winter. Greater recent forest harvesting may offer different habitat selection strategies, and as a result, multiple competing supported models. Habitat Richness was an important parameter in all three study areas. The driest study area (Big Creek) had selection for Wetted areas in all seasons. There was support for our hypothesis that moose avoid high proportions of clear-cuts and high road density in areas with a high degree of MPB salvage logging. Mature forest cover was also highly used regardless of MPB salvage logging intensity among study areas (Appendices C – E). Selection of New Cutblocks was important in all seasons except Calving in PG South. Consequently, seasonal HR selection by female moose suggests trade-offs between reducing vulnerability and increasing access to browse.

All supported seasonal selection models for Entiako contained the Habitat Richness variable (number of unique cover classes within a HR). Habitat richness at the HR scale is a measure of diversity; therefore, female moose in Entiako appear to be selecting for a more complex habitat at the HR scale. Moose are expected to benefit when habitats are heterogeneous (Peek 1998). Although we could not measure forage intake or number of browsed species relative to HR selection, a greater number of vegetation cover classes within an individual's HR could ultimately increase the number of browse species. If female moose are selecting for a greater range of vegetation cover classes within their HR, this would allow for greater diet mixing, and potentially greater intake of nutrients (Wang et al. 2010), thereby buffering against the potential accumulation of plant secondary metabolites (Iason and Villalba 2006).

Big Creek was least similar geographically to the other two study areas because it is on a high plateau with a dry climate and slow forest regeneration time (B. Cadsand, pers. comm.). In this area, supported selection models varied by season and were quite general.

Saturated models were in all competing model sets except for Summer, and the vegetation cover classes with coefficients that showed the greatest support in each model set made up a very small proportion of female moose HRs. Similar to Entiako, Big Creek showed support for having diverse HRs with multiple vegetation cover classes. Likely because of the hotter, dry climate in this study area, Wetted cover classes were highly selected in HRs in all seasons. This study area also had the greatest daily movements and the largest seasonal HRs; female moose may be spending a greater proportion of their time searching for sufficient forage due to local climatic conditions in deciduous-poor new clear-cuts (Dawe and Boutin 2016).

Prince George South had the most variable supported models among seasons, but selection for individual variables was relatively consistent. In this area, high road densities were avoided, and mature forest cover classes were selected in all seasons except Early Winter. In all seasons, except Calving, New Cutblocks were selected at the HR scale. Because roads and cutblocks are highly related (i.e., aerial-logging activities are extremely rare in British Columbia's interior), and this area has been heavily modified by logging, female moose appear to space their HRs away from the greatest proportion of logging and to select areas where New Cutblocks and mature forest are plentiful on the border of mature forest stands as logging activities expand further away from main haul roads. Trade-offs between forage and security cover (Wasser et al. 2011) may be associated with HR selection in PG South. This trend was not observed in the other two study areas, potentially due to the high degree of logging activity in PG South.

Calving represents a critical time for population growth, and different calving strategies are used by moose (Poole et al. 2007). In the study area with the greatest proportion of cutblocks (PG South), female moose selected wetlands and lakes, and avoided high road densities, likely to increase access to browse provided near wetlands and lakes (McGraw et al. 2014) and reduce vulnerability to predation. Wolves travel two to three times faster on roads than in forest cover (Dickie et al. 2017), and wolf predator efficiency is greater near linear corridors (James and Stuart-Smith 2000). Kunkel and Pletscher (2000), however, showed that moose kill sites were more likely to be in low road density areas (0.6 km•km^{-2}), compared to random sites (0.9 km•km^{-2}). In our study, collared moose avoided areas with high road density, which could expose them (and their calves) to higher risk of wolf predation if wolves are also avoiding high road density. The response to predation risk in much higher road density (>1 km•km^{-2}) areas such as in this study is unknown.

Seasonal selection patterns are consistent with reducing limiting factors at the HR scale. Calving represents a sensitive period for female moose and their offspring where we found selection for “safe” areas hypothesized to reduce predation events and provide adequate forage for neonate development. Alternatively, during Early Winter, collared moose HRs included areas less “safe” to include more cutblocks and roads indicating a trade-off for forage acquisition being of higher priority that security cover. Late Winter then shows a trade-off for greater cover for security and energy conservation with reduced forage areas.

Results from use and availability and from the HR selection models should be interpreted together. Attributes of moose HRs in this study were generally similar to availability and HR selection model inconsistencies across study areas and season were likely due to study area differences, moose individuality, and large HRs confounding differences. We observed that models describing HR selection by female moose were highly variable due to individuality and differing HR selection strategies. Predictive accuracy of supported case-matched logistic regression models was poor or low (Table 2.6); we believe that we correctly classified individuals used and available HRs, but available HRs encompassing HRs used by other individual moose was unaccounted for and may not separate used from available (misclassification). Therefore, caution should be used when applying the models to the 'average' female moose as this study has shown that moose are quite dynamic and individualistic. Collared female moose did not select for HRs with less forest harvesting activity in any study area. In fact, many models showed selection for recent forest harvesting at the HR scale. High road density, however, was avoided (in 14 of the 17 supported models where the coefficient was present). This suggests female moose select HRs on the periphery of large-scale disturbance and avoid homogenous areas containing vast proportions of cutblocks and negligible cover. The study area with the highest model variability (PG South) was also the study area that had the greatest amount of disturbance; possibly because it was harder for female moose to find sufficient high-quality moose habitat, and therefore, there were multiple HR selection strategies. This trend is problematic in areas with highly disturbed landscapes such as PG South because it reduces the potential area available for moose home ranges being selected (therefore reducing the effective carrying capacity of the landscape) and increases vulnerability. Our analyses have shown that female moose did not avoid recently disturbed landscapes, but they avoided the most disturbed portions of it, suggesting a threshold of disturbance (i.e., Intermediate Disturbance Hypothesis; Levin and Paine 1974, Connell 1978) acceptable for female moose HR selection.

Other researchers have shown this threshold of disturbance to be linked to the Intermediate Disturbance Hypothesis, which suggests that highest biological diversity and species richness is maintained at an intermediate scale of disturbance where a landscape or ecosystem is always in perpetual change, without severe disturbances (Levin and Paine 1974, Connell 1978). Beyer et al. (2013) noted that thresholds to landscape change can have disproportionately large effects on wildlife; their hypothesis holds true for these data from our study areas as early seral stages from cutblocks may provide forage for moose, but moose also rely on cover; in addition, a certain amount of disturbance (e.g., fires, clear-cuts) benefits a species, and has negative consequences at a certain threshold. A continuum of disturbed landscapes was used in our study, all of which had declining moose densities (Kuzyk and Heard 2014) following the MPB outbreak. The Intermediate Disturbance Hypothesis does not account for landscape productivity during and after disturbance, whereby diversity relationships can be negative or positive depending on productivity (Proulx and Mazumder 1998).

Management implications

Our results emphasize that female moose utilize forest cover, heterogeneous landscapes, and areas with browse abundance in large clearcut landscapes. Other researchers have shown that following large-scale bark beetle outbreaks, without the intervention of clear-cutting practices, forests maintain heterogeneity in vertical and horizontal structure, diversity of understory species, and high stocking standards (Alfaro et al. 2015, Winter et al. 2015). Our work also highlights that if clear-cutting of MPB-killed pine stands continues in these study areas, the effective carrying capacity of the landscape for female moose may continually decrease if forest harvesting occurs at a rate that exceeds the regrowth of forestry plantations that produce adequate moose habitat. Given the current state of logging practices in central BC, moose habitat would be expected to benefit from: 1) a reduction in salvaging

MPB-killed pine stands; 2) reducing silvicultural treatments such as brush-cutting (unless used to increased biomass and accessibility of willow (*Salix* spp.) and reduction of alder (*Alnus* spp.) and other non-preferred deciduous species) and the use of herbicides on palatable herbaceous species selected by moose; and 3) avoiding excessively high road densities and rehabilitating roads through decommissioning and replanting (accessible only to humans by walking, and reducing line of sight for predators). Future research would benefit from: 4) assessing productivity of dry sites containing lodgepole pine forests post logging with respect to moose habitat and forage nutrition; 5) researching the effects of mechanical treatments on moose browse in central BC to improve moose habitat; 6) better documentation of individual moose HR selection across more study areas; as well as 7) researching the effects of female moose survival in areas with differing degrees of MPB salvage logging.

Chapter 3 : Habitat and space use of female moose in central British Columbia following a mountain pine beetle outbreak

ABSTRACT

The loss of heterogeneity on the landscape can result in a loss of biological diversity and loss of megafauna. Anthropogenic landscape changes resulting from progressive salvage logging following a mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreak have changed areas in the central interior of British Columbia (BC) from a heterogenous mosaic to a more uniform homogenous state. Female moose (*Alces alces*) were equipped with GPS-radio collars in three study areas in central BC following a MPB outbreak and subsequent forest harvesting. We investigated within home-range selection using mixed-effects logistic regression for 173 female moose resulting in 134,631 used location points over 3 years. Pine (*Pinus* spp.) was the most used vegetation cover class in all three study areas, regardless of the main canopy being open because of dead standing trees. The use of New Cutblocks differed substantially among study areas and seasons. Deciduous-leading stands were the only vegetation cover class selected by collared moose in every study area and season regardless of the proportion of cutblocks present. Trade-offs between browse quantity and cover by season and study area were evident, whereby differing limiting factors in each study area resulted in differences in habitat selection by collared female moose. Our findings indicate that forest harvesting of MPB-killed pine stands after over a decade of regeneration reduced suitable moose range, and the cutblocks remaining have different outcomes for habitat selection depending on limiting factors and landscape differences.

INTRODUCTION

Landscape change is often regarded negatively when there is associated loss of biological diversity (Hanski 2005), and loss of megafauna (Johnson 2002). Anthropogenic disturbances to landscapes and negative effects on wildlife include the loss of intact forests due to forestry practices, agriculture, mining and other natural resource developments (Gill et al. 1996, Arlettaz et al. 2015, MacNearney et al. 2016, Wilson 2016, Stewart and Komers 2017). Progressive landscape change due to forest harvesting can alter ecosystems from a heterogenous state to a more homogenous one (Scheffer et al. 2001). Frequently, high-priority wildlife species in North America are studied to understand the effects and driving factors of species decline in areas where human-accelerated land-use change has occurred (Courbin et al. 2014, Ehlers et al. 2014, Johnson and Russell 2014, Cristescu et al. 2016, Lamb et al. 2017).

How animals use the landscape in which they live is a hierarchical process in which animals satisfy their requirements at different spatial scales (Johnson 1980), whether it be geographically (Moorcroft 2012), through the selection of home ranges (see Chapter 2), or through habitat selection (Manly et al. 2007). At specific spatial scales, animals utilize landscape features to reduce limiting factors (Dussault et al. 2005*b*), such as the use of cover (Bjørneraas et al. 2011) and the need for high-quality food sources (VanBeest et al. 2011). Habitat selection can be consistent across spatial scales, or different across spatial scales (Boyce 2006, McGarigal et al. 2016) depending on the animals' needs in a given environment. Researchers have investigated habitat selection by moose (*Alces alces*) at numerous spatial scales (Cederlund and Okarma 1988, Darimont et al. 2005, Stolter et al.

2005, Dussault et al. 2006), and differing environmental systems allow flexibility in moose habitat selection (Courtois et al. 2002, Osko et al. 2004).

Our objectives were to test a landscape-change hypothesis predicting that changes in the proportion of cutblocks, road density, and use across a landscape negatively affect moose (Kuzyk and Heard 2014), 15 years after a mountain pine beetle (*Dendroctonus ponderosae*; MPB) infestation and subsequent salvage logging. To do this, we examined seasonal habitat selection by female moose across landscapes altered to varying extents by MPB and subsequent salvage logging. Our hypotheses about within home-range selection (3rd-order), and subsequent selection of candidate models and covariates were informed by results of 2nd-order selection (i.e., seasonal home-range; see Chapter 2). For moose, habitat selection is believed to be more pronounced at a finer scale (Courtois et al. 2002), whereby if a resource is selected at a broader scale, that resource will also be selected at a finer scale. We predicted that because collared moose avoided areas with the greatest disturbance when selecting seasonal ranges, female moose would have strong avoidance of roads within home-range selection. We also predicted that because mature cover and browse vegetation classes were selected at the home-range scale, selection by moose for mature timber edge as escapement cover and distance to browse may also be spatially important (Courtois et al. 2002) within their home ranges. We expected that the use of mature cover would be more evident in 3rd-order selection, and that beetle-killed pine stands that were not salvage-logged would be highly selected because they provided connectedness, horizontal cover and diverse understory vegetation following the MPB outbreak (Campbell and Antos 2015).

METHODS

This study was conducted as part of a larger moose survival study (BC Provincial Animal Care Permit CB17-277227) ongoing since December 2013 (Kuzyk and Heard 2014, Kuzyk et al. 2016). Three study areas in central BC were chosen to offer a range of landscapes modified by MPB and subsequent salvage logging (Figure 3.1). The three study areas were Entiako, Big Creek, and Prince George South (PG South, hereafter; additional study area information available in Chapter 2). Entiako (~850 – 1900 m), as the epicenter of the MPB outbreak, was vegetated primarily by lodgepole pine *(Pinus contorta* var. *latifolia)* and was located among two provincial parks. Big Creek (~1100 – 2450 m), the southernmost study area on a high-elevation plateau, was characterized by a warm dry climate with concentrated logging activity in the north where new clear-cuts experience very slow regeneration time, and virtually no logging in the south because of two provincial parks. Prince George South had the lowest elevation (~550 – 1400 m), the greatest precipitation and the highest proportion of roads (1.9 km•km^{-2}) and cutblocks. Cutblocks since 1975 make up 33% of the total land cover of this study area.

Female moose were fitted with a GPS Plus Vertex Survey collars (VECTRONIC Aerospace, Berlin, Germany (Vectronic)) or an ATS Iridium GPS G2110E collar (Advanced Telemetry Systems Inc., Insanti, MN (ATS)) by the BC Ministry of Forests Lands and Natural Resource Operations and Rural Development (FLNRORD) staff. Location data from collared female moose between January 15, 2014 – April 25, 2017 were used for analysis. Depending on collar brand or model, collars received one, two, or four locations points a day. Collar information from 173 female moose resulting in 134,631 used location points was used for analysis (Table 3.1).

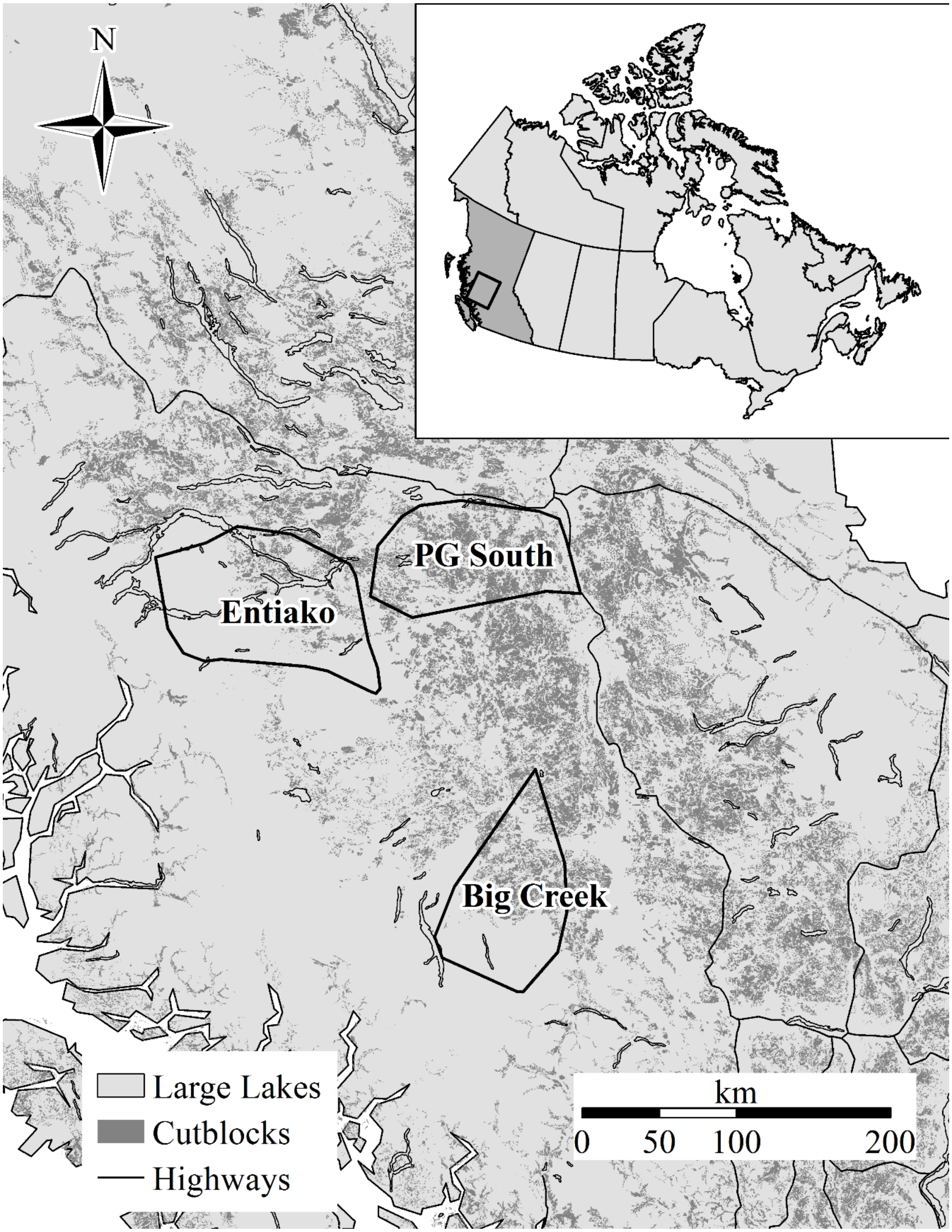

Figure 3.1. Location of three study areas (Entiako, Big Creek, and PG South) for GPS-collared female moose in central British Columbia.

Table 3.1. Collar information from 173 GPS-collared (Advanced Telemetry System (ATS), all other Vectronic Survey collars) female moose in three study areas in central British Columbia used for within home-range selection analysis between January 15, 2014 – April 25, 2017.

Study Area	Number of Individuals	Number of locations	Mean Fix Rate	Standard Error
Entiako - ATS	16	34680	93.1	3.31
Entiako	51	31405	76.8	2.66
Big Creek	58	41302	89.8	1.61
PG South	48	27244	72.5	2.96

Locations of female moose were divided into five biologically relevant seasons (Late Winter: January 15 – April 25, Calving: April 26 – June 20, Summer: June 21 – September 12, Fall: September 13 – November 20, Early Winter: November 21 – January 14) adapted from Gillingham and Parker (2008b) and Chapter 2, trends observed in the three study areas, and from local and expert knowledge. A minimum of 30 location points per individual in a single season were required to be included in our analysis. We believe that using a minimum of 30 locations points ensured that no individual's seasonal contribution would be underrepresented in model selection, and for project consistency (Chapter 2).

Used location points were screened for abnormalities in fix transmission or satellite transmission errors by identifying mortality events and screening locations before then, as well as removing locations that appeared to be errant or had unrealistic elevation measurements. A post-hoc examination of location points showed that average location error was <10 m away from the centroid of points, consistent with other researchers having an average precision of 10 – 28 m for GPS collars (D'Eon et al. 2002, Cain et al. 2005, Hansen and Riggs 2008). Our indices were from a collar that was not retrieved after a mortality in the Entiako study area near a creek where the collar continued to send location points from the same location for over 2 years.

Models can be biased if fix locations from denser vegetation cover are underrepresented (i.e., fewer location points for dense forest than forest openings). Therefore, we tested to determine if there was a fix bias using these GPS collars. To better understand the potential effects of missing fixes and habitat biases due to crown closure, we used recovered collars (usually from mortalities) to compare uploaded points to additional points that were stored on the collar (but not uploaded). Downloaded collars had 10.5, 20.1, and 18.2 % more fixes stored on-board (Big Creek, Entiako, PG South, respectively; Appendix A). We determined that there were differences between uploads and direct downloads, and vegetation cover effects on collar transmission rate. As such, there was ~15% chance of missing fixes in any given cover class (Appendix B). Because of differences in fix time for collars, ATS collars programmed for four fixes a day were analyzed to determine if vegetation cover class use differed by time of day. Female moose used Pine cover slightly more (14%) during the late morning and afternoon than they did at night, and they used Wetted areas and New Cutblocks more at night (38 and 30%, respectively) than during late morning and afternoon (Figure 3.2). Assuming female moose in other study areas responded to cover and wet features similarly, and most Vectronic collars having only one location point in the late morning, Wetted features may be significantly under-represented for those animals, and the use of Pine cover may be slightly over-represented for animals with collars that only received one fix per day.

To assess resource selection, five random (i.e., available) points were generated for each used location point (Burnham and Anderson 2001). To do this, we calculated the individual's 95th longest seasonal daily movement (Gillingham and Parker 2008*b*), and randomly assigned available location points within the generated buffer distance surrounding each used location point. This distance represents the maximum distance an animal would likely travel, excluding rare movements (e.g., predator avoidance), without under-representing availability for animals that did not move as much. For each animal, all random points were screened to ensure that they did not fall within 10 m of a used point to ensure that the same location was not considered both used and available. We removed a total of 37 available location points from the analysis.

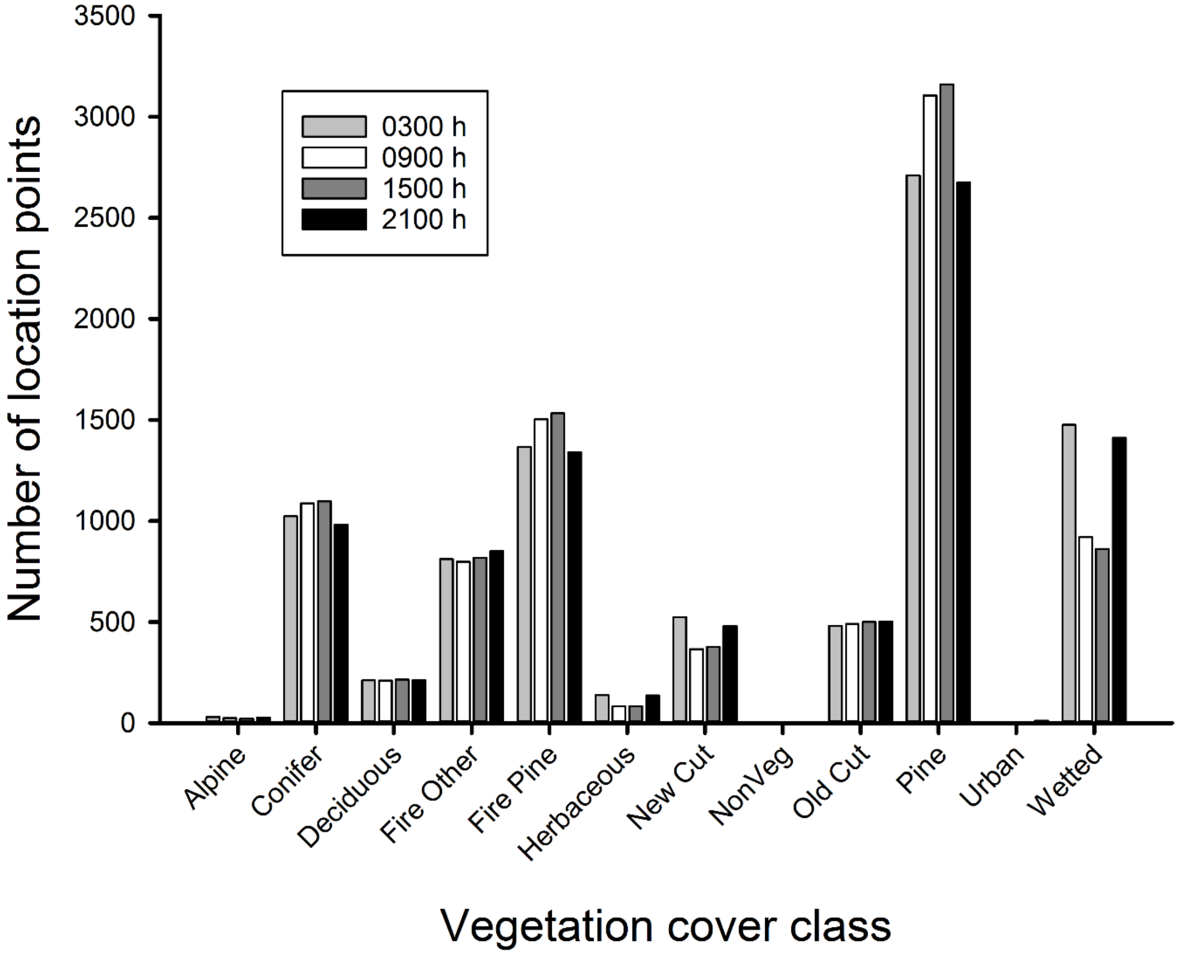

Figure 3.2. Time of day differences in vegetation cover use by female moose (*n* = 16) in the Entiako study area using four fix-a-day ATS (Advanced Telemetry Systems) Iridium collars; 34,680 location points.

Spatial data

We obtained forest-cover information (Vegetation Resource Inventory,VRI, veg_comp_lyr_r1_poly), and data for wetlands (fwa_wetlands_poly), lakes (fwa_lakes_poly), roads (dra_digital_road_atlas_line_sp, abr_road_section_line, resultsroads, ften_road_section_lines_svw, trim_transportation_lines, og_petrlm_dev_rds_pre06_pub_sp, og_petrlm_dev_roads_pub_sp, og_petrlm_access_roads_pub_sp), wildfires (prot_historical_fire_polys_sp) and cutblocks (rslt_opening_svw) from 1:20,000 map sheets to designate forest types by leading species and age (DataBC Distribution Service 2015). An additional VRI layer from TFL52 (South-East portion of PG South) was generously provided by West Fraser Mills (Quesnel, BC). Pine-leading forest cover was removed from other conifer forest cover due to the MPB outbreak, with our assumption being that most mature Pine were dead standing due to MPBs. The most recent VRI layer we used was from 2016, and the most current wetland, lake, road, wildfire, and cutblock layers were from 2015. We generated a non-overlapping map sheet in ArcGIS 10.2.2 (ESRI Corp. 2014) by year because of changes in landcover from logging and wildfire activity over study years; seasonal location data were queried with their respective year of spatial vegetation cover classes. With this technique, all seasonal location data for 2014 were queried on a spatial map without the disturbance that occurred after 2014; the 2015 and 2016 seasonal location data were queried with all changes to the vegetation cover map. We did this to ensure that location data were matched to the most up-to-date physical landscape at that time as was possible.

We used ArcGIS 10.2.2 (ESRI Corp. 2014) to calculate distances from used and available location points for moose (vegetation cover class and roads; Table 3.2) to generate

Table 3.2. Vegetation cover class, anthropogenic, and distance-to variables used in analysis of within home-range (3nd-order) selection by female moose in central British Columbia.

Variables		
A	Alpine	Area above treeline, dominated by shrubs
C	Conifer	All coniferous-leading forest stands except for *Pinus* spp.
PI	Pine	All Pinus spp.-leading forest stands
D	Deciduous	All deciduous-leading forest stands. Includes tall shrub-leading
W	Wetted	All water features, and annually permanent wet areas
NC	New Cutblock	All areas logged between 2000 – 2015
NV	Non-Veg	Area with no vegetation (e.g., gravel pit)
OC	Old Cutblock	All areas logged between 1975 – 2000
FP	Pine Fire	Wildfires occurring between 2000 – 2015 in *Pinus* spp.-leading forest stands
FO	Other Fire	Wildfires occurring between 2000 – 2015 in any species-leading forest stand except for *Pinus* spp.-leading
OF	Old Fire	All wildfires between 1975 – 2000 in any forest stand
U	Urban	Generally agricultural areas owned privately
RD	Road Distance	Distance (m) from an established road.
DM	Distance Mature	Distance (m) to a mature stand (Conifer, Pine, Deciduous) edge
ED	Escapement Cover	Distance (m) to mature stand (Conifer, Pine, Deciduous) of trees if in the open (New Cutblocks, Pine Fire, Wetted)

‘distance-to’ variables. Distance to road, distance to mature edge (food – cover boundary), and distance to escapement cover (distance away from cover, 0 if within cover) were calculated with this technique.

Topographical variables were derived from a digital elevation model (DEM) raster file (DataBC Distribution Service 2015) using ArcGIS 10.2.2 (ESRI Corp. 2014) with 25-m resolution. Elevation and aspect were extracted for all used and available location points. Elevation was also considered as a quadratic to determine if female moose were selecting for mid elevations. To reduce the number of categorical variables, two continuous variables (Northness and Eastness) were generated (Gillingham and Parker 2008*b*) as measures of aspect that range from -1.0 to 1.0 where Northness is the cosine of aspect and Eastness is the sine of aspect. Slopes <5° were not considered to have aspect and were assigned Northness and Eastness values of 0.We intersected used and available location points with their corresponding year vegetation cover-class layer, and topographical variables in ArcGIS 10.2.2 (ESRI Corp. 2014).

Use and availability

We determined relative use and availability of cover classes for female moose by season and study area. These data were used primarily to examine the importance of specific vegetation cover class relative to selection or avoidance — often used cover classes may be important to moose even if they are avoided (i.e., used less than availability) and the importance of rare cover classes may be overestimated even if they are highly selected (Stewart et al. 2002).

Statistical analysis

We assessed resource selection in an Information Theoretic framework (Burnham and Anderson 2002) for female moose by study area and season. We developed 10 *a priori* competing models (Table 3.3) to examine both the landscape-change hypothesis as well as to examine potential limiting factors for female moose seasonally. These models were based on study area geography (Base Topography), avoidance of ‘risky’ areas (Anthropogenic Disturbance, Access/Stress/Vulnerability, Edge, Escapement Cover Distance, Avoidance), browse and cover availability (Vegetation, and a combination of both browse availability and risk avoidance (Cover/Browse). Due to the numerous ecological effects associated with elevation and aspect across the three study areas, and because available locations are inherently generated further from the centroid of the study area than used points, we included elevation and aspect variables in each model and used a base model with only those covariates to determine if the effects of geography outweighed predictive covariates for the landscape-change hypothesis. We suspected that vegetation cover classes would be used differently throughout the year; however, vegetation was a categorical variable so whenever it was used in a model, all cover classes were tested at the same time relative to each other. We predicted that Conifer, Pine, and Deciduous would be selected in all seasons because of the cover these classes provide. Further we expected that New Cutblock, Old Cutblock, Other Fire, and Old Fire would be selected in all seasons but summer because of their forage potential — in summer these cover classes provide very little thermal cover. Finally, we expected Wetted and Alpine to be selected during growing seasons (calving, summer, fall) for browse and thermal relief, and Non Veg, Pine Fire, and Urban to be avoided in all seasons because of insufficent cover and forage.

Table 3.3. Competing models used for analyzing selection of within home-range locations of female moose with mixed-effects logistic regression in three study areas during five seasons within central British Columbia. Variables are defined in Table 3.2.

Model	Model Name	Variables								
		Elevation	Elevation^2	Easting	Northing	Year	Veg. Cover Class	Distance to Road	Distance to Mature Edge	Escapement Cover Distance
1	Base Topography	✓	✓	✓	✓	✓				
2	Anthropogenic Disturbance	✓	✓	✓	✓	✓		✓	✓	
3	Access/Stress/Vulnerability	✓	✓	✓	✓	✓		✓		
4	Edge	✓	✓	✓	✓	✓			✓	
5	Cover/Browse	✓	✓	✓	✓	✓	✓		✓	
6	Escapement cover distance	✓	✓	✓	✓	✓	✓			✓
7	Vegetation	✓	✓	✓	✓	✓	✓			
8	Avoidance	✓	✓	✓	✓	✓	✓	✓		
9	Saturated 1	✓	✓	✓	✓	✓	✓	✓	✓	
10	Saturated 2	✓	✓	✓	✓	✓	✓	✓		✓

Hypotheses for each Model number:

1. Geographic covariates predict other measurable covariates (such as vegetation) due to soil moisture, shading effects, wind, etc.
2. Avoidance of roads and selection for proximity of cover due to predation risk associated with anthropogenic openings.
3. Avoidance of risky areas such as roads from predation risk, stress associated with vehicle traffic, and vulnerability due to visibility on linear corridors.
4. Selection to be near a mature edge for accessibility to foraging areas, and cover for predator avoidance, thermal relief and snow interception regardless of what vegetation cover is being used.
5. Selection for cover and browse near a mature cover edge to facilitate efficient feeding and bedding sites, reducing energetic expenditures needed to travel between cover and browse, and reducing predator encounters by moving less.
6. Selection for close proximity to a Mature Edge when in a foraging area (New Cutblock, Old Fire, Other Fire, Wetted) and predator avoidance during browsing.
7. Selection for the best cover and foraging areas seasonally. See text for seasonal hypotheses for cover classes.
8. Avoidance of recent disturbances associated with roads to minimize predator encounters and stress; moose would be most vulnerable near a road associated with an opening.

Categorical vegetation cover-class variables were examined relative to a reference category with deviation coding (Hendrickx 1999) using desmat in Stata 14 (StataCorp 2015). To avoid issues with complete or near-complete separation, we identified and dropped vegetation cover classes when use or availability locations were ≤4 (Menard 2002) from individual/season models sets as appropriate. Consequently, one to three vegetation cover classes were removed from each model set (Appendix F). Each competing model was assessed by study area (*n* = 3) and season (*n* = 5) with mixed-effects logistic regressions (melogit in Stata 14) comparing used and available locations; individuals were tracked in the analyses through random intercepts. To prevent collinearity, covariates were not included in the same model if tolerance scores were >0.20 (Menard 2002). Competing models were checked for uninformed parameters (Burnham and Anderson 2002, Arnold 2010); as a result, one model was dropped from the supported models. Competing models were ranked using Akaike's Information Criterion (Akaike 1973) corrected (AIC_c) for small sample sizes (Burnham and Anderson 2002). Akaike's weights (w_i) were calculated to indicate the relative weight of evidence for the supported models, but we considered any model within a ΔAIC_c of 2.0 of the top model (providing the competing model contained no uninformed parameters) to be a supported model.

We assessed the validity of each supported model (Mac Nally et al. 2018) in two ways. As described in more detail in Chapter 2, using the area under the receiver operator curve (ROC) assumes that true presence and true absence data are being used (Fielding and Bell 1997, Pearce and Ferrier 2000). Resultant ROC values between 0.5 – 0.7 are considered to have low discrimination ability, 0.7 – 0.9 are considered to be good, and >0.9 have excellent discrimination ability (Manel et al. 2001). For point locations with collared moose, however, there is both the possibility that a collared animal may have used a random location when a fix was not obtained, or that other animals may have used available points. Therefore, we also used k-fold partitioning (Boyce et al. 2002, see also Chapter 2), which is less sensitive to errors in the correct classification of points. Typical implementation of k-fold validation in mixed models (package adehabitat (Calenge 2006) in R (R Core Team 2017) versions 3.4.1) involves holding back a subset of all data (and not of individuals). Therefore, the assessment is of how well the model fits the data collected as opposed to testing how sensitive are the results to the individuals (as was the case in Chapter 2). Models with significant r_s values ($r_{s\_critical,\ 10} = 0.648$, Zar 1999) were considered valid models.

RESULTS

Use and availability

We first qualitatively describe use and availability to assist with the subsequent interpretation of resource selection by female moose. Differences in use and availability for collared female moose were evident among study areas and seasons. Female moose primarily used Mature Cover vegetation cover classes and browse classes such as Cutblocks and Wetted areas in all seasons, although proportions of use differed. Pine stands were the most available forest vegetation cover class in all study areas and seasons. Use of Pine stands varied by study area and season. Pine was also by far the most used cover class in all study areas and seasons except during Early Winter in Big Creek and PG South, and during Late Winter in PG South (Figures 3.3 – 3.5). In all study areas, Pine stands were used most during the Summer (28 – 54%) and least during Early Winter (16 – 26%; Figure 3.6).

Conifer cover was used in proportion to availability on the landscape, but use varied

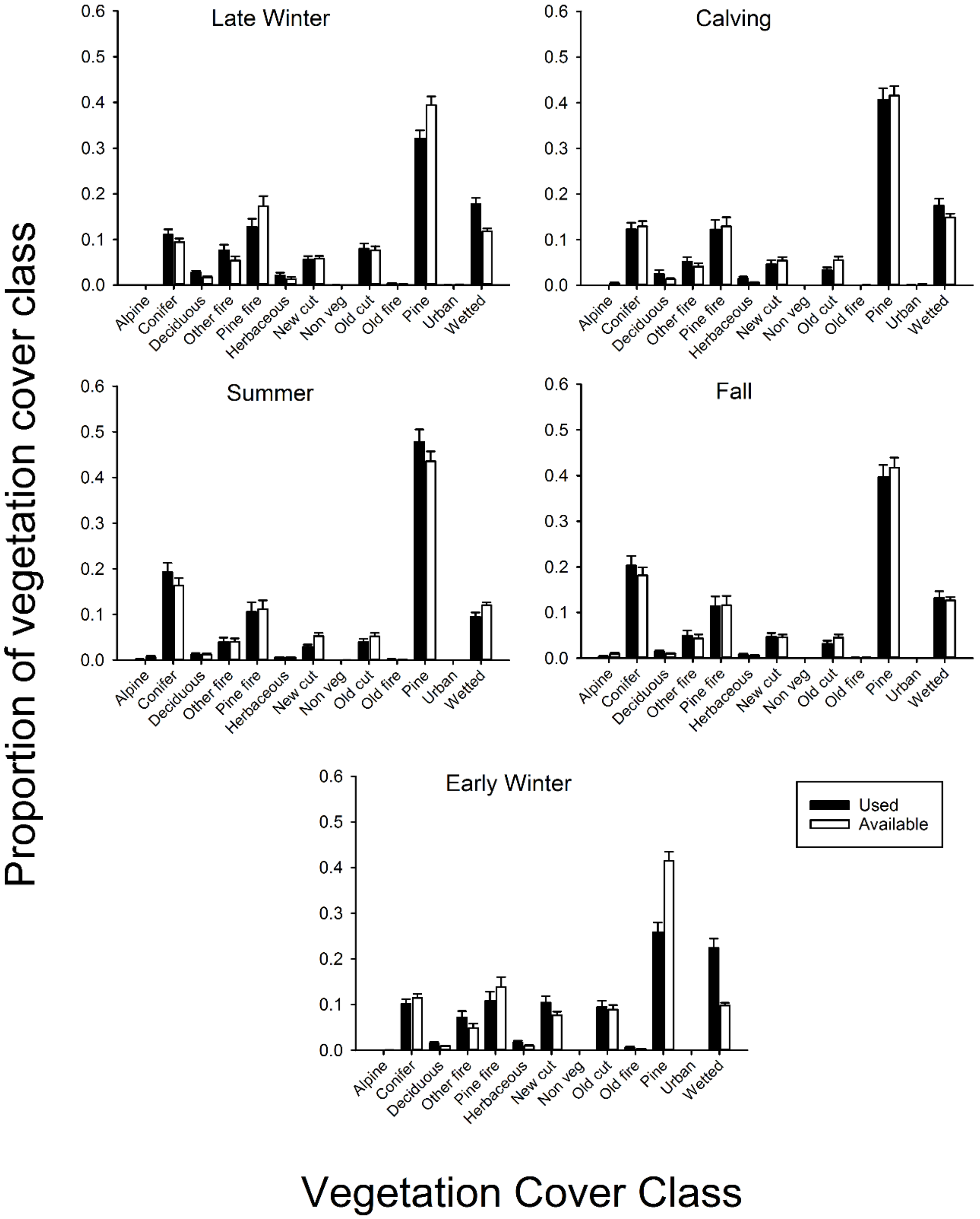

Figure 3.3. Use and availability ($\bar{x}$ + SE) of vegetation cover classes for within home-range selection analyses for female moose in the Entiako study area between January 15, 2014 – April 25, 2017 during five seasons.

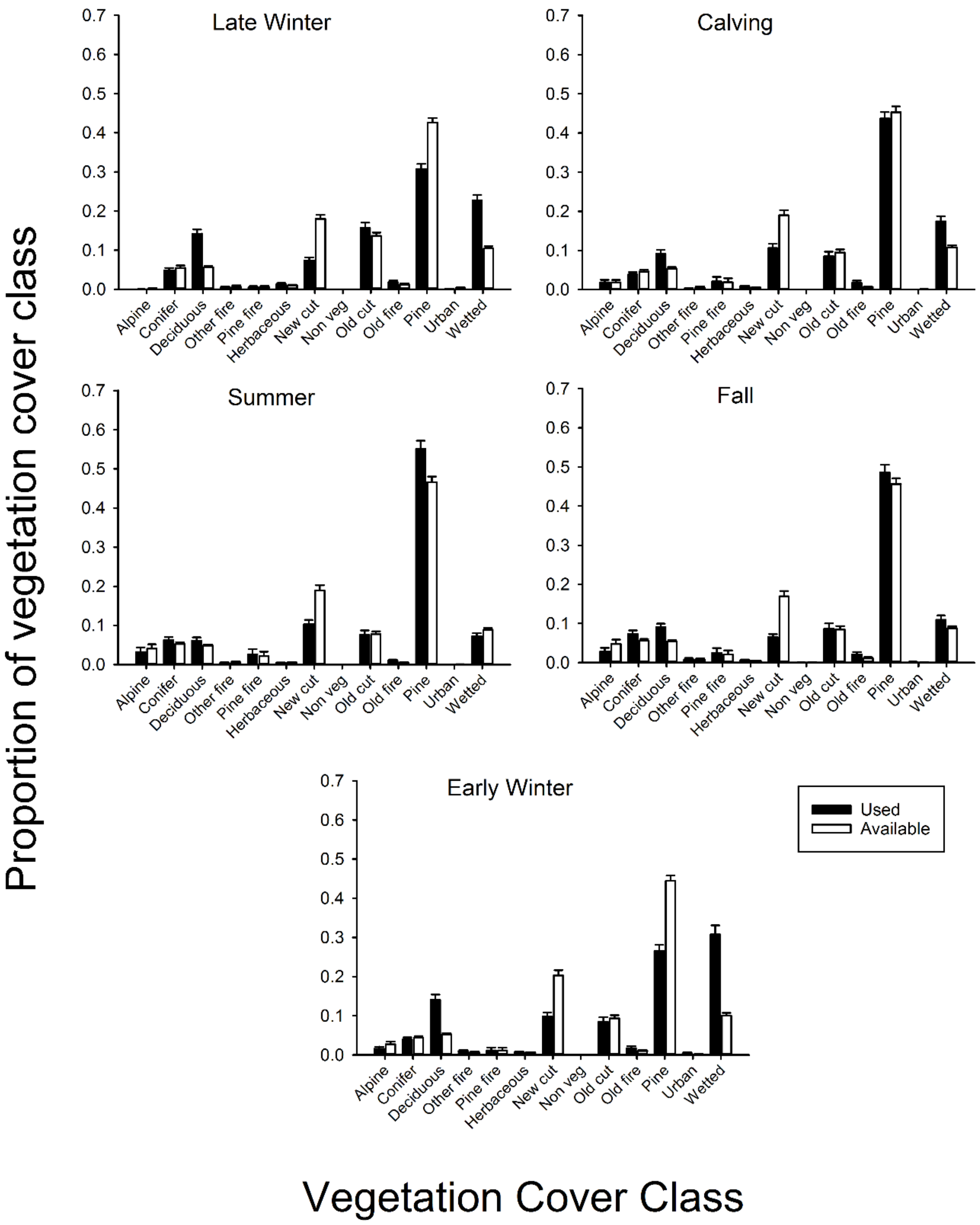

Figure 3.4. Use and availability ($\bar{x}$ + SE) of vegetation cover classes for within home-range selection analyses for female moose in the Big Creek study area between January 15, 2014 – April 25, 2017 during five seasons.

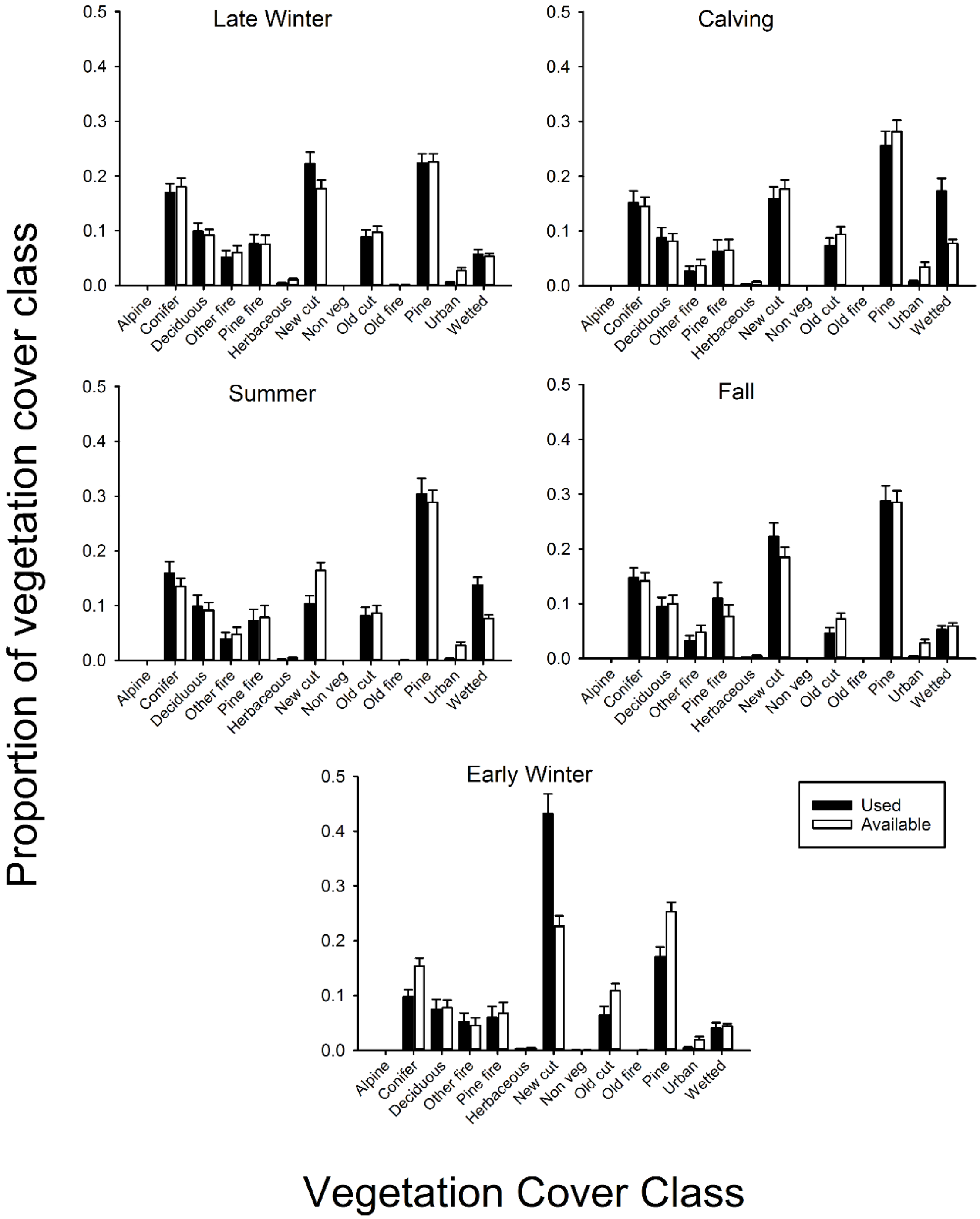

Figure 3.5. Use and availability ($\bar{x}$ + SE) of vegetation cover classes for within home-range selection analyses for female moose in the PG South study area between January 15, 2014 – April 25, during five seasons.

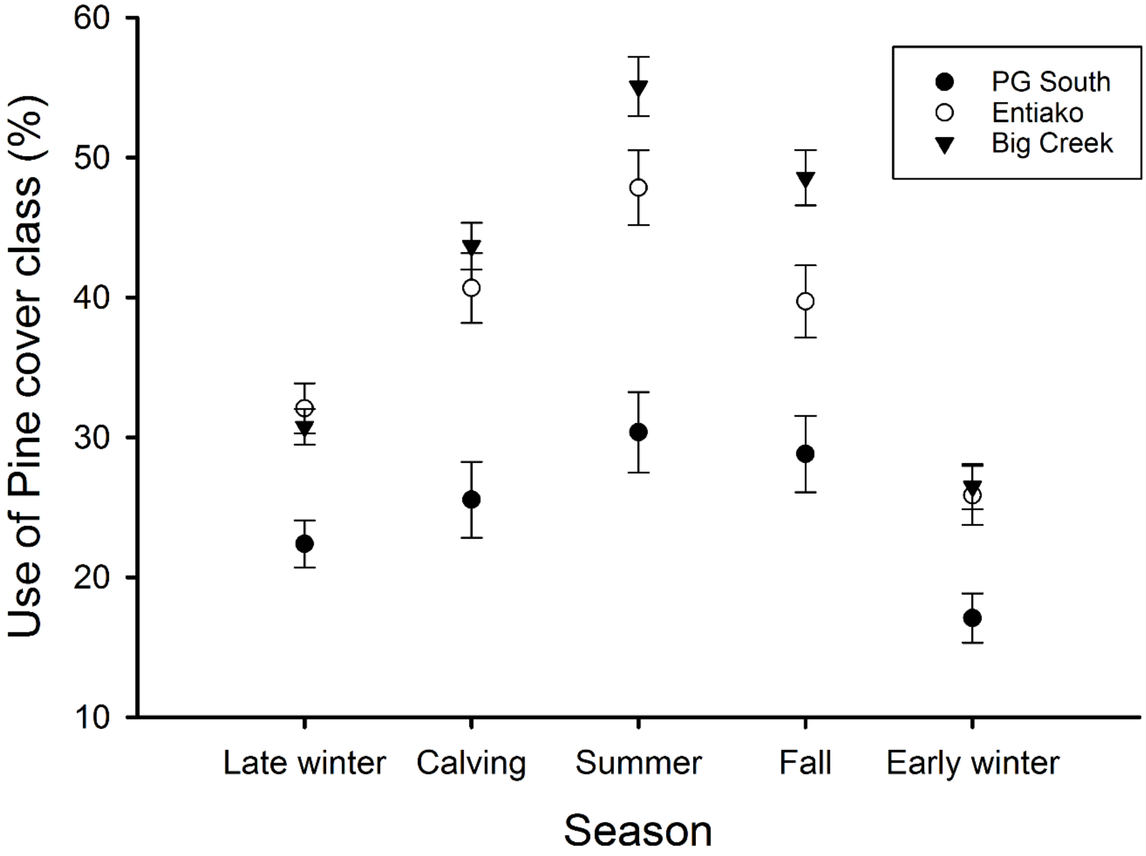

Figure 3.6. Percent use ($\bar{x}$ ± SE) of Pine vegetation cover class in three study areas in central British Columbia between January 15, 2014 – April 25, 2017 during five seasons using GPS-collar locations from 173 female moose.

by study area. Collared female moose in PG South and Entiako utilized conifer stands (~13%) throughout the entire year with the least use in Early Winter where other vegetation cover classes such as Wetted and New Cutblocks were utilized more for browse potential (Figures 3.3 – 3.5). In Big Creek, use of Conifer cover was always <7% (Figure 3.4).

Wetted areas were used most by moose during Early Winter in Entiako and Big Creek (19% [Figure 3.3] and 31% [Figure 3.4], respectively), whereas moose in PG South used these areas the least at this time of year (4%). Alternatively, during the summer, Big Creek and Entiako collared moose used Wetted areas the least of all seasons, and PG South moose used Wetted areas most during Spring and Summer. During Early Winter, PG South and Entiako moose had the greatest use of New Cutblocks (42% and 11%) exceeding availability. During Summer, however, collared moose in PG South avoided New Cutblocks. The use of New Cutblocks in Big Creek was minimal (<11%) during all seasons (Figure 3.3 – 3.5).

Old Cutblocks were a nominal portion of used vegetation cover classes (<10%), although use was usually greatest during Late Winter. Big Creek-collared moose used Old Cutblocks two times more than New Cutblocks during Late Winter. Deciduous stands were also used in all study areas; however, their use was proportional to availability except notably in Big Creek in Early and Late Winter when it was used much more than available (Figure 3.3 – 3.5).

By pooling all female moose location points from each study area and season, we observed that female moose used Old Cutblocks in the same proportion as they were available to them. Relative to stand age, cutblocks that were harvested between 2002 – 2005

(13 – 10 years) were preferred, and cutblocks harvested after 2006 (<9 years) were avoided by the collared female moose (Figure 3.7).

Resource selection

In all study areas and seasons, 30 mixed-effects logistic regression models were supported (Table 3.4). All supported models included vegetation cover (Table 3.5). Deciduous was the only cover class selected in every supported model and it was positively selected by moose. All other parameters were not consistently selected or avoided across study areas and seasons, but there were trends in selection of individual parameters. Supported models identify the selection for browse and cover, varying by study area. Pine cover was avoided in Early Winter in each study area. New and Old Cutblocks (except Late Winter) were avoided in every season in Big Creek; conversely, New Cutblocks were selected in all seasons except Summer in PG South (Table 3.4). Predictive accuracy of supported mixed-effects logistic regression models was poor to excellent (Table 3.4). All but two k-folds were robust to subsampling of the data, but only one ROC score sufficiently predicted good model accuracy (Table 3.4). We have provided the ROC results just for completeness but believe that the k-fold validations likely provide a better measure of how well models fit the collected data.

VEGETATION COVER

Vegetation cover classes were treated as categorical variables and assigned deviation coding for analysis. Coefficients are therefore relative to one another and cannot be interpreted as the percent of selection or avoidance in supported models (as for continuous variables). They do, however, represent the relative weight of selection or avoidance of

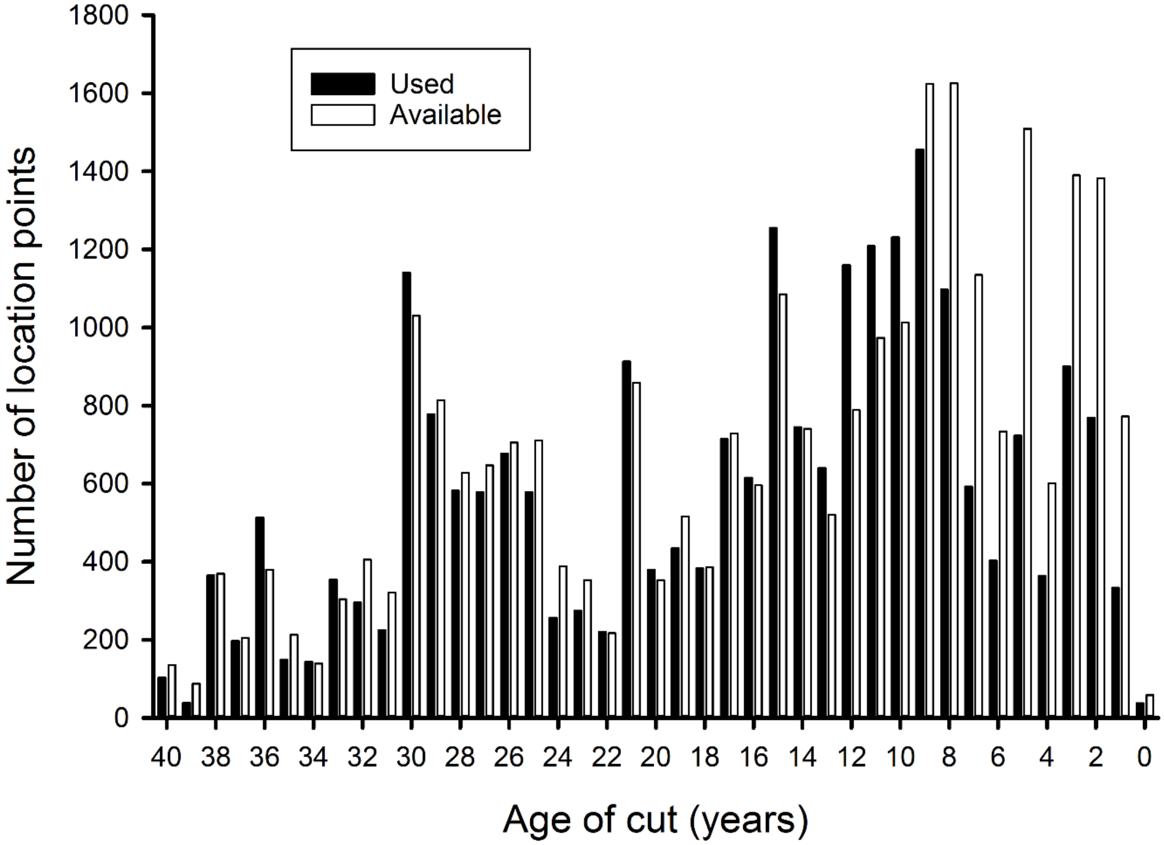

Figure 3.7. Comparison of used and available (corrected to number of used locations by dividing number of available locations in each cutblock year by 5) location points for GPS-collared female moose in cutblocks harvested from 1975 (Age 40 relative to the start of the study) and 2015 (Age 0) in central British Columbia between January 15, 2014 – April 25, 2017.

Table 3.4. Supported models for within home-range selection by female moose in three study areas during five seasons (LW: Late Winter, C: Calving, S: Summer, F: Fall, EW: Early Winter) in central British Columbia using mixed-effects logistic regression indicating the chi squared goodness of fit test statistic (*P*), the log likelihood (LL), number of parameters (*k*), number of home ranges (*n*), Akaike information Criterion corrected for small sample size (AIC_c), change in AIC from top model (ΔAIC_c), Akaike weight (w_i), area under the receiver-operating curve (ROC), and k-fold cross validation value. Model numbers are described in Table 3.3.

Season	Study Area	Model	*P*	LL	*k*	*n*	AICc	ΔAIC_c	w_i	ROC	k-fold
LW	Entiako	6	<0.001	-55091.02	21	151	110231.20	–	0.40	0.58	0.93
		10	<0.001	-55089.72	22	151	110231.35	0.15	0.37	0.58	0.94
	Big Creek	9	<0.001	-39688.46	22	160	79428.30	–	0.58	0.67	0.99
		5	<0.001	-39690.12	21	160	79428.94	0.64	0.42	0.67	0.99
	PG South	9	<0.001	-29035.72	21	114	58123.48	–	0.42	0.55	0.88
		5	<0.001	-29037.52	20	114	58124.06	0.58	0.31	0.55	0.89
		10	<0.001	-29036.64	21	114	58125.32	1.84	0.17	0.55	0.86
C	Entiako	5	<0.001	-27211.48	18	123	54465.54	–	0.35	0.56	0.58
		7	<0.001	-27212.97	17	123	54465.77	0.24	0.32	0.56	0.59
	Big Creek	5	<0.001	-16131.39	19	118	32308.54	–	0.78	0.60	0.95
	PG South	8	<0.001	-9911.53	18	69	19872.75	–	0.51	0.59	0.75
		7	<0.001	-9914.21	17	69	19874.41	1.67	0.22	0.59	0.77
S	Entiako	5	<0.001	-38076.57	19	119	76198.81	–	0.27	0.54	0.79
		7	<0.001	-38078.02	18	119	76198.89	0.08	0.26	0.54	0.73
		6	<0.001	-38076.89	19	119	76199.45	0.64	0.20	0.54	0.80
	Big Creek	5	<0.001	-20068.89	19	108	40184.41	–	0.58	0.59	0.97
		9	<0.001	-20067.69	20	108	40185.03	0.62	0.42	0.60	0.98

Table 3.4. Continued.

Season	Study Area	Model	P	LL	k	n	AICc	ΔAIC_c	w_i	ROC	k-fold
S	PG South	8	<0.001	-12327.98	18	67	24706.20	–	0.43	0.58	0.88
		7	<0.001	-12330.31	17	67	24707.11	0.90	0.28	0.58	0.87
F	Entiako	7	<0.001	-31664.88	18	111	63373.19	–	0.48	0.53	0.69
		8	<0.001	-31664.31	19	111	63375.98	1.78	0.20	0.54	0.71
	Big Creek	9	<0.001	-17044.75	21	105	34142.62	–	0.63	0.60	0.87
		5	<0.001	-17046.86	20	105	34143.72	1.10	0.36	0.60	0.88
	PG South	9	<0.001	-10782.76	19	66	21620.05	–	0.51	0.57	0.82
		5	<0.001	-10785.37	18	66	21621.29	1.25	0.27	0.57	0.78
EW	Entiako	9	<0.001	-24528.56	19	111	49103.48	–	0.72	0.63	0.88
	Big Creek	9	<0.001	-13868.00	21	107	27788.87	–	1.00	0.71	0.96
	PG South	8	<0.001	-10350.61	18	71	20750.36	–	0.36	0.64	0.95
		7	<0.001	-10353.00	17	71	20751.55	1.19	0.20	0.64	0.92
		9	<0.001	-10349.63	19	71	20752.17	1.80	0.15	0.64	0.94

Table 3.5. Visual representation of coefficient values (positive or negative) from supported models (see Table 3.4) for within home-range selection by female moose in three study areas during five seasons (LW: Late Winter, C: Calving, S: Summer, F: Fall, EW: Early Winter) in central British Columbia using mixed-effects logistic regression.

Cover Class	Study Area	Season				
		LW	C	S	F	EW
Alpine	Entiako			—	—	
	Big Creek	—	+	+	—	—
	PG South					
Conifer	Entiako	+	—	+	+	—
	Big Creek	+	—	+	+	—
	PG South	+	+	+	+	—
Deciduous	Entiako	+	+	+	+	+
	Big Creek	+	+	+	+	+
	PG South	+	+	+	+	+
Fire Other	Entiako	+	+	+	+	+
	Big Creek	+	—	—	—	+
	PG South	—	—	+	+	+
Fire Pine	Entiako	—	—	—	—	—
	Big Creek	+	+	+	+	+
	PG South	+	+	+	+	+
Herbaceous	Entiako	+	+	+	+	+
	Big Creek	+	+	—	+	—
	PG South	—	—	—	—	—

Table 3.5. Continued.

Cover Class	Study Area	Season				
		LW	C	S	F	EW
New Cut	Entiako	—	—	—	+	+
	Big Creek	—	—	—	—	—
	PG South	+	+	—	+	+
Old Cut	Entiako	+	—	—	—	—
	Big Creek	+	—	—	—	—
	PG South	+	—	+	—	—
Old Fire	Entiako	+		+	—	+
	Big Creek	+	+	+	+	+
	PG South	+				
Pine	Entiako	—	—	+	—	—
	Big Creek	—	—	+	—	—
	PG South	+	+	+	+	—
Urban	Entiako	—	—			
	Big Creek	—			+	+
	PG South	—	—	—	—	—
Wetted	Entiako	+	—	—	—	+
	Big Creek	+	+	—	+	+
	PG South	+	+	+	+	+

vegetation cover classes by collared female moose and are discussed as such for the supported models.

We separated Conifer and Pine to determine differences in selection based on reduced canopy cover. Collared female moose in PG South selected Conifer and Pine throughout the year. In Big Creek and Entiako they only selected for Pine during the summer and showed selection for Conifer in Late Winter and Fall (Table 3.5; Appendix G). New Cutblocks and Old Cutblocks were separated to determine differences in ages and logging practices before and after the MPB-outbreak. Old Cutblocks were avoided by female moose in every season among study areas except for Late Winter when they were selected (exception: selection for Old Cutblocks in Summer in PG South). Conversely, New Cutblocks were selected in every season except Summer in PG South, completely avoided in Big Creek, and only selected in Fall and Early Winter in Entiako (Table 3.5, Appendix G). Wetted areas were selected in Early and Late Winter among all study areas, and only selected during Summer in PG South.

DISTANCE METRICS

No single distance metric was supported in all top seasonal and study-area models. In general, roads were avoided by moose, except during the Fall in Entiako, and during Calving in PG South (Appendix G). Distances to Mature Forest and Escapement cover were never included in the same model set due to collinearity. Collared female moose appeared to select for Mature Forest edges in Big Creek in all seasons, whereas Escapement cover distance was never included in any supported model in Big Creek (Table 3.4).

ELEVATION AND ASPECT

The base Topography model (comprised of elevation and aspect) was never supported by itself in any season or study area. Because Elevation and Aspect were included in every model, however, we could not make inferences about their statistical importance in the context of the other candidate models. Their inclusion was our attempt to use them as ecological surrogates for unavailable variables such as biogeoclimatic zones, moisture retention, shading, snow depth, etc. Generally, female moose selected low – mid elevations within their study area, except in PG South during Calving where they avoided mid elevations and selected for low and high elevations (Figure 3.8).

Selection for Aspect changed seasonally and by study area. Female moose in Entiako selected SW aspects in Late Winter, NW aspects in Calving, NE aspects in Summer and Fall, and NW aspects in Early Winter. Female moose in Big Creek selected NE aspects in Late Winter, Calving and Summer, and NW aspects in Fall and Early Winter. Prince George South animals selected SE aspects in Late Winter, NW aspects in Calving, NE aspects in Summer, SE aspects in Fall, and NW aspects in Early Winter.

DISCUSSION

Our study examined how collared female moose used three landscapes with differing degrees of MPB salvage logging about 14 years after most mature Pine in the study areas died due to a MPB outbreak (British Columbia Ministry of Forests 2007, Ritchie 2008, Walton 2010, Alfaro et al. 2015). Pine was the most used vegetation cover class in all three study areas, regardless of the main canopy being open due to dead standing trees. The use of New Cutblocks differed between study areas and seasons. Deciduous-leading stands were the only vegetation cover class selected in every study area and season regardless of the proportion of cutblocks. Trade-offs between browse quantity and cover, by season and study area were evident, where limiting factors in each study area result in differences in habitat selection for collared female moose in central BC.

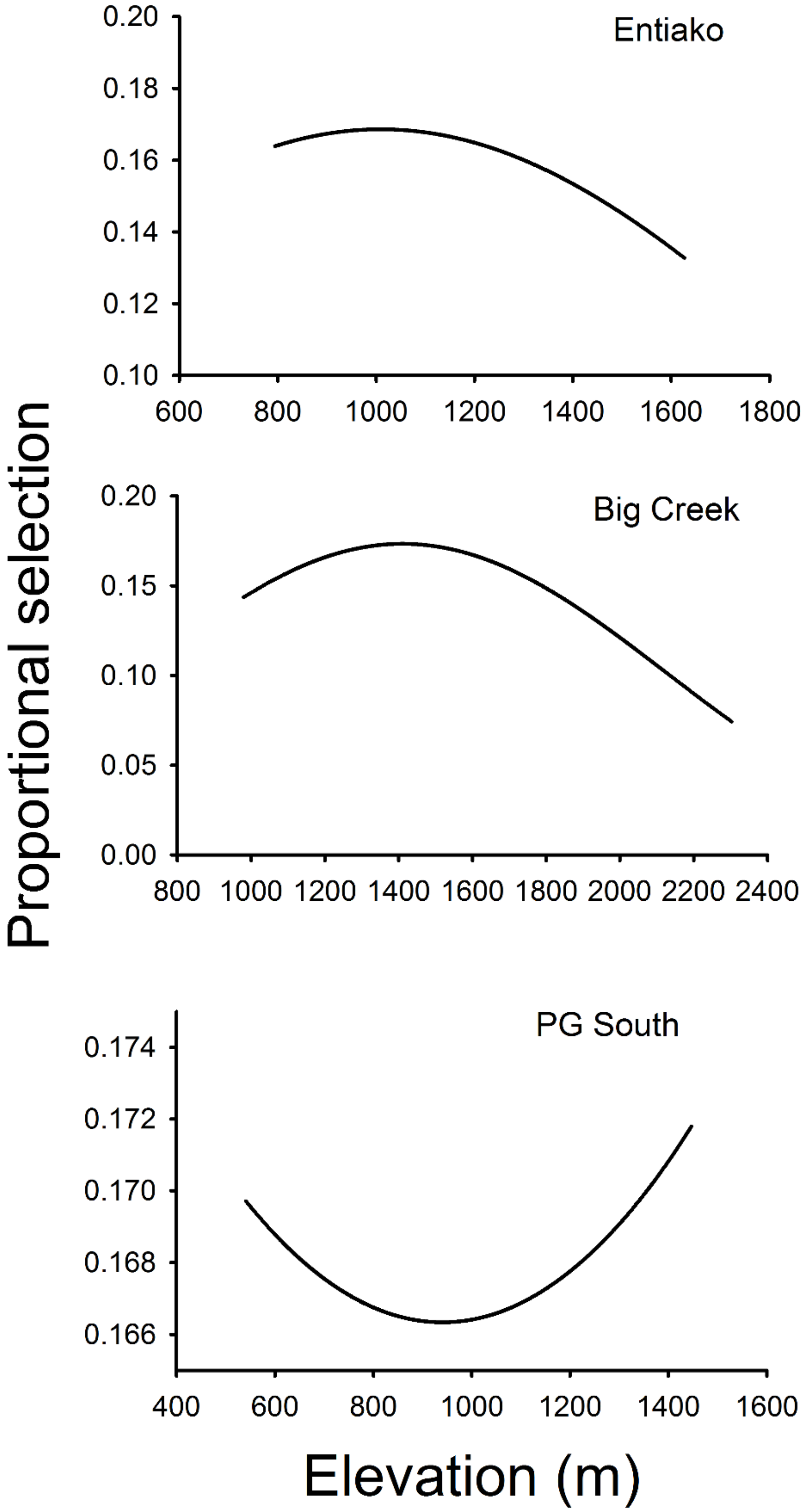

Figure 3.8. Example of predictive means based on the quadratic function for elevation from supported mixed-effects logistic regression models describing selection by GPS-collared female moose during Calving with data collected between April 25, 2014 – June 20, 2016 in Entiako, Big Creek, and PG South, central British Columbia.

A large-scale MPB outbreak significantly changed the landscape in a short time, followed by high intensity salvage logging (Alfaro et al. 2015) in all three study areas (Appendix E), but the landscapes and proportions of the landscape harvested differed. Habitat selection of collared female moose varied among study areas and seasons, suggesting that selection patterns are not consistent across their geographic range, landscape range, or home range (see also Chapter 2), and that they may ameliorate limiting factors or environmental needs (Courtois et al. 2002, Osko et al. 2004, Boyce 2006, McGarigal et al. 2016). We expected female moose to select for Pine stands killed by MPB that were not salvage-logged in response to the remaining habitat connectedness, horizontal cover (Ritchie 2008), and diverse, heterogeneous understories (Campbell and Antos 2015). We also predicted that other mature forest stands (Conifer and Deciduous) not harvested would be selected, as well as their interface edge to browse cover classes (Courtois et al. 2002).

Pine cover represented the most used cover classes (also the most available cover class; see Chapter 2) in all study areas (except Early and Late Winter in PG South), but it was not always selected seasonally. Conifer represented all other leading mature conifer stands (besides Pine) and we used it to help separate differences between living and dead conifer canopy cover. Compared to Pine, there were fewer locations in Conifer seasonally, but it was selected in more study areas seasonally than Pine. The use and selection of New Cutblocks created since the MPB outbreak differed tremendously among study areas which may be an artifact of the yearly categorical variables we used, regeneration differences, and silvicultural differences among study areas. Mature forest cover and browse interface (selection of Edge) was tested against Escapement Distance; female moose were more likely to be near a mature forest edge regardless of whether their location point was inside or outside of Mature Forest. Female moose avoided the highest road densities in these study areas when selecting home ranges (see Chapter 2) and avoided road proximity in the supported models for selection within home ranges. Between the two spatial scales studied, female moose tended to avoid anthropogenic corridors on the landscape following the MPB outbreak, and the selection for these features may be a by-product of landscape saturation.

More homogeneous landscapes are created through progressive landscape change (Scheffer et al. 2001) such as the salvage logging of vast expanses of MPB-killed lodgepole pine forests, reducing mature conifer cover and creating great proportions of early seral stage vegetation. The most evident example of this is from PG South, where 33% of the total study area has been harvested (1975 – 2015), not accounting for deforestation through the process of road building, farmlands, gravel pits, and other anthropogenic changes, reducing matrix habitat and mature forest cover. Open areas with no cover have been reported to be an average of 6°C warmer than conifer cover (Pigeon et al. 2016). In PG South, female moose are faced with the choice of selecting for remaining forest cover or browse created by early seral forest stands. Forest cover was highly selected in all seasons except for Early Winter, and New Cutblocks were selected in all seasons except Summer (Old Cutblocks selected for during the Summer). The proportion of used location points in New Cutblocks during Early Winter was over 40%, representing a tradeoff between cover and browse during this season.

During Early Winter, ambient temperatures are typically lower than Summer and Fall, and snow cover low enough to allow female moose to utilize potentially high-biomass browse areas; however, during the summer when ambient temperatures increase, it is likely that female moose avoid New Cutblocks and stay within cover to reduce thermal stress. In contrast, in Big Creek where the temperature is warmest, female moose selected for Conifer cover during Late Winter, Summer and Fall, and for Pine stands during the Summer, while avoiding New Cutblocks in all seasons. Female moose may avoid these areas due to thermoregulation costs, as well as reduced browse opportunities, because regenerating stands in this study area take much longer for sufficient browse to grow. These two study areas rapidly lost conifer cover through deforestation (11% and 19% of total landscape in Big Creek and PG South, respectively, since 2000; Appendix E), allowing for an increase in overall study area temperature and potentially resulting in female moose reaching the upper limit of thermoneutrality faster during all seasons than they may have otherwise. Because moose are sensitive to temperature (Renecker and Hudson 1986, Karns 1998), warmer temperatures may have cumulative impacts on survival (Lenarz et al. 2009). Studies with carnivores have shown reduced activity patterns and use of New Cutblocks during warm summer months, thereby reducing their ability to feed as efficiently (McLellan and McLellan 2015, Pigeon et al. 2016). Habitat selection by female moose suggests a response to high temperatures by utilizing Wetlands and New Cutblocks more during the twilight hours than during the day (Figure 3.2), as well as using Pine cover more during the Summer than any other season (Figure 3.6). This strategy may allow female moose to reduce the effects of a warming landscape (Melin et al. 2014, Street et al. 2015a), but may not allow female moose to forage efficiently or adequately to meet energetic requirements (Renecker and Hudson 1986, Murray et al. 2006, Kuzyk et al. 2016).

New Cutblocks were all harvested since 2000, aligning with pre-and post-salvage logging operations, when the size of cutblocks increased, and reserve zones between cutblocks decreased (to hinder spread of MPB) in order to salvage as much wood as possible before loss of marketability (Taylor and Carroll 2003). Old Cutblocks were <40 years old until the year 2000. Ritchie (2008) hypothesized that moose likely benefit from the creation of early seral habitat following the MPB outbreak in BC. We observed that the use of New Cutblocks and Old Cutblocks was approximately the same in Big Creek and Entiako, but the use of New Cutblocks was far greater than Old Cutblocks in PG South. This may be due to regeneration time, re-stocking standards, and silvicultural treatments to harvested cutblocks in these study areas as PG South has faster regeneration than Big Creek, and as a result, more intensive removal of deciduous species to get to free-to-grow stage. Old Cutblocks were primarily avoided in this study. Researchers commonly use 40 years as the cutoff between regenerating forests and mature cover (Kinley and Apps 2001, Poole et al. 2007, Lesmerises et al. 2012, Muhly 2016), where this seral stage of regenerating forest stands benefits moose (Bunnell et al. 2004, Janz 2006). Forest silvicultural practices have changed since the accepted stratification (<40 year old cutblocks provide beneficial forage for moose) trend commenced (Gasaway 1986), but the 40-year cutoff may be an overestimation based on the avoidance by moose (RSF models), little use, and selection of only recently harvested cutblocks (Table 3.4). Old Cutblocks may not contain sufficient vertical cover if they have been subjected to stand-tending, and historically high stocking standards in Pine plantations reduce available palatable browse for moose in these study areas. The temporal period that cutblocks are beneficial to moose may be significantly less than previously thought in areas where commercial logging places high priority on stand-tending and high stocking standards for non-palatable browse species (e.g., lodgepole pine; see Figures 3.5 and 3.7).

Lodgepole pine forests may not be considered suitable to moose, and salvage logging is believed to have few negative impacts on moose (Bunnell et al. 2004). The transition of the lodgepole pine forests following MPB, however, returns the stand to an earlier seral stage with diverse stand structure and deciduous regeneration (Campbell and Antos 2015) — in our study Pine was utilized by female moose. The benefits to moose of conserving dead standing lodgepole pine stands following the MPB outbreak likely outweigh the benefits from salvage logging these stands (>15 years post outbreak) with already reduced concealment and escapement cover, specifically in areas with slow regeneration of browse.

How moose perceive risk, vulnerability, or being in a risky area is unknown, but they often cannot avoid areas where predators live (Theuerkauf and Rouys 2008). Moose are more likely to be killed further from a forest edge (Kunkel and Pletscher 2000), and more likely to be killed near a road due to predator efficiency on linear corridors (James and Stuart-Smith 2000, Dickie et al. 2017). Our results suggest that female moose try to reduce their vulnerability to predation by selecting to be near forest edges in all seasons in Big Creek. In the other two study areas, however, collared female moose did not consistently select or avoid edge, potentially due to the provincial parks within the study area (and reduced forest-edge area in that area) or differing seasonal selection patterns in Entiako and PG South. Courtois et al. (2002) also observed that moose locations were located closer to edge between cover and browse than were random locations, especially during Late Winter. Others reported that female moose with calves avoided open areas (Dalton 1989, Eason 1989, Dussault 2002, Gillingham and Parker 2008*a*), and females with calves stayed closer to an edge than did females without calves (Thompson and Euler 1987). We did not observe a seasonal trend among the three study areas for selection of edge. Selection related to distance from a road also was not consistent across study areas or seasons. Linear corridors represent an easy pathway for moose to follow, reducing energetic expenditures, and the presence of roadside vegetation often offers palatable browse for moose (Rea 2003, Laurian et al. 2008). Roads have unknown consequences for the risk of mortality in these study areas, but road networks are known to increase landscape fragmentation, and allow hunters and predators access to landscapes otherwise more difficult for people and wolves. Research on grizzly bears (*Ursus arctos*) demonstrated that bear mortality rates were higher near roads, where it is easier for large mammals to travel, and thereby may spend more time on them (Kite et al. 2016). We suspect that back-tracking of collared moose in our study would reveal that moose use roads for travel (under-representation of roads; see Serrouya et al. 2017); however, due to the saturation (high road density) of roads and correlation between roads and anthropogenic seral stands, they were neither selected nor avoided consistently across study areas and seasons.

Deciduous cover was the only covariate with uniform selection in all study areas and seasons. This cover class was used significantly more than available, and the cover class was relatively rare on the landscape (Table 3.5, Figure 3.3-3.5, Appendix 2). Hence, deciduous-leading forest stands represent an important cover class to moose in all seasons regardless of the extent of salvage logging.

This study emphasizes that female moose have variable selection strategies across seasons and study areas, but in general, trade-offs between cover and browse drive their selection. Predictive accuracy of supported mixed-effects logistic regression models was good (Table 3.4, k-folds). Even though there often were multiple supported models for each season and study area, these supported models never conflicted or had opposing coefficients. Our analysis indicates that animals did not avoid Pine stands (predominantly dead standing canopy) following a MPB outbreak. New Cutblocks created from salvage logging these areas were not avoided consistently across all study areas or within a season. The benefit of young cutblocks to moose in areas with slow regeneration and clear-cutting operations, however, is likely very limited.

Anthropogenic changes to natural landscapes are often studied to determine if high-priority megafauna are negatively affected by these changes (Scheffer et al. 2001, Courbin et al. 2014, Ehlers et al. 2014, Johnson and Russell 2014, Cristescu et al. 2016, Lamb et al. 2017). The transition of landscapes from heterogeneous mosaics to homogeneous stands of regenerating coniferous forests or other monoculture plots can have negative consequences for wildlife (Gill et al. 1996, Arlettaz et al. 2015, MacNearney et al. 2016, Wilson 2016, Stewart and Komers 2017). Biological diversity is lost when heterogeneous landscapes are altered to homogenous ones (Hanski 2005), and the loss of megafauna has been observed through such landscape changes (Johnson 2002).

Management implications

Our results emphasize that female moose have variability in habitat selection like other studies before have reported (Courtois et al. 2002, Gillingham and Parker 2008*a*), and no single management decision is likely to benefit all moose across a landscape. Habitat selection by female moose is based on trade-offs among limiting factors affecting individual moose at independent spatial scales (Johnson 1980, Dussault et al. 2005*b*). Management recommendations differ depending on what goals are desired, and what limiting factors the species face in that area or season. In our study area of dry ecosystems with slow regeneration, palatable browse species could be planted near the edges of forest openings to enhance browse in New Cutblocks, and the benefits of edge for female moose. In systems where cutblocks represent a greater proportion than suitable mature forests, the need for leave-tree patches between cutblocks and a reduction in linear corridors is apparent. In all study areas, female moose utilized pine stands killed by MPBs. Resource managers need to determine at what cost salvaging pine beetle-killed wood and the additional road building and reduction in matrix habitat is to ensure suitable moose range in perpetuity.

Chapter 4 : Overview of habitat selection by female moose in a clear-cut world

THESIS SYNTHESIS

Moose (*Alces alces*) are a keystone species, and play an important role in predator-prey systems, nutrient cycling, and forest succession (Molvar et al. 1993, McLaren and Peterson 1994). Moose are considered an iconic species of the north: culturally important, offering subsistence, recreational, and economic values. Prior to 1860, there were no known records of moose in British Columbia's (BC) interior (Franzmann and Schwartz 1998), but during the 'invasion' of the BC interior in the late 19th century (Peterson 1955, Hatter 1970, Telfer 1984, Spalding 1990) and the coastal rainforests in the mid 1900's (Darimont et al. 2005), moose expanded their range throughout much of BC and their populations grew considerably. Forest harvesting since the mid-19th century created early seral stage habitats suitable for this expansion. Over the last 100 years, BC forests have transitioned from a natural state to a managed state, where natural disturbances such as fire are suppressed and forest harvesting has become the main disturbance agent on the landscape (Taylor and Carroll 2003).

Naturally occurring forest pests and pathogens commonly create outbreaks across small sections of a landscape (Martinat et al. 1987, Peltonen et al. 2002, Taylor and Carroll 2003, Romme et al. 2006). Most recently, a mass die-off of lodgepole pine (*Pinus contorta* var. *latifolia*) caused by an unprecedented outbreak of mountain pine beetle (*Dendroctonus ponderosae;* MPB) spread across western North America, including BC's central interior (Kurz et al. 2008). Subsequently, logging rates in BC have soared to over 15 million m^3 annually to salvage wood before it degrades to a point it cannot be used for profit, and thereby creating clear-cuts with little to no regenerating trees or course woody debris (Parfitt 2007).

Salvage logging of MPB-killed pine stands and other commercially valuable tree species were concurrent with observed changes in moose populations across certain areas of BC experiencing 50 – 70 % declines in moose numbers (Bunnell et al. 2004, Kuzyk and Heard 2014). Although it is not known whether the removal of MPB-killed forest stands would negatively affect moose populations, forest openings and linear corridors created by logging can increase susceptibility to predation and hunting pressure because of increased visibility until the plantations suitably regenerate (Forman and Alexander 1998, James and Stuart-Smith 2000, Janz 2006, Gillingham and Parker 2008*b*, Laurian et al. 2008, Dickie et al. 2017). Alternatively, early seral stages created by forest harvesting can provide abundant food sources for moose (Parker 1978, Schwartz et al. 1987, Lemke 1998, Courtois et al. 2002, Rea 2003, Dussault et al. 2005*a*). Cumulative impacts to moose are not well understood, but research in parasite transmission (Terry 2015), metabolic change due to movements and thermoregulation (Renecker and Hudson 1986, Karns 1998, Ritchie 2008), and lack of adequate cover for predator avoidance and snow interception (Dussault et al. 2005*b*, Beyer et al. 2010) are all concerns that wildlife managers are faced with following landscape change cause by forest harvesting.

To better understand how moose respond to MPB-killed lodgepole pine stands and clear-cuts as a result of salvage logging, the BC Provincial Government undertook a five-year study to examine causative factors associated with the perceived moose population declines in central BC (Kuzyk and Heard 2014, Kuzyk et al. 2016, Marshall et al. 2016, Werner and Anderson 2017). My research focused on a portion of the previously mentioned study by acquiring GPS locations from collared female moose to determine habitat selection at two spatial scales. Here, I review my major findings, link habitat selection for female moose across spatial scales, and propose recommendations for management of landscapes affected by MPB with recent forest harvesting activities.

Female moose were captured using aerial net-gunning or aerial chemical immobilization between December 2013 and March 2016 (BC Provincial Animal Care Permit CB17-277227) and fitted with a GPS Plus Vertex Survey collar (VECTRONIC Aerospace, Berlin, Germany (Vectronic)) or an ATS Iridium GPS G2110E collar (Advanced Telemetry Systems Inc., Insanti, MN (ATS)) by the BC Ministry of Forests Lands and Natural Resource Operations and Rural Development (FLNRORD) staff. Location data from three study areas and a total of 173 female moose between January 15, 2014 and April 25, 2017 were used for analysis (total number of animals differs between spatial scales; see Chapter 2 and Chapter 3). Location points of female moose were divided into five biologically relevant seasons (Late Winter: January 15 – April 25, Calving: April 26 – June 20, Summer: June 21 – September 12, Fall: September 13 – November 20, Early Winter: November 21 – January 14) adapted from Gillingham and Parker (2008*a*), trends observed in the three study areas, and from local and expert knowledge. A minimum of 30 location points per individual in a single season was required for an individual's seasonal data to be used in analyses.

Habitat selection is a hierarchical process with animals making decisions at different spatial scales (Johnson 1980). Therefore, location points of female moose were analyzed at two spatial scales: at a course scale (landscape or home-range scale, 2nd-order) and at a finer scale (within home-range, 3rd-order selection). I constructed individual seasonal home ranges (HRs) by buffering location points (Arthur et al. 1996, Walker et al. 2007) by each animal's 70th longest consecutive daily movement distance within that season. I then created circular replicates of the same area (available HRs) for each seasonal HR that were randomly distributed on the landscape and constrained to be 2 – 5 radii from the centroid of the used HR to avoid substantial overlap. For comparative purposes with other studies, I also constructed 100% minimum convex polygons (MCP) HRs (Eddy 1977) for each animal-season combination. To assess within home-range selection, I generated five available location points (Burnham and Anderson 2001) for each used location point, randomly within each individual's 95th longest seasonal daily movement buffer (Gillingham and Parker 2008*a*). The distances used for home-range and within home-range selection represent the most reasonable distance an animal would likely travel under normal movements, excluding rare movements, without underrepresenting availability for animals that do not move as much within that season.

Daily movements were greatest in Big Creek and shortest in PG South, with exceptions in Late Winter and Calving (Chapter 2). Daily movements were also longest during the Summer and shortest in Late Winter in all study areas. Pine-leading forests were the most prevalent cover class and made up the greatest proportion of moose HRs; they also were the most used vegetation cover class within home-ranges for most seasons, regardless of the main forest canopy being dead standing or wind-thrown dead pine with subsequent forest succession. New Cutblocks created by forest harvesting of these Pine stands and others were not unanimously selected or avoided among study areas and seasons. Study area differences and forestry practices likely contribute to the use of early successional stands by female moose.

Female moose had shorter daily movements during the winter than they did during the summer, which is consistent with other studies (Phillips et al. 1973, Gillingham and Parker 2008*b*). Seasonal home ranges were smaller in PG South — the study area with the greatest proportion of forest harvesting than in the other study areas. Daily movement distances and home-range size did not increase with increasing road densities as other researchers have reported (Courtois et al. 2002).

Vegetation cover was intrinsically linked to within home-range selection; however, home-range selection differed where animals avoided landscape attributes, rather than selecting for them. These differences reveal how animals respond on the landscape at different spatial scales in response to limiting factors or environmental needs (Courtois et al. 2002, Osko et al. 2004, Boyce 2006, McGarigal et al. 2016). Comparing use and availability of both spatial scales revealed that female moose selected for geographic areas and sites that provided the heterogeneous habitats they use most often.

Home-range selection is the spatial scale that most directly impacts animal fitness (Leblond et al. 2013). Female moose HRs were mostly comprised of Pine in every study area and season except for PG South in Early Winter where female moose used a greater proportion of New Cutblocks. The same trend was observed within home ranges where female moose used Pine more than any other cover class except during Early Winter in Big Creek and PG South, and Late Winter in PG South. Regardless of study area, Pine cover was used most during the Summer, and least during Early Winter. Pine stands in each of the study areas are presumed to be dead due to the MPB outbreak, and therefore, the canopy provided as vertical cover is likely greatly reduced for thermal protection and snow interception (Boon 2012). Even with the reduced vertical cover, horizontal cover for predator avoidance may have increased because of the MPB outbreak (due to early seral flush, and windblown trees). Use of Pine by female moose is likely a result of the security cover provided, which is not available in high salvage-logged areas, as well as the diverse understory of browse available through succession since the MPB outbreak, and the habitat connectedness remaining as potential travel corridors between salvage-logged areas (Campbell and Antos 2015).

The increased use of New Cutblocks by moose during the Early Winter is likely based on trade-offs between cover and browse acquisition. New Cutblocks, if silvicultural treatments such as mechanical and chemical removal of deciduous species have not been implemented, can create an early seral stage providing abundant browse and horizontal cover for moose. Home-range selection with avoidance of New Cutblocks was not parsimonious among study areas, seasons, or spatial scales. Homogenous landscapes created by monoculture crops, and extensive landscape change through salvage-logged forests, were avoided at the scale of home-range selection, but selection of cutblocks within home ranges was mixed depending on study area and season. Broadly, female moose living in drier landscapes avoided cutblocks more often than in wetter landscapes (such as PG South), which may be due to the greater quantities of regenerating browse in wetter landscapes before extensive stand tending that physically or chemically removes deciduous species. Older cutblocks in drier areas experienced more use by moose than newer ones, although were only selected for during Late Winter in Entiako and Big Creek (3rd-order selection), indicating that our cutblock age class designation may not characterize moose browse abundance similarly across the central interior of BC. Alternatively, with reduced browse and warmer temperatures, female moose may avoid open areas created by salvage logging due to thermoregulation constraints (Renecker and Hudson 1986, Karns 1998), which may have cumulative impacts on fitness (Lenarz et al. 2009). Female moose showed differential selection of cutblocks depending on where they lived and time of year.

Where browse is lower due to slow regeneration of cutblocks in areas where moose lived prior to extensive landscape change, lakes, wetlands, and shrubby cover would likely be the most important cover classes. In Big Creek and Entiako, female moose used Wetted areas more during the winter than Summer. This may reflect a trade-off between browse-poor cutblocks and naturally occurring browse from Wetted areas. In contrast, in PG South where female moose increase their use in cutblocks, the number of visits to Wetted areas (based on GPS locations) decreased during the winter (although Wetted was selected for in all seasons in PG South). Besides the trade-off between alternate high-biomass browse sources, female moose used Wetted areas more often during the night or twilight hours of the day than they did during the daylight.

The only covariate in my study consistently selected across study areas and season was Deciduous cover. Deciduous cover made up a small proportion of each study area (1 – 6%); however, this vegetation cover class was visited significantly more than available and, therefore, represents an important cover class to moose in all seasons regardless of extent of salvage logging.

Because there were differences in selection at the home-range (Chapter 2) and within home-range (Chapter 3) scales, I compared vegetation use and availability at both spatial scales using selection ratios (Manly et al. 2007). I standardized the selection ratios so any selection ratio >0.11 indicates positive selection (based on nine vegetation cover classes; see

Manly et al. 2007). Changes in selection ratios between spatial scales indicate a switch in selection between where home ranges are located and what animals select within those home ranges.

Selection ratio indices calculated for female moose indicate that selection across spatial scales was similar (Figures 4.1 – 4.3), suggesting that selection at the HR scale reduces limiting factors, and within HR selection shows preferred vegetation cover to facilitate daily requirements. Differences between spatial scales were less common. During the Summer in Entiako, female moose avoided Pine Fire and Other Fire in their choice of HR, but increased their use of these two classes within their HR (Figure 4.1). This may be due to browse availability within these new fire areas, but because a recent large wildfire present in Entiako, the relationship was not observed at the HR scale. Alternatively, in Big Creek during the Fall, the opposite trend was observed relative to Other Fires as new fires were much less common (Appendix E) — female moose selected for them at the HR scale, but avoided them within their HR (Figure 4.2). Selection indices for PG South were consistent across spatial scales except for New Cutblocks and Old Cutblocks in Summer and Early Winter, respectively (Figure 4.3). Female moose selected for these vegetation classes in their choice of HR, but avoided them within their HR potentially due to thermal stress, and preferred browse locations, respectively.

My study is limited by the number of moose locations (fixes) received per day (and missing fixes from un-collected collars) and the scale at which I could investigate differences. All study areas had a large portion of their landscape altered by the MPB. Because a large component of each study area was Pine and most of it died, there was no comparative data for use of living mature pine forests. This research is also limited because

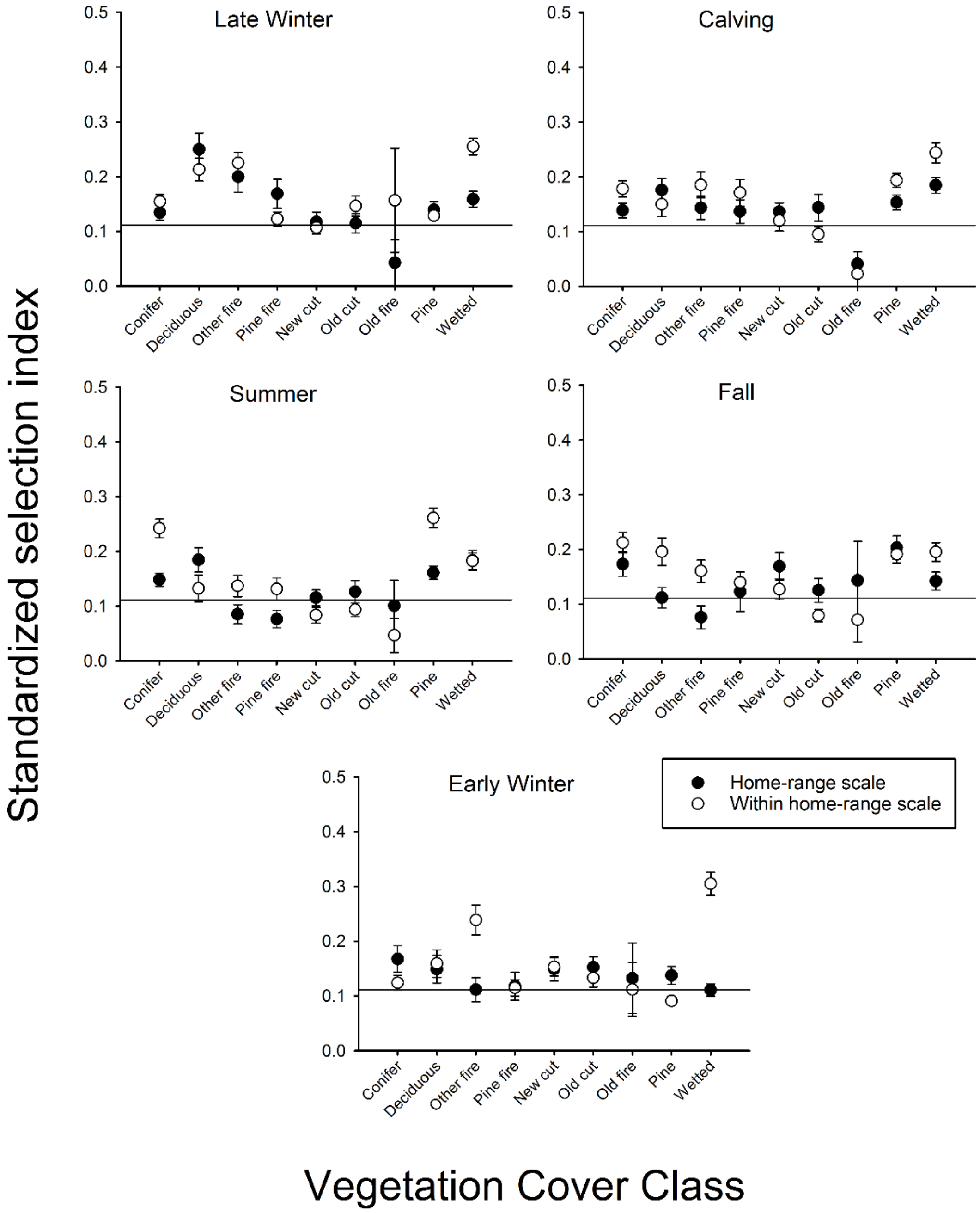

Figure 4.1. Comparison of used proportions (± SE) of vegetation cover classes for female moose in home range and within home range selection in Entiako using standardized selection ratio indices. Horizontal reference line indicates either positive (above the line) or negative (below the line) selection for that cover class given individual animal selection. Vegetation cover classes are described in Table 3.2.

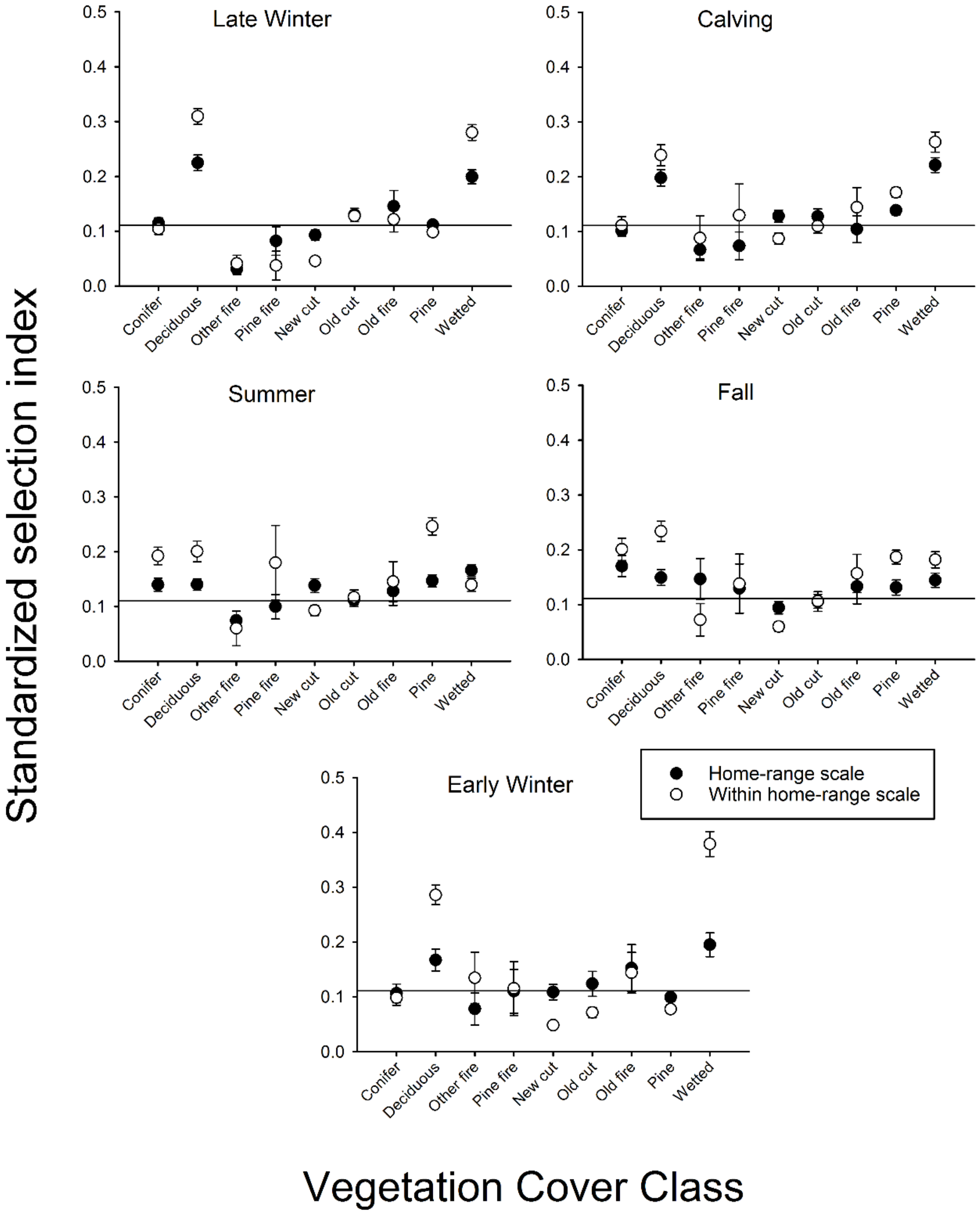

Figure 4.2. Comparison of used proportions (± SE) of vegetation cover classes for female moose in home range and within home range selection in Big Creek using standardized selection ratio indices. Horizontal reference line indicates either positive (above the line) or negative (below the line) selection for that cover class given individual animal selection. Vegetation cover classes are described in Table 3.2.

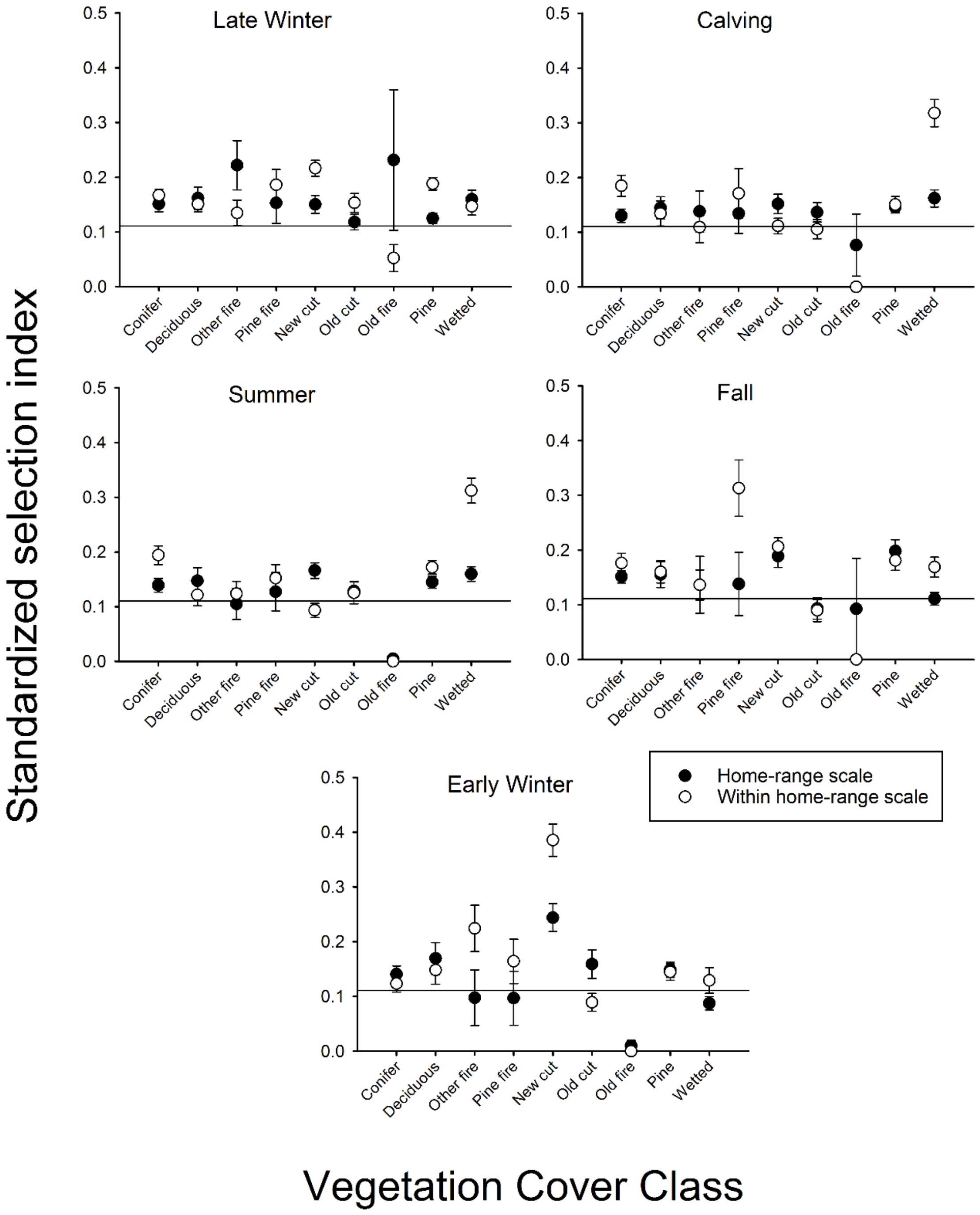

Figure 4.3. Comparison of used proportions (± SE) of vegetation cover classes for female moose in home range and within home range selection in PG South using standardized selection ratio indices. Horizontal reference line indicates either positive (above the line) or negative (below the line) selection for that cover class given individual animal selection. Vegetation cover classes are described in Table 3.2.

all study areas have predators with unknown densities, and I was unable to test theories of escapement cover or dash-distance differences on high and low predation landscapes. Lastly, I could not include a variable for parturient females versus females with no calves to test whether habitat selection by female moose differed depending on calf status.

In summary, female moose utilized dead standing Pine forests, but the cumulative effect on demography is unknown. Logging following the MPB outbreak increased the number of linear corridors; cutblocks were selected or avoided based on the assumed browse availability in the blocks; and areas with the greatest proportion of roads and forest openings were avoided. The need for sufficient cover is evident with the avoidance of highly logged areas of landscapes and the use of conifer and deciduous cover during all seasons. This avoidance is likely based on the Intermediate Disturbance Hypothesis, whereby clear-cut areas may provide browse, but when clear-cuts exceed a threshold on the landscape, they no longer provide sufficient moose habitat.

MANAGEMENT RECOMMENDATIONS

Over the course of this research, evidence of high variability in habitat selection among female moose became increasingly evident. Individual moose appear to have consistent habitat-selection strategies, but individuals are quite different, and study area differences exacerbate the variance. Because of differences in habitat selection among collared female moose in central BC, there is no single management action that would improve fitness for all moose on the landscape. There are, however, management levers that I believe would benefit most moose on the landscape, depending on what their limiting factors appear to be geographically.

Worldwide, megafauna and biological diversity are lost due to progressive anthropogenic landscape change (Johnson 2002, Hanski 2005). Forest harvesting can alter ecosystems from a heterogeneous state to a more homogeneous one (Scheffer et al. 2001). Following the MPB outbreak and subsequent salvage logging, plantations are carefully stand-tended to remove deciduous browse, creating an environment for moose where browse is limited, temperatures are warmer, predator efficiency is heightened, and disease transmission may be accelerated. In this study, female moose avoided homogeneous landscapes and selected heterogenous home ranges, avoiding the highest proportions of disturbance on the landscape. I propose that if managers want more moose, smaller clearings should be considered with more mature timber between stands to provide adequate food-cover areas for female moose, in combination with reductions in linear corridors. Spatial distribution of small clearings and mature forest would spatially distribute moose more evenly across the landscape. DeLong and Tanner (1996) proposed that larger cutblocks could be implemented with the lack of large wildfire-replacing events (due to increased forest fire fighting), but their concept was contingent on having numerous unburned (or uncut) patches within the clearing. In contrast, salvage-logged blocks are generally very large and have little to no leave-tree patches, inconsistent with DeLong and Tanner's (1996) recommendations.

Although my research did not investigate survival or risk of moose relative to linear features, female moose avoided the highest road densities at the HR scale, and avoided proximity of roads within home-range selection. Roads represent travel corridors not only for moose, but also for predators where efficiency of predation on moose is greatly increased (James and Stuart-Smith 2000, Dickie et al. 2017). I recommend rehabilitation of roads to reduce access and sightability by predators and humans. If clear-cuts are to represent natural stand-replacing events to an earlier seral stage, I also see merit in replanting linear corridors such as spur-roads with a mix of deciduous and coniferous species to not only provide browse and cover for moose, but to reduce road density, re-establish continuous forests, and restore corridors to a productive forested site.

Pine forests that were not cut following the MPB outbreak are highly utilized by female moose. I propose leaving the remaining MPB-killed Pine stands intact as they maintain forest heterogeneity in vertical and horizontal structure, diversity of understory species, and high stocking standards (Alfaro et al. 2015, Winter et al. 2015). I believe if forest harvesting of MPB-killed Pine stands continues in these study areas, moose populations will continue to decline as the rate of deforestation greatly exceeds the regrowth needed to provide adequate moose habitat. We may also wish to 'learn from this past' relative to moose response following large-scale beetle infestations because many parts of BC are currently experiencing the greatest Spruce beetle (*Dendroctonus rufipennis*) outbreak since the 1980s (FLNRORD 2016), and subsequent salvage logging is similar to clear-cutting practices used for MPB.

Selection of New Cutblocks varied greatly among study areas. I believe this is based on two factors: the geography and local climate within the study areas, and the forestry stand-tending practices within the study areas. If managers wish to improve moose browse and cover within clear-cuts, I recommend reducing stand-tending regulations for the free-to-grow stage so deciduous species that moose require will be more prevalent on the landscape. Additionally, on dry sites, I recommend planting species such as willow (*Salix* spp.), red-osier dogwood (*Cornus stolonifera*), high-bush cranberry (*Viburnum edule*), and other preferred species to help speed up succession where regeneration is slow, primarily focusing on the perimeter of clear-cuts where female moose select for edge.

My research shows in heavily deforested areas, that female moose exhibit trade-offs between cover and browse areas; by allowing deciduous browse to freely grow, negative impacts of reduced cover may be mitigated with plentiful food sources, reducing cumulative impacts with ease of accessing browse. This trade-off would only be viable if the remaining mature forests were protected from forest harvesting for intrinsic wildlife values given the enormity of landscape disturbance already present and uncertainty in future forest health. By no means do these study areas represent the most disturbed landscapes in the province of British Columbia, and results from my thesis may highlight mid-levels of disturbance; more heavily modified landscapes likely will or have seen a more drastic reduction in moose population numbers. Future research should assess productivity of dry Pine stands in relation to suitable moose habitat, define strategies that female moose with calves use to minimize calf mortality, and investigate landscape attributes that result in mortality of female moose in central BC.

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Appendix A. GPS collar fix rate differences between uploaded and downloaded collars

Table A1. Differences in GPS-collar fix rate ($\bar{x}$ and parenthetic SD) between uploaded (received through GPS Plus X Vectronic software) and downloaded (using Vectronic key to manually download collars following a mortality) Globalstar GPS Plus Vertex Survey collars (*n* = 44) on female moose between January 15, 2014 and April 25, 2017 in three study areas in central British Columbia. Results show that collars store on board an average of 10 – 20% more location points, and once downloaded, fix rates were >90%. Resource managers should be aware of implications of not downloading collars after retrieval if they are experiencing low fix rates.

Study Area	*n*	Download %	Upload %	Difference %
Entiako	12	93.8 (15.8)	73.7 (17.7)	20.1 (10.9)
Big Creek	22	98.9 (1.1)	88.5 (9.3)	10.5 (8.5)
PG South	10	96.7 (2.4)	78.4 (8.7)	18.2 (6.8)

Appendix B. Differences in assessing the use of vegetation class by female moose with locations received via satellite transmission and locations directly downloaded from GPS collars

Introduction

Researchers are understandably concerned when Global positioning system (GPS) collars fail to retrieve 100% of their fix locations, and often associate the missing fixes with vegetation, topography (Webb et al. 2013) and animal behaviour (Heard et al. 2008). Any missing fixes can result in a potential bias associated with data interpretation (Frair et al. 2004), particularly if any attribute of interest, for example vegetation cover, affects GPS fix acquisition (Frair et al. 2010). Several attempts at correcting for missing fixes have been developed (Nielson et al. 2009, Webb et al. 2013), but those corrections tend to be targeted at correcting for missing cover classes, and do not correct for locations of animals when the fix was missed — something that is needed in resource selection models that contain 'distance-to' attributes.

The number of programmed fixes per day potentially influences fix success. For example, the time-to-fix varies depending on how long it has been since the GPS receiver last received a fix — longer time between fixes increases the time-to-fix, which is also affected by satellite geometry and vegetation cover (see https://www.maptoaster.com/maptoaster-topo-nz/articles/how-gps-works/how-gps-works.html for an example). Further, the loss of one or two fixes per day in an hourly fix schedule is far less problematic for telemetry studies than is one or two consecutive missed fixes when a collar is programmed to only receive one fix per day.

More recent advances in GPS technology have enabled collars to remotely transmit received data via satellite or cellular networks. To upload collar-stored GPS fixes via satellite, however, requires separate collar-satellite communication, which can be further affected by transmitting and receiving conditions. Our objective here is to compare estimates of vegetation cover class use between data remotely uploaded by GPS collars during deployment on female moose and data from the same collars obtained via direct download (once those collars were recovered) to determine if there were any systematic biases in the GPS-uploaded data (the only data available if collars were not recovered).

Methods

This appendix includes data collected by Vectronic GPS Plus Survey collars (VECTRONIC Aerospace, Berlin, Germany), which were set for one location point per day. Data were regularly uploaded from GPS Plus X software (referred to as uploads, hereafter), although missing fixes existed in this database. Following mortalities of collared moose, however, collars were recovered, and data were retrieved from them (referred to as collar downloads, hereafter) by directly downloading information on the collar to an attached computer. The collars were set to receive the uploaded fix for only three minutes to conserve battery life. If the fix failed to send during that time, the fix was stored onboard the collar and could only be downloaded if the collar was retrieved either by end of study, or during mortality investigations.

Locations for uploaded and downloaded data were queried in the GIS using ArcMap (ESRI Corp. 2014) to determine the vegetation cover class for each fix. Vegetation cover classes were determined post hoc using spatial data provided by BC Data Distribution Services; spatial layers were queried for dominant (leading) cover species to determine the predominant cover class for each location point. We then calculated the proportion of cover-class use by animal for all points (i.e., from download) and for only uploaded data. For each vegetation cover class, we then regressed the proportion of use from the download on the proportion of use from the uploaded data. If the confidence interval (95% CI) around the slope of a regression included the value of 1, we considered there to be no bias in the uploaded data. Regressions for vegetation cover classes with slope significantly >1 indicated classes that were under represented in the uploaded data, and of potential concern. Regressions with slopes significantly <1 (i.e., there was a higher proportion of a vegetation cover class in the upload than in the download) were also of concern but were likely the result of other classes being underestimated given the dependence of proportional use across all cover classes. All statistical analyses were conducted with Stata 14 (StataCorp 2015).

Results and Discussion

In all cases (n = 33), recovered collars contained more fixes than had been uploaded through the Globalstar satellite system. Fix success improved from 53.0 – 97.2 % ($\bar{x}$ = 85.9%) for the uploaded data to 93.6 – 100.0% ($\bar{x}$ = 98.6%) for the downloaded data. We therefore suspected that any bias was not with the acquisition of the GPS location because the downloaded fix rates were so high that there was little room for bias, but rather with the relay of that information through the satellite uplink.

There were no differences in the proportion of use of Alpine, Deciduous, Fire Other, Old Cut, and Old Fire Vegetation Cover Classes (Table B1) between uploaded and downloaded collar data for female moose. The uploaded data, however, appeared to overestimate use of Fire Pine (by 2%), Herbaceous (by 19%), New Cut (by 13%), Urban (by 10%) and Wetted (by 9%) Vegetation Cover Classes. Concurrently, uploaded data

Table B1. Results of regressing proportion of vegetation cover classes in GPS-collar downloads on collar uploads (see text). Vegetation cover classes with slopes significantly <1 (^{U} superscript on Cover Class) or significantly >1 (^{O} superscript on Cover Class) were significantly under or overestimated with points from the collar upload, respectively. Cover classes are defined in Table 3.2.

Cover Class	Slope	SE	Lower CI	Upper CI	Comment
Alpine	1.00	0.001	0.999	1.002	
Conifer^U	1.05	0.019	1.012	1.091	Underestimated by 5%
Deciduous	1.02	0.025	0.964	1.066	
Fire Other	0.99	0.020	0.949	1.031	
Fire Pine^O	0.99	0.006	0.973	0.998	Overestimated by 2%
Herbacious^O	0.81	0.014	0.781	0.836	Overestimated by 19%
New Cut^O	0.87	0.023	0.827	0.921	Overestimated by 13%
Old Cut	0.99	0.010	0.968	1.010	
Old Fire	1.03	0.018	0.994	1.067	
Pine^U	1.06	0.024	1.015	1.112	Underestimated by 6%
Urban^O	0.91	0.020	0.865	0.944	Overestimated by 10%
Wetted^O	0.91	0.022	0.865	0.954	Overestimated by 9%

underestimated the use of Conifer (by 5%) and Pine (by 6%) use by collared moose. Taken together this suggests that it is the openness of the vegetation type during upload and not GPS signal acquisition that introduces fix bias for these collars.

Our second approach was to look to see if there were any relationships between the proportion of missed fixes and cover type. Missed fixes were expressed as a proportion of the total number of fixes in a cover class so that differences were not just mirroring use information. The proportion of missing fixes by animal and cover type were then calculated. Results from proportions of missing fixes by cover type indicate that other than Urban class, for which there is very little use by moose, none of the cover types had appreciably different missing fix rates (Figure B1). Additionally, across animals and seasons, there is approximately a 15 % chance of missing fixes in any given cover class (Figure B1) except for Urban where the likelihood of missing a fix is less common.

Although in most RSF studies, it is impossible to retrieve all collars to download for additional data (due to animals surviving, collar failure, data collection cut off prior to study end date, etc.), we wanted to determine if there were any systematic biases in fix transmission associated with vegetation cover classes, i.e., habitat bias. At the time of any moose mortality, all data from the collar were uploaded from GPS Plus X software from the time of collar deployment to time of mortality. Data were sorted by date, and all fixes with missing geographic locations were removed from the data set. Once collars were recovered from mortality investigations, collars were downloaded and all fixes that successfully acquired a location were added to a spreadsheet. Both uploads and collar downloads were sorted by date in the same spreadsheet and then duplicate fixes were removed (if upload was

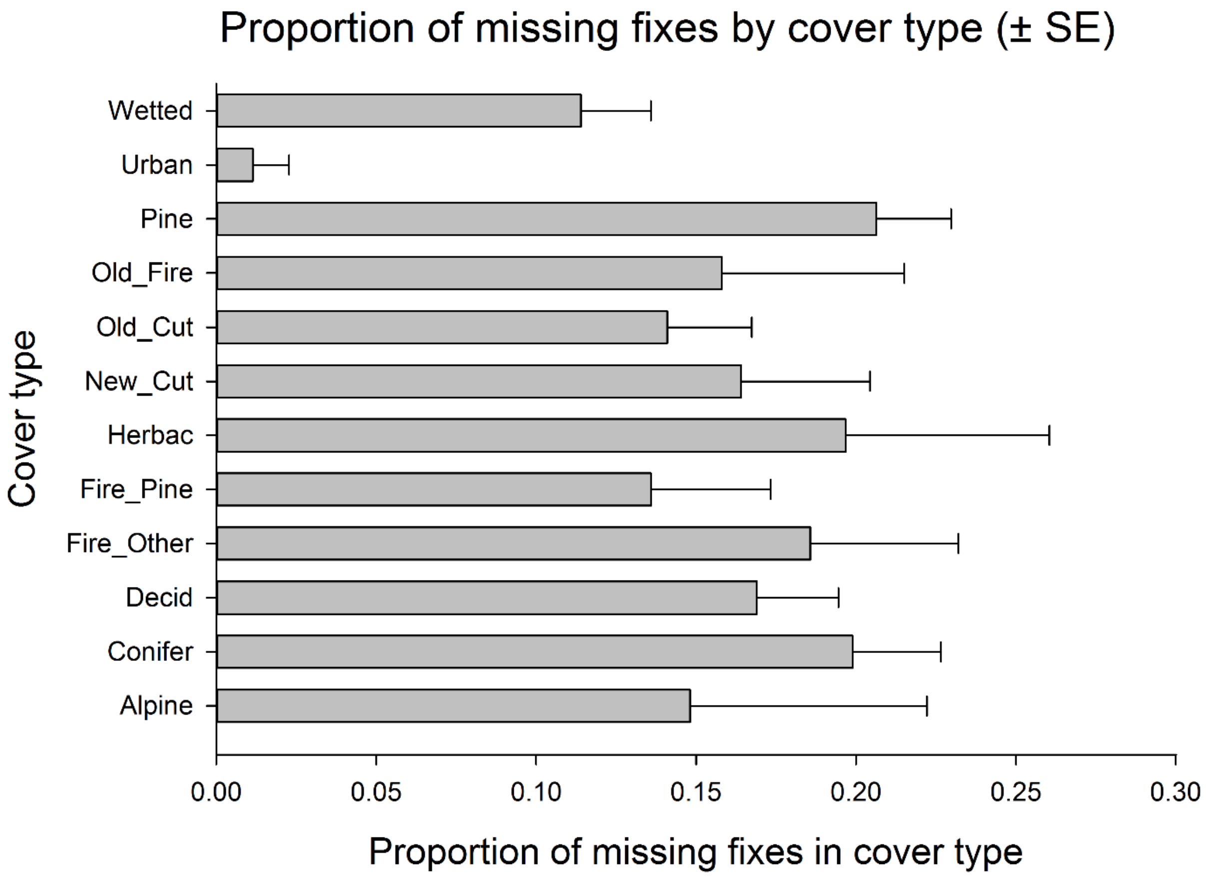

Figure B.1. Proportion of missing fixes relative to proportion of used cases in each cover class using one fix-a-day GPS collars on female moose in central British Columbia.

present, collar download was removed; if upload was not present, collar download increased fix rate). Once all retrieved collars were downloaded, we summarized data by animal, source of data (upload or download), and vegetation cover class type at the time of fix. We then calculated the fix rate of uploads only, and then the fix rate using both sources of location data.

Conclusions

Given the results and previous studies, there are no corrections that can be made suitable for RSF studies including ‘distance-to’ parameters, and therefore, the only way to increase fix rate is to directly download GPS collars following retrieval. Un-retrieved collars may still have low fix rates, which equates to having fewer points for analysis. Unfortunately, this study illustrates that any vegetation cover class is susceptible to having missing fixes, and classes with more canopy cover are more likely to have underrepresentation in RSF than classes with open canopies. Recommendations for researchers who are concerned about low fix rates would be to recover all collars if study objectives permit (e.g., use of drop off mechanism) or to use Iridium collars that continually attempt uploads until confirmation of upload is received by the collar. Future studies could further refine this bias test by adding topographical variables which are known to affect collar performance (Lewis et al. 2007). This study was conducted on relatively flat plateaus, and therefore, topography was believed to have negligible effects.

Appendix C. Pearson correlation coefficients for female moose home-range size of female moose and landscape attributes

Table C1. Pearson correlation coefficients (*r*) for home-range size (km^2) of female moose and: proportion of cutblocks, road density (km•km^{-2}), and habitat richness in central British Columbia. The number of individual home ranges is indicated by n. *P*-values indicate correlation test results. Significant *P* (≤ 0.05) values are indicated by an *.

Season	Study Area	*n*	Proportion of Cutblocks		Road Density		Habitat Richness	
			P	*r*	*P*	*r*	*P*	*r*
LW	Entiako	91	0.596	0.056	0.301	0.110	0.003	0.305*
	Big Creek	126	0.093	0.150	0.799	-0.023	0.011	0.226*
	PG South	80	0.166	0.157	0.563	0.066	0.019	0.262*
C	Entiako	95	0.430	0.082	0.161	0.145	0.138	0.153
	Big Creek	118	0.000	0.353*	0.005	0.258*	0.000	0.324*
	PG South	68	0.106	0.198	0.986	-0.002	0.347	0.116
S	Entiako	93	0.408	0.087	0.845	0.021	0.142	0.154
	Big Creek	107	0.084	0.168	0.046	0.193*	0.014	0.238*
	PG South	66	0.640	0.059	0.019	-0.288*	0.562	0.073
F	Entiako	52	0.438	-0.110	0.245	-0.164	0.767	0.042
	Big Creek	67	0.588	-0.068	0.126	-0.189	0.032	0.263*
	PG South	35	0.401	0.147	0.470	-0.126	0.044	0.342*
EW	Entiako	55	0.265	-0.153	0.396	-0.117	0.009	0.348*
	Big Creek	72	0.838	0.025	0.284	-0.128	0.054	0.228
	PG South	40	0.716	0.060	0.073	-0.287	0.313	0.164

Appendix D. Coefficients for supported models for home-range selection by female moose in central British Columbia.

Table D1. Coefficients (with parenthetic SE) for supported models for female moose in central British Columbia within three study areas and five seasons (LW = Late Winter, C = Calving, S = Summer, F = Fall, and EW = Early Winter). Parameters include Conifer (CO), Pine (PI), Deciduous (D), Water (W), New Cutblock (NC), Old Cutblock (OC), Pine Fire (FP), Other Fire (FO), Old Fire (OF), Road density km•km^{-2} (RD), Habitat Richness (HR), and Mature Forest (MF). Blanks indicate that the specific coefficient was not present in the model.

Season	Study Area	Model	Parameter											
			CO	PI	D	W	NC	OC	FP	FO	OF	RD	HR	MF
LW	Entiako	Hab. Rich.											0.9 (0.13)	
	Big Creek	Saturated	13.08 (6.1)	9.29 (5.13)	41.97 (7.54)	27.52 (6.09)	9.77 (5.41)	14 (5.33)	16.96 (8.52)	-23.23 (13.11)	13.02 (7.22)	0.63 (0.3)	0.97 (0.17)	
	PG South	Hab. Rich.											0.55 (0.13)	
		Saturated	2.97 (2.51)	1.08 (2.61)	2.27 (3.04)	-3.12 (4.12)	2.57 (2.45)	1.25 (2.74)	5.25 (3.04)	4.64 (3.11)	37.32 (30.25)	-0.22 (0.22)	0.73 (0.15)	
		Anthropog Dist.					0.38 (0.99)					-0.26 (0.18)	0.57 (0.13)	
C	Entiako	Hab. Rich.											0.72 (0.12)	
	Big Creek	Saturated	-1.47 (2.97)	0.79 (2.12)	12.76 (3.54)	6.36 (2.34)	2.31 (2.23)	2.99 (2.66)	3.21 (2.78)	-9.62 (7.3)	15.63 (8.77)	-0.2 (0.27)	0.46 (0.13)	
	PG South	Access/ Stress										-0.29 (0.19)		
		Vulnerability										-0.42 (0.22)		-1.18 (0.89)
		Water				2.15 (1.92)								
		Hab. Rich.											0.12 (0.12)	

Table D1. Continued.

Season	Study Area	Model	Parameter											
			CO	PI	D	W	NC	OC	FP	FO	OF	RD	HR	MF
S	Entiako	Hab. Rich.											0.72 (0.12)	
	Big Creek	Anthropog. Disturb					2.28 (1.07)					-0.48 (0.24)	0.33 (0.11)	
		Hab. Rich.											0.28 (0.11)	
	PG South	Accessibility					1.52 (1.43)		4.37 (2.03)	-1.87 (2.86)		-0.44 (0.22)		
		Access/ Stress										-0.46 (0.2)		
		Vulnerability										-0.6 (0.24)		-1.21 (0.95)
F	Entiako	Anthropog. Disturb					7.34 (3.2)					-0.91 (0.46)	0.5 (0.16)	
		Saturated	13.08 (6.1)	9.29 (5.13)	41.97 (7.54)	27.52 (6.09)	9.77 (5.41)	14 (5.33)	16.96 (8.52)	-23.23 (13.11)	13.02 (7.22)	0.63 (0.3)	0.97 (0.17)	
	Big Creek	Saturated	6.42 (4.26)	1.1 (2.35)	10.78 (5.35)	5.1 (3.32)	1.29 (2.87)	-0.62 (3.75)	3.57 (3.41)	3.69 (8.11)	54.99 (17.78)	0.06 (0.48)	0.58 (0.2)	
		Water & Natural Browse			8.89 (4.06)	2.06 (2.14)				10.04 (7.33)	54.75 (16.12)			
	PG South	Saturated	15.13 (7.34)	19.25 (7.79)	23.94 (9.21)	5.41 (8.66)	18.23 (7.32)	14.53 (7.3)	26.02 (9.86)	7.82 (11.7)	-4 (76.63)	-0.6 (0.4)	0.23 (0.24)	
		Access/ Stress										-0.73 (0.31)		

Table D1. Continued.

Season	Study Area	Model	Parameter											
			CO	PI	D	W	NC	OC	FP	FO	OF	RD	HR	MF
EW	Entiako	Anthropog. Disturb					4.97 (2.82)					0 (0.39)	0.7 (0.15)	
		Hab. Rich.											0.66 (0.14)	
	Big Creek	Water & All Browse			16.03 (4.22)	14.19 (2.8)	3.49 (1.4)	2.7 (2.08)		7.3 (9.32)	22.02 (8.18)			
		Saturated	2.68 (7.4)	4.53 (4.99)	21.42 (7.41)	19.87 (6.01)	8.19 (5.23)	8.06 (5.77)	5.66 (6.33)	3.53 (10.66)	22.51 (9.99)	-0.43 (0.46)	0.48 (0.17)	
	PG South	Water & All Browse			3.98 (2.06)	-15.19 (6.74)	5.43 (1.76)	-3.06 (2.47)		4.78 (2.96)	-630.91 (916.11)			

Appendix E. Composition (%) of vegetation cover classes in three study areas in central British Columbia

Table E1. Percent of vegetation cover classes within each study area in central British Columbia using the study area boundaries in Figure 2.1 and Figure 3.1. Study area boundaries represent the 100% MCP of all used locations of female moose between January 15, 2014 – April 25, 2017. Cover percentages represent the actual proportions within the study areas as opposed to what was obtained using availability for each individual home range (HR) and within HR selection.

Vegetation Cover Class	Study Areas		
	Entiako	Big Creek	PG South
Alpine	1.38	15.14	<0.01
Bryoid	0.01	<0.01	<0.01
Conifer	18.91	13.09	12.77
Deciduous	1.15	3.60	5.52
Fire Other	3.90	0.77	2.23
Fire Pine	12.41	1.16	3.21
Herbaceous	0.68	1.69	0.93
New Cut	4.71	9.68	19.08
Non-Veg	0.04	0.21	0.08
Old Cut	4.47	8.80	14.29
Old Fire	0.16	0.41	0.36
Pine	39.19	38.93	32.70
Urban	0.13	0.37	1.28
Wetted	12.88	6.16	7.54

Appendix F. Vegetation cover classes removed from mixed-effects logistic regression models

Table F1. Vegetation cover classes removed from mixed-effects logistic regression model sets for within home-range selection by female moose to avoid complete separation following methods by Menard (2002) in central British Columbia during five seasons: Late Winter (LW), Calving (C), Summer (S), Fall (F) and Early Winter (EW). Cover classes are defined in Table 3.2.

Season	Study Area	Vegetation cover class
LW	Entiako	Alpine
	Big Creek	Non-Veg
	PG South	Alpine, Non-Veg
C	Entiako	Alpine, Non-Veg, Old Fire
	Big Creek	Non-Veg, Urban
	PG South	Alpine, Non-Veg, Old Fire
S	Entiako	Non-Veg, Urban
	Big Creek	Non-Veg, Urban
	PG South	Alpine, Non-Veg, Old Fire
F	Entiako	Non-Veg, Urban
	Big Creek	Non-Veg
	PG South	Alpine, Non-Veg, Old Fire
EW	Entiako	Alpine, Non-Veg, Urban
	Big Creek	Non-Veg
	PG South	Alpine, Non-Veg, Old Fire

Appendix G. Details for supported seasonal resource selection model coefficients for collared female moose in central British Columbia.

Table G1. Results of supported seasonal resource selection function (RSF) model coefficients using mixed-effects logistic regression for GPS-collared female moose in three study areas during five seasons in central British Columbia. Variables are defined in Table 3.2, models are described in Table 3.3.

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Late Winter	9	elevkm	3.26	1.00	3.26	<0.001	1.30	5.23
Big Creek	Late Winter	9	elevkm2	-1.19	0.36	-3.29	<0.001	-1.89	-0.48
Big Creek	Late Winter	9	east	0.05	0.01	3.32	<0.001	0.02	0.07
Big Creek	Late Winter	9	north	0.13	0.01	9.76	<0.001	0.11	0.16
Big Creek	Late Winter	9	Alpine	-1.98	0.55	-3.63	<0.001	-3.05	-0.91
Big Creek	Late Winter	9	Conifer	0.13	0.07	1.99	0.05	0.00	0.26
Big Creek	Late Winter	9	Decid	1.06	0.06	17.10	<0.001	0.94	1.18
Big Creek	Late Winter	9	Fire_Other	0.02	0.14	0.16	0.87	-0.26	0.30
Big Creek	Late Winter	9	Fire_Pine	0.31	0.14	2.30	0.02	0.05	0.58
Big Creek	Late Winter	9	Herbac	0.48	0.09	5.29	<0.001	0.30	0.66
Big Creek	Late Winter	9	New_Cut	-0.80	0.06	-12.56	<0.001	-0.93	-0.68
Big Creek	Late Winter	9	Old_Cut	0.28	0.06	4.51	<0.001	0.16	0.40
Big Creek	Late Winter	9	Old_Fire	0.78	0.09	8.85	<0.001	0.61	0.96
Big Creek	Late Winter	9	Pine	-0.20	0.06	-3.35	<0.001	-0.31	-0.08
Big Creek	Late Winter	9	Urban	-0.98	0.22	-4.57	<0.001	-1.41	-0.56
Big Creek	Late Winter	9	Wetted	0.89	0.06	14.77	<0.001	0.78	1.01
Big Creek	Late Winter	9	road_distkm	0.03	0.02	1.85	0.06	0.00	0.06
Big Creek	Late Winter	9	mature_distkm	-0.90	0.07	-13.53	<0.001	-1.03	-0.77
Big Creek	Late Winter	9	2015	0.05	0.04	1.52	0.13	-0.02	0.13

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Late Winter	9	2016	0.02	0.04	0.59	0.55	-0.05	0.09
Big Creek	Late Winter	9	2017	0.05	0.04	1.36	0.17	-0.02	0.13
Big Creek	Late Winter	9	Constant	-3.91	0.69	-5.70	<0.001	-5.26	-2.57
Big Creek	Late Winter	5	elevkm	2.96	0.98	3.01	<0.001	1.03	4.89
Big Creek	Late Winter	5	elevkm2	-1.07	0.35	-3.02	<0.001	-1.76	-0.37
Big Creek	Late Winter	5	east	0.05	0.01	3.30	<0.001	0.02	0.07
Big Creek	Late Winter	5	north	0.13	0.01	9.77	<0.001	0.11	0.16
Big Creek	Late Winter	5	Alpine	-1.97	0.55	-3.61	<0.001	-3.04	-0.90
Big Creek	Late Winter	5	Conifer	0.13	0.07	1.96	0.05	0.00	0.26
Big Creek	Late Winter	5	Decid	1.06	0.06	17.08	<0.001	0.94	1.18
Big Creek	Late Winter	5	Fire_Other	0.02	0.14	0.17	0.86	-0.26	0.31
Big Creek	Late Winter	5	Fire_Pine	0.33	0.14	2.41	0.02	0.06	0.59
Big Creek	Late Winter	5	Herbac	0.48	0.09	5.29	<0.001	0.30	0.66
Big Creek	Late Winter	5	New_Cut	-0.81	0.06	-12.71	<0.001	-0.93	-0.68
Big Creek	Late Winter	5	Old_Cut	0.27	0.06	4.38	<0.001	0.15	0.39
Big Creek	Late Winter	5	Old_Fire	0.78	0.09	8.81	<0.001	0.61	0.95
Big Creek	Late Winter	5	Pine	-0.20	0.06	-3.36	<0.001	-0.31	-0.08
Big Creek	Late Winter	5	Urban	-0.99	0.22	-4.60	<0.001	-1.41	-0.57
Big Creek	Late Winter	5	Wetted	0.90	0.06	14.79	<0.001	0.78	1.01
Big Creek	Late Winter	5	mature_distkm	-0.88	0.07	-13.40	<0.001	-1.01	-0.75
Big Creek	Late Winter	5	2015	0.06	0.04	1.55	0.12	-0.01	0.13
Big Creek	Late Winter	5	2016	0.02	0.04	0.59	0.56	-0.05	0.09
Big Creek	Late Winter	5	2017	0.05	0.04	1.35	0.18	-0.02	0.13
Big Creek	Late Winter	5	Constant	-3.72	0.68	-5.49	<0.001	-5.04	-2.39
Big Creek	Calving	5	elevkm	4.57	1.10	4.14	<0.001	2.40	6.73

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Calving	5	elevkm2	-1.60	0.37	-4.31	<0.001	-2.33	-0.87
Big Creek	Calving	5	east	0.07	0.02	3.13	<0.001	0.02	0.11
Big Creek	Calving	5	north	0.01	0.02	0.49	0.62	-0.03	0.05
Big Creek	Calving	5	Alpine	0.39	0.13	2.91	<0.001	0.13	0.65
Big Creek	Calving	5	Conifer	-0.39	0.07	-5.27	<0.001	-0.54	-0.25
Big Creek	Calving	5	Decid	0.28	0.06	4.82	<0.001	0.17	0.40
Big Creek	Calving	5	Fire_Other	-0.56	0.24	-2.35	0.02	-1.02	-0.09
Big Creek	Calving	5	Fire_Pine	0.65	0.14	4.79	<0.001	0.38	0.91
Big Creek	Calving	5	Herbac	0.16	0.16	0.98	0.33	-0.16	0.47
Big Creek	Calving	5	New_Cut	-0.81	0.05	-15.25	<0.001	-0.92	-0.71
Big Creek	Calving	5	Old_Cut	-0.41	0.06	-6.97	<0.001	-0.52	-0.29
Big Creek	Calving	5	Old_Fire	0.76	0.12	6.35	<0.001	0.53	0.99
Big Creek	Calving	5	Pine	-0.29	0.04	-6.76	<0.001	-0.38	-0.21
Big Creek	Calving	5	Wetted	0.22	0.05	4.42	<0.001	0.12	0.32
Big Creek	Calving	5	mature_distkm	-0.40	0.06	-7.16	<0.001	-0.51	-0.29
Big Creek	Calving	5	2015	-0.01	0.03	-0.21	0.83	-0.08	0.06
Big Creek	Calving	5	2016	0.02	0.03	0.65	0.51	-0.05	0.09
Big Creek	Calving	5	Constant	-4.51	0.81	-5.56	<0.001	-6.10	-2.92
Big Creek	Summer	5	elevkm	6.97	0.87	8.00	<0.001	5.27	8.68
Big Creek	Summer	5	elevkm2	-2.31	0.28	-8.11	<0.001	-2.86	-1.75
Big Creek	Summer	5	east	0.09	0.02	4.95	<0.001	0.06	0.13
Big Creek	Summer	5	north	0.18	0.02	9.42	<0.001	0.14	0.22
Big Creek	Summer	5	Alpine	0.42	0.10	4.31	<0.001	0.23	0.61
Big Creek	Summer	5	Conifer	0.10	0.06	1.81	0.07	-0.01	0.22
Big Creek	Summer	5	Decid	0.19	0.06	3.35	<0.001	0.08	0.30

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Summer	5	Fire_Other	-0.36	0.19	-1.95	0.05	-0.73	0.00
Big Creek	Summer	5	Fire_Pine	0.53	0.11	4.96	<0.001	0.32	0.74
Big Creek	Summer	5	Herbac	-0.26	0.19	-1.39	0.16	-0.62	0.11
Big Creek	Summer	5	New_Cut	-0.80	0.05	-16.21	<0.001	-0.89	-0.70
Big Creek	Summer	5	Old_Cut	-0.20	0.05	-3.72	<0.001	-0.31	-0.10
Big Creek	Summer	5	Old_Fire	0.66	0.13	4.96	<0.001	0.40	0.92
Big Creek	Summer	5	Pine	0.00	0.04	0.08	0.94	-0.07	0.08
Big Creek	Summer	5	Wetted	-0.28	0.05	-5.25	<0.001	-0.39	-0.18
Big Creek	Summer	5	mature_distkm	-0.26	0.05	-5.68	<0.001	-0.34	-0.17
Big Creek	Summer	5	2015	-0.01	0.03	-0.33	0.74	-0.07	0.05
Big Creek	Summer	5	2016	0.00	0.03	0.15	0.88	-0.06	0.07
Big Creek	Summer	5	Constant	-6.65	0.66	-10.07	<0.001	-7.94	-5.35
Big Creek	Summer	9	elevkm	7.35	0.91	8.08	<0.001	5.57	9.13
Big Creek	Summer	9	elevkm2	-2.44	0.30	-8.16	<0.001	-3.02	-1.85
Big Creek	Summer	9	east	0.09	0.02	5.00	<0.001	0.06	0.13
Big Creek	Summer	9	north	0.18	0.02	9.33	<0.001	0.14	0.22
Big Creek	Summer	9	Alpine	0.42	0.10	4.28	<0.001	0.23	0.61
Big Creek	Summer	9	Conifer	0.10	0.06	1.74	0.08	-0.01	0.22
Big Creek	Summer	9	Decid	0.19	0.06	3.30	<0.001	0.08	0.30
Big Creek	Summer	9	Fire_Other	-0.36	0.19	-1.94	0.05	-0.73	0.00
Big Creek	Summer	9	Fire_Pine	0.53	0.11	4.99	<0.001	0.32	0.74
Big Creek	Summer	9	Herbac	-0.26	0.19	-1.41	0.16	-0.63	0.10
Big Creek	Summer	9	New_Cut	-0.79	0.05	-16.01	<0.001	-0.89	-0.69
Big Creek	Summer	9	Old_Cut	-0.20	0.05	-3.61	<0.001	-0.31	-0.09
Big Creek	Summer	9	Old_Fire	0.66	0.13	4.98	<0.001	0.40	0.92
Big Creek	Summer	9	Pine	0.00	0.04	0.01	0.99	-0.07	0.07

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Summer	9	road_distkm	0.01	0.01	1.56	0.12	0.00	0.02
Big Creek	Summer	9	mature_distkm	-0.26	0.05	-5.79	<0.001	-0.35	-0.17
Big Creek	Summer	9	2015	-0.01	0.03	-0.33	0.74	-0.07	0.05
Big Creek	Summer	9	2016	0.00	0.03	0.06	0.95	-0.06	0.06
Big Creek	Summer	9	Constant	-6.91	0.69	-10.08	<0.001	-8.26	-5.57
Big Creek	Fall	9	elevkm	5.50	1.00	5.52	<0.001	3.55	7.46
Big Creek	Fall	9	elevkm2	-1.75	0.32	-5.47	<0.001	-2.38	-1.12
Big Creek	Fall	9	east	0.09	0.02	4.50	<0.001	0.05	0.13
Big Creek	Fall	9	north	-0.03	0.02	-1.56	0.12	-0.07	0.01
Big Creek	Fall	9	Alpine	-0.34	0.11	-3.21	<0.001	-0.55	-0.13
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Big Creek	Fall	9	Conifer	0.08	0.07	1.09	0.28	-0.06	0.21
Big Creek	Fall	9	Decid	0.36	0.06	5.58	<0.001	0.23	0.49
Big Creek	Fall	9	Fire_Other	-0.04	0.15	-0.28	0.78	-0.33	0.25
Big Creek	Fall	9	Fire_Pine	0.39	0.12	3.39	<0.001	0.17	0.62
Big Creek	Fall	9	Herbac	0.06	0.17	0.37	0.72	-0.27	0.40
Big Creek	Fall	9	New_Cut	-1.14	0.07	-17.08	<0.001	-1.27	-1.01
Big Creek	Fall	9	Old_Cut	-0.19	0.07	-2.90	<0.001	-0.32	-0.06
Big Creek	Fall	9	Old_Fire	0.46	0.11	4.38	<0.001	0.26	0.67
Big Creek	Fall	9	Pine	-0.17	0.05	-3.16	<0.001	-0.27	-0.06
Big Creek	Fall	9	Urban	0.52	0.44	1.16	0.25	-0.35	1.39
Big Creek	Fall	9	Wetted	0.01	0.06	0.15	0.88	-0.11	0.13
Big Creek	Fall	9	road_distkm	0.01	0.01	2.07	0.04	0.00	0.02
Big Creek	Fall	9	mature_distkm	-0.26	0.05	-5.27	<0.001	-0.36	-0.16
Big Creek	Fall	9	2015	0.00	0.03	-0.08	0.94	-0.07	0.07
Big Creek	Fall	9	2016	0.01	0.03	0.23	0.82	-0.06	0.08

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Fall	9	Constant	-5.62	0.77	-7.31	<0.001	-7.12	-4.11
Big Creek	Fall	5	elevkm	4.85	0.94	5.19	<0.001	3.02	6.68
Big Creek	Fall	5	elevkm2	-1.52	0.30	-5.12	<0.001	-2.11	-0.94
Big Creek	Fall	5	east	0.09	0.02	4.43	<0.001	0.05	0.13
Big Creek	Fall	5	north	-0.03	0.02	-1.44	0.15	-0.07	0.01
Big Creek	Fall	5	Alpine	-0.35	0.11	-3.23	<0.001	-0.56	-0.14
Big Creek	Fall	5	Conifer	0.08	0.07	1.19	0.24	-0.05	0.22
Big Creek	Fall	5	Decid	0.37	0.06	5.67	<0.001	0.24	0.49
Big Creek	Fall	5	Fire_Other	-0.04	0.15	-0.27	0.79	-0.33	0.25
Big Creek	Fall	5	Fire_Pine	0.40	0.12	3.44	<0.001	0.17	0.62
Big Creek	Fall	5	Herbac	0.06	0.17	0.37	0.71	-0.27	0.40
Big Creek	Fall	5	New_Cut	-1.15	0.07	-17.24	<0.001	-1.28	-1.02
Big Creek	Fall	5	Old_Cut	-0.20	0.07	-3.04	<0.001	-0.33	-0.07
Big Creek	Fall	5	Old_Fire	0.46	0.11	4.36	<0.001	0.25	0.67
Big Creek	Fall	5	Pine	-0.16	0.05	-3.06	<0.001	-0.26	-0.06
Big Creek	Fall	5	Urban	0.51	0.44	1.15	0.25	-0.36	1.38
Big Creek	Fall	5	Wetted	0.01	0.06	0.23	0.82	-0.11	0.14
Big Creek	Fall	5	mature_distkm	-0.26	0.05	-5.18	<0.001	-0.35	-0.16
Big Creek	Fall	5	2015	0.00	0.03	-0.06	0.95	-0.07	0.07
Big Creek	Fall	5	2016	0.01	0.03	0.42	0.67	-0.05	0.08
Big Creek	Fall	5	Constant	-5.15	0.73	-7.09	<0.001	-6.57	-3.73
Big Creek	Early Winter	9	elevkm	2.29	1.23	1.87	0.06	-0.11	4.69
Big Creek	Early Winter	9	elevkm2	-0.77	0.41	-1.88	0.06	-1.57	0.03
Big Creek	Early Winter	9	east	0.10	0.02	4.48	<0.001	0.06	0.15
Big Creek	Early Winter	9	north	-0.02	0.02	-0.95	0.34	-0.07	0.02

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Big Creek	Early Winter	9	Alpine	-0.54	0.15	-3.56	<0.001	-0.84	-0.24
Big Creek	Early Winter	9	Conifer	-0.40	0.08	-5.17	<0.001	-0.55	-0.25
Big Creek	Early Winter	9	Decid	0.73	0.06	13.03	<0.001	0.62	0.84
Big Creek	Early Winter	9	Fire_Other	0.45	0.16	2.88	<0.001	0.14	0.76
Big Creek	Early Winter	9	Fire_Pine	0.50	0.15	3.30	<0.001	0.20	0.80
Big Creek	Early Winter	9	Herbac	-0.14	0.16	-0.85	0.39	-0.46	0.18
Big Creek	Early Winter	9	New_Cut	-1.03	0.06	-17.79	<0.001	-1.14	-0.91
Big Creek	Early Winter	9	Old_Cut	-0.36	0.06	-5.86	<0.001	-0.48	-0.24
Big Creek	Early Winter	9	Old_Fire	0.37	0.12	3.06	<0.001	0.13	0.61
Big Creek	Early Winter	9	Pine	-0.79	0.05	-17.03	<0.001	-0.88	-0.70
Big Creek	Early Winter	9	Urban	0.32	0.23	1.40	0.16	-0.13	0.77
Big Creek	Early Winter	9	Wetted	0.88	0.05	17.22	<0.001	0.78	0.98
Big Creek	Early Winter	9	road_distkm	0.05	0.01	4.64	<0.001	0.03	0.07
Big Creek	Early Winter	9	mature_distkm	-0.91	0.09	-10.63	<0.001	-1.08	-0.74
Big Creek	Early Winter	9	2015	-0.05	0.05	-1.16	0.25	-0.15	0.04
Big Creek	Early Winter	9	2016	0.16	0.05	3.24	<0.001	0.06	0.26
Big Creek	Early Winter	9	Constant	-2.97	0.91	-3.28	<0.001	-4.75	-1.19
Entiako	Late Winter	6	elevkm	5.42	0.93	5.83	<0.001	3.60	7.25
Entiako	Late Winter	6	elevkm2	-2.46	0.43	-5.74	<0.001	-3.31	-1.62
Entiako	Late Winter	6	east	-0.03	0.01	-2.91	<0.001	-0.06	-0.01
Entiako	Late Winter	6	north	-0.06	0.01	-5.15	<0.001	-0.08	-0.04
Entiako	Late Winter	6	Conifer	0.11	0.06	2.02	0.04	0.00	0.23
Entiako	Late Winter	6	Decid	0.32	0.07	4.75	<0.001	0.19	0.45
Entiako	Late Winter	6	Fire_Other	0.26	0.06	4.46	<0.001	0.14	0.37
Entiako	Late Winter	6	Fire_Pine	-0.41	0.06	-7.31	<0.001	-0.52	-0.30
Entiako	Late Winter	6	Herbac	0.63	0.08	8.33	<0.001	0.48	0.78

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Late Winter	6	New_Cut	-0.06	0.06	-1.10	0.27	-0.18	0.05
Entiako	Late Winter	6	Nonveg	0.47	0.36	1.30	0.19	-0.23	1.17
Entiako	Late Winter	6	Old_Cut	0.01	0.06	0.17	0.86	-0.10	0.12
Entiako	Late Winter	6	Old_Fire	0.41	0.19	2.20	0.03	0.04	0.78
Entiako	Late Winter	6	Pine	-0.22	0.05	-4.15	<0.001	-0.32	-0.11
Entiako	Late Winter	6	Urban	-1.95	0.38	-5.11	<0.001	-2.70	-1.21
Entiako	Late Winter	6	Wetted	0.44	0.05	8.13	<0.001	0.33	0.55
Entiako	Late Winter	6	Escape_cov	0.02	0.01	3.48	<0.001	0.01	0.03
Entiako	Late Winter	6	2015	-0.08	0.02	-3.46	<0.001	-0.12	-0.03
Entiako	Late Winter	6	2016	-0.04	0.03	-1.56	0.12	-0.09	0.01
Entiako	Late Winter	6	2017	0.00	0.03	-0.13	0.90	-0.06	0.05
Entiako	Late Winter	6	Constant	-4.48	0.50	-8.90	<0.001	-5.47	-3.50
Entiako	Late Winter	10	elevkm	5.52	0.93	5.94	<0.001	3.70	7.34
Entiako	Late Winter	10	elevkm2	-2.50	0.43	-5.84	<0.001	-3.34	-1.66
Entiako	Late Winter	10	east	-0.03	0.01	-2.96	<0.001	-0.06	-0.01
Entiako	Late Winter	10	north	-0.06	0.01	-5.03	<0.001	-0.08	-0.03
Entiako	Late Winter	10	Conifer	0.11	0.06	1.97	0.05	0.00	0.22
Entiako	Late Winter	10	Decid	0.32	0.07	4.77	<0.001	0.19	0.45
Entiako	Late Winter	10	Fire_Other	0.26	0.06	4.42	<0.001	0.14	0.37
Entiako	Late Winter	10	Fire_Pine	-0.41	0.06	-7.35	<0.001	-0.52	-0.30
Entiako	Late Winter	10	Herbac	0.63	0.08	8.32	<0.001	0.48	0.78
Entiako	Late Winter	10	New_Cut	-0.06	0.06	-1.05	0.29	-0.18	0.05
Entiako	Late Winter	10	Nonveg	0.47	0.36	1.31	0.19	-0.23	1.17
Entiako	Late Winter	10	Old_Cut	0.01	0.06	0.23	0.82	-0.10	0.12
Entiako	Late Winter	10	Old_Fire	0.41	0.19	2.20	0.03	0.05	0.78
Entiako	Late Winter	10	Pine	-0.22	0.05	-4.22	<0.001	-0.32	-0.12

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Late Winter	10	Urban	-1.95	0.38	-5.10	<0.001	-2.70	-1.20
Entiako	Late Winter	10	road_distkm	0.00	0.00	1.63	0.10	0.00	0.01
Entiako	Late Winter	10	Escape_cov	0.02	0.01	3.33	<0.001	0.01	0.03
Entiako	Late Winter	10	2015	-0.08	0.02	-3.56	<0.001	-0.12	-0.03
Entiako	Late Winter	10	2016	-0.05	0.03	-1.88	0.06	-0.10	0.00
Entiako	Late Winter	10	2017	-0.01	0.03	-0.33	0.74	-0.06	0.04
Entiako	Late Winter	10	Constant	-4.54	0.50	-9.03	<0.001	-5.53	-3.56
Entiako	Calving	5	elevkm	3.90	1.03	3.77	<0.001	1.87	5.93
Entiako	Calving	5	elevkm2	-1.80	0.47	-3.81	<0.001	-2.72	-0.87
Entiako	Calving	5	east	0.11	0.02	6.43	<0.001	0.07	0.14
Entiako	Calving	5	north	-0.11	0.02	-6.80	<0.001	-0.14	-0.08
Entiako	Calving	5	Conifer	-0.07	0.04	-1.76	0.08	-0.15	0.01
Entiako	Calving	5	Decid	0.59	0.07	8.19	<0.001	0.45	0.73
Entiako	Calving	5	Fire_Other	0.24	0.05	4.63	<0.001	0.14	0.34
Entiako	Calving	5	Fire_Pine	-0.20	0.04	-4.70	<0.001	-0.29	-0.12
Entiako	Calving	5	Herbac	0.97	0.09	10.51	<0.001	0.79	1.15
Entiako	Calving	5	New_Cut	-0.12	0.05	-2.37	0.02	-0.23	-0.02
Entiako	Calving	5	Old_Cut	-0.65	0.06	-11.17	<0.001	-0.77	-0.54
Entiako	Calving	5	Pine	-0.16	0.03	-5.18	<0.001	-0.22	-0.10
Entiako	Calving	5	Urban	-0.55	0.20	-2.83	0.01	-0.94	-0.17
Entiako	Calving	5	Wetted	-0.03	0.04	-0.73	0.46	-0.10	0.04
Entiako	Calving	5	mature_distkm	-0.02	0.01	-1.72	0.09	-0.04	0.00
Entiako	Calving	5	2015	0.00	0.03	-0.05	0.96	-0.05	0.05
Entiako	Calving	5	2016	0.01	0.03	0.43	0.66	-0.05	0.07
Entiako	Calving	5	Constant	-3.57	0.56	-6.34	<0.001	-4.67	-2.46

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Calving	7	elevkm	3.75	1.03	3.64	<0.001	1.73	5.77
Entiako	Calving	7	elevkm2	-1.73	0.47	-3.69	<0.001	-2.65	-0.81
Entiako	Calving	7	east	0.11	0.02	6.36	<0.001	0.07	0.14
Entiako	Calving	7	north	-0.11	0.02	-6.77	<0.001	-0.14	-0.08
Entiako	Calving	7	Conifer	-0.07	0.04	-1.63	0.10	-0.14	0.01
Entiako	Calving	7	Decid	0.60	0.07	8.29	<0.001	0.46	0.74
Entiako	Calving	7	Fire_Other	0.22	0.05	4.39	<0.001	0.12	0.32
Entiako	Calving	7	Fire_Pine	-0.24	0.04	-6.49	<0.001	-0.32	-0.17
Entiako	Calving	7	Herbac	0.98	0.09	10.65	<0.001	0.80	1.16
Entiako	Calving	7	New_Cut	-0.12	0.05	-2.20	0.03	-0.22	-0.01
Entiako	Calving	7	Old_Cut	-0.65	0.06	-11.06	<0.001	-0.76	-0.53
Entiako	Calving	7	Pine	-0.16	0.03	-5.00	<0.001	-0.22	-0.09
Entiako	Calving	7	Urban	-0.55	0.20	-2.80	0.01	-0.93	-0.16
Entiako	Calving	7	Wetted	-0.03	0.04	-0.71	0.48	-0.10	0.05
Entiako	Calving	7	2015	0.00	0.03	0.03	0.98	-0.05	0.05
Entiako	Calving	7	2016	0.02	0.03	0.64	0.52	-0.04	0.08
Entiako	Calving	7	Constant	-3.50	0.56	-6.24	<0.001	-4.60	-2.40
Entiako	Summer	5	elevkm	3.83	0.78	4.92	<0.001	2.30	5.35
Entiako	Summer	5	elevkm2	-1.74	0.34	-5.07	<0.001	-2.41	-1.07
Entiako	Summer	5	east	0.00	0.01	0.21	0.84	-0.02	0.03
Entiako	Summer	5	north	0.00	0.01	0.07	0.94	-0.03	0.03
Entiako	Summer	5	Alpine	-0.65	0.25	-2.64	0.01	-1.13	-0.17
Entiako	Summer	5	Conifer	0.29	0.04	6.39	<0.001	0.20	0.37
Entiako	Summer	5	Decid	0.20	0.07	2.74	0.01	0.06	0.34
Entiako	Summer	5	Fire_Other	0.23	0.06	4.07	<0.001	0.12	0.34
Entiako	Summer	5	Fire_Pine	-0.06	0.05	-1.15	0.25	-0.16	0.04

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Summer	5	Herbac	0.14	0.13	1.09	0.28	-0.11	0.40
Entiako	Summer	5	New_Cut	-0.30	0.06	-4.69	<0.001	-0.42	-0.17
Entiako	Summer	5	Old_Cut	-0.10	0.06	-1.67	0.09	-0.22	0.02
Entiako	Summer	5	Old_Fire	0.17	0.28	0.60	0.55	-0.38	0.72
Entiako	Summer	5	Pine	0.14	0.04	3.31	<0.001	0.06	0.23
Entiako	Summer	5	Wetted	-0.06	0.05	-1.26	0.21	-0.16	0.03
Entiako	Summer	5	mature_distkm	0.01	0.01	1.71	0.09	0.00	0.03
Entiako	Summer	5	2015	0.01	0.02	0.44	0.66	-0.03	0.05
Entiako	Summer	5	2016	0.01	0.03	0.40	0.69	-0.04	0.06
Entiako	Summer	5	Constant	-3.79	0.43	-8.81	<0.001	-4.63	-2.95
Entiako	Summer	7	elevkm	3.92	0.78	5.05	<0.001	2.40	5.44
Entiako	Summer	7	elevkm2	-1.78	0.34	-5.20	<0.001	-2.45	-1.11
Entiako	Summer	7	east	0.00	0.01	0.15	0.88	-0.03	0.03
Entiako	Summer	7	north	0.00	0.01	0.09	0.93	-0.02	0.03
Entiako	Summer	7	Alpine	-0.64	0.25	-2.60	0.01	-1.12	-0.16
Entiako	Summer	7	Conifer	0.28	0.04	6.27	<0.001	0.19	0.37
Entiako	Summer	7	Decid	0.20	0.07	2.68	0.01	0.05	0.34
Entiako	Summer	7	Fire_Other	0.24	0.06	4.39	<0.001	0.13	0.35
Entiako	Summer	7	Fire_Pine	-0.03	0.05	-0.57	0.57	-0.12	0.07
Entiako	Summer	7	Herbac	0.13	0.13	1.02	0.31	-0.12	0.39
Entiako	Summer	7	New_Cut	-0.31	0.06	-4.85	<0.001	-0.43	-0.18
Entiako	Summer	7	Old_Cut	-0.11	0.06	-1.82	0.07	-0.22	0.01
Entiako	Summer	7	Old_Fire	0.16	0.28	0.57	0.57	-0.39	0.71
Entiako	Summer	7	Pine	0.14	0.04	3.17	<0.001	0.05	0.22
Entiako	Summer	7	Wetted	-0.06	0.05	-1.32	0.19	-0.16	0.03
Entiako	Summer	7	2015	0.01	0.02	0.41	0.68	-0.03	0.05

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Summer	7	2016	0.00	0.03	0.19	0.85	-0.04	0.05
Entiako	Summer	7	Constant	-3.83	0.43	-8.90	<0.001	-4.67	-2.99
Entiako	Summer	6	elevkm	3.85	0.78	4.95	<0.001	2.33	5.37
Entiako	Summer	6	elevkm2	-1.74	0.34	-5.10	<0.001	-2.42	-1.07
Entiako	Summer	6	east	0.00	0.01	0.18	0.86	-0.02	0.03
Entiako	Summer	6	north	0.00	0.01	0.06	0.95	-0.03	0.03
Entiako	Summer	6	Alpine	-0.65	0.25	-2.63	0.01	-1.13	-0.17
Entiako	Summer	6	Conifer	0.29	0.04	6.41	<0.001	0.20	0.37
Entiako	Summer	6	Decid	0.20	0.07	2.79	0.01	0.06	0.35
Entiako	Summer	6	Fire_Other	0.23	0.06	4.06	<0.001	0.12	0.34
Entiako	Summer	6	Fire_Pine	-0.06	0.05	-1.10	0.27	-0.16	0.04
Entiako	Summer	6	Herbac	0.14	0.13	1.07	0.28	-0.12	0.40
Entiako	Summer	6	New_Cut	-0.30	0.06	-4.72	<0.001	-0.43	-0.18
Entiako	Summer	6	Old_Cut	-0.10	0.06	-1.71	0.09	-0.22	0.01
Entiako	Summer	6	Old_Fire	0.17	0.28	0.59	0.55	-0.38	0.71
Entiako	Summer	6	Pine	0.14	0.04	3.34	<0.001	0.06	0.23
Entiako	Summer	6	Wetted	-0.06	0.05	-1.29	0.20	-0.16	0.03
Entiako	Summer	6	Escape_cov	0.01	0.01	1.51	0.13	0.00	0.03
Entiako	Summer	6	2015	0.01	0.02	0.43	0.67	-0.03	0.05
Entiako	Summer	6	2016	0.01	0.03	0.35	0.73	-0.04	0.06
Entiako	Summer	6	Constant	-3.80	0.43	-8.83	<0.001	-4.64	-2.96
Entiako	Fall	7	elevkm	0.45	0.66	0.67	0.50	-0.85	1.74
Entiako	Fall	7	elevkm2	-0.27	0.29	-0.96	0.34	-0.83	0.29
Entiako	Fall	7	east	0.03	0.02	2.14	0.03	0.00	0.06
Entiako	Fall	7	north	0.04	0.01	2.78	0.01	0.01	0.07

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Fall	7	Alpine	-0.16	0.13	-1.30	0.20	-0.41	0.08
Entiako	Fall	7	Conifer	0.18	0.05	3.64	<0.001	0.08	0.28
Entiako	Fall	7	Decid	0.28	0.10	2.92	<0.001	0.09	0.47
Entiako	Fall	7	Fire_Other	0.21	0.06	3.67	<0.001	0.10	0.32
Entiako	Fall	7	Fire_Pine	-0.10	0.05	-1.99	0.05	-0.20	0.00
Entiako	Fall	7	Herbac	0.39	0.13	2.89	<0.001	0.13	0.65
Entiako	Fall	7	New_Cut	0.01	0.07	0.09	0.93	-0.12	0.13
Entiako	Fall	7	Old_Cut	-0.31	0.07	-4.59	<0.001	-0.44	-0.18
Entiako	Fall	7	Old_Fire	-0.39	0.40	-0.99	0.32	-1.17	0.38
Entiako	Fall	7	Pine	-0.04	0.05	-0.86	0.39	-0.13	0.05
Entiako	Fall	7	Wetted	-0.06	0.05	-1.13	0.26	-0.16	0.04
Entiako	Fall	7	2015	0.00	0.02	0.12	0.90	-0.04	0.05
Entiako	Fall	7	2016	0.01	0.03	0.40	0.69	-0.04	0.07
Entiako	Fall	7	Constant	-1.77	0.38	-4.70	<0.001	-2.51	-1.03
Entiako	Fall	8	elevkm	0.35	0.67	0.53	0.60	-0.95	1.66
Entiako	Fall	8	elevkm2	-0.23	0.29	-0.79	0.43	-0.79	0.34
Entiako	Fall	8	east	0.03	0.02	2.15	0.03	0.00	0.06
Entiako	Fall	8	north	0.04	0.01	2.68	0.01	0.01	0.07
Entiako	Fall	8	Alpine	-0.15	0.13	-1.20	0.23	-0.40	0.10
Entiako	Fall	8	Conifer	0.19	0.05	3.75	<0.001	0.09	0.28
Entiako	Fall	8	Decid	0.28	0.10	2.89	<0.001	0.09	0.47
Entiako	Fall	8	Fire_Other	0.21	0.06	3.70	<0.001	0.10	0.33
Entiako	Fall	8	Fire_Pine	-0.10	0.05	-1.95	0.05	-0.20	0.00
Entiako	Fall	8	Herbac	0.39	0.13	2.88	<0.001	0.12	0.65
Entiako	Fall	8	New_Cut	0.00	0.07	0.00	1.00	-0.13	0.13
Entiako	Fall	8	Old_Cut	-0.32	0.07	-4.66	<0.001	-0.45	-0.18

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
Entiako	Fall	8	Old_Fire	-0.40	0.40	-1.01	0.32	-1.18	0.38
Entiako	Fall	8	Pine	-0.04	0.05	-0.86	0.39	-0.13	0.05
Entiako	Fall	8	road_distkm	0.00	0.00	-1.06	0.29	-0.01	0.00
Entiako	Fall	8	2015	0.00	0.02	0.13	0.89	-0.04	0.05
Entiako	Fall	8	2016	0.01	0.03	0.49	0.62	-0.04	0.07
Entiako	Fall	8	Constant	-1.72	0.38	-4.52	<0.001	-2.46	-0.97
Entiako	Early Winter	9	elevkm	4.30	1.01	4.27	<0.001	2.33	6.28
Entiako	Early Winter	9	elevkm2	-1.76	0.44	-4.03	<0.001	-2.61	-0.90
Entiako	Early Winter	9	east	0.01	0.02	0.36	0.72	-0.03	0.04
Entiako	Early Winter	9	north	0.00	0.02	-0.23	0.82	-0.04	0.03
Entiako	Early Winter	9	Conifer	-0.40	0.05	-8.35	<0.001	-0.50	-0.31
Entiako	Early Winter	9	Decid	0.18	0.09	2.09	0.04	0.01	0.36
Entiako	Early Winter	9	Fire_Other	0.13	0.05	2.52	0.01	0.03	0.23
Entiako	Early Winter	9	Fire_Pine	-0.76	0.05	-15.65	<0.001	-0.85	-0.66
Entiako	Early Winter	9	Herbac	0.79	0.09	9.05	<0.001	0.62	0.96
Entiako	Early Winter	9	New_Cut	0.08	0.05	1.69	0.09	-0.01	0.17
Entiako	Early Winter	9	Old_Cut	-0.20	0.05	-4.38	<0.001	-0.29	-0.11
Entiako	Early Winter	9	Old_Fire	0.33	0.23	1.41	0.16	-0.13	0.79
Entiako	Early Winter	9	Pine	-0.71	0.04	-18.78	<0.001	-0.78	-0.63
Entiako	Early Winter	9	Wetted	0.56	0.04	14.01	<0.001	0.48	0.64
Entiako	Early Winter	9	road_distkm	0.01	0.00	3.00	<0.001	0.00	0.02
Entiako	Early Winter	9	mature_distkm	0.04	0.01	3.81	<0.001	0.02	0.07
Entiako	Early Winter	9	2015	0.05	0.03	1.60	0.11	-0.01	0.12
Entiako	Early Winter	9	2016	0.07	0.04	1.83	0.07	0.00	0.14
Entiako	Early Winter	9	Constant	-3.97	0.57	-6.91	<0.001	-5.09	-2.84

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Late Winter	9	elevkm	1.76	0.95	1.86	0.06	-0.10	3.62
PG South	Late Winter	9	elevkm2	-1.17	0.53	-2.23	0.03	-2.20	-0.14
PG South	Late Winter	9	east	-0.03	0.01	-1.80	0.07	-0.06	0.00
PG South	Late Winter	9	north	0.11	0.02	6.76	<0.001	0.08	0.14
PG South	Late Winter	9	Conifer	0.16	0.04	4.17	<0.001	0.09	0.24
PG South	Late Winter	9	Decid	0.32	0.04	7.13	<0.001	0.23	0.40
PG South	Late Winter	9	Fire_Other	-0.07	0.06	-1.14	0.25	-0.18	0.05
PG South	Late Winter	9	Fire_Pine	0.11	0.05	2.04	0.04	0.00	0.21
PG South	Late Winter	9	Herbac	-0.72	0.13	-5.60	<0.001	-0.97	-0.47
PG South	Late Winter	9	New_Cut	0.46	0.04	12.57	<0.001	0.39	0.53
PG South	Late Winter	9	Old_Cut	0.18	0.04	4.10	<0.001	0.09	0.26
PG South	Late Winter	9	Old_Fire	0.36	0.19	1.90	0.06	-0.01	0.73
PG South	Late Winter	9	Pine	0.22	0.04	5.99	<0.001	0.15	0.29
PG South	Late Winter	9	Urban	-1.40	0.14	-9.88	<0.001	-1.68	-1.12
PG South	Late Winter	9	Wetted	0.39	0.05	8.50	<0.001	0.30	0.48
PG South	Late Winter	9	road_distkm	0.09	0.05	1.90	0.06	0.00	0.18
PG South	Late Winter	9	mature_distkm	0.05	0.02	3.32	<0.001	0.02	0.08
PG South	Late Winter	9	2015	0.03	0.06	0.55	0.58	-0.09	0.16
PG South	Late Winter	9	2016	0.00	0.06	0.00	1.00	-0.12	0.12
PG South	Late Winter	9	2017	0.00	0.06	0.08	0.93	-0.11	0.12
PG South	Late Winter	9	Constant	-2.54	0.43	-5.90	<0.001	-3.38	-1.70
PG South	Late Winter	5	elevkm	1.76	0.95	1.86	0.06	-0.10	3.62
PG South	Late Winter	5	elevkm2	-1.16	0.53	-2.20	0.03	-2.19	-0.13
PG South	Late Winter	5	east	-0.03	0.01	-1.77	0.08	-0.05	0.00
PG South	Late Winter	5	north	0.11	0.02	6.84	<0.001	0.08	0.14
PG South	Late Winter	5	Conifer	0.17	0.04	4.29	<0.001	0.09	0.24

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Late Winter	5	Decid	0.33	0.04	7.41	<0.001	0.24	0.41
PG South	Late Winter	5	Fire_Other	-0.08	0.06	-1.31	0.19	-0.19	0.04
PG South	Late Winter	5	Fire_Pine	0.11	0.05	2.10	0.04	0.01	0.21
PG South	Late Winter	5	Herbac	-0.73	0.13	-5.63	<0.001	-0.98	-0.47
PG South	Late Winter	5	New_Cut	0.45	0.04	12.43	<0.001	0.38	0.52
PG South	Late Winter	5	Old_Cut	0.17	0.04	3.87	<0.001	0.08	0.25
PG South	Late Winter	5	Old_Fire	0.36	0.19	1.93	0.05	-0.01	0.73
PG South	Late Winter	5	Pine	0.22	0.04	6.21	<0.001	0.15	0.29
PG South	Late Winter	5	Urban	-1.40	0.14	-9.91	<0.001	-1.68	-1.13
PG South	Late Winter	5	Wetted	0.40	0.05	8.76	<0.001	0.31	0.49
PG South	Late Winter	5	mature_distkm	0.05	0.02	3.37	<0.001	0.02	0.09
PG South	Late Winter	5	2015	0.03	0.06	0.52	0.60	-0.09	0.16
PG South	Late Winter	5	2016	0.00	0.06	-0.05	0.96	-0.12	0.11
PG South	Late Winter	5	2017	0.00	0.06	-0.02	0.98	-0.12	0.12
PG South	Late Winter	5	Constant	-2.53	0.43	-5.87	<0.001	-3.38	-1.69
PG South	Late Winter	10	elevkm	1.75	0.95	1.85	0.07	-0.11	3.61
PG South	Late Winter	10	elevkm2	-1.17	0.53	-2.22	0.03	-2.20	-0.14
PG South	Late Winter	10	east	-0.03	0.01	-1.78	0.08	-0.05	0.00
PG South	Late Winter	10	north	0.11	0.02	6.79	<0.001	0.08	0.14
PG South	Late Winter	10	Conifer	0.17	0.04	4.24	<0.001	0.09	0.24
PG South	Late Winter	10	Decid	0.32	0.04	7.17	<0.001	0.23	0.41
PG South	Late Winter	10	Fire_Other	-0.06	0.06	-1.03	0.30	-0.18	0.06
PG South	Late Winter	10	Fire_Pine	0.11	0.05	2.09	0.04	0.01	0.22
PG South	Late Winter	10	Herbac	-0.73	0.13	-5.64	<0.001	-0.98	-0.47
PG South	Late Winter	10	New_Cut	0.46	0.04	12.50	<0.001	0.39	0.53
PG South	Late Winter	10	Old_Cut	0.17	0.04	4.02	<0.001	0.09	0.26

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Late Winter	10	Old_Fire	0.35	0.19	1.88	0.06	-0.02	0.72
PG South	Late Winter	10	Pine	0.22	0.04	6.00	<0.001	0.15	0.29
PG South	Late Winter	10	Urban	-1.41	0.14	-9.92	<0.001	-1.68	-1.13
PG South	Late Winter	10	Wetted	0.39	0.05	8.43	<0.001	0.30	0.48
PG South	Late Winter	10	road_distkm	0.10	0.05	2.06	0.04	0.00	0.19
PG South	Late Winter	10	Escape_cov	0.05	0.02	3.03	<0.001	0.02	0.08
PG South	Late Winter	10	2015	0.03	0.06	0.54	0.59	-0.09	0.16
PG South	Late Winter	10	2016	0.00	0.06	-0.04	0.97	-0.12	0.11
PG South	Late Winter	10	2017	0.00	0.06	0.04	0.97	-0.12	0.12
PG South	Late Winter	10	Constant	-2.53	0.43	-5.87	<0.001	-3.38	-1.69
PG South	Calving	8	elevkm	-0.34	1.28	-0.27	0.79	-2.84	2.16
PG South	Calving	8	elevkm2	0.27	0.68	0.40	0.69	-1.06	1.61
PG South	Calving	8	east	0.03	0.03	1.14	0.25	-0.02	0.08
PG South	Calving	8	north	-0.06	0.03	-2.12	0.03	-0.11	0.00
PG South	Calving	8	Conifer	0.25	0.06	4.12	<0.001	0.13	0.37
PG South	Calving	8	Decid	0.28	0.07	3.85	<0.001	0.14	0.42
PG South	Calving	8	Fire_Other	-0.13	0.09	-1.34	0.18	-0.31	0.06
PG South	Calving	8	Fire_Pine	0.13	0.07	1.89	0.06	0.00	0.27
PG South	Calving	8	Herbac	-0.35	0.26	-1.35	0.18	-0.85	0.16
PG South	Calving	8	New_Cut	0.05	0.06	0.78	0.44	-0.07	0.16
PG South	Calving	8	Old_Cut	-0.03	0.07	-0.44	0.66	-0.17	0.11
PG South	Calving	8	Pine	0.07	0.05	1.34	0.18	-0.03	0.17
PG South	Calving	8	Urban	-1.39	0.20	-7.09	<0.001	-1.78	-1.01
PG South	Calving	8	Wetted	1.12	0.06	19.64	<0.001	1.01	1.23
PG South	Calving	8	road_distkm	-0.17	0.08	-2.29	0.02	-0.32	-0.03
PG South	Calving	8	2015	-0.01	0.05	-0.23	0.82	-0.12	0.09

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Calving	8	2016	-0.07	0.05	-1.29	0.20	-0.17	0.03
PG South	Calving	8	Constant	-1.65	0.59	-2.81	0.01	-2.81	-0.50
PG South	Calving	7	elevkm	-0.19	1.27	-0.15	0.88	-2.69	2.31
PG South	Calving	7	elevkm2	0.16	0.68	0.23	0.82	-1.17	1.49
PG South	Calving	7	east	0.03	0.03	1.12	0.26	-0.02	0.08
PG South	Calving	7	north	-0.06	0.03	-2.15	0.03	-0.11	-0.01
PG South	Calving	7	Conifer	0.24	0.06	3.99	<0.001	0.12	0.36
PG South	Calving	7	Decid	0.27	0.07	3.73	<0.001	0.13	0.41
PG South	Calving	7	Fire_Other	-0.11	0.09	-1.20	0.23	-0.29	0.07
PG South	Calving	7	Fire_Pine	0.12	0.07	1.66	0.10	-0.02	0.25
PG South	Calving	7	Herbac	-0.34	0.26	-1.34	0.18	-0.84	0.16
PG South	Calving	7	New_Cut	0.07	0.06	1.16	0.25	-0.05	0.18
PG South	Calving	7	Old_Cut	-0.01	0.07	-0.09	0.93	-0.14	0.13
PG South	Calving	7	Pine	0.05	0.05	1.03	0.30	-0.05	0.16
PG South	Calving	7	Urban	-1.38	0.20	-7.04	<0.001	-1.77	-1.00
PG South	Calving	7	Wetted	1.09	0.06	19.54	<0.001	0.99	1.20
PG South	Calving	7	2015	-0.01	0.05	-0.25	0.80	-0.12	0.09
PG South	Calving	7	2016	-0.06	0.05	-1.22	0.22	-0.16	0.04
PG South	Calving	7	Constant	-1.73	0.59	-2.95	<0.001	-2.88	-0.58
PG South	Summer	8	elevkm	1.40	1.03	1.36	0.18	-0.62	3.43
PG South	Summer	8	elevkm2	-0.84	0.53	-1.59	0.11	-1.88	0.20
PG South	Summer	8	east	0.01	0.02	0.54	0.59	-0.03	0.06
PG South	Summer	8	north	0.10	0.02	3.99	<0.001	0.05	0.15
PG South	Summer	8	Conifer	0.51	0.07	7.52	<0.001	0.38	0.64
PG South	Summer	8	Decid	0.39	0.08	5.07	<0.001	0.24	0.54

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Summer	8	Fire_Other	0.24	0.08	3.00	<0.001	0.08	0.40
PG South	Summer	8	Fire_Pine	0.22	0.07	3.04	<0.001	0.08	0.36
PG South	Summer	8	Herbac	-0.65	0.33	-1.96	0.05	-1.30	0.00
PG South	Summer	8	New_Cut	-0.06	0.07	-0.87	0.39	-0.20	0.08
PG South	Summer	8	Old_Cut	0.34	0.08	4.44	<0.001	0.19	0.49
PG South	Summer	8	Pine	0.38	0.06	6.03	<0.001	0.25	0.50
PG South	Summer	8	Urban	-2.29	0.35	-6.61	<0.001	-2.97	-1.61
PG South	Summer	8	Wetted	0.92	0.07	13.44	<0.001	0.78	1.05
PG South	Summer	8	road_distkm	0.12	0.05	2.18	0.03	0.01	0.23
PG South	Summer	8	2015	0.01	0.05	0.11	0.92	-0.09	0.10
PG South	Summer	8	2016	0.02	0.05	0.45	0.65	-0.07	0.11
PG South	Summer	8	Constant	-2.57	0.50	-5.16	<0.001	-3.55	-1.60
PG South	Summer	7	elevkm	0.93	1.01	0.92	0.36	-1.05	2.91
PG South	Summer	7	elevkm2	-0.54	0.51	-1.06	0.29	-1.54	0.46
PG South	Summer	7	east	0.01	0.02	0.53	0.59	-0.03	0.06
PG South	Summer	7	north	0.10	0.02	4.00	<0.001	0.05	0.15
PG South	Summer	7	Conifer	0.52	0.07	7.69	<0.001	0.39	0.65
PG South	Summer	7	Decid	0.39	0.08	5.17	<0.001	0.24	0.54
PG South	Summer	7	Fire_Other	0.24	0.08	2.93	<0.001	0.08	0.40
PG South	Summer	7	Fire_Pine	0.23	0.07	3.24	<0.001	0.09	0.38
PG South	Summer	7	Herbac	-0.65	0.33	-1.97	0.05	-1.30	0.00
PG South	Summer	7	New_Cut	-0.08	0.07	-1.13	0.26	-0.22	0.06
PG South	Summer	7	Old_Cut	0.32	0.08	4.22	<0.001	0.17	0.47
PG South	Summer	7	Pine	0.39	0.06	6.23	<0.001	0.26	0.51
PG South	Summer	7	Urban	-2.30	0.35	-6.64	<0.001	-2.98	-1.62
PG South	Summer	7	Wetted	0.93	0.07	13.72	<0.001	0.80	1.07

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Summer	7	2015	0.00	0.05	-0.08	0.94	-0.10	0.09
PG South	Summer	7	2016	0.01	0.05	0.22	0.83	-0.08	0.10
PG South	Summer	7	Constant	-2.36	0.49	-4.82	<0.001	-3.31	-1.40
PG South	Fall	9	elevkm	-1.00	0.95	-1.05	0.29	-2.87	0.87
PG South	Fall	9	elevkm2	0.45	0.48	0.94	0.35	-0.49	1.38
PG South	Fall	9	east	0.00	0.02	-0.09	0.93	-0.05	0.04
PG South	Fall	9	north	0.06	0.03	2.30	0.02	0.01	0.11
PG South	Fall	9	Conifer	0.34	0.07	4.75	<0.001	0.20	0.47
PG South	Fall	9	Decid	0.24	0.08	3.04	<0.001	0.08	0.39
PG South	Fall	9	Fire_Other	0.19	0.10	2.01	0.04	0.01	0.38
PG South	Fall	9	Fire_Pine	0.84	0.08	10.61	<0.001	0.68	0.99
PG South	Fall	9	Herbac	-0.84	0.38	-2.20	0.03	-1.59	-0.09
PG South	Fall	9	New_Cut	0.51	0.07	7.81	<0.001	0.38	0.64
PG South	Fall	9	Old_Cut	-0.04	0.09	-0.42	0.68	-0.21	0.14
PG South	Fall	9	Pine	0.28	0.06	4.38	<0.001	0.15	0.41
PG South	Fall	9	Urban	-1.73	0.27	-6.45	<0.001	-2.26	-1.20
PG South	Fall	9	Wetted	0.21	0.08	2.50	0.01	0.05	0.38
PG South	Fall	9	road_distkm	0.12	0.05	2.31	0.02	0.02	0.22
PG South	Fall	9	mature_distkm	-0.09	0.03	-3.38	<0.001	-0.14	-0.04
PG South	Fall	9	2015	0.01	0.05	0.25	0.81	-0.09	0.12
PG South	Fall	9	2016	-0.04	0.05	-0.87	0.39	-0.15	0.06
PG South	Fall	9	Constant	-1.41	0.46	-3.04	<0.001	-2.32	-0.50
PG South	Fall	5	elevkm	-1.15	0.95	-1.21	0.23	-3.02	0.71
PG South	Fall	5	elevkm2	0.57	0.47	1.21	0.23	-0.36	1.50
PG South	Fall	5	east	0.00	0.02	-0.06	0.95	-0.05	0.05

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Fall	5	north	0.06	0.03	2.32	0.02	0.01	0.11
PG South	Fall	5	Conifer	0.35	0.07	4.99	<0.001	0.21	0.49
PG South	Fall	5	Decid	0.25	0.08	3.18	<0.001	0.10	0.40
PG South	Fall	5	Fire_Other	0.18	0.10	1.88	0.06	-0.01	0.37
PG South	Fall	5	Fire_Pine	0.85	0.08	10.74	<0.001	0.69	1.00
PG South	Fall	5	Herbac	-0.84	0.38	-2.20	0.03	-1.59	-0.09
PG South	Fall	5	New_Cut	0.49	0.07	7.57	<0.001	0.36	0.62
PG South	Fall	5	Old_Cut	-0.06	0.09	-0.69	0.49	-0.23	0.11
PG South	Fall	5	Pine	0.30	0.06	4.65	<0.001	0.17	0.42
PG South	Fall	5	Urban	-1.74	0.27	-6.47	<0.001	-2.26	-1.21
PG South	Fall	5	Wetted	0.23	0.08	2.68	0.01	0.06	0.39
PG South	Fall	5	mature_distkm	-0.09	0.03	-3.36	<0.001	-0.14	-0.04
PG South	Fall	5	2015	0.01	0.05	0.21	0.83	-0.10	0.12
PG South	Fall	5	2016	-0.05	0.05	-0.96	0.34	-0.15	0.05
PG South	Fall	5	Constant	-1.34	0.46	-2.90	<0.001	-2.25	-0.43
PG South	Early Winter	8	elevkm	-2.21	1.43	-1.54	0.12	-5.02	0.60
PG South	Early Winter	8	elevkm2	1.30	0.72	1.82	0.07	-0.10	2.71
PG South	Early Winter	8	east	0.03	0.02	1.29	0.20	-0.02	0.08
PG South	Early Winter	8	north	0.06	0.03	2.11	0.04	0.00	0.11
PG South	Early Winter	8	Conifer	-0.16	0.07	-2.27	0.02	-0.30	-0.02
PG South	Early Winter	8	Decid	0.18	0.08	2.20	0.03	0.02	0.34
PG South	Early Winter	8	Fire_Other	0.40	0.08	4.77	<0.001	0.23	0.56
PG South	Early Winter	8	Fire_Pine	0.26	0.08	3.29	<0.001	0.10	0.41
PG South	Early Winter	8	Herbac	-0.33	0.29	-1.14	0.25	-0.90	0.24
PG South	Early Winter	8	New_Cut	0.97	0.06	16.01	<0.001	0.85	1.08
PG South	Early Winter	8	Old_Cut	-0.16	0.08	-2.04	0.04	-0.31	-0.01

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Early Winter	8	Pine	-0.10	0.06	-1.64	0.10	-0.22	0.02
PG South	Early Winter	8	Urban	-1.34	0.26	-5.12	<0.001	-1.85	-0.83
PG South	Early Winter	8	Wetted	0.29	0.09	3.28	<0.001	0.12	0.46
PG South	Early Winter	8	road_distkm	-0.19	0.09	-2.16	0.03	-0.37	-0.02
PG South	Early Winter	8	2015	0.07	0.07	1.11	0.27	-0.06	0.20
PG South	Early Winter	8	2016	0.01	0.06	0.19	0.85	-0.11	0.13
PG South	Early Winter	8	Constant	-1.01	0.70	-1.43	0.15	-2.39	0.37
PG South	Early Winter	7	elevkm	-2.17	1.44	-1.51	0.13	-4.99	0.65
PG South	Early Winter	7	elevkm2	1.25	0.72	1.74	0.08	-0.16	2.65
PG South	Early Winter	7	east	0.03	0.02	1.28	0.20	-0.02	0.08
PG South	Early Winter	7	north	0.06	0.03	2.06	0.04	0.00	0.11
PG South	Early Winter	7	Conifer	-0.17	0.07	-2.47	0.01	-0.31	-0.04
PG South	Early Winter	7	Decid	0.17	0.08	2.10	0.04	0.01	0.33
PG South	Early Winter	7	Fire_Other	0.41	0.08	4.98	<0.001	0.25	0.57
PG South	Early Winter	7	Fire_Pine	0.24	0.08	3.08	<0.001	0.09	0.39
PG South	Early Winter	7	Herbac	-0.32	0.29	-1.10	0.27	-0.89	0.25
PG South	Early Winter	7	New_Cut	0.99	0.06	16.48	<0.001	0.87	1.10
PG South	Early Winter	7	Old_Cut	-0.13	0.08	-1.73	0.08	-0.28	0.02
PG South	Early Winter	7	Pine	-0.12	0.06	-1.90	0.06	-0.24	0.00
PG South	Early Winter	7	Urban	-1.33	0.26	-5.10	<0.001	-1.84	-0.82
PG South	Early Winter	7	Wetted	0.27	0.09	3.05	<0.001	0.09	0.44
PG South	Early Winter	7	2015	0.07	0.06	1.07	0.29	-0.06	0.20
PG South	Early Winter	7	2016	0.01	0.06	0.21	0.83	-0.11	0.14
PG South	Early Winter	7	Constant	-1.04	0.71	-1.46	0.14	-2.42	0.35
PG South	Early Winter	9	elevkm	-2.26	1.44	-1.58	0.12	-5.08	0.55

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)

Table G.1 Continued

Study Area	Season	Model	Variable	Coef.	SE	z	*P*	95% Conf. Interval	
PG South	Early Winter	9	elevkm2	1.33	0.72	1.86	0.06	-0.07	2.74
PG South	Early Winter	9	east	0.03	0.02	1.29	0.20	-0.02	0.08
PG South	Early Winter	9	north	0.06	0.03	2.12	0.03	0.00	0.11
PG South	Early Winter	9	Conifer	-0.14	0.07	-1.96	0.05	-0.28	0.00
PG South	Early Winter	9	Decid	0.20	0.08	2.39	0.02	0.04	0.36
PG South	Early Winter	9	Fire_Other	0.33	0.10	3.42	<0.001	0.14	0.52
	Early Winter	9	Fire_Pine	0.19	0.09	2.02	0.04	0.01	0.37
PG South	Early Winter	9	Herbac	-0.31	0.29	-1.07	0.29	-0.88	0.26
PG South	Early Winter	9	New_Cut	0.99	0.06	15.87	<0.001	0.87	1.11
PG South	Early Winter	9	Old_Cut	-0.14	0.08	-1.74	0.08	-0.29	0.02
PG South	Early Winter	9	Pine	-0.08	0.06	-1.28	0.20	-0.20	0.04
PG South	Early Winter	9	Urban	-1.32	0.26	-5.04	<0.001	-1.83	-0.80
PG South	Early Winter	9	road_distkm	-0.19	0.09	-2.17	0.03	-0.37	-0.02
PG South	Early Winter	9	mature_distkm	0.04	0.03	1.40	0.16	-0.02	0.10
PG South	Early Winter	9	2015	0.07	0.07	1.07	0.29	-0.06	0.20
PG South	Early Winter	9	2016	0.01	0.06	0.16	0.88	-0.11	0.13
PG South	Early Winter	9	Constant	-1.01	0.71	-1.43	0.15	-2.39	0.37

Note: Model # (Name): 1 (Base Topography), 2 (Anthropogenic Disturbance), 3 (Access/Stress/Vulnerability), 4 (Edge), 5 (Cover/Browse), 6 (Escapement cover distance), 7 (Vegetation), 8 (Avoidance), 9 (Saturated 1), 10 (Saturated 2)