Evaluating Habitat Use of Female Moose in Response to Large Scale Salvage Logging Practices in British Columbia, Canada

by

Alexandra Francis
Bachelor of Natural Resource Science, Thompson Rivers University, 2010

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Supervisory Committee

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Professor John P. Volpe, School of Environmental Studies
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Abstract

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Dr. John P. Volpe, School of Environmental Studies
Co-supervisor

Global biodiversity is in decline as a result of unprecedented human alterations to the earth’s land cover. Understanding the ecological mechanisms of these large-scale changes in biodiversity is imperative in furthering our knowledge on the effects these alterations may have on animal behaviour and consequently on populations, allowing researchers and managers to effectively conserve species. During the last decade, there have been reports of moose populations both increasing and decreasing in North America due to a variety of factors (e.g., climate change, habitat disturbance, disease, etc.). Within British Columbia, wildlife managers have reported moose population declines of up to 50 – 70%, while other areas have remained stable. These changes have coincided, spatially and temporally, with the largest recorded mountain pine beetle (*Dendroctonus ponderosae)* outbreak. The outbreak resulted in extensive logging and road building in attempts to recover economic value from the beetle killed trees, resulting in drastic changes to the landscape. Understanding the effects that a highly disturbed landscape has on a species is critical for effective management and conservation.

To investigate this, I examined the seasonal response of female moose to landscape change caused by the Mountain Pine Beetle outbreak and attendant salvage logging infrastructure in the Interior of British Columbia on the Bonaparte Plateau. First, I used a cluster analysis framework to develop biologically relevant seasons for female moose using individual movement and habitat use. I then used this temporal framework to develop seasonal home ranges for each individual moose. Second, I modelled the seasonal habitat selection of female moose to examine how moose respond to salvage logging infrastructure (i.e., dense road network and extensive cutblocks) using resource selection functions in an information-theoretic framework. We tested whether predation risk, forage availability or the cumulative effects of salvage logging best predicted moose space-use.

Moose movement data clustered into five biologically relevant seasons, which were consistent with our biological and ecological knowledge of moose in the study area; however, these seasons and the size of the range differed from other seasons defined using alternative methods in the region. Across all seasons, the cumulative effects of forage availability and risk best predicted female moose distribution. In the calving and fall seasons, the top risk model best predicted moose habitat selection while the top forage availability model better explained moose habitat selection in spring, summer, and winter. Our results identified the importance of defining biological seasons using empirical data and how these seasons can differ from arbitrarily defined seasons, as well as the implications these can have in subsequent analysis and management. Additionally, we found that moose are seasonally trading the benefits of foraging for predation risk in these highly disturbed landscapes, using some aspects of salvage logging. My results bring perspective on how moose are using a highly disturbed landscape at the seasonal scale and a nuanced approach to landscape management.

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Chapter 1: General Introduction

1.1 Research Context

Moose (*Alces alces)* are the largest member of the deer (*Cervidae)* family. They have a circumboreal distribution, being found in the northern forests across Eurasia (i.e., from Scandinavia to eastern Russia) and across North America (i.e., from Alaska/British Columbia (B.C.) to Labrador/Nova Scotia) (Blood 2000). Their biogeographical distribution is limited by forage, climate, and habitat composition in the north and hot temperatures (>27ºC) and the absence of thermal refugia in the south (Timmermann and McNicol 1988). Their widespread distribution is indicative of their ability to utilize a variety of habitats.

Within their home range, defined as the area an animal moves in when performing its normal activities (Harris et al. 1990), moose movements and habitat use represent trade-offs between minimizing predation risk, managing energy expenditure, and accessing high quality forage (Fryxell and Sinclair 1988, Rettie and Messier 2000, Dussault et al. 2005). In general moose utilise a mosaic of habitat types that provide forage as well as thermal and security cover (Timmermann and McNicol 1988). Thermal cover is defined as canopies that provide shelter from microclimatic extremes (e.g., vegetation that reduces an animal's exposure to solar radiation) (Dussault et al. 2004) and security cover is habitat that generally reduces visibility and provides protection from predators (Timmermann and McNicol 1988). The use and need of these various habitats shift seasonally as the species' physiological requirements shift and environmental conditions change.

Calving typically occurs in late May (Hauge and Keith 1981, Larsen et al. 1989) with second estrous events occurring in June. During this time females must balance meeting nutritional requirements due to the demands of lactation and neonate development with the risk of predation, particularly as predation on neonates can be significant during the first few weeks after birth (Severud et al. 2019). Existing data on calving and post-parturition site selection are variable (Poole et al. 2007, Severud et al. 2019), with a number of habitat types reported to be important for calving (e.g., security/hiding cover, proximity to water, islands, and elevation) (Langley and Pletscher 1994). Despite this variation, it is generally agreed that females trade-off forage for predator avoidance during this time (Testa et al. 2000, Severud et al. 2019).

In summer, moose forage substantially more than in the winter, as they require an increase in nutrients when females are lactating, males are developing antlers, and they must store fat for winter (Timmermann and McNicol 1988). Moose use aquatic areas that provide both aquatic vegetation for foraging and relief from warm temperatures and insects (Timmermann and McNicol 1988). The species is well adapted to cold temperatures, but are less tolerant to high temperatures in the summer and winter. Renecker and Hudson (1986) found the threshold for thermal stress for moose is 14℃ in summer, consequently thermal cover (e.g., mature coniferous stands) is critical during this period (Demarchi and Bunnell 1993). For females with young, predation risk of calves is still high (Larsen et al. 1989), and as such summer habitat must also provide security cover.

Fall is marked by the onset of the breeding season. The rut is a very energetically-expensive period (Mysterud et al. 2004) and generally lasts about three weeks from mid-September to early-October, depending on the geographic area. Females are usually less active than males at this time (Cederlund and Sand 1994) and interestingly males reduce their foraging dramatically during the rut (Miquelle 2020). With winter approaching, moose forage on remaining green species and aspen leaf litter in attempts to extend the period of weight gain (Timmermann and McNicol 1988).

Winter is considered a season of negative energy balance for moose, as they reduce their metabolic rate in response to snow conditions and have a decreased foraging rate (Timmermann and McNicol 1988). Moose tend to use habitat of high browse production (e.g., cutblocks) foraging on deciduous woody trees and shrubs. Snow depth is a driving factor of distribution in late winter (Timmermann and McNicol 1988, Gillingham and Parker 2008) and once snow depths are > 65cm, moose movements can be restricted (Timmermann and McNicol 1988). During these times, moose will select for mature timber that intercepts the snow, offers cover from predators, and provides thermal protection. In spring, moose start to use areas that receive high solar radiation where plants may green-up earlier (Leblond et al. 2010).

Predators play an important role in regulating moose populations (Gasaway et al. 1992). In unexploited, lightly harvested, multi-predator systems, moose abundance is generally at a low-density (i.e., 400 moose per 1000 km^2). In areas with either a single or no predators, densities normally exceed 400 moose per 1000km^2 (Gasaway et al. 1992). Typical predators of moose include grizzly bears (*Ursus arctos)*, black bears (*Ursus americanus)*, wolves (*Canis lupus)*, and cougars (*Felis concolor)*. Both bears and wolves predate heavily on moose calves within the first few months of birth (Patterson et al. 2013, Severud et al. 2019), with wolf predation continuing through the winter. In systems where wolves are the sole moose predator, moose make up greater than 90% of the biomass in wolf diet (Vucetich et al. 2011). Cougars occupy a different global distribution than moose, with ranges only overlapping in parts of northwestern North America (Ross and Jalkotzy 1996). In southwestern Alberta, cougars were found to be a significant predator of moose, with moose being a substantial portion of their winter diet (Ross and Jalkotzy

1996). Other sources of moose mortality include disease and parasites, vehicle collisions, and human harvest (Danks and Porter 2010, Kuzyk et al. 2019).

Over the last decade in North America, there have been reports of both increasing and decreasing populations of moose (Timmermann and Rodgers 2015). Various studies have investigated the causes of these changes (e.g., (Darimont et al. 2005, Wattles and DeStefano 2011, Timmermann and Rodgers 2015) with declines being attributed to climate change, disease or parasites, habitat disturbance and vehicle collisions, while population increases or expansions being attributed to climate, habitat restoration, and changing harvest restrictions. Presently, moose are not considered to be of conservation concern and are globally ranked as “G5” (i.e., demonstrably widespread, abundant, and secure).

At the provincial scale, since the early 2000’s in central B.C., there has been increasing concern over changes in moose populations. In some regions of the province, moose population declines of up to 50 – 70% have been documented, whereas other populations have been considered stable or even increasing (Kuzyk, 2017). The B.C. moose populations was most recently estimated in 2014 at 120,000 to 205,000 moose, declining by approximately 27,500 moose from 2011 (Ministry of Forests Lands and Natural Resource Operations 2013). Moose are currently “Yellow-listed” in B.C. (i.e., apparently secure and not at risk of extinction) (B.C. Conservation Data Center, 2020).

The changes in moose abundance in B.C. have temporally and spatially coincided with the largest recorded Mountain Pine Beetle (*Dendroctonus ponderosae)* outbreak (Kuzyk et al. 2019). The outbreak has been attributed to natural and human influences (Ritchie 2008) and as of 2015 had killed approximately 54% (731 million m^3) of B.C.’s merchantable pine (BC FLNRO

2020). In an attempt to recover economic timber value, large scale salvage logging occurred throughout the interior of B.C. (Ritchie 2008), resulting in in an increased logging rate of more than 15 million cubic meters over previous levels (Parfitt 2007). This has significantly altered the landscape with extensive cutblocks and resulting road networks.

Of significant interest is the effect that these changes to the landscape have on wildlife, and in particular on moose, given the noted population changes coinciding with the M.P.B outbreak. Logging creates extensive early seral habitat which provides abundant forage for moose in regenerating forests. However, these cutblocks with extensive forage in them are inevitably associated with road networks. An extensive road network modifies the landscape by fragmenting habitat and can facilitate predator travel and human access. A landscape extensively marked with these features has the potential leave moose vulnerable to predation from both predators and humans.

Human driven landscape change is one of the most significant factors contributing to the global decline in biodiversity (Maxwell et al. 2016, Segan et al. 2016). Landscape disturbance can favor some species while at the same time disadvantaging others (Fisher and Burton 2018), thus it is critical to monitor and understand the effects of landscape change on all wildlife. Moose, a globally abundant species that is considered apparently secure, play a key role in ungulate food webs, nutrient cycling and forest succession (Molvar et al. 1993, Danell et al. 1998). Understanding the effects that disturbance has on moose behaviour is key in understanding the impacts to the web of ecological processes that moose are tied to.

1.2 Research Focus and Objectives

In 2013, the B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development launched a provincially coordinated research program to investigate factors affecting moose population change. Prior to this, in 2012, a study on the Bonaparte Plateau, north of Kamloops, B.C., was initiated in response to concerns over declining moose populations from First Nations and timber harvesting companies (Pers. Com. Chris Procter, B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development). The Bonaparte Plateau project was then integrated into the provincial program which has focused on five main study areas: Big Creek, Entiako, Prince George South, John Prince Research Forest, and the Bonaparte Plateau (Figure 1.1). The main objective of the program was to evaluate a landscape change hypothesis that predicted that moose had increased in vulnerability as a result of the changes to the landscape from the MPB outbreak (Kuzyk et al. 2019). This thesis focuses on the southern-most study area, the Bonaparte Plateau, where I examined the seasonal response of female moose to landscape change as a result of the MPB outbreak and subsequent salvage logging infrastructure (i.e., cutblocks, roads).

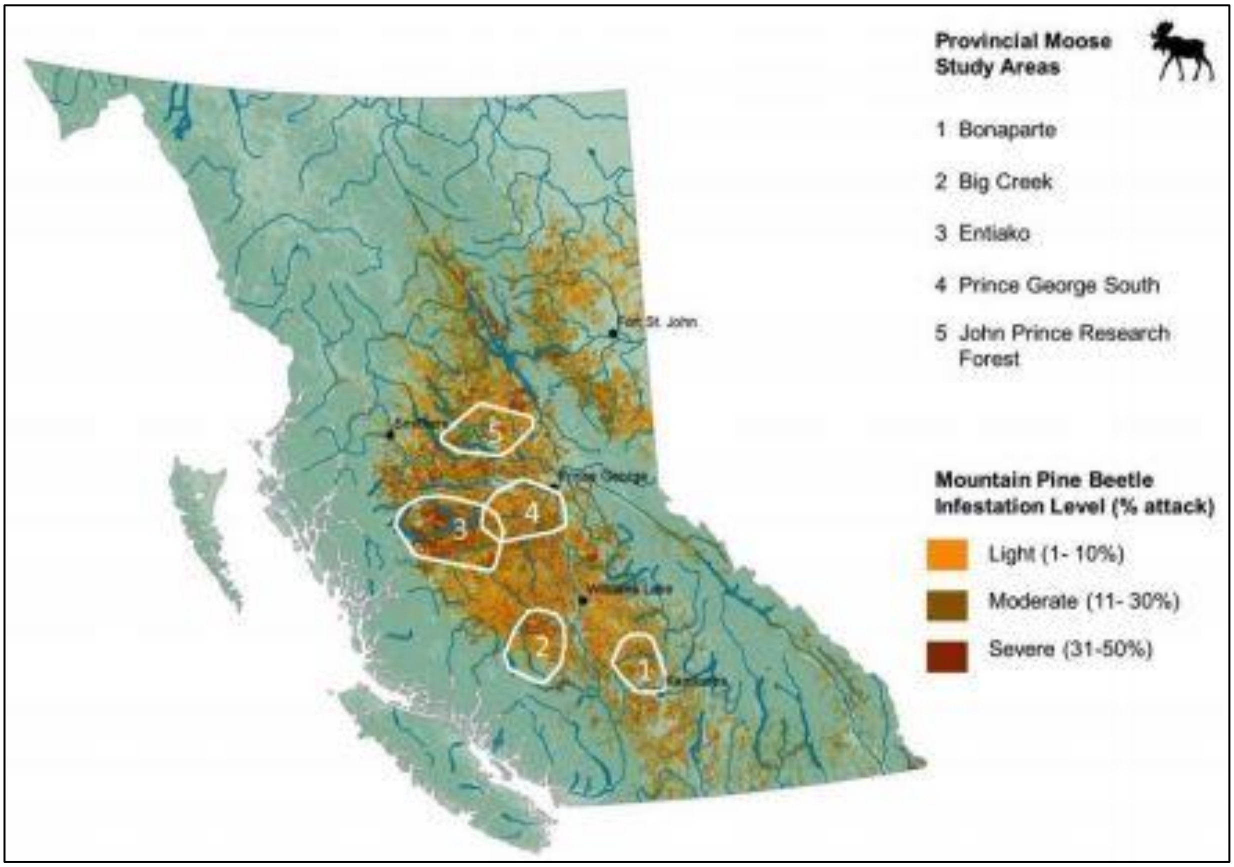

Figure 1.1 Five study areas within central British Columbia used to examine the factors affecting moose population change in relation to mountain pine beetle infestation level. The southern-most study area, Bonaparte Plateau, is the focus of this thesis (map provided from Kuzyk et al. 2019).

1.3 Thesis Structure

In Chapter 2, *Biological seasons defined by cluster analysis provide a different lens on seasonal fluctuations in home-range sizes for moose,* I used a cluster analysis framework developed by Basille et al. (2013), to determine biologically relevant seasons for female moose on the Bonaparte Plateau, in the Interior of B.C. I hypothesized that biological seasons will be defined by individual behaviour, measured by movement and habitat use, and that these seasons would coincide with climatic and physiological processes. I used these temporal periods to build spatial seasonal home ranges. I hypothesized that the size of the seasonal range would reflect the movement patterns of that season. I compared the differences in calendar dates between seasons derived empirically to those derived seemingly arbitrarily or using a single variable. In addition, I compared the size of seasonal ranges between different methodologies. These findings were then used in Chapter 3 to examine habitat selection.

In Chapter 3, *Female moose prioritize forage over mortality risk seasonally*, I examined the seasonal differences in female moose habitat selection in response to landscape change from mountain pine beetle salvage logging infrastructure (i.e., dense road network and intensive forest cutblocks). I tested whether altered resource availability, altered risk, or the cumulative effects of salvage logging best explained female moose distribution. I hypothesized that both altered resource and altered risk would influence seasonal moose distribution; however, the combinations of both these factors, the cumulative effects of salvage logging, would best explain moose space-use. I developed seasonal resource selection function models to test these hypotheses and develop management strategies based on the results.

In the final chapter, I summarize my findings from each data chapter and provide recommendations for management as well as future research.

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Chapter 2: Biological seasons defined by cluster analysis provide a different lens on seasonal fluctuations in home-range sizes for moose.

2.1 Introduction

Seasonal changes in environmental conditions strongly influence the behaviour of terrestrial mammals. For large herbivores, migration between seasonal ranges is thought to have evolved in response to the availability and quality of forage (Hebblewhite et al. 2008), predation avoidance or risk (Fryxell and Sinclair 1988), and shifts in temperature and precipitation (Rudolph and Drapeau 2012). For non-migratory populations of large herbivores, localized movements between seasonal ranges are common (Timmermann and McNicol 1988) and similarly are in response to forage availability and weather (Leblond et al. 2010). Seasonality also controls many life history events such as reproduction, recruitment, growth, and dispersal (Basille et al. 2013). Identifying these temporal shifts in animal movement and habitat use contributes to our knowledge of an animal's behaviour in addition to our understanding of an animal's response to its environment.

As the "season" is often the temporal foundation for animal space-use studies, it is essential that consideration be given as to how seasons are defined. Approaches used to define seasons have varied greatly and include using calendar dates (Beier and McCullough 1990), local and expert knowledge (Houle et al. 2009), environmental proxies (e.g., snow depth or plant phenology) (Beyer et al. 2013), movement rates (Rudolph and Drapeau 2012), and more recently by incorporating movement behaviour in combination with biological and physical variables (Vander Wal and Rodgers 2009, Basille et al. 2013).

Defining seasons into seemingly arbitrary periods is problematic, as this may lead to inaccurate conclusions in subsequent analysis and the development of ineffective management strategies. In the absence of fine scale movement and habitat use data, local and expert knowledge is a valuable source of information; however, limitations of this type of data include individual bias or knowledge being limited to a sample of a study area or individuals. Furthermore, arbitrary divisions of seasons may hide key shifts in an animal's behaviour (Harris et al. 1990). Using a single proxy to define seasonal boundaries is troublesome as it likely does not represent all of the factors that influence an animal's behaviour over time and it may fail to capture individual variation (Vander Wal and Rodgers 2009). We contend that a more scientifically sound alternative is to define biological seasons empirically, based on observed (rather than assumed) changes in movement and habitat use, especially where seasons provide the temporal framework for space-use studies.

The main spatial unit for wildlife research is an animal's home range (Long and Nelson 2012) defined as the area in which an animal moves when performing its normal activities (Harris et al. 1990). While there are a number of factors that influence a species' home range size, including both biological (e.g., age, size, and sex (Cederlund and Sand 1994)) and environmental factors (e.g., landscape structure and configuration (Anderson et al. 2005)), the "season" provides the temporal structure for spatially defining seasonal ranges. Several methods exist to spatially define home ranges, including minimum convex polygon, Kernel Density estimation, and more recently the Potential Path area (Long and Nelson 2012). Despite the various methods available to estimate home range size and the variability that these can introduce into analysis (Harris et al. 1990, Long and Nelson 2012)), we assert that accurately defining seasons based on biological data, may have a profound impact on the size and location of that range. Seasonal ranges are generally the foundation for habitat use studies, and as such the accurate temporal definition of the range, and subsequently the spatial definition, is imperative.

Examining the response of wildlife to landscape change from a seasonal lens is a common approach in wildlife studies (e.g., (Nielsen et al. 2004, Hornseth and Rempel 2016) and studies have shown that impacts or disturbance thresholds are often seasonal in nature (Beyer et al. 2013). For example, Beyer et al. (2013) examined the seasonal response of moose to road crossing and found that moose had a functional response to road crossings which varied seasonally as a function of road density. Understanding effects of development at the correct temporal scale allows wildlife managers to recommend management recommendations at a comparable, relevant scale.

Beginning in the early 2000's, moose populations in some areas of British Columbia have declined substantially (e.g.., by 50 – 70%) while other areas have remained stable or increased (Kuzyk and Heard 2014). These population changes coincided with a Mountain Pine Beetle (*Dendroctonus ponderosae)* outbreak which resulted in extensive salvage logging to recover economic value from the beetle-killed lumber. This large-scale disturbance has substantially changed the landscape (Alfaro et al. 2015, Kuzyk et al. 2019) and given the current climate of moose populations changing variably throughout B.C., it is imperative to understand the response of moose to landscape change, particularly in respects to salvage logging infrastructure.

Knowing that moose inhabit seasonal environments throughout their range (e.g., use aquatic habitats for foraging, cooling, and insect relief in the summer and mature timber in the winter to intercept snow), our primary goal was to determine biologically relevant seasons for moose within our study area and examine the differences between these seasons. Using GPS collar data from 83 female moose in the interior of British Columbia, we used a cluster analysis framework, developed by Basille et al. 2013, to define biologically relevant seasons. This empirically based method of delineating seasons incorporates both animal movement and habitat data. We hypothesized that biological seasons will be defined by changes in movement and habitat use, coinciding with climatic and physiological processes. We predicted that female moose would have increased movement rates through the growing seasons, utilizing forest cover that provides forage and that movement rates will decrease in the winter because of increased snow cover and movement constraints. Our second goal was to develop individual seasonal home ranges. We hypothesized that the size of the seasonal range would reflect the movement patterns of that season, with summer being the largest range and winter the smallest. These findings will be further used in subsequent analysis to examine the seasonal response of female moose to salvage logging infrastructure.

2.2 Study Area

Our research took place on the Bonaparte Plateau, north of the city of Kamloops, British Columbia (50º46’ to 51º30’N and 120º34’ to 121º34W), predominately within provincial Wildlife Management Units 3-29 and 3-20 (Figure 2.1.). The topography of the area is low-relief rolling terrain with elevations ranging from 1,000 m to 1,800 m above sea level. There is an abundance of small lakes throughout the study area. Historic weather data from Bridge Lake (located at the northern part of study area), reports daily averages of -2ºC to -8ºC in the winter (November to March) and 8ºC to 14ºC in the summer (May to September). Average annual rainfall is 385.1mm and annual average snowfall is 214.3cm, with the majority of snow falling in November (38.5cm), December (54.6cm) and January (55.4cm) (Government of Canada 2011).

Low elevation areas (400 – 1400m. a.s.l) consist of mixed seral stands of Douglas-fir (*Pseadotsuga menziesii)* and lodgepole pine (*Pinus contorta).* At mid-elevations (1250 – 1700m a.s.l.) there are extensive stands of even-aged lodgepole pine. The sub-boreal pine-spruce Biogeoclimatic zone (850 – 1500m) is dominated by lodgepole pine with spruce (Picea spp.) on moist sites (Meidinger and Pojar 1991). Large-scale commercial forestry and cattle ranching have resulted in a mosaic of disturbance across the study area predominately consisting of an extensive road network and cutblocks of varying ages.

Moose population density within the study area was estimated to be 296 ± 18 (SE) moose/ 1,000 km^2 in 2013 and 254 ± 41 (SE) moose/ 1,000 km^2. Predators of moose in the study area include wolves (estimated density: 10 wolves/1000km2 (Kuzyk and Hatter 2014)), cougars (*Puma concolor*), and black bears (*Ursus americanus*), with sporadic occurrences of grizzly bears (*Ursus arctos horribilis*). Little is known about density or space use of other prey or predators on the Bonaparte Plateau. Other ungulates in our study area includes mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and a small number of Rocky Mountain elk (*Cervus canadensis*).

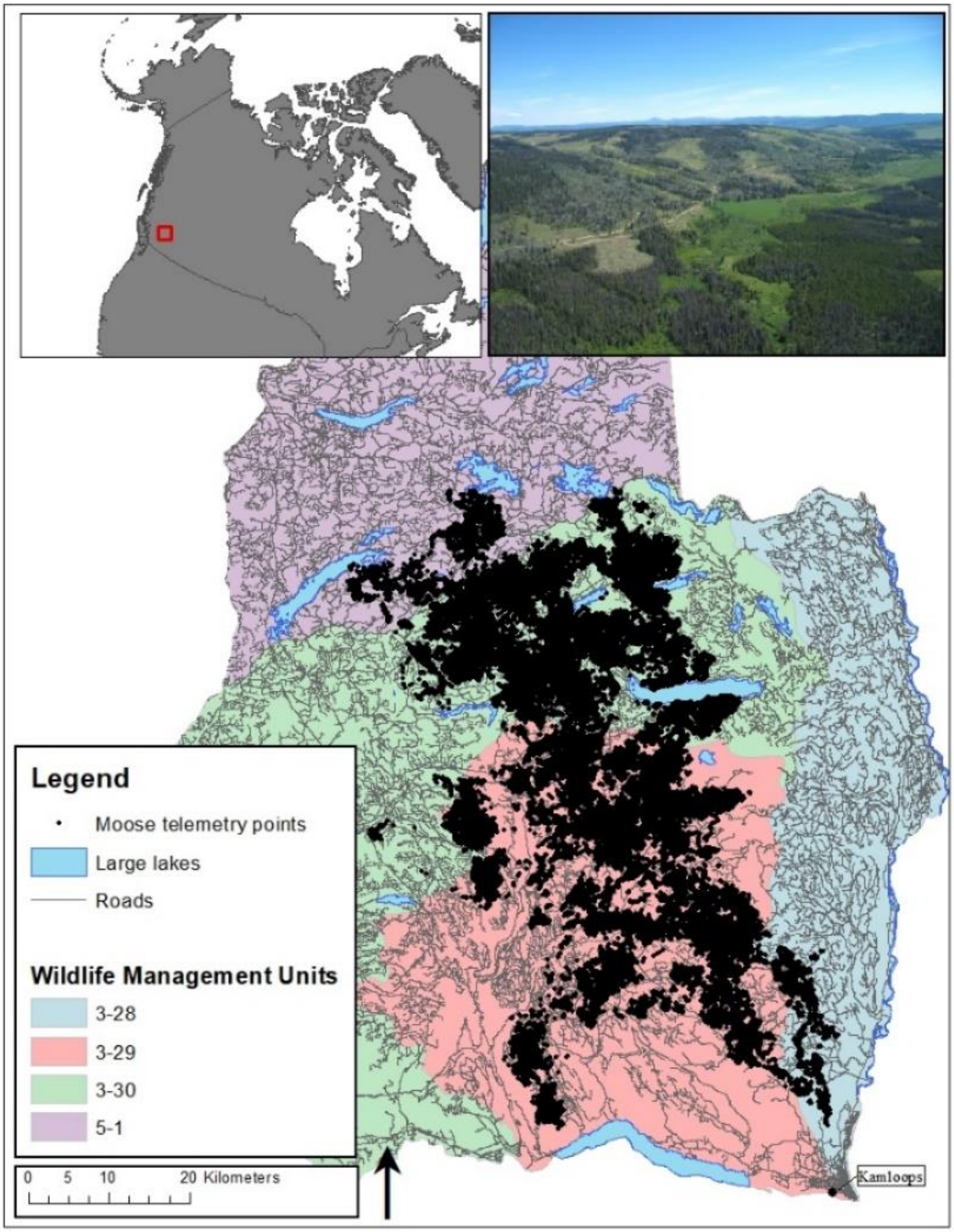

Figure 2.1 The study area is located on the Bonaparte Plateau, north of Kamloops, British Columbia, Canada. Moose telemetry locations (black dots) are distributed across the landscape predominately in Wildlife Management Units 3-29 and 3-30, with some extending in 3-28 and 5-1.

2.3 Methods

2.3.1 Moose Location Data

From February 2012 to January 2015, eighty-three G2110E Iridium Global Positioning System (GPS) collars were applied to female moose using helicopter-based net gunning techniques or chemical immobilization with a combination of carfentanil citrate and xylazine hydrochloride (Kuzyk and Heard 2014, Roffe et al. 2015). In February 2012, nine moose were collared followed by 29 in December 2012/January 2013, 14 in February 2014 and 31 in January 2015. Standard handling protocols were followed and were in accordance with the B.C. Ministry of Environment Animal Care Committee (Animal Care Permit Number CB17-277227).

The collars were programmed to acquire locations every four hours from March 1 to August 31 and every 1.5 hours from September 1 to February 28. The variable fix schedule was set by the B.C. Government as it was hypothesized that there would be more moose mortalities in the winter and a higher fix rate (i.e., one point every 1.5 hours) would allow fine scale investigation into female moose behavior leading up to the mortalities. The collars also collected time of data collection, ambient air temperature, horizontal dilution of precision (HDOP), number of satellites, and fix time. Mortality warnings were triggered after 12 hours of inactivity and investigations of mortalities were conducted within 24 hours of a notification. Data were cleaned to exclude location data for five days post-captures to account for potential effects that collaring may have on animal activity (Northrup et al. 2014), low accuracy points (i.e., 2D with HDOP >10 (D’eon and Delparte 2005), and outliers.

2.3.2 Determining Biological Seasons

We stratified moose location points into seasons using a cluster analysis framework following Basille et al. (2013). This approach defines seasons as homogenous periods where movements (i.e., speed and turning angle) and habitat use (i.e., in this case the vegetation in which the telemetry point is located) are more similar than in other periods. We used moose speed and turning angle, and elevation and vegetation cover where the location points were located to identify these states.

2.3.2.1 Moose Movement Data

Movement was characterized by calculating speed and turning angle between subsequent moose location points. We measured speed as the Euclidean distance between two successive points, divided by the time elapsed between successive relocations. Turning angle was estimated as the direction formed by the previous, current, and next locations (Basille et al. 2013). Individual location points were built into trajectories as an *ltraj* class using the ADE habitat package (Calenge 2015).

2.3.2.2 GIS Spatial Layers

We characterized habitat (i.e., topography and vegetation) in the study area using a geographic information system (GIS; ArcGIS 10.2, Esri). The Vegetation Resource Inventory (VRI; BR Ministry of Forests and Range 2007) spatial layer was used to characterize vegetation into 8 vegetation classes which we hypothesized as important for moose. These included: burned forest (<20 years old), deciduous, fir, water (i.e., wetlands and small lakes), mixed coniferous/deciduous, mixed coniferous, pine, and spruce. Forest stands were classified by the dominant species and were not considered mixed if they had > 70% of the leading species. Lakes were considered small if they were < 178 ha. This cut-off was determined using the natural breaks tool (jenks) in ArcGIS 10.2. Large lakes were generally unexploited by moose and were excluded. A digital elevation model with a scale of 1:20,000 and spatial resolution of 25m was used to estimate elevation (m) of the location data.

2.3.2.3 Cluster Analysis Framework

To characterize space use of each individual in each year, we used a 15-day moving window (7 days before and 7 days after the focal day) that summarized movement and habitat use data. For each GPS location for each day, the moving window summarized eleven variables including mean speed (m/day), turning angle, mean elevation, and the proportion of locations in burns, deciduous, fir, pine, spruce, mixed coniferous, mixed coniferous-deciduous, and water. The moving window approach smoothed temporal trends and provided more consistent seasons by removing fine-grained spatio-temporal variation and facilitated the use of data collected on different fix schedules (Basille et al. 2013).

We range-standardized variables using $z_i = \frac{x_i - \min(x)}{\max(x) - \min(x)}$ where x represents each variable of interest, so each had the same clustering weight (Steinley 2006). Standardization was completed for each individual-year measurement, and then averaged first by individual, and then for the set of individuals to ensure that behaviors displayed one year did not contribute more than others (Basille et al. 2013). We subsequently then standardized each variable in the resulting data frame.

We used the difference of difference-weighted (DD-weighted) gap method to determine the optimal number of clusters in the data (Yan and Ye 2007). The gap statistic, defined as: $\text{gap}_k = E^*\{\log(W_{kb})\} - \log(W_k)$, contrasts the observed within-cluster homogeneity from the expected within-cluster homogeneity. E^* denotes expectation under a sample size of n from the reference distribution, Wk is the pooled within-cluster sum of squares around the cluster mean with B equivalent to the random multivariate data sets that are generated (with *b* = 1,..., B) (Tibshirani et al. 2001). The optimal number of clusters identified was used to define the number of seasons and each day of the year was then represented by a cluster, which defined a space-use state. A season was then defined as the period wherein a species has the same space-use state (Basille et al. 2013)

Using a bootstrapping approach, we assessed the robustness of the delineation of the seasons by randomly re-sampling 100 sets of individual year units, with replacement, from the original data to match the same sample size as the observed data set (Basille et al. 2013). We then used K-means clustering to estimate the number of clusters for the entire data set (Basille et al. 2013). From the bootstrap sample, we estimated a distribution of daily weights corresponding to the likelihood that a given day would start a new season. Days that were in the top 20% of the weight distribution were retained as the start of a season and the remaining values were dropped. Seasons that were shorter than 5 days were combined with the previous season (Basille et al. 2013).

2.3.2.4 Seasonal Home Ranges

Within each season, a home range size was estimated for each individual moose using kernel density estimations (KDE; Laver and Kelly 2008) in Geospatial Modelling Environment (GME). The KDE method transforms the data into a continuous density surface by placing a three-dimensional kernel on each telemetry location. The kernel weights nearby points more heavily than those further away, giving estimates of local density ((O'Sullivan and Unwin 2010)). The Gaussian kernel estimator was used. Bandwidth was set to least squares cross validation (LSCV). The LSCV method was chosen as it has been suggested as the most reliable bandwidth for KDE analysis (Walter et al. 2011). Following this, a 95% isopleth was created around the kernel, delineating the home range (Worton 1989). The size of each individual seasonal home range (ha) was calculated in ArcGIS.

2.4 Results

Moose data were structured temporally, with data clustering into five biologically defined seasons. The DD-weighted gap statistic clustered into 6 groups (DD-gap = 0.21) which corresponded to five biological seasons. Seasons started January 7, March 29, April 30, June, 28, and September 21, which we defined as winter, spring, calving, summer, and fall, respectively (Figure 2.2). Two breakpoints were removed as they were not within the top 20% of the weight distribution, as indicated by dashed black lines in Figure 2.2.

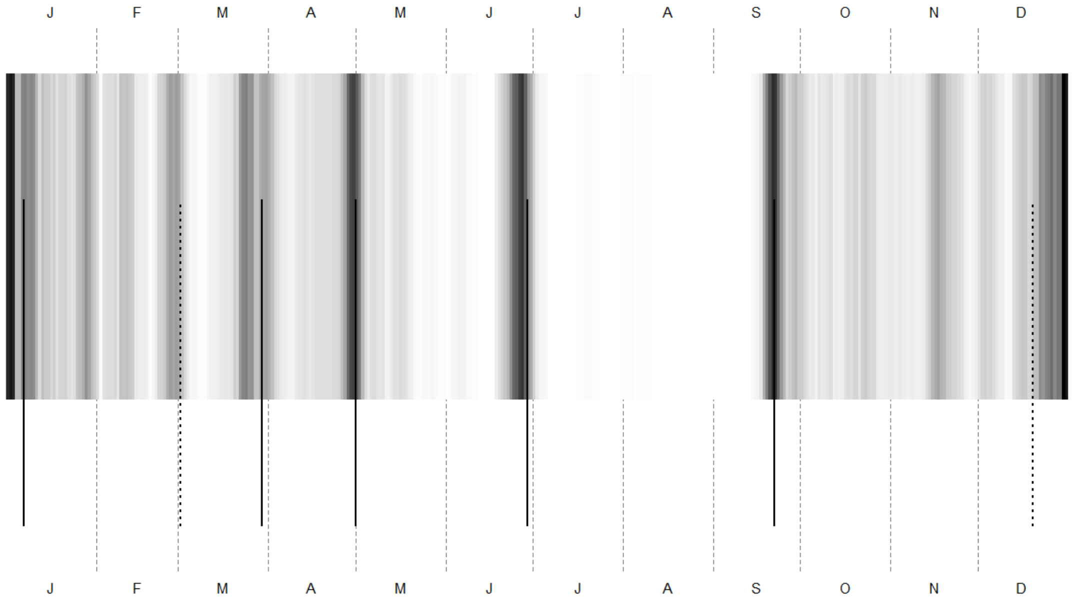

Figure 2.2. Weight distribution for each day of the year. Darker shades reflect higher weights. Seasons that were retained are represented by a black line and seasons that were dropped are represented by a dashed line. Months of the year are shown on the bottom and top of the graph consecutively from left to right, January to December.

Moose had the highest travel rate (i.e., speed) in the summer (Jun 28 – Sep 20) followed by the calving season (Apr 30 – Jun 27) and the fall (Sep 21 – Jan 6), with the lowest speeds observed in the winter (Jan 7 – Mar 28) and the spring (Mar 29 – Apr 29). Turning angles were lowest in the summer and highest, indicating less directional travel, in the calving season. Moose moved progressively into higher elevations from the winter through to the fall. Small lakes and wetlands were used more in the calving and the summer seasons compared to other seasons. Burned areas were used throughout all seasons; however, the least in the summer. Forest stands were used variably throughout the year. Deciduous, fir, and mixed coniferous/deciduous stands were used in the winter, with pine, spruce, and mixed coniferous/deciduous stands used in the spring. The summer and the fall were predominately defined by the use of mixed coniferous, pine, and spruce stands (Figure 2.3).

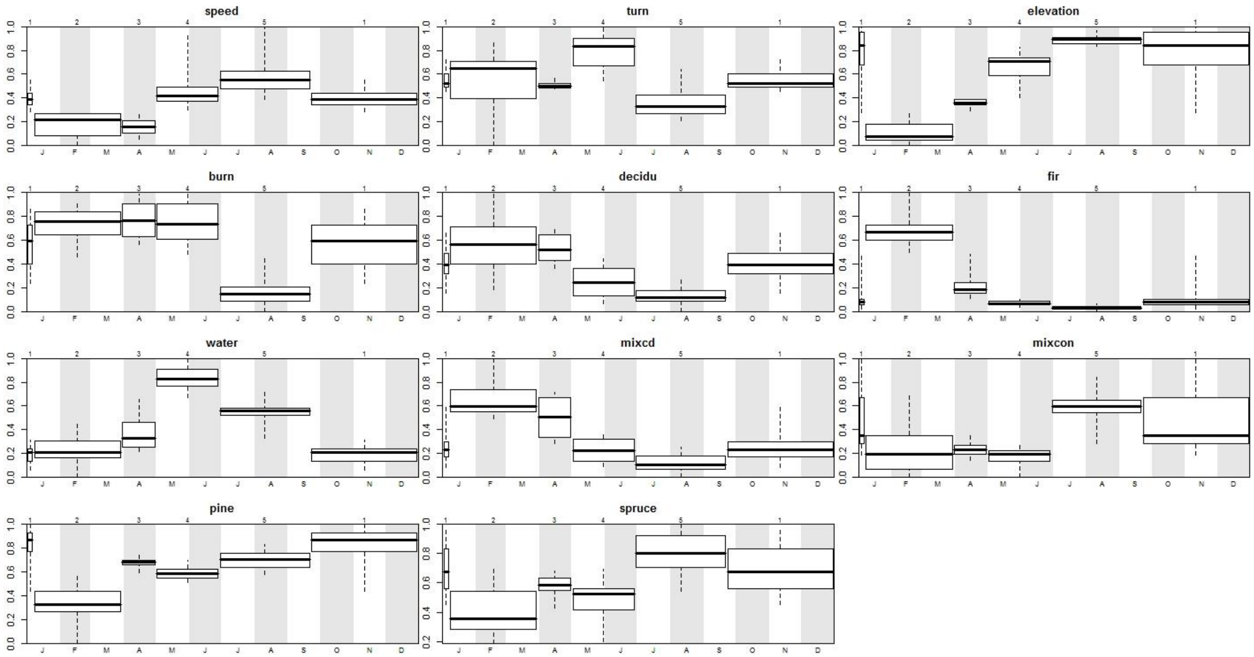

Figure 2.3. Detailed characteristics of variables throughout the year. Months of the year are shown on the bottom of each graph consecutively from left to right, January to December. Variables that were included in the analysis include biological (i.e., speed and tortuosity) topographic (i.e., elevation) and forest cover data (i.e., burn, deciduous, fir, water (wetland and small lakes), mixed coniferous/deciduous stands, mixed coniferous stands, pine, and spruce).

Average individual seasonal range size was similar among seasons: winter (2985.23 ha ± 624.09, n = 52), spring (2412.63 ha ± 655.24, n = 98), calving (2981.0 ha ± 254.81, n = 94), summer (2828.8 ha ± 199.99, n = 89), with the exception of fall where the largest average home range was observed (4742.85 ha ± 656.96, n = 60) (Figure 2.4).

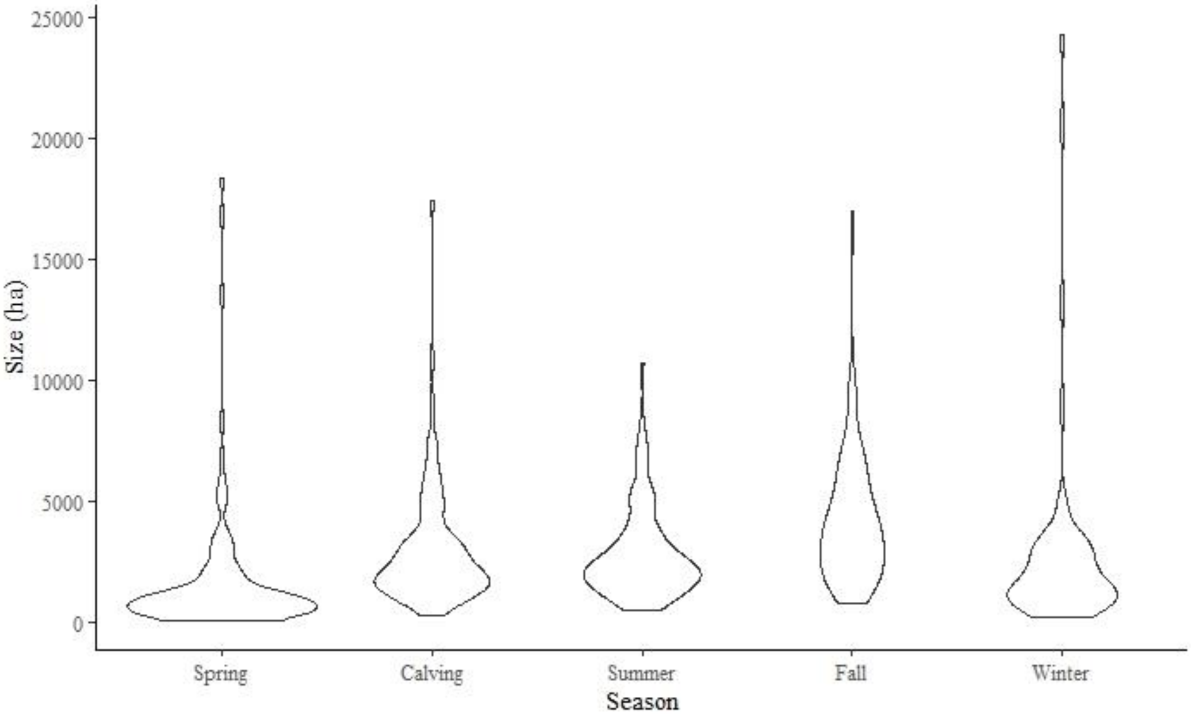

Figure 2.4 Size (ha) of seasonal ranges of female moose on the Bonaparte Plateau, British Columbia from 2012 to 2016. Average individual seasonal range size was similar among seasons: winter (2985.23 ha ± 624.09), spring (2412.63 ha ±655.24), calving (2981.0 ha ± 254.81), summer (2828.8 ha ± 199.99), but significantly larger in fall (4742.85 ha ± 656.96).

2.5 Discussion

Moose movement clustered biologically important periods of the species' annual life-history cycle, with implications for subsequent analysis, management, and conservation of this iconic species. Seasonality is a key feature of species ecology and evolution (Fretwell 1972, Boyce 1979, Hebblewhite et al. 2008) and biological data partitioned by seasons are used globally for a range of analyses on a variety of species (Nielsen et al. 2002, Ryan et al. 2006, Périquet and le Roux 2018). The method in which we define seasons will affect how we interpret successive analyses and seasonality in species space use, influence management recommendations and decisions, and guide conservation initiatives. We demonstrated how biologically defined seasons can differ from arbitrarily defined seasons and the implications that these differences may have on subsequent analysis.

Following the methodology presented by Basille et al. (2013), we found that movements and habitat use of female moose in the B.C. interior clearly revealed five biologically relevant seasons: spring (Mar 29 – Apr 29), calving (Apr 30 – Jun 27), summer (Jun 28 – Sept 20), fall (Sept 21 – Jan 6), and winter (Jan 7 – Mar 28). These seasons are consistent with our biological and ecological knowledge of moose in the study area; however, interestingly, differ temporally from other studies within the interior of British Columbia that used different variables (e.g., local/expert knowledge or movement rates) to measure seasons (e.g., (Lemke 1998, Gillingham and Parker 2008*a*, Scheideman 2018). Through incorporating both movement and habitat metrics we show that the biological seasons reported in this paper accurately depict moose space-use in the interior of B.C.

The timing and changes observed in seasonal moose movement rates reflect climatic cycles (i.e., plant green up) and physiological processes (i.e., parturition and rut). We observed the lowest movement rates in the winter and spring, with rates increasing as the growing season progressed. This pattern has been observed in other populations of moose in Canada (e.g., Mcculley 2004, Gillingham and Parker 2008, Vander Wal and Rodgers 2009). During the growing season, moose are maximizing their forage intake, consuming 2.6 – 3.2% of their body weight in dry matter to exploit available forage, accommodation lactation, and store fat, with consumption declining through the fall (i.e., rut) to a low of 1.2 – 1.3% in winter (Schwartz et al. 1984). As such, movement rates in summer are higher as moose are actively searching for food (Vander Wal and Rodgers 2009). As fall and winter approach, forage quality and availability decrease and moose switch their diet from green forage to twigs and buds. In addition, snow levels increase and this is generally marked by a decrease in movement (Vander Wal and Rodgers 2009). While this pattern is generally consistent between sexes throughout the year, male moose may increase their movements during the rut (Garner and Porter 1990). The turning angle between animal location points is representative of an animal's response to its environment, with an increase in turning angle signifying searching behaviour (i.e., non-directional movement, Etzenhouser et al. 1998). In combination with speed, turning angle can be used to characterize animal behaviour and can be indicative of an animal spending more time foraging than moving (Etzenhouser et al. 1998). In the calving season, we observed a low turning angle indicative of female moose spending more time foraging or potentially in a similar location. We observed the lowest turning angle and highest speeds in the summer suggesting that moose are travelling between foraging areas.

Similar to moose movement patterns reflecting climatic and physiological cycles, habitat use by moose also reflected their changing seasonal requirements. During the calving season, moose used pine and spruce stands and there was a notable increase in use of water features (i.e., small lakes and wetlands) compared to other seasons. Studies on calving site selection by moose have provided inconsistent results (Mclaren et al. 2017); however, based on results from our resource selection function analysis in Chapter 3, water features in our study area, in particular wetlands, are a very important feature during this season. The summer season was defined by the continued use of water features (albeit less than calving season), as well as an increase in use of spruce, pine and mixed coniferous stands. The use of these habitats is likely to avoid heat stress by selecting wet and shaded areas (Melin et al. 2014). The fall season was characterized by the use of coniferous (i.e., pine, spruce, and mixed stands) and deciduous stands and similarly, the winter and spring seasons were characterized by the use of pine and fir, mixed coniferous-deciduous, and deciduous stands. Both deciduous and coniferous stands provide critical functions in the winter, with mixed deciduous stands provide important forage (i.e., aspen leaf litter) (Renecker and Hudson 1988) and mature coniferous stands intercepting snow, thus aiding in moose movement (Lemke 1998).

The biological seasons defined in this study differ to varying degrees compared to other moose studies in comparable climates (e.g., Lemke 1998, Gillingham and Parker 2008*b*, Scheideman 2018). Lemke (1998) examined seasonal habitat requirement of moose on the Bonaparte Plateau (Wildlife Management Unit 3-29). Four seasons were defined using previous data as well as reviewing relevant moose literature and include: winter (Dec 1 – Mar 31), spring (April 1 – Jun 30), summer (Jul 1 – Sept 15), and autumn (Sept 16 to Nov 30). While the calendar dates are comparable to the dates we defined, Lemke (1998) combined what we defined as spring and calving seasons into a single season spanning the timeframe of our two seasons. This could have implications regarding the identification of important calving habitat or behaviours associated with calving habitat, the interpretation of results, as well as the ability to compare results between studies. Gillingham and Parker (2008*b*) used biological and ecological characteristics to define five seasons for moose for studies in northern British Columbia. Seasons were defined as winter (Nov 1 – Feb 28), late winter (Mar 1 – May 15), calving (May 16 – Jun 15), summer (Jun 16 – Aug 15), and fall (Aug 16 – Oct 31). Scheideman (2018) adapted these using trends from the local study area and local and expert knowledge and refined those seasons as: early winter (Nov 21 – Jan 14), late winter (Jan 15 – Apr 25), calving (Apr 26 – Jun 20), summer (Jun 21 – Sept 12), and fall (Sept 13 – Nov 20). Scheideman's (2018) seasons are comparable to our results with the exception of fall (Sept 13 – Nov 20 compared to Sept 21 to Jan 6) and winter (Nov 21 to Jan 14 compared to Jan 7 to Mar 28). These differences may be attributed to the geographic, and therefore climatic, differences in study areas; however, this is difficult to conclude as the seasons were defined using different approaches. An empirical based method reduces the bias from this process. Between the aforementioned studies, calving season is defined differently (i.e., Lemke (1998) included calving with spring, Gillingham and Parker (2008b) defined it as a month long period, while Scheideman (2018) has defined it as a two month long period. These differences make it challenging to compare results between studies, as the degree to which the periods include pre and post calving movements and habitat use vary substantially. Through looking at movement rates associated with parturition events, we found that median day of parturition was between May 21 and May 26 from 2012 to 2015, thus our calving period (i.e., Apr 30 – Jun 27) includes both pre and post calving movements. By failing to properly identify seasons (e.g., lumping seasons together), it is possible to increase the variability of movement and consequently habitat use within that season, thus increasing the potential of inducing a Type II error into subsequent analysis. Empirically defined seasons should reduce noise or variability within the seasons and will allow for finer-scale responses to be detected.

We used the biological seasons developed in this chapter as the foundation for developing seasonal home ranges. The seasonal ranges defined by the cluster analysis differed in size from other studies where seasons were more arbitrarily defined. Contrary to our predictions, seasonal range size was comparable between seasons, apart from fall, where the average size was 1.6 times larger than the next largest seasonal range, winter. As movement rates are highest in the summer and lowest in the winter, we expected seasonal ranges to reflect this, with summer ranges being significantly larger than winter ranges. Other studies have found summer ranges to be the largest and calving and winter ranges to be smallest (Gillingham and Parker 2008*a*, Cederlund and Okarma 2014); however, Mcculley 2004 found that female moose had the largest range in the early winter and smallest in the late winter. An increased range size in fall may be a function of the abundance of females compared to males (Cederlund and Okarma 2014). In a situation where the density of females is low compared to males, females may have to increase their movements, and subsequently have larger fall ranges, to find males during the mating season. Comparing seasonal home range sizes between studies is challenging when the temporal scale (i.e., season) used to delineate the range is based on different methods. This is further compounded by the varying methods researchers use to develop seasonal range (e.g., Minimum Convex Polygon, Kernel Density). As the seasonal range is often the primary spatial unit to study animal space use (e.g., habitat studies, predator-prey dynamics), it is imperative to utilize a method that most accurately represents the biological reality of a species, thereby minimizing the potential to misinterpret results or to fail to detect a response.

The value of applying a seasonal perspective to space-use studies has been well documented and we highlight the importance of defining biologically relevant seasons, particularly when using these seasons in subsequent home range analyses and space-use studies. Biological season can be defined in a variety of ways, including using expert or local knowledge, environmental data, resource availability, and the modelling of movement rates. Recently several frameworks have been developed to assist researchers in taking the approach of generally focusing on using movement metrics to define biological seasons (see Vander Wal and Rodgers 2009*a*, Birkett et al. 2012, van Beest et al. 2013), with Basille et al. (2013) incorporating habitat metrics into the method. These methods are advantageous as they define seasonality empirically, centered on animal behaviour (i.e., movement and habitat use) rather than singularly on one variable (e.g., plant phenology) or an individual’s knowledge. Limitations may arise if precise high frequency animal location data or sufficient land cover data are not available. While the empirically based methods (e.g., Basille et al. 2013) are more onerous than simply using calendar dates or expert knowledge, they provide a repeatable, empirical approach to defining seasons that is rooted in animal behaviour. Accurately defining the temporal framework that subsequent analysis is centered on is key in furthering our understanding of an animal’s response to its environment and researchers’ abilities to make meaningful and relevant management decisions and guide conservation efforts.

2.6 Management Implications

The method used to define seasons, the temporal framework for many animal space-use studies, has implications for the spatial definition of a home range and subsequent space-use analysis, thereby influencing our ability to make meaningful management decisions. With the goal of furthering our understanding of a species seasonal response to its environment, the approach we used (i.e., (Basille et al. 2013) has many advantages, as it is based on an individual animal’s behaviour, rather being arbitrarily defined or based on a single variable. Furthermore, this empirically based method allows us to spatially define an animal’s seasonal ranges more accurately. Identifying the location and size of seasonal ranges are key for (1) accurately assessing habitat selection and a species seasonal response to its environment, (2) the identification and protection of key habitat and (3) for calculating densities and therefore the population management of a species. We recommend that researchers use an empirically based approach, rooted in animal behaviour, to delineate temporal and spatial seasonal ranges.

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Chapter 3: Female Moose Prioritize Forage Over Mortality Risk Seasonally

A revised version of this chapter, which included the methods from Chapter 2, was submitted to the Journal of Wildlife Management and was accepted pending revisions in March 2020.

3.1 Abstract

Over the last decade, several moose (*Alces alces)* populations have declined across North America. These declines are believed to be broadly related to climate and landscape change. At the western reaches of moose continental range, in the interior of British Columbia, Canada, wildlife managers reported widespread declines of moose populations. Disturbances to forests from a mountain pine beetle (*Dendroctonum ponderosae)* outbreak and associated salvage logging infrastructure in British Columbia (B.C.) are suspected as a mechanism manifested in moose behavior and habitat selection. We examined seasonal differences in moose habitat selection in response to landscape change from mountain pine beetle salvage logging infrastructure: dense road networks and large intensive forest harvest cutblocks. We used 157,447 global positioning system (GPS) locations from 83 adult female moose from 2012 to 2016 on the Bonaparte Plateau at the southern edge of the Interior Plateau of central B.C. to test whether increased forage availability, landscape features associated with increased mortality risk, or the cumulative effects of salvage logging best explain female moose distribution using resource selection functions in an information-theoretic framework. We tested these hypotheses across biological seasons, defined using a cluster analysis framework. The cumulative effects of forage availability and risk best predicted resource selection of female moose in all seasons;

however, the covariates included in the cumulative models varied between seasons. The top forage availability model better explained moose habitat use than the top risk model in all seasons, except for the calving and fall seasons where the top risk model (distance to road) better predicted moose space use. Selection of habitats that provide forage in winter, spring, and summer suggests that moose seasonally trade predation risk for the benefits of foraging in early seral habitat in highly disturbed landscapes. Our results identified the need for intensive landscape scale management to stem moose population declines. Additional research is needed on predator densities and space use as well as calf survival in relation to salvage logging infrastructure.

3.2 Introduction

When populations of a circumboreal species are variably changing across space, the blame logically falls to regional-scale changes in resources, mortality, or both as potential mechanisms. Parsing apart why regional declines occur, in the context of those local habitat changes, yields valuable insight into population processes that are important to effective management decisions. For example, within North America, there have been reports of increasing and decreasing populations of moose (*Alces alces)* over the last decade (Timmermann and Rodgers 2015). Across the range, different factors including climate change, habitat loss or degradation, disturbance, harvest, disease, predation, and vehicle collisions have been suggested as causes of declines (West 2009, Timmermann and Rodgers 2015), while changing harvest regulations, habitat restoration, and climate have facilitated population increases or range expansion (Darimont et al. 2005, Wattles and Destefano 2013). Although moose resource selection has been studied extensively, those studies are limited to specific foci. Anderson et al. (2018) focussed on the role of elevation, and Gagné et al. (2016) focussed on moose-caribou (*Rangifer* *tarandus caribou)*-wolf (*Canis lupus)* movement along an elevational gradient. Courbin et al. 2014 modelled individual behaviour and movement relative to nodes in a planar network. In summary, little to no synthetic information exists to help extrapolate reasons for moose declines across landscapes and systems, precipitating the need for additional research. This is the case for moose declines in British Columbia, Canada (B.C.).

Since the mid-2000s B.C. moose population surveys have indicated declines up to 70% in some regions of the province, while other areas remained stable or increasing (Kuzyk 2016, Kuzyk et al. 2018a). Coinciding temporally with these changes, the ecological landscape has recently been subject to unprecedented change, arising from significant road building and timber harvest due to the largest and most severe recorded outbreak of mountain pine beetle (*Dendroctonus ponderosae*) in the province (Kurz et al. 2008). Large-scale salvage logging of beetle-killed trees was more intensive and extensive than traditional forms of forest harvest (e.g., larger cut sizes, extensive road networks; Radeloff et al. 2000, Lindermayer and Noss 2006). A landscape change hypothesis has been proposed that suggests increased roads and cutblocks from mountain pine beetle salvage logging facilitates predators and hunters putting moose at increased risk of mortality (Kuzyk and Heard 2014). Several research projects within B.C. are examining aspects of this hypothesis (e.g., Kuzyk et al. 2018b, Scheideman 2018).

We posited that evidence for the mechanisms of declines could be garnered through examination of female moose habitat selection in relation to mountain pine beetle infestation, logging features, and other natural and anthropogenic landscape features. Habitat selection is a hierarchical behavioral process wherein habitat use decisions are made at multiple spatial scales (Johnson 1980). At the largest scale, an animal establishes a home range from within the species' range and within the home range makes movement decisions in response to environmental conditions, typically measured as resource availability. These decisions are a series of trade-offs, influenced by the need to meet nutritional requirements with adequate forage and cover, and to minimize mortality risk (Fryxell et al. 1988, Rettie and Messier 2000, Dussault et al. 2005). For prey species in particular, the decision between foraging and predation risk is a key driver of habitat selection (Fryxell et al. 1988, Dussault et al. 2005). Prey species balance anti-predator behaviors (e.g., vigilance, group size, group structure) with the acquisition of resources (Lima and Dill 1990, Ferrari et al. 2009, Nicholson et al. 2014). Ungulate species may opt for energy gain through foraging in early-seral habitats against the risk of predation (Dussault et al. 2004, 2005).

It is hypothesized that prey respond to these risk trade-offs in a hierarchical nature (Johnson 1980). In theory (but without empirical test), animals are expected to select for habitats that reduce the factors with the greatest potential to reduce individual fitness, such as predation, at a large scale (Rettie and Messier 2000, Street et al. 2016). Once animals meet requirements at this scale, selection at smaller scales meets specific needs such as foraging requirements or cover (Courtois et al. 2002, Kittle et al. 2008, Leblond et al. 2010). At these smaller scales (i.e., within the home range), prey respond to predation risk by adjusting their behaviors through spatial changes in habitat selection and activity patterns (Thaker et al. 2011), thereby selecting for habitats that provide cover and security when predation risk is high.

Predation risk is typically associated with nonhuman predators; however, many ecologists have observed that anthropogenic disturbances such as habitat alterations, resource exploitation, and human presence may elicit a behavioral response in prey species similar to that of predation risk (Beauchesne et al. 2013, Smith et al. 2017). Landscape features associated with an increased probability of predator presence are considered a cue of of predation risk, thus vulnerability to predation can be attributed to specific habitat features rather than direct predator presence (i.e., roads; Hebblewhite et al. 2005). Behavioral changes are often then reflected in alterations to a species use of space, interactions (i.e., competition and predation), distribution, and movement patterns (Turner 1989, Lindenmayer and Fischer 2006). In contrast, disturbances that lead to an increase in early seral stage vegetation (i.e., forage) and a mosaic of landscape types are beneficial for moose (Fisher and Wilkinson 2005). Mature coniferous forests are also important habitat for moose for escape cover (Kunkel and Pletscher 2000) and thermal needs (Dussault et al. 2004) and the juxtaposition of this habitat with foraging habitat is crucial (Fisher and Wilkinson 2005).

Early seral vegetation stemming from forest harvest is necessarily associated with road networks, and there is considerable evidence that linear features can affect the distribution and behavior of various species (Jalkotzy et al. 1997, Fahrig and Rytwinski 2009). Gray wolves use linear features to increase movement and distance travelled (Dickie et al. 2016) thereby increasing their hunting efficiency (Latham et al. 2011, Whittington et al. 2011, Mckenzie et al. 2012). Roads also provide vehicular access for hunters to areas that are otherwise inaccessible; hunters and hunting success has been documented to increase with use of vehicles (Rempel et al. 1997, Schmidt et al. 2005). Roads may have a negative effect on moose by facilitating predator travel and hunter access, thereby increasing their exposure to potential predation; a landscape with an extensive road network juxtaposed with extensive early seral habitat offering high visibility as a result of salvage logging has the potential to be a risky landscape for moose.

Building on these specific foci, we took a multi-mechanism approach and competed multiple hypotheses about forage, risk, elevation, topography, and other metrics of resource heterogeneity. We sought best support among those hypotheses, to describe selection within a rapidly declining moose population in a multi-predator system. We examined female moose response to resources and risk using a relationship between habitat alteration from salvage logging and seasonal moose resource selection. In addition to natural features on the landscape (i.e., topography and forest cover type), we tested whether altered resource availability, altered risk, or the cumulative effects of salvage logging best explain female moose distribution at the seasonal range scale. We tested 3 competing (but not mutually exclusive) hypotheses.

1. Altered resource availability as a result of the creation of early seral habitat from extensive harvesting will influence seasonal moose distribution because of the increased availability of forage; however, this use will be limited by the risk posed by roads and the lack of security cover as a result of extensive, large cutblocks.
2. Altered mortality risk from increased linear features from salvage logging will influence seasonal female moose distribution in all seasons. We expect moose to avoid roads in all seasons: during calving and summer when calves are young and susceptible to predation, in fall when hunting season occurs, and in winter and spring when moose may be susceptible to predation and predator travel through snow is expedited by roads.
3. Salvage logging infrastructure (i.e., roads and cutblocks) influence seasonal patterns of habitat use for female moose and that the cumulative effects of salvage logging, which include both risk and resources, will best explain moose distribution.

3.3 Study Area

Our study was conducted on the Bonaparte Plateau at the southern edge of the Interior Plateau of central B.C. from February 2012 to March 2016 as part of a large-scale provincial-wide study investigating factors affecting moose population change (Kuzyk et al. 2018b). Moose densities in 2018 were estimated at 254 ± 41(SE) moose/1,000 km^2, declining from an estimated 296 ± 18 moose/1,000 km^2 in 2013 (Procter and Iredale 2018).

The Bonaparte Plateau study area, approximately 3,500 km^2 in size, is located in south-central B.C. (50º46’ to 51º30’N and 120º34’ to 121º34W, Figure 3.1). The plateau is characterized by low-relief rolling terrain with abundant lakes (van Poorten et al. 2012) and elevations ranging from 1,000 m to 1,800 m above sea level. The climate is characterized by short, hot, dry summers (i.e., June – August) and long, cold winters (i.e., December to March), predominately influenced by the rain shadow of the Coast Mountains. The long term mean annual temperature is 4.2 ºC, with average long term winter temperatures ranging from -4 to -37 ºC and summer temperatures ranging from 9 to 29 ºC (Environment Canada 2019). The region receives an average of 496 mm of precipitation annually (Environment Canada 2019).

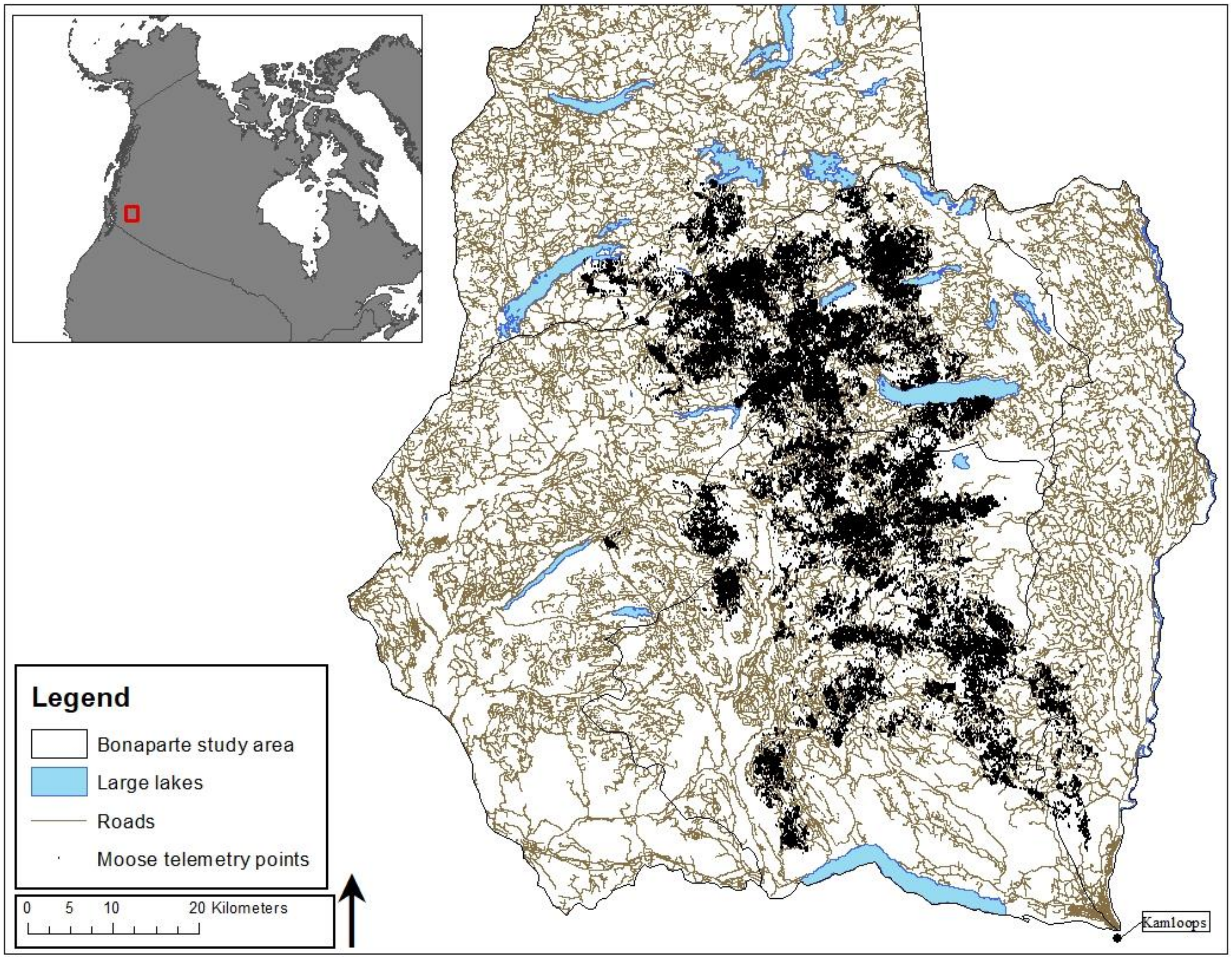

Figure 3.1 Distribution of moose location data (black dots) (*n* = 83, 157,447 location points) on the Bonaparte Plateau, south-central British Columbia, Canada, 2012-2016. Brown lines represent the road system and large lakes are in blue.

Three dominant Biogeoclimatic Ecosystem Classification Zones characterize this region: interior Douglas fir (IDF), sub-boreal pine-spruce (SBPS), and montane spruce (MS; Meidinger and Pojar 1991). The IDF zone occurs at lower elevations (400 – 1,400 m) and includes mixed seral stands of Douglas-fir (*Pseudotsuga menziesii)* and lodgepole pine (*Pinus contorta*; Meidinger and Pojar 1991). The SBPS occurs at mid elevations and is dominated by lodgepole pine with spruce (*Picea* spp.) occurring on moist sites. The MS zone occurs at mid elevations (1,250 – 1,700 m). The Engelmann spruce sub-alpine fir, sub-boreal spruce, bunchgrass, and ponderosa pine zones occur relatively infrequently throughout the study area (Meidinger and Pojar 1991, Kuzyk et al. 2018b).

Large-scale commercial forestry and cattle ranching dominate the landscape. Logging has increased to an unprecedented rate since 2010 due to the largest recorded outbreak of mountain pine beetle (British Columbia Ministry of Forests and Range 2006, Heinrich 2007, Ritchie 2008, Lewis 2009, Alfaro et al. 2015). The outbreak resulted in extensive tree mortality and subsequent salvage logging, leading to abundant cutblocks and road development across the landscape. The estimated proportion of the landscape affected by mountain pine beetle is considered to be pervasive (i.e., 71 to 100 %, Kuzyk et al. 2018b). Between 2012 to 2016, 4.7 to 8.2 % (166 – 289 km^2) of the study area was between 0 and 2 years in age (i.e., freshly logged) and 13.5 to 18.1% (474 – 635 km^2) was between 3 and 14 years of age (i.e, regenerating cut blocks; Figure 3.2). Regeneration of the logged blocks is from both planting and natural seeding.

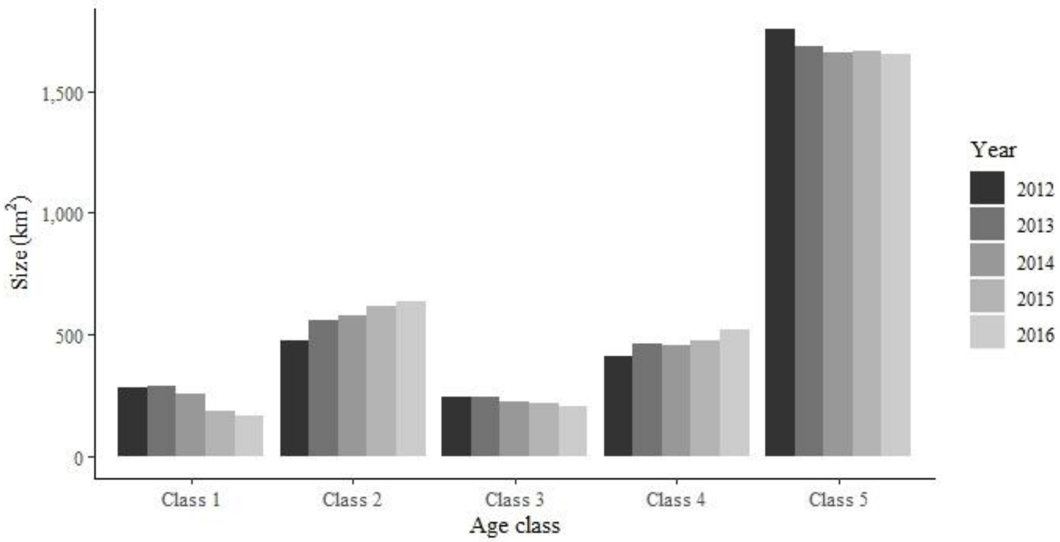

Figure 3.2 Area (km^2) of various age classes on the Bonaparte Plateau, British Columbia from 2012 to 2016. Class 1 represents stands that are 0-2 years old, Class 2 are 3-14 years, Class 3 are 15 to 25 years, Class 4 are 26-79 years, and Class 5 are >80 years in age.

Predators in the study area include wolves (estimated density: 10 wolves/1000km^2 (Kuzyk and Hatter 2014)), cougars (*Puma concolor*), and black bears (*Ursus americanus*), with recent sporadic occurrences of grizzly bears (*Ursus arctos horribilis*). Other ungulates in the area include mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and a small number of Rocky Mountain elk (*Cervus canadensis*). Very little is known about densities or space use of these species within the study area. Moose harvest by First Nations and resident and non-resident hunters occurs within the study area. First Nations harvest moose within their traditional territory for food, social and ceremonial purposes and licensed hunting opportunities are offered through limited entry hunts for males and females in October and November and an open season for spike-fork males from 1 - 15 November.

3.4 Methods

3.4.1 Moose Location Data

We captured 83 female moose via helicopter-based net gunning and chemical immobilization with a combination of carfentanil citrate and xylazine hydrochloride (Roffe et al. 2001, G. Kuzyk et al. 2018b) between February 2012 and January 2015. Nine, 29, 14 and 31 moose were captured during winters 2011 - 2012, 2012 - 2013, 2013 - 2014 and 2014 - 2015, respectively. We targeted adult female moose randomly for capture, and we attempted to evenly distribute collars throughout the study area. Standard protocols for handling were approved in accordance with the B.C. Ministry of Environment Animal Care Committee (Animal Care Permit Number CB17-277227).

We fitted female moose with G2110E Iridium GPS-collars (Advanced Telemetry Systems, Isanti MN, USA) programmed to acquire locations every 4 hours from 1 March – 31 August and every 1.5 hours from 1 September – 28 February. In addition, the collars report time of data collection, ambient air temperature, horizontal dilution of precision (HDOP), number of satellites, and fix time. We excluded location data for 5 days post-capture to account for the potential effects that collaring may have on animal activity (Northrup et al. 2014).

The raw data collected from GPS collars can contain bias and error (D’eon et al. 2002), with the largest source of this being from missing data which is often associated with topography and vegetation cover type (D’eon and Delparte 2005). This can be problematic in a resource selection study as certain vegetation types may then be over or underrepresented, leading to bias and potentially inaccurate conclusions (D’eon et al. 2002). To examine the potential error in our collar data, we calculated the fix rate of the collars (i.e., observed fixed rate vs expected fix rate). Data were also cleaned for low accuracy points (i.e., 2D locations with a horizontal dilution of precision >10 (D’eon and Delparte 2005) and outliers. We subset the remaining GPS location points to 6 location points/day to maintain consistency across seasons for resource selection analysis.

3.4.2 Development of GIS Spatial Layers

We characterized moose habitat using spatial data within a geographic information system (GIS; ArcGIS 10.2, Esri, Redlands, CA, USA). We selected covariates that we hypothesized were biologically relevant for moose habitat selection (i.e., topography, vegetation, salvage logging infrastructure [i.e., roads and cutblocks], (Appendix 1, Table 3.5)).

These data spanned 2 main sources. We used a 1:20,000 scale digital elevation model (DEM) with a spatial resolution of 25m to estimate elevation (m), slope (degrees), and aspect (obtained from the Ministry of Forests, Lands, Natural Resource Operations and Rural Development). Aspect was converted to a categorical variable with four classes: east (45 - 135°), south (136 - 225°), west (226 - 315°), and north (316 - 44°). Degree of slope ranged from 0 to

90º, with 90º being vertical. Landcover was the second data source, characterized using a combination of Vegetation Resource Inventory (VRI; BC Ministry of Forests and Range 2007) and Reporting Silviculture Updates and Land Status Tracking System (RESULTS) spatial layers. We reclassified data into ten landcover types we hypothesized are important to moose: burned forest (< 20 yrs old), deciduous, fir, pine, spruce, mixed coniferous, and mixed coniferous-deciduous stands, small lakes, wetlands, and cutblocks. Mixed coniferous stands were withheld as the reference category. Lakes were classified as small (< 178 ha) or large (> 178 ha) using the natural breaks tool (jenks) in ArcGIS 10.2. Large lakes (> 178 ha) were not included in the Resource Section Function analysis as these were considered unexploited by moose. Distance to water features (i.e., lakes, wetlands) was measured using Euclidean distance (m) for each location point to the nearest water features as a proxy for use of riparian areas associated with these features (i.e., smaller distances > 0, indicated use of zones around lake-wetland) (Table 3.5; Appendix 1).

Roads and cutblocks associated with salvage logging were characterized using the RESULTS layers and the Cumulative Effects Grizzly Bear Road spatial layer (B.C. Ministry of Forests Lands and Natural Resource Operations 2014). Five age class categories were established: 0 - 2 years, 3 - 14 years, 15 - 25 years, 26 - 79 years, and ≥ 80 years. These categories were established to capture the habitat values (i.e., forage, security and thermal cover) provided for moose by different aged stands (Fisher and Wilkinson 2005). Forest stands from 26 to 75 years in age (Class 4) were withheld as the reference category as these stands are common across the landscape and were hypothesized to provide the least habitat value for moose. A sub-sample of various aged stands were assessed in the field for moose habitat values to aid in the delineation of age classes. Cutblocks <14 years in age (i.e., Class 1 and 2 that do not provide security cover) were categorized into three size classes: small (<40 ha), medium (40-80 ha), and large (>80ha). We developed the GIS layers for each year (2012 to 2016) and matched with telemetry data to capture the temporal and spatial changes in salvage logging.

We used road layers from the RESULTS database and the Cumulative Effects Grizzly Bear Road spatial layer (B.C. Ministry of Forests Lands and Natural Resource Operations 2014) to characterize the spatial distribution of roads on the Bonaparte Plateau. We measured the distance to road (m) from each moose GPS location and a raster layer was developed to measure road density (km/km^2).

3.4.3 Habitat Selection

Following Johnson (1980), we modelled selection at the third order (seasonal range) scale with five seasons, which we determined based on movement rates and habitat use. Resource Selection Function modelling was completed within the home range as management decisions are generally made at this scale (Walker et al. 2007). To estimate resource selection, we compared used resources to available resources using a logistic regression analysis (Manly et al. 2002). We followed a Design III type analysis where use and availability were calculated and analysed at the scale of the individual’s seasonal range, allowing for differences in individuals to manifest among models (Manly et al. 2002).

3.4.4 Determining Biological Seasons

Assigning calendar dates to define resource selection seasons is somewhat arbitrary and we contend a better alternative is to define biological seasons empirically, based on observed (rather than assumed) changes to moose movement and habitat selection. We stratified location points into five seasons using a cluster analysis framework following Basille et al. (2013). This approach defines seasons as homogenous periods with similar space-use, state of movement, and habitat use, which leads to more accurate conclusions of species habitat use in comparison to the more common approach of defining seasons based on assumptions around moose responses to changing conditions (Basille et al. 2013). This approach was described and outlined in Chapter 2.

3.4.5 Resource Selection Function Models

Within each of the five biological seasons, we estimated individual seasonal ranges using kernel density estimations (KDE; Laver and Kelly 2008). We calculated a 95% fixed-kernel estimate using least-squares cross-validation as a smoothing parameter (Worton 1989) and generated five random locations for each used location within individual seasonal ranges to compare differences between used and available locations. We sub-sampled location points to six locations per day to ensure sampling was consistent across seasons. The mean number of locations per moose used in our analysis was 473 ± 19.6(SD), 187 ± 6.6, 342 ± 15.5, 490 ± 14.9, and 634 ± 22.9 by moose for spring, calving, summer, fall, and winter, respectively.

We assessed habitat selection using logistic regression (Manly et al. 2002). The model structure was: $w(x) = exp(ß_1 x_1 + ß_2 x_2 + \ldots + ß_i x_i)$, where w(x) is the RSF or relative probability of selection based on the predictor variables (x_i) and ßi, the estimated coefficients using the lme4 package in R (R Core Team, 2016). Collinearity of model covariates was evaluated using Pearson correlation coefficient (r). Correlated variables with $r > 0.7$ were not used in the same model. Numerical variables were standardized ($\bar{x} = 0$, SD = 1) using the scale function in R (R Core Team, 2016). To account for variation among individuals, we included individual ID as a random effect (Gillies et al. 2006).

We developed seven a priori candidate models to investigate the influence of salvage logging on seasonal moose resource selection (Table 3.1). The core model included topographical variables (i.e., elevation, slope, aspect), ten different forest cover types, and distance to water features (i.e., lakes and wetlands). We expected this core model to explain natural variability in moose habitat selection, and we iteratively added covariates relevant to salvage logging to evaluate and isolate factors that may be important influences on moose habitat selection.

We developed two themes of candidate models: altered resource availability and altered risk. Moose response to altered resource availability was assessed by adding three covariates individually to the core model: age class of forest, distance to cutblock, and size of cutblock. We evaluated moose response to altered risk through two candidate models. First, road density was added to the core model to assess the response of moose to landscape level disturbance. Distance to the nearest road assessed the response of moose to individual road features. Finally, to test for the cumulative effects of salvage logging on moose distribution, we included the top risk model (i.e., roads) and top resource availability model (i.e., cutblocks) in the final model. We compared weight of evidence for our hypothesis models to the core model to assess which covariates best explained moose distribution.

We used Akaike's Information Criterion (AIC) to rank candidate models in each season as relative support for each model and its corresponding hypothesis. The model with the lowest AIC score (> 2 AIC from next model) was considered the top model. Both model fit (log likelihood [LL]) and number of parameters (K) were considered in evaluating model performance (Burnham and Anderson 2002). The predictive ability of the models were evaluated using *k*-fold cross validation and Spearman's rank correlation (r_s; Boyce et al. 2002).

The coefficient of determination R^2 was calculated following Nakagawa et al. (2017) for the top models in each season to provide an estimate of the variance explained by the model, including both fixed and random effects.

Table 3.1 Female moose population scale candidate resource selection models used to examine factors that influence female moose habitat selection in relation to salvage logging infrastructure on the Bonaparte Plateau, south-central British Columbia, Canada, 2012 to 2016. The core model consists of topography and natural landscape features (i.e., elevation, slope, aspect, forest cover, distance to water). Subsequent models include salvage logging variables that describe altered resource availability as a result of cutblocks and altered risk as a result of roads. The cumulative effects model is composed of the core model, top road model and top cutblock model.

Description		**Model variables**	**Hypothesis: Moose resource selection is explained by:**
1	Core model	E+S+A+C+DW	Topography and natural features
2	Landscape level linear features	E+S+A+C+DW+RD	Road density as a measure of landscape scale linear disturbance
3	Individual linear features	E+S+A+C+DW+DR	Distance to individual roads as a measure of indirect predation risk
4	Forage and cover	E+S+A+C+DW+AC	Forest age class as a measure of forage availability, thermal cover, and security cover.
5	Size of cutblocks	E+S+A+C+DW+CS	Size of cutblocks as a measure of indirect predation risk.
6	Proximity to cutblocks	E+S+A+C+DW+DC	Distance to cutblocks (0-14 yrs old) as a measure of forage availability and indirect predation risk.
7	Cumulative effects	E+S+A+C+DW+top road model + top cutblock model	The cumulative effects of topography and natural features as well as salvage logging infrastructure

*E = Elevation, S = Slope, A = Aspect, C = Cover, DW = Distance to Water, DR = Distance to Road, DC = Distance to cut block, RD = Road Density, AC = Age Class, CS = Cutblock Size.

3.5 Results

We collected 157,447 GPS locations from 83 individual female moose from 2012 to 2016, including spring (18,365 points, 11.6%), calving (33,272 points, 21.1%), summer (43,625 points, 27.7%), fall (38,077 points, 24.2%), and winter (24,108 points, 15.3%). Fix success rates from the collars ranged from 74.6% to 100% with an average fix success rate of 95.96 % (SE = 0.49).

3.5.1 Biological Seasons

The DD-weighted gap statistic clustered into 6 groups (DD-gap = 0.21) which corresponded to five biological seasons. Seasons started January 7, March 29, April 30, June, 28, and September 21, which we defined as winter, spring, calving, summer, and fall, respectively (Details in Chapter 2).

3.5.2 Habitat Selection

Cumulative effects of salvage logging best explain seasonal moose distribution. - Female moose habitat selection was best explained by a combination of physical features, forest cover, and salvage logging infrastructure, suggesting the cumulative effects of these different landscape characteristics affect moose space-use (Table 3.2). All top seasonal RSF models had high k-fold cross validation scores, indicating high predictability for each season (i.e., spring: $r_s = 0.903$, $P = <0.000$, $w_i = 1.0$; calving: $r_s = 0.988$, $P = <0.000$, $w_i = 1.0$, summer: $r_s = 0.996$, $P = <0.000$, $w_i = 1.0$, fall: $r_s = 0.989$, $P = <0.000$, $w_i = 1.0$, winter: $r_s = 0.985$, $P = <0.000$, $w_i = 1.0$; Table 3.3). The random effect of individual moose in the top seasonal models had a standard deviation of 0.334, 0.267, 0.281, 0.245, and 0.140 for winter, spring, calving, summer, and fall respectfully.

Table 3.2 Candidate models and ranking, based on for female moose seasonal resource selection on the Bonaparte Plateau in south-central British Columbia, 2012 to 2016, based on AIC score.

Hypothesis		**Model Covariates**	**Model Rank**
Spring			
Core Model	Elevation + slope + aspect + forest cover + distance to water	E+S+A+C+DW	6
Altered Risk	Landscape level linear features	Core+RD	7
	Individual linear features	Core+DR	5
Altered Resource Availability	Forage and cover	Core+AC	2
	Size of cutblocks	Core+CS	3
	Proximity to cutblocks	Core+DC	4
Cumulative Effects	Core + individual linear features + forage and cover	Core+DR+AC	1
Calving			
Core Model	Elevation + slope + aspect + forest cover + distance to water	E+S+A+C+DW	7
Altered Risk	Landscape level linear features	Core+RD	6
	Individual linear features	Core+DR	2
Altered Resource Availability	Forage and cover	Core+AC	3
	Size of cutblocks	Core+CS	4
	Proximity to cutblocks	Core+DC	5
Cumulative Effects	Core + individual linear features + forage and cover	Core+DR+AC	1
Summer			
Core Model	Elevation + slope + aspect + forest cover + distance to water	E+S+A+C+DW	7
Altered Risk	Landscape level linear features	Core+RD	6
	Individual linear features	Core+DR	3
Altered Resource Availability	Forage and cover	Core+AC	5
	Size of cutblocks	Core+CS	4
	Proximity to cutblocks	Core+DC	2
Cumulative Effects	Core + individual linear features + proximity to cutblocks	Core+DR+DC	1
Fall			
Core Model	Elevation + slope + aspect + forest cover + distance to water	E+S+A+C+DW	7
Altered Risk	Landscape level linear features	Core+RD	5
	Individual linear features	Core+DR	2
Altered Resource Availability	Forage and cover	Core+AC	4
	Size of cutblocks	Core+CS	3
	Proximity to cutblocks	Core+DC	6
Cumulative Effects	Core + individual linear features + size of cutblocks	Core+DR+CS	1
Winter			
Core Model	Elevation + slope + aspect + forest cover + distance to water	E+S+A+C+DW	6
Altered Risk	Landscape level linear features	Core+RD	5
	Individual linear features	Core+DR	4
Altered Resource Availability	Forage and cover	Core+AC	2
	Size of cutblocks	Core+CS	3
	Proximity to cutblocks	Core+DC	7
Cumulative Effects	Core + individual linear features + forage and cover	Core+DR+AC	1

While the cumulative effects models best predicted resource selection of female moose in all seasons, the covariates included in the cumulative models varied between seasons (Table 3.2). Distance to road was included in the cumulative effects model in all seasons. The top resource availability covariate varied between spring (core + age class + distance to road, calving (core +age class + distance to road), summer (core + distance to cutblock + distance to road), fall (core + cutblock size + distance to road), and winter (core + age class + distance to road)). The top resource availability model explained moose habitat use better than the top risk model in spring (core + age class), summer (core + distance to cutblock), and winter (core + cutblock size), whereas in calving and fall, the top risk model (i.e., core + distance to road) better explained female moose distribution than the resource availability model (Table 3.3, Figure 3.3).

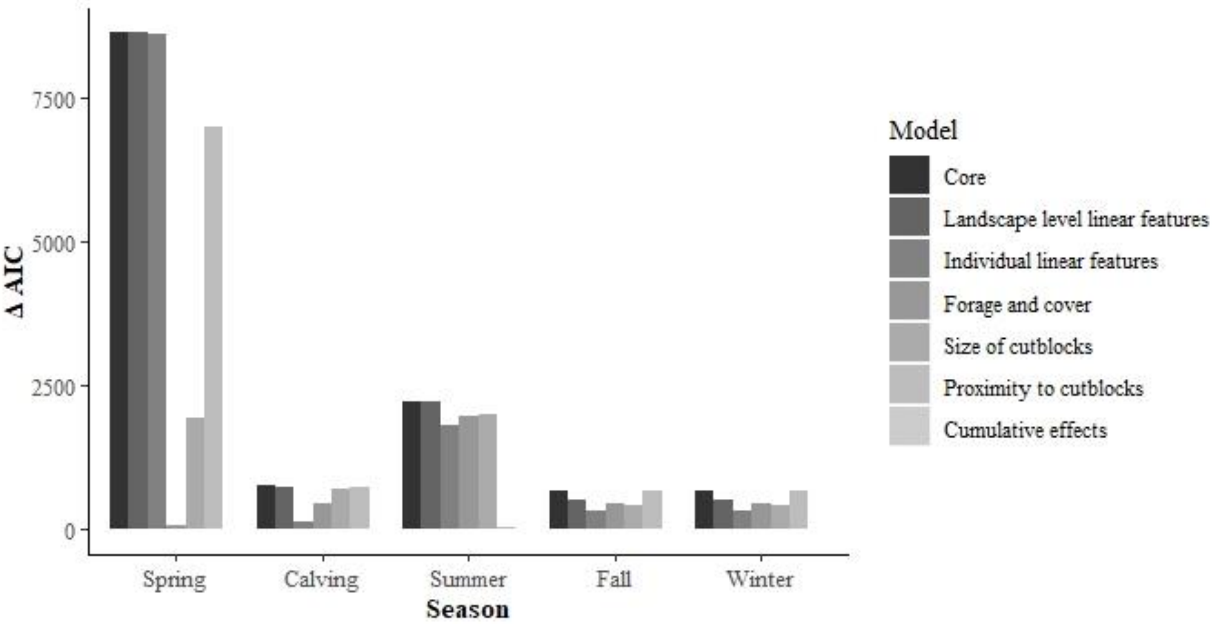

Figure 3.3 Akaike's Information Criterion (ΔAIC) values for each of the competing hypothesis in spring, calving, summer, fall, and winter. The top model was the cumulative effects model (ΔAIC = 0) in each season.

Table 3.3 Candidate models for female moose seasonal resource selection on the Bonaparte Plateau in south-central British Columbia, 2012 to 2016, based on Akaike's Information Criterion (AIC). Statistics include the number of parameters in the model (K), deviance (Dev), Log Likelihood (LL) and AIC score. Model performance was evaluated by k-fold cross validation and statistics include the Spearman Rank coefficient (R_s) and associated p-value. The co-efficient of determination R^2 was calculated to quantify the proportion of variance explained by the top model.

Model	**K_i**	**Dev**	**LL**	**AIC**	**ΔAIC**	**W_1**	**R_s**	**P-value**	**Pseudo R^2**
Spring (n=78 individual moose, 18550 locations)									
Core	7	88186.6	-44093.3	88200.6	8614.7	0.0	0.989	<0.001	-
2	8	88184.8	-44092.4	88200.8	8614.9	0.0	0.992	<0.001	-
3	8	88181.9	-44091.0	88197.9	8612.0	0.0	0.992	<0.001	-
4	8	79632.7	-39816.4	79648.7	62.8	0.0	0.903	<0.001	-
5	8	81504.7	-40752.4	81520.7	1934.8	0.0	0.806	0.008	-
6	8	86572.1	-43286.1	86588.1	7002.2	0.0	0.915	<0.001	-
7	9	79567.9	-39784.0	79585.9	0.0	1	0.903	<0.001	0.503
Calving (n=77 individual moose, 33272 locations)									
Core	7	161858.2	-80929.1	161844.2	754.9	0.0	0.961	<0.001	-
2	8	161849.4	-80924.7	161833.4	748.1	0.0	0.957	<0.001	-
3	8	161226.9	-80613.5	161210.9	125.6	0.0	0.985	<0.001	-
4	8	161551.5	-80775.8	161567.5	450.2	0.0	0.966	<0.001	-
5	8	161797.9	-80899.0	161813.9	696.6	0.0	0.988	<0.001	-
6	8	161842.2	-80921.1	161858.2	740.9	0.0	0.988	<0.001	-
7	9	161099.3	-80549.7	161117.3	0.0	1.0	0.988	<0.001	0.207
Summer (n=71 individual moose ,44120 locations)									
Core	7	218109.2	-109054.6	218123.2	2225.2	0.0	0.988	<0.001	-
2	8	218102.5	-109051.3	218118.5	2220.5	0.0	0.963	<0.001	-
3	8	217685.7	-108842.9	217701.7	1803.7	0.0	0.996	<0.001	-
4	8	217853.8	-108926.9	217869.8	1971.8	0.0	0.975	<0.001	-
5	8	217876.5	-108938.3	217892.5	1994.5	0.0	0.957	<0.001	-
6	8	215928.0	-107964	215944.0	46.0	0.0	0.992	<0.001	-
7	9	215880.0	-107940	215898.0	0.0	1.0	0.996	<0.001	0.182
Fall (n=51 individual moose, 38077 locations)									
Core	7	194163.1	-97081.6	194177.1	668.6	0.0	0.927	<0.001	-
2	8	194022.8	-97011.4	194038.8	530.3	0.0	0.963	<0.001	-
3	8	193816.5	-96908.3	193832.5	324.0	0.0	0.951	<0.001	-
4	8	193935.5	-96967.8	193951.5	443.0	0.0	0.921	<0.001	-
5	8	193912.7	-96956.4	193928.7	420.2	0.0	0.964	<0.001	-
6	8	194150.8	-97075.4	194166.8	658.3	0.0	0.953	<0.001	-
7	9	193491	-96745	193509.0	0	1.0	0.989	<0.001	0.117
Winter (n=47 individual moose, 25054 locations)									
Core	7	114014.0	-57007.0	114028.0	619.0	0.00	0.982	<0.001	-
2	8	113964.6	-56982.3	113980.6	571.6	0.00	0.972	<0.001	-
3	8	113848.6	-56924.3	113864.6	455.6	0.00	0.971	<0.001	-
4	8	113641.5	-56820.8	113657.5	248.5	0.00	0.992	<0.001	-
5	8	113804.3	-56902.2	113820.3	411.3	0.00	0.975	<0.001	-
6	8	114099.8	-57049.9	114115.8	706.8	0.00	0.982	<0.001	-
7	9	113391.0	-56695.5	113409.0	0.0	1.00	0.985	<0.001	0.298

Response to altered resource availably varies seasonally. - Age of cutblocks and stands (resource availability), best explained moose distribution in spring, calving, and winter. In spring, moose strongly avoided younger cutblocks (0-2 yrs: $\beta = -4.02 \pm 0.067$; 3-14 yrs: $\beta =$ -

1.76 ± 0.044) and selected for stands aged 15 to 25 yrs (β = 0.68 ± 0.051) and mature forest (>80 yrs; β = 0.27 ± 0.032). During the calving season, moose selected new cutblocks (0-2 yrs, β = 0.36 ± 0.24) and mature forest (β = -0.068 ± 0.023) and avoided stands aged 3-14 and 15-25 (β = -0.15 ± 0.030; β = -0.014 ± 0.025). A similar pattern was observed in winter, wherein moose strongly selected new cutblocks and selected mature forest (β = 2.76 ± 0.20; β = 0.21± 0.027) and avoided stands aged 3-14 and 15-25 (β = -0.16 ± 0.032, β = -0.015 ± 0.042). In summer, moose distribution was best explained by distance to cutblock, with moose selecting habitat further from cutblocks (β = 0.30 ± 0.0070). In fall, the size of cutblock best explained moose distribution with moose selecting for small cutblocks (β = 0.35 ± 0.023), 50% more often than medium cutblocks (β = 0.26±0.022), and 27 times more often than large cutblocks (β = 0.013±0.020) over mature stands (Table 3.4).

Response to altered risk from linear features varies seasonally. - Of the risk models, individual response to linear features (i.e., distance to road) consistently best explained moose response to altered risk on the landscape, whereas the larger-scale measure road density consistently performed poorly (i.e, high AIC values) across all seasons and was never included in the cumulative effects model. Female moose selected habitat closer to roads in the winter (β = -0.14 ± 0.0090) and spring (β = -0.094 ± 0.0012), but farther from roads the remainder of the year (April 30 to Jan 6) in calving (β = 0.16 ± 0.0075), summer (β = -0.046 ± 0.0067), and fall (β = 0.14 ± 0.0067) seasons (Table 3.4, Figure 3.4; Supplementary Material). The effect sizes of response to linear features was typically smaller than response to forage availability.

Forest cover and topography additionally influence seasonal moose habitat selection. -Female moose selected different forest cover types in different seasons. Moose selected for burns (<20 yrs) in the spring (β = 0.66 ± 0.084) but avoided this habitat type in all other seasons. In spring and calving, moose selected deciduous (β = 0.605 ± 0.060l; β = 0.13 ± 0.040) and mixed deciduous-coniferous stands (β = 0.61 ± 0.044; β=0.10 ± 0.029). Moose selected deciduous stands in the fall (β = 0.20 ± 0.032), but both deciduous and mixed deciduous/coniferous stands were avoided from the summer to winter. Moose consistently avoided fir stands in all seasons, and pine stands in calving (β = -21 ± 0.021), summer (β = -0.20 ± 0.017), and fall (β = -0.23 ± 0.018). In the spring, summer, and fall, moose selected for spruce stands. Moose avoided small lakes in all seasons; however, wetlands were selected for in all seasons apart from winter. Habitat closer to wetlands and small lakes were selected for by moose in calving, summer, and winter. Female moose strongly selected for cutblocks (0 - 14 yrs) in the spring (β = 4.74 ± 0.049) (Table 3.4).

Physical landscape characteristics also contributed to female moose distribution. Moose selected low elevations in each season except for spring and summer when higher elevations were selected. Shallow slopes were selected for in spring, calving, and summer, with steeper slopes being selected for in fall and winter. Moose selected west-facing aspects in all seasons with the exception of spring where south facing slopes were selected (Table 3.4).

Table 3.4 Top models explaining the factors that influence seasonal habitat selection of female moose on the Bonaparte Plateau in south-central British Columbia from 2012 to 2016. Model coefficients and standard errors (ß ± SE) are presented for the most supported model for spring, calving, summer, fall, and winter seasons.

Variables		Season				
		Spring (ß ± SE)	**Calving (ß ± SE)**	**Summer (ß ± SE)**	**Fall (ß ± SE)**	**Winter (ß ± SE)**
Physical						
Elevation		0.059 ± 0.015	-0.055 ± 0.011	0.102 ± 0.012	-0.051 ± 00092	-0.079 ± 0.013
Slope		-0.11 ± 0.011	-0.152 ± 0.0080	-0.100 ± 0.0066	0.0063 ± 0.0069	0.052 ± 0.0091
Aspect	North	-0.057 ± 0.026	-1.35 ± 0.019	-1.38 ± 0.017	-1.23 ± 0.017	-1.14 ± 0.023
	East	-0.0051 ± 0.027	-1.26 ± 0.020	-1.28 ± 0.018	-1.21 ± 0.019	-1.21 ± 0.024
	South	0.015 ± 0.025	-1.31 ± 0.018	-1.34 ± 0.016	-1.08 ± 0.016	-1.26 ± 0.022
	West	Reference category				
Forest Cover						
Burn		0.66 ± 0.084	-0.34 ± 0.044	-0.66 ± 0.057	-0.27 ± 0.046	-0.27 ± 0.061
Deciduous		0.605 ± 0.060	0.13 ± 0.040	-0.097 ± 0.039	0.20 ± 0.032	-0.19 ± 0.040
Fir		-0.083 ± 0.053	-0.59 ± 0.042	-0.70 ± 0.042	-0.48 ± 0.037	-0.27 ± 0.033
Mix coniferous/ deciduous		0.61 ± 0.044	0.10 ±0.029	-0.05 ± 0.025	-0.051 ± 0.025	-0.21 ± 0.030
Mix coniferous		Reference category				
Pine		0.51 ± 0.036	-0.21 ± 0.021	-0.20 ± 0.017	-0.23 ± 0.018	0.71 ± 0.027
Spruce		0.45 ± 0.061	-0.062 ± 0.031	0.14 ± 0.023	0.094 ± 0.026	-2.0 ± 0.035
Small lake		-2.2 ± 0.096	-1.61 ± 0.057	-0.92 ± 0.046	-1.43 ± 0.056	-1.62 ± 0.080
Wetland		3.28 ± 0.052	0.96 ± 0.029	0.78 ± 0.025	0.55 ± 0.029	-0.34 ± 0.039
Cutblock		4.74 ±0.049	-0.80 ± 0.24	-0.075 ± 0.027	-0.34 ± 0.029	-3.15 ± 0.20
Distance to water						
Distance to water		0.33 ± 0.010	-0.096 ± 0.029	-0.016 ± 0.0074	0.0013 ± 0.0074	-0.10 ± 0.010
Age class						
Class 1		-4.02 ± 0.067	0.36 ± 0.24	-	-	2.76 ± 0.20
Class 2		-1.76 ± 0.044	-0.15 ± 0.030	-	-	-0.16 ± 0.032
Class 3		0.68 ± 0.051	-0.014 ± 0.025	-	-	-0.015 ± 0.042
Class 4		Reference category				
Class 5		0.27 ± 0.032	0.068 ± 0.023	-	-	0.21 ± 0.027
Cutblock size						
Small		-	-	-	0.35 ± 0.023	-
Medium		-	-	-	0.26 ± 0.022	-
Large		-	-	-	0.013 ± 0.020	-
Distance to cutblock						
Distance to cutblock		-	-	0.30 ± 0.0070	-	-
Road						
Road density		-	-	-	-	-
Distance to road		-0.094 ± 0.012	0.16 ± 0.0075	0.046 ± 0.0067	0.14 ± 0.0067	-0.14 ± 0.0090

3.6 Discussion

The changing landscapes of B.C. provide both increased resources through forage, and increased risk through linear features; both affect moose habitat selection but female moose generally prioritize acquisition of forage over minimizing risk, and we hypothesize this behavioural choice may be a contributory mechanism to moose declines. Moose make trade-offs between the forage subsidies and the increased predation risk provided by spatially expansive and intensive salvage logging, and though female moose seasonally prioritize forage acquisition over risk avoidance, they respond differently throughout the year. Seasonality suggests greatest avoidance of risky habitats in calving season (i.e., when offspring are youngest) and during fall (i.e., hunting season). In the winter, spring, and summer increased forage availability drives female moose habitat selection more than increased risk on the landscape. Similarly, in Yukon, Mcculley et al. (2017) observed female and male moose responding to risk seasonally; however, contrary to our results, female moose did not avoid risk from predation by bears during the calving season.

The consistent prioritization of forage subsidies suggests that moose trade predation risk for the benefits of foraging in early seral habitat in this highly modified landscape in the spring, summer, and winter. We predicted that new cutblocks (i.e., 0 - 2 yrs (age class 1) would pose some degree of risk to moose due to the lack of security cover and their association with roads; however, apart from spring, female moose strongly selected for these new cutblocks. Interestingly, females avoided 3 - 14 year old stands in spring, summer, and winter, which we predicted would be risky yet would provide forage, and mature forests were used in all seasons. This suggests that despite altered resource availability driving seasonal moose habitat selection, trade-offs are being made at smaller scales.

We predicted that indirect risk from increased linear features associated with salvage logging would drive seasonal female moose distribution and that moose would avoid roads in all seasons; however, this effect was seasonal and only observed in the calving and fall seasons.

During the calving season, parturient females make a trade-off between avoiding predation risk and meeting nutritional requirements, often selecting birth sites that may not have the highest quality or quantity of forage (Bowyer et al. 1999, McGraw et al. 2014). During the calving season on the Bonaparte Plateau, female moose appear to be prioritizing minimizing risk by avoiding roads while utilizing wetlands and new cutblocks (although there is a degree of correlation between cutblocks and roads, presenting a difficult trade-off). While cutblocks provide abundant forage and sometimes cover, they are also used by post-denning black bears – an important predator of moose calves (Garneau et al. 2008). Roads facilitate predator travel (Dickie et al. 2016) as well as inducing neophobia, and play a similar role as predation risk in influencing prey behaviour (Beyer et al. 2013). Moose calves are susceptible to predation particularly within the months following birth (i.e., June/July) by bears (Patterson et al. 2013) and wolves (Severud et al. 2019) . In eastern interior Alaska, predation, predominantly by black bears and grizzly bears, was found to be responsible for 92% of known calf mortality (Bertram and Vivion 2002). We posit the avoidance of roads during calving and the subsequent months following parturition is likely a strategy to mitigate risk to calves.

Female moose are behaving similarly in the fall, by avoiding roads yet using habitat with increased forage availability (i.e., wetlands, cutblocks). Brown et al. (2018) reported that during the hunting season in Alaska, hunter access from trails and roads affected male moose movement and habitat selection to avoid risk. While licensed harvest is predominately focused on male moose in our study area, we anticipate female moose to behave similarly in the fall due to risk of mortality from subsistence harvest. During our study (2012 - 2016), 4.8% (*n* = 5) of collared moose mortalities were from human harvest. Other studies found ungulates used habitats providing cover during the hunting season (Bjørneraas et al. 2011, Bonnot et al. 2013, Brown et al. 2018); however, we did not explicitly observe that. Contrary to our prediction, moose selected for areas closer to roads in winter and spring. This may be a result of the perceived risk being lower for individuals with calves, as calves are older and more mobile, as well, in the spring and winter, there is naturally less activity on the roads due to snow cover.

Larger-scale road density was not an important factor explaining moose habitat selection patterns. Moose response to mortality risk (i.e., defined by linear features in our study) may be to immediately visible local cues rather than large-scale landscape disturbance – at least at the scale of individual selection (as opposed to population-scale selection) within seasonal ranges. A landscape scale analysis (i.e., 2nd order selection) may show different patterns if that decision is already reflected in where female moose establish seasonal ranges. Beyer et al. (2013) reported moose responded to roads at varying scales; at a landscape scale, moose favored areas of moderate road density, yet at a finer scale, moose avoided roads. North of the Bonaparte Plateau near Prince George, a comparable study found at the landscape level in areas of high salvage logging disturbance female moose selected for habitats with a low road density (Scheideman 2018).

Caveats

Other techniques can be used to estimate population-level models by developing individual-based models, then using the average coefficient from multiple individuals to examine selection. Nielsen et al. (2002) used this approach to model grizzly bear habitat selection and found there are likely biases incurred using this approach, and high individual variability overall decreased the predictive power of the population level models. We opted to develop population level models primarily due to our large sample size and computing time for models for 83 individuals; however, we do recognize that individuals may respond uniquely to salvage logging infrastructure and that population models do not capture this level of individual behavior. Given that individual behavioural differences were not the focus of this study we elected to use the population level approach. However, to account for individual variation in our models, we included individual moose identification as a random effect. The standard deviation of the random effect of individual identification was greatest in the winter and lowest in the fall. This indicates that variation in individual behaviour contributes to the models and this also varies seasonally. We would expect to see these differences as some female moose would have calves and would behave differently from barren females. Furthermore, the results of our study are specific to female moose. While understanding male moose selection patterns is also important, female moose are one of the important drivers of moose population change and as such were the focus of this study (Kuzyk et al. 2018b). During the time of this study, 2012 to 2016, significant salvage logging was occurring on the Bonaparte Plateau. Moose location data were matched to spatial data associated with logging (i.e., age class) annually to attempt to capture this change. Spatial representation of the roads was only available in 2016 and therefore includes all roads present at that time, and time stamped data were not available to identify when roads were built. For example, if a road had been built in 2015, moose location points from 2012 would show moose utilizing that area, even though in 2012 the road would not have been present. Future studies in areas with rapid anthropogenic change should aim to temporally match location data to spatial data as close as possible. However, we would expect these data issue only to increase variability around our estimates not to induce any systematic bias that would lead to spurious conclusions.

We examined female moose selection at the third order (home range) scale, recognizing that this is generally the scale at which land management decisions are made (Nielsen et al.

2002). Examining resource selection at the second-order (landscape) scale may provide different results as selection patterns examined in this study do not reflect prior decisions by female moose to establish seasonal ranges where they did and may be useful for comparing varying levels of landscape disturbance from the pine beetle and associated logging.

Changes to the landscape on the Bonaparte Plateau and in much of the interior of B.C. from intense insect kill and attendant salvage logging is unprecedented. These large-scale landscape changes are novel to moose, and in the spring, summer, and winter, moose are prioritizing obtaining food over reducing risk. Our results suggest moose may not yet have adapted to assess the trade-offs between forage acquisition and risk in such a landscape, and given that moose populations have declined through the research period, ultimately their behaviour may be negatively influencing their survival, or survival of their calves. In an alternative interpretation, roads and linear features may not actually pose a risk at all. If true this would run counter to observations in nearby systems (Dickie et al. 2016) and the reasons for the marked declines observed here would remain unknown, resting on other mechanisms as yet to be hypothesized. This study, and future research in this region, would benefit regional-based research on predator densities and space-use. Additionally, future research should focus on calf survival in relation to these features; should this behaviour lead to increased predation of adults or their calves, as hypothesized, then landscape change from salvage logging may impose a potential ecological trap for moose (Sih et al. 2011). Moreover, the value of this study is greatest when taken as one of multiple tests of moose declines (or ungulates writ large) across the circumboreal. Regional declines of circumboreal species are a useful collection of “natural experiments” to understand how changes in resources and mortality sources affect population responses.

3.7 Management Implications

Both anthropogenic and natural features influence moose habitat selection at the seasonal range scale; moose are not behaviourally avoiding salvage logging infrastructure, rather are selecting aspects of it. However, wholescale habitat loss, as would have been evidenced by outright moose avoidance of this extensive landscape disturbance, is not the reason for moose declines. Instead, changes to how the landscape functions to support moose, is a likely contender to explain declines. Landscape management thus requires a more nuanced (and perhaps expensive) approach to moose recovery. If salvage logged areas are ecological traps, then management must consider restoration or deactivation of aspects of salvage logging (i.e., roads) to discourage use by predators (i.e., wolves and humans) potentially inducing increased mortality rates, which is particularly critical when roads are located adjacent to key habitat that moose are selecting for (e.g., wetlands, young cutblocks); landscape scale restoration of these areas through conifer planting and other forestry interventions to remove the resource subsidy drawing moose into the trap which is neither practical or socially palatable; or addressing how these areas function to potentially contribute to increase mortality. Management options such as establishing screening cover around cutblocks and key habitat features for visual obstruction and leaving woody debris in cutblocks to aid moose in escaping predation may benefit moose. In synthesis, moose are selecting these intensively logged areas and are declining within them, and equally intensive landscape management appears necessary to stem these declines.

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3.9 Appendix A: Chapter 3 Supplementary Information

Figure 3.4 Model coefficients for the distance to road variable in population-level seasonal models of radiocollared female moose from 2012 to 2016 on the Bonaparte Plateau in south-central British Columbia. Distance to road (m) is a continuous variable measured as the distance to nearest road.

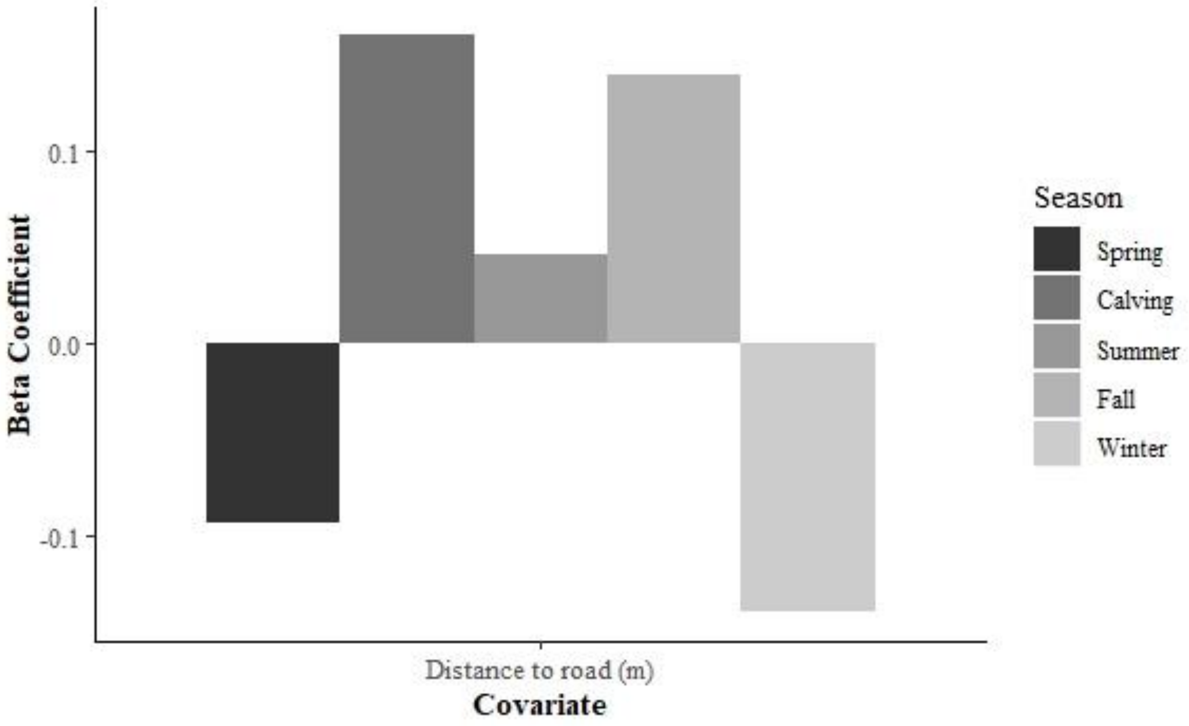

Table 3.5 Geographic information system landscape spatial layers used to examine factors that influence female moose habitat selection in relation to salvage logging infrastructure on the Bonaparte Plateau, south-central British Columbia, Canada, 2012 to 2016.

Variable	Source	Description
Physical		
Elevation	DEM	Meters (a.s.l.)
Slope	DEM	Degrees
Aspect	DEM	North (315 to 45°), South (135 to 225°), East (45 to 135°), West (225 to 315°)
Forest cover		
Burn	VRI	Previously burned areas; <20 years in age
Deciduous	VRI	All deciduous (>70%)
Fir	VRI	All fir (>70%)
Pine	VRI	All Pine (>70%)
Spruce	VRI	All spruce (>70%)
Mixed coniferous	VRI	All coniferous (<70% of a single coniferous species)
Mixed coniferous/ deciduous	VRI	Mixed Coniferous/Deciduous (<70% coniferous or deciduous species)
Large lake	VRI	Open water (>178ha)
Small lake	VRI	Open water (<178ha)
Wetland	VRI	Wetlands/swamps/marshes
Cutblock	VRI	Forest harvested cutblocks (0-15 years of age).
Distance to water	VRI	Distance (m) to nearest water feature (large lake, small lake or wetland)
Age class		
Class 1	RESULTS/ VRI	0-2 years: Fresh cutblocks which generally do not provide forage and consistently provide no security or thermal cover.
Class 2	RESULTS/ VRI	3-14 years: Cutblocks that provide forage but generally poor cover.
Class 3	RESULTS/ VRI	15-25 years: Regenerating stands that provide security cover but generally reduced forage.
Class 4	RESULTS/ VRI	26-79 years: Regenerating stands that provide security and thermal cover, but generally little forage.
Class 5	RESULTS/ VRI	80+ years: Mature forest. Provides security and thermal cover and forage in many cases.
Size of cutblocks		
Small	RESULTS	Forested harvested cutblock (0 to 40ha)
Medium	RESULTS	Forested harvested cutblocks (41 to 80ha)
Large	RESULTS	Forested harvestd cutblocks (>80ha)
Distance to cutblock	RESULTS	Distance (m) to cutblock (0-15yrs)
Roads		
Road density	Cumulative effects layer	Density of road (km/km^2)
Distance to road	Cumulative effects layer	Distance (m) to road.

* Field visits to a sub-sample of various aged stands were completed to assess tree height relative to cutblock age with respect to habitat values (i.e. security and thermal cover and forage values) for moose. We then made a histogram of age classes for the entire study area to delineate natural breaks in the data corresponding to biological values provided.

Chapter 4: Conclusion

4.1 Summary

Globally, human dominated landscapes are replacing natural ecosystems (Tscharntke et al. 2012) and the habitat loss associated with this is the largest threat to global biodiversity loss (Maxwell et al. 2016). Landscape change and anthropogenic disturbances can alter animal behaviour and demography, with consequences for both individuals and populations. Understanding the mechanisms leading to population declines is critical in understanding the ecological processes affecting wildlife species' persistence and for effective management of the landscape to mitigate these effects.

Our research investigated the response of female moose to landscape change from the Mountain Pine Beetle outbreak and subsequent salvage logging on the Bonaparte Plateau and contributed to the BC Ministry of Forests, Lands, Natural Resource Operations and Rural Developments larger provincial wide program. This program hypothesized that "Moose declines coincided with a MPB outbreak because habitat change, increased salvage logging and associated road building resulted in greater vulnerability to moose attributed to hunting, predation, nutritional constraints, age/health conditions, and environmental conditions" (Kuzyk et al. 2019). We found that moose seasonally trade predation risk for the benefits of foraging in early seral habitat, such as those created by salvage logging cutblocks, in these disturbed landscapes. In line with the provincial hypothesis, the habitat change caused by salvage logging is leaving moose more vulnerable to predation (i.e., wolves and humans), particularly when moose are not always behaviourally avoiding these features but are actually selecting them. The results of this study contribute to our understanding of how changes in resources and potential mortality risk affect population responses in addition to increasing our knowledge of the mechanisms in highly disturbed landscapes that lead to species declines.

In Chapter 2, I developed biologically relevant seasons for female moose in the interior of British Columbia based on movement rates and habitat use patterns using a cluster analysis framework. I developed seasonal ranges based on these newly defined seasons. Misidentifying or using arbitrarily defined seasons can lead to erroneous results in seasonally based studies. We recommend that researchers use these biologically relevant seasons within this region to study other aspects of moose behaviour (e.g., fine scale movement) or predatory-prey dynamics. Furthermore, we broadly recommend this approach to defining seasons in all wildlife studies, as it is empirically based and rooted in animal behaviour. We also found that the seasonal home ranges in our study were different sizes than in other studies in the same area, which may be a result both of the method used to define the temporal and the spatial framework of the seasons. The identification of the seasonal ranges, from a temporal and spatial perspective, is a critical piece in identifying and protecting key habitats and estimating densities when managing wildlife populations.

In Chapter 3, we found that moose made seasonal trade-offs between forage acquisition and minimizing their exposure to risk. Moose avoided risky habitat in the calving and fall seasons, but chose habitats that provide foraging opportunities over risk in the winter, spring, and summer. As such, we found that moose are not always avoiding salvage logging infrastructure but rather are selecting portions of it. We concluded that salvage logging areas may be ecological traps for moose, and management should take a nuanced approach to landscape management to remove the resource subsidy drawing moose into these traps. We recommend (1) restoration or deactivation of aspects of salvage logging (i.e., roads) to discourage use by predators, (2) landscape scale restoration of these areas (i.e., planting of diverse species), and (3) the use of screening cover around cutblocks and key habitat features to visually obscure moose.

4.2 Future Research

Future research should be focused on furthering our understanding of the mechanisms leading to moose population declines. This could include a focus on calf survival in relation to salvage logging features that contribute to our ecological trap theory. Additionally, it would be beneficial to collect data (either through radio collars or camera trapping) to better characterize the predator populations in the study area. These data could be used to develop predation risk layers that would be used in future movement or habitat selection studies. Furthermore, developing dynamic spatial layers of roads in the study area (i.e., distinguishing the year roads were built) and characterising high use roads compared to low use roads would help us tease out the fine-scale response of moose to these features, recognizing that moose likely do not response to all roads equally.

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Chapter 5: Appendix B - Thesis Supplementary Information

Table 5.1 Detailed description of moose collar data from 2012 to 2016 on the Bonaparte Plateau. Columns are defined as: ID = unique identifier given to each animal; Collar = Collar ID; Start date = date moose was collared; End date = date collar failed or moose died; Total days = total number of days animal was collared; Total useable locations = total telemetry points after outliers removed and 2D locations with a horizontal dilution of precision <10 removed, % 3D locations = percent of location that were a 3D fix.

ID	**Collar**	**Start date**		**End date**		**Total days**	**Total useable locations**	**Fix success**	**%3D locations**
		Day	**Year**	**Day**	**Year**				
1	31265	64	2012	40	2014	699	7,323	95.18	96.98
2	31261	64	2012	36	2014	703	7,430	97.78	97.86
3	31260	64	2012	314	2014	979	9,911	97.02	97.22
4	31262	64	2012	340	2013	642	6,538	98.49	97.34
5	31259	64	2012	340	2013	423	4,273	98.27	98.2
6	31266	65	2012	340	2013	642	6,486	97.8	98.34
7	31267	65	2012	364	2014	1029	10,843	98.51	97.73
8	31263A	65	2012	41	2013	363	3,947	98.82	98.83
9	31264	65	2012	36	2014	702	7,426	97.6	98.21
10	31558A	352	2012	338	2013	353	3,717	98.09	96.6
11	31545A	353	2012	39	2014	419	4,784	98.67	97.91
12	31609	358	2012	248	2013	257	2,200	97.17	95.55
13	31557	359	2012	265	2014	637	6,136	94.12	95.81
14	31546A	358	2012	340	2013	350	3,680	98.29	97.53
15	31608	359	2012	238	2013	245	2,094	97.12	97.85
16	31541A	358	2012	338	2013	347	3,685	98.65	98.29
17	31607	358	2012	251	2013	259	2,315	99.14	98.66
18	31556A	361	2012	338	2013	344	3,616	98.93	97.15
19	31554A	362	2012	35	2014	405	4,604	99.22	98.15
20	31543A	362	2012	35	2014	405	4,565	98.55	97.65
21	31560A	362	2012	35	2014	405	4,615	99.46	98.78

ID	Collar	Start date		End date		Total days	Total useable locations	Fix success	%3D locations
		Day	Year	Day	Year				
22	31575A	361	2012	352	2013	358	3,629	93.13	97.21
23	31544	19	2013	333	2014	678	7,345	98.02	97.13
24	31578A	20	2013	37	2014	366	3,888	90.86	94.89
25[1]	31576A	20	2013	36	2014	275	2,024	67.06	95.45
26	31548A	20	2013	35	2014	382	4,218	99.08	97.04
27	31549A	20	2013	129	2013	110	1,054	98.69	97.25
28	31571	20	2013	275	2013	256	2,146	95.12	93.49
29	31542A	21	2013	37	2014	382	4,162	97.63	96.2
30	31552A	21	2013	36	2014	381	4,202	99.1	98.74
31	31577A	21	2013	39	2014	385	4,144	96.17	95.92
32	31574	21	2013	37	2014	382	4,211	98.78	99.03
33	31572A	21	2013	35	2014	380	4,192	98.82	98.26
34	31580A	21	2013	31	2014	376	3,636	86.86	95.34
35	31559	21	2013	37	2014	382	4,227	98.92	97.92
36	31551	22	2013	37	2014	381	4,248	99.03	98.52
37	31573A	21	2013	37	2014	382	4,251	99.89	97.95
38	31555A	21	2013	81	2013	61	762	99.47	98.34
39	31547A	22	2013	35	2014	379	4,172	98.75	98.56
40	032923	55	2014	89	2016	757	7,976	95.56	96.65
41	032680	55	2014	89	2016	760	8,132	98.33	97.98
42	032684	53	2014	365	2015	673	7,060	98.35	97.5
43	032678	56	2014	251	2015	557	5,175	97.27	96.44
44	32677	53	2014	340	2014	286	2,698	97.47	96.55
45	32683	54	2014	97	2015	409	4,108	94.78	95.2
46	032676	55	2014	365	2015	670	7,016	98.34	97.83
47	031555B	55	2014	89	2016	756	7,953	95.98	96.33
48	32682	55	2014	72	2014	17	168	100	99.4
49	032679	54	2014	89	2016	759	8,059	97.26	97.4

ID	Collar	Start date		End date		Total days	Total useable locations	Fix success	%3D locations
		Day	Year	Day	Year				
50	31549B	56	2014	244	2014	189	1,182	100	92.99
51	032681	54	2014	89	2016	754	8,040	97.03	97.77
52	032922	54	2014	303	2015	613	5,743	93.06	94.15
53	31263B	55	2014	88	2014	34	262	99%	98.47
54	031541B	26	2015	365	2015	337	3,454	95.97	95.63
55	031542B	30	2015	365	2015	326	3,021	85.44	94.04
56	031543B	30	2015	365	2015	334	3,365	95.16	96.35
57	031545B	30	2015	360	2015	322	2,577	74.57	93.14
58	031546B	27	2015	365	2015	336	3,411	95.17	94.4
59	031547B	27	2015	243	2015	209	1,401	85.84	92.38
60	031548B	31	2015	306	2015	273	2,335	91.14	91.49
61	31552B	30	2015	97	2015	66	685	97.8	96.75
62	031554B	28	2015	89	2016	419	4,557	98.96	96.92
63	031556B	29	2015	89	2016	417	4,435	94.64	97.84
64	031558B	25	2015	365	2015	316	3,268	90.37	94.16
65	031560B	29	2015	89	2016	419	4,490	96.02	97.44
66	031572B	25	2015	89	2016	420	4,463	93.94	95.14
67	031573B	31	2015	365	2015	332	3,309	94	94.93
68	031575B	31	2015	89	2016	424	4,299	86.67	93.18
69	031576B	28	2015	89	2016	419	4,471	95.08	96.22
70	031577B	28	2015	365	2015	336	3,390	95.01	94.96
71	031578B	30	2015	89	2016	418	4,517	96.72	99.14
72	031580B	27	2015	89	2015	420	4,373	93	94.63
73	033395	28	2015	365	2015	337	2,848	79.82	91.15
74	033516	25	2015	89	2016	423	4,428	93.22	96.18
75	033517	29	2015	359	2015	329	3,692	106.82	98.94
76	033518	28	2015	89	2016	420	4,475	95.17	97.11
77	033519	26	2015	89	2016	420	4,511	95.29	98.36

ID	Collar	Start Date		End Date		Total Days	Total Useable Locations	Fix Success	%3D Locations
		Day	Year	Day	Year				
78	033520	25	2015	89	2016	422	4,544	95.66	96.61
79	033521	30	2015	360	2015	331	3,844	111.23	96.96
80	033522	25	2015	89	2016	423	4,577	96.36	97.09
81[2]	33523	23	2015	n/a	n/a	n/a	n/a	n/a	n/a
82	033524	26	2015	89	2016	422	4,556	96.89	98.24
83	033525	26	2015	89	2016	422	4,555	96.22	97.69
84	033526	25	2015	365	2015	339	3,495	96.64	95.57

1. Moose 25 was a male and was not used in the analysis.
2. Moose 81 died shortly after collaring and was not used in the analysis.

Table 5.2: Details of collar failures and mortalities of moose on the Bonaparte Plateau from 2012 to 2016.

ID	**Collar**	**Mortality**	**Date**	**Cause**
1	31265	N	10-Feb-2014	Collar failure
2	31261	N	06-Feb-2014	Collar failure
3	31260	N	11-Nov-2014	Collar failure
4	31262	N	07-Dec-2013	Collar failure
5	31259	N	29-Apr-2013	Collar failure
6	31266	N	07-Dec-2013	Collar failure
7	31267	N	31-Dec-2014	Collar failure
8	31263A	Y	03-Mar-2013	Mortality: starvation
9	31264	N	06-Feb-2014	Collar failure
10	31558A	N	04-Dec-2013	Collar failure
11	31545A	N	09-Feb-2014	Collar failure
12	31609	Y	05-Sep-2013	Mortality - health related
13	31557	N	23-Sep-2014	Collar failure
14	31546A	N	07-Dec-2013	Collar failure
15	31608	N	26-Aug-2013	Collar failure
16	31541A	N	04-Dec-2013	Collar failure
17	31607	Y	09-Sep-2013	Mortality: Motor vehicle collision/septicemia
18	31556A	N	04-Dec-2013	Collar failure
19	31554A	N	05-Feb-2014	Collar failure
20	31543A	N	05-Feb-2014	Collar failure
21	31560A	N	05-Feb-2014	Collar failure
22	31575A	N	18-Dec-2013	Collar failure
23	31544	N	30-Nov-2014	Collar failure
24	31578A	N	06-Feb-2014	Collar failure
25[1]	31576A	N	06-Feb-2014	Collar failure
26	31548A	N	.5-Feb-2014	Collar failure
27	31549A	N	09-May-2013	Collar failure
28	31571	N	09-Feb-2014	Collar failure
29	31542A	N	06-Feb-2014	Collar failure
30	31552A	N	05-Feb-2014	Collar failure
31	31577A	N	09-Feb-2014	Collar failure
32	31574	Y	17-Mar-2016/26-Jun-2016	Collar failure/ Mortality: predation
33	31572A	N	05-Feb-2014	Collar failure
34	31580A	N	31-Jan-2014	Collar failure
35	31559	Y	14-Oct-2015	Mortality: unlicensed hunting
36	31551	N	06-Feb-2014	Collar failure

ID	Collar	Mortality	Date	Cause
37	31573A	N	06-Feb-2014	Collar failure
38	31555A	Y	22-Mar-2013	Mortality: health related/old age
39	31547A	N	05-Feb-2014	Collar failure
40	032923	N	22-Jun-2016	Release
41	032680	N	22-Jun-2016	Release
42	032684	N	01-Apr-2016	Collar failure
43	032678	N	17-Mar-2016	Collar failure
44	32677	N	06-Dec-2014	Mortality: unregulated hunting
45	32683	N	11-Jun-2015	Collar failure
46	032676	Y	19-Jan-2016	Mortality: unregulated hunting
47	031555B	N	29-Jul-2016	Collar failure
48	32682	N	14-Mar-2014	Collar failure
49	032679	Y	18-May-2016	Mortality: wolf predation
50	31549B	N	17-Nov-2014	Collar failure
51	032681	N	22-Jun-2016	Release
52	032922	Y	30-Oct-2015	Mortality: unregulated hunting
53	31263B	Y	29-Mar-2014	Mortality: wolf predation
54	031541B	N	03-Apr-2016	Collar failure
55	031542B	N	16-Feb-2016	Collar failure
56	031543B	N	09-Nov-2016	Collar failure
57	031545B	N	25-May-2016	Collar failure
58	031546B	N	07-Aug-2016	Collar failure
59	031547B	N	04-Jun-2016	Collar failure
60	031548B	Y	02-Nov-2015	Mortality: licensed resident hunting
61	31552B	Y	07-Apr-2015	Mortality: probable starvation
62	031554B	N	09-Nov-2016	Collar failure
63	031556B	N	09-Jun-2016	Collar failure
64	031558B	N	17-Feb-2016	Collar failure
65	031560B	N	09-Nov-2016	Collar failure
66	031572B	Y	13-Jan-2018	Mortality: unregulated hunting
67	031573B	N	09-Nov-2016	Release
68	031575B	N	27-Nov-2016	Collar failure
69	031576B	N	09-Nov-2016	Release
70	031577B	N	09-Nov-2016	Release
71	031578B	N	09-Nov-2016	Release
72	031580B	N	09-Jun-2016	Release
73	033395	N	24-Jul-2016	Collar failure
74	033516	N	09-Nov-2016	Release
75	033517	N	30-May-2016	Collar failure
76	033518	N	09-Nov-2016	Release
77	033519	N	09-Nov-2016	Release

ID	Collar	Mortality	Date	Cause
78	033520	N	09-Nov-2016	Collar failure
79	033521	N	09-Nov-2016	Release
80	033522	N	09-Nov-2016	Release
81[2]	33523	Y	25-Jan-2014	Mortality: capture related
82	033524	N	28-Nov-2016	Collar failure
83	033525	N	09-Nov-2016	Collar failure
84	033526	N	09-Nov-2016	Release

Detailed information on Geographic Information System Layers used to describe the Bonaparte Plateau.

Physical Characteristics

A digital elevation model (DEM) was obtained for the study are from the BC Ministry of Forests Lands and Natural Resource and Rural Operations and was used to develop both the aspect and slope rasters. The DEM raster has a cell size of 25m. The aspect raster was developed using the Aspect 3D Analyst tool and the slope raster was developed using the Slope 3D Analyst tool in ARCGIS 10.3.

Roads

The grizzly bear cumulative effects road layer was obtained from the B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development and was used as the primary source for information on roads in the study area. The dataset consists of nine different road layers that were consolidated into a final product (Table 5.3).

Table 5.3 Input layers for the consolidated roads database.

Priority	Description	Source
1	Digital Road Atlas	WHSE_BASEMAPPING.DRA_DIGITAL_ROAD_ATLAS_LINE_SP
2	As-built Roads	WHSE_FOREST_TENURE.ABR_ROAD_SECTION_LINE
3	RESULTS Forest Roads	WHSE_FOREST_VEGETATION.RSLT_FOREST_COVER_INV_SVW
4	Forest Tenure Roads - Active	WHSE_FOREST_TENURE.FTEN_ROAD_SECTION_LINES_SVW
5	Forest Tenure Roads – Pending or Retired	WHSE_FOREST_TENURE.FTEN_ROAD_SECTION_LINES_SVW
6	TRIM Roads	WHSE_BASEMAPPING.TRIM_TRANSPORTATION_LINES
7	OGC Petroleum Development Roads Pre-2006	WHSE_MINERAL_TENURE.OG_PETRLM_DEV_RDS_PRE06_PUB_SP
8	OGC Petroleum Development Roads	WHSE_MINERAL_TENURE.OG_PETRLM_DEV_ROADS_PUB_SP
9	OGC Petroleum Access Roads	WHSE_MINERAL_TENURE.OG_PETRLM_ACCESS_ROADS_PUB_SP