MULTI-SCALE RESOURCE SELECTION BY WOODLAND CARIBOU IN SASKATCHEWAN'S BOREAL SHIELD: A FUNDAMENTAL STEP TOWARDS MANAGING A THREATENED SPECIES

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By

KATHRINE MARY STEWART

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ABSTRACT

Resource selection is a dynamic behavioural process by which individuals choose resource units (e.g., pixels or points on a landscape) disproportionate to their availability in order to maximize fitness. Because it influences how individuals, and thus populations, are distributed through space and time, understanding how animals choose resource units is fundamental to developing effective, long-term resource management and species' conservation strategies. One of the first steps in assessing conservation prospects for a species is identifying critical habitat, which is habitat necessary for a species to carry out all of its life functions (e.g., breeding, foraging, migrating etc.). Resource selection functions (RSFs), which are functions proportional to the probability of use of a resource unit, provide a means to both quantify animal-environment interactions and predict species' probability of occurrence on a given landscape. When linked to information concerning a species survival and reproduction (e.g., birth, death and recruitment rates), RSFs can be used to determine which resource units constitute critical habitat for a species. I used RSFs to model seasonal resource selection at two spatial scales by a population of woodland caribou (*Rangifer tarandus caribou*) in Saskatchewan's Boreal Shield. Across much of Canada, woodland caribou populations are declining due to anthropogenic-driven habitat loss, fragmentation and alteration; as a result, they are listed as 'Threatened' on Canada's Species at Risk Act. However, compared to other caribou populations in Canada, caribou in Saskatchewan's Boreal Shield are exposed to unusually low levels of human activity (est. 3% landscape disturbed by humans) but relatively high levels of natural forest fires (est. 55% of landscape burned in the past 40 years). My thesis offers valuable, benchmark insight into how caribou use resources relative to their availability under this largely natural disturbance regime, which likely reflects the pristine conditions under which the species evolved. Ultimately, the RSFs developed here offer a first step towards effective land management decisions pertaining to woodland caribou in Saskatchewan's Boreal Shield.

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1.0 CHAPTER ONE: GENERAL INTRODUCTION

1.1 Introduction

Loss of biodiversity at the genetic, population, species and ecosystem levels is a growing global issue (Cardinale et al. 2012, Hooper et al. 2012). Reduced biodiversity has been shown to negatively affect primary productivity (Hector et al. 1999), decomposition (Gessner et al. 2010; Handa et al. 2014), susceptibility to invasive species (Stachowicz et al. 1999) and other important ecosystem properties, often with corresponding detrimental impacts on ecosystem goods (e.g., supplies of timber minerals, food and pharmaceutical compounds), and services (e.g., water filtration, flood protection and climate regulation; as reviewed in the Millennium Ecosystem Assessment [MEA 2015]). Despite commitments by world leaders in 2002 to reduce biodiversity loss (Secretariat of the Convention on Biological Diversity, 2005), Butchart et al. (2010) found that based on 31 biodiversity indicators the overall rate of biodiversity loss has not slowed; in fact, pressures on biodiversity may be increasing. One of the major causes of reduced species diversity is human alteration and fragmentation of landscapes for industry, urbanization and agriculture (MEA 2005); therefore, the development and implementation of effective land management strategies that balance species conservation with sustainable resource extraction have a crucial role to play in helping to curb biodiversity loss.

The development of management strategies aimed at maintaining or restoring biodiversity requires a sound understanding of the extrinsic and intrinsic factors governing species' population dynamics and distributions (Morris 2003, Franklin 2010). Fundamental to this is the study of how animals select resources, which may be defined as discrete spatial units characterized by a suite of abiotic and/or biotic factors (Manly et el. 2002), or more simply as single resources, such as den sites or specific forage species (Resource selection dictates the distribution of animals through space and time, often with ramifications for intraspecific population dynamics, interspecific interactions and coevolution (Rosenzweig 1991, Morris 2003). It can be defined as a behavioural process by which animals occupy resource units (e.g., points or pixels on a landscape) or select specific resources (e.g., forage species) in order to maximize their fitness under existing ecological and physiological conditions (Fretwell and

Lucas 1969, Manly et al. 2002). Resource selection is often modelled using logistic regression to compare resource units that are known to be occupied by an animal to a set of resource units that are either available to or known to be unoccupied by that animal (Manly et al. 2002; Boyce et al. 2002). These models typically take the form of a resource selection function (hereafter 'RSF'), which are functions proportional to the probability of use of a resource unit (e.g., a point or pixel in space; Manly 2002). RSFs provide a means to: (a) quantitatively evaluate the animal-environment interactions underlying species' distributions (e.g., Rettie and Messier 2000, Ryan et al. 2006, DeCesare et al. 2012); and (b) characterize and map a species' relative probability of occurrence within a given landscape (Boyce 2002, Manly 2002). When coupled with demographic data (births and deaths), resource selection patterns can be used to identify habitat critical to a population's or species' survival and/or reproductive success (e.g., McLoughlin et al. 2006). Thus, resource selection studies are integral to the development of effective animal conservation strategies, and, by extension, effective land management strategies that preserve biodiversity. Recent efforts to conserve woodland caribou (*Rangifer tarandus caribou*) in Canada present one example where resource selection analyses are being used to address biodiversity loss. . Here, the study of resource selection is intimately tied to our understanding of why caribou populations may be at risk throughout much of their distribution. In particular, analyses of resource selection have allowed us to explore how human disturbances may affect predator-prey relationships and the ability of caribou to use habitat to minimize predation.

Woodland caribou are one of four subspecies of caribou recognized in Canada and can be classified into two broad behavioural ecotypes: the forest-dwelling ecotype, which occupies forested habitat year-round, and forest-tundra ecotype, which migrates between the boreal forest and the arctic tundra (Environment Canada 2012). Forest-dwelling woodland caribou can be further sub-divided into six geographically distinct populations or conservation units (Fig.1.1): **(i)** the Boreal population, which has been divided into 57 local populations (also known as designatable units because population boundaries are somewhat arbitrary [Callaghan et al. 2010]) spread across seven provinces and two territories; **(ii)** the Northern Mountain population, which is comprised of 45 sub-populations ranging from northern British Columbia to the Yukon Territory and the Northwest Territories; **(iii)** the Central Mountain population, which is distributed across 10 small sub-populations in east-central British Columbia and west-central Alberta; **(iv)** the Southern Mountain population, which occurs in southeastern British Columbia and along the northern fringes of Washington State and Idaho; **(v)** the Atlantic-Gaspésie population, which is concentrated in three mountainous regions within and adjacent to Gaspésie Provincial Park, Quebec; and **(vi)** the insular Newfoundland population, which resides on the island of Newfoundland in eastern Canada. The Committee for the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the Atlantic-Gaspésie and Central Mountain populations as Endangered, the Boreal and Southern Mountain populations as Threatened, and the Northern Mountain population as Special Concern. The insular Newfoundland population was last assessed as ‘not at risk’ (COSEWIC 2002).

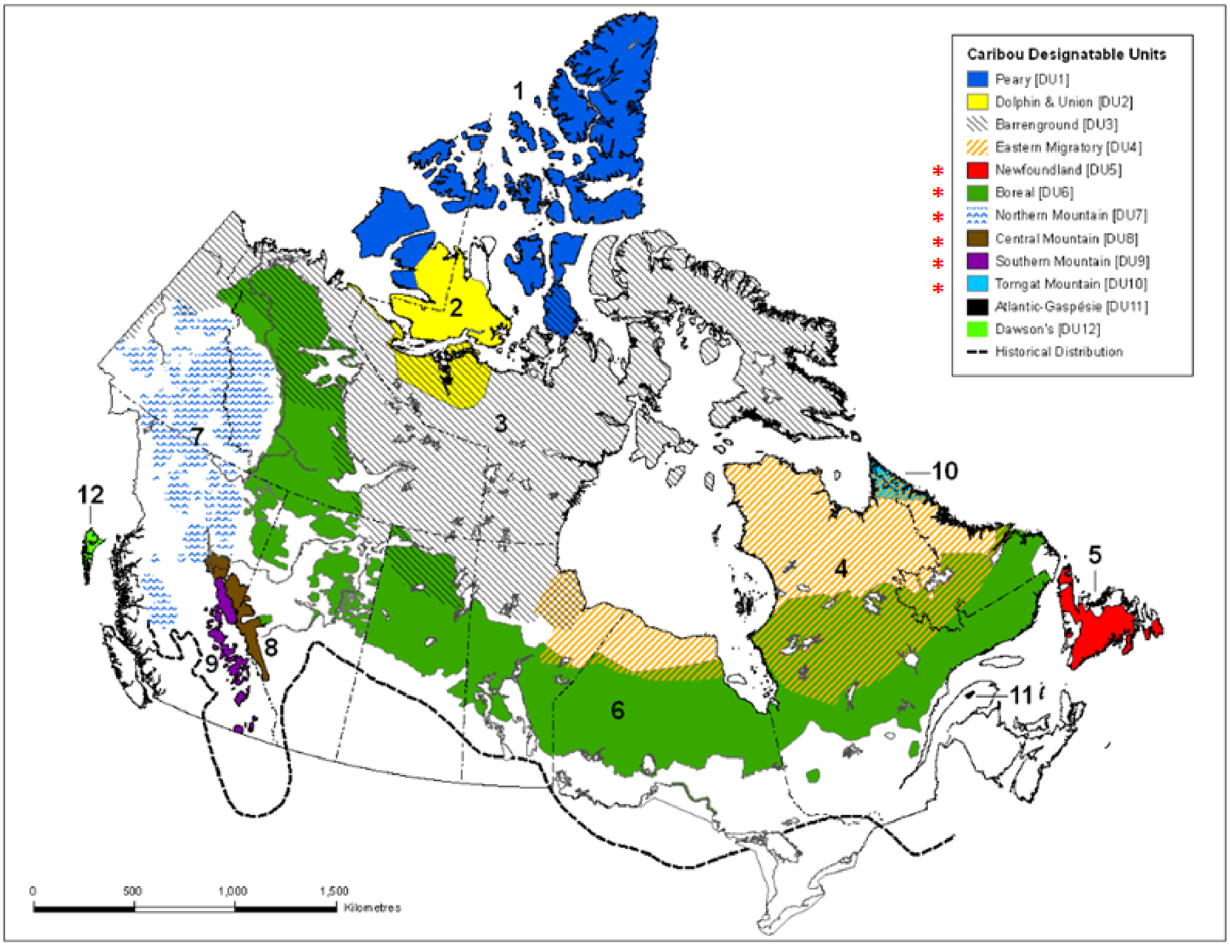


Fig. 1.1: Twelve designatable units of caribou (*Rangifer tarandus*) defined in Canada (COSEWIC 2011). Note that the Dawson’s unit encompasses the range of an extinct sub-species of woodland caribou known as *Rangifer tarandus dawsoni*. The large green polygon delineates the range of boreal woodland caribou (*Rangifer tarandus caribou*, Boreal Population), which are the focus of this thesis. Boreal woodland caribou are one of six ecotypes of forest-dwelling woodland caribou (denoted by a red asterisks in the legend). [Figure reproduced from COSEWIC 2011:82].

Reasons for the at-risk status of woodland caribou throughout much of their distribution are varied; however, the role of human disturbance is likely significant. The ranges of many forest-dwelling populations of caribou overlap lucrative pockets of timber, oil, natural gas, mineral, peat and/or other commodities. In accessing and extracting these resources, humans have significantly altered, fragmented or destroyed important tracts of habitat (Environment Canada 2012; COSEWIC 2014), which has had negative consequences for woodland caribou population dynamics (COSEWIC 2002; McLoughlin et al. 2003, Hervieux et al. 2013; Johnson et al. 2015).

The direct effects of humans on caribou, including the numerical effects of human hunting (Schmelzer 2013) and caribou-vehicle collisions (Smith 2004), are relatively minor; however, the indirect effects of human activity on caribou populations appear to be more severe. Indirect effects, which are generally defined as effects mediated by an intermediary species (Strauss 1991: 206), are predominantly the predator-mediated effects of humans on woodland caribou, precipitated by our disturbances of habitat. One of the most significant of these appears to be the exacerbation of apparent competition (Holt 1997) between woodland caribou and alternate prey species such as moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*) and North American elk (*Cervus canadensis*). Apparent competition is a form of asymmetric, indirect competition between two or more prey species that arises from the numerical response of a shared predator to one or more of the prey species. In the case of woodland caribou, it is hypothesized that human conversion of mature conifer forests to early seral forests causes an increase in the densities of alternate prey species, which in turn support a greater number of predators (e.g., wolves (*Canis lupus*), black bears (*Ursus americanus*), mountain lions (*Puma concolor*), wolverines (*Gulo gulo*) and/or coyotes (*Canis latrans*)). The numerical response of predators to their primary prey species may inflate encounter rates between woodland caribou and these predators, ultimately resulting in increased caribou mortality. For example, Wittmer et al. (2007) found that survival among populations of woodland caribou in southern British Columbia generally declined with increasing proportions of early- and mid-seral forests. Encounter rates between woodland caribou and their predators (especially wolves) are also hypothesized to increase with an increase in the densities of linear features (e.g., human-built roads, seismic lines, fire breaks etc.). Although there is evidence suggesting caribou avoid linear features (e.g., James and Stuart-Smith 2000, Oberg 2001, DeCesare et al. 2012), McLoughlin et al. (2016, in review) argue that more robust analyses are needed to link increased predation on caribou with the presence of linear features.

Despite the difficulty in teasing apart the predator-mediated effects of humans on woodland caribou, researchers generally agree woodland caribou populations are declining due to human-induced increases in caribou predation rates (McLoughlin et al. 2003, Wittmer et al. 2005). Predation risk has been shown to be a primary factor driving woodland caribou resource selection at coarser spatial and temporal scales (e.g., home range scale (Gustine et al. 2006a) and seasonal range scale [Rettie and Messier 2000]); in other words, at broader spatial scales, woodland caribou tend to select resource units that minimize predation risk. For example, female woodland caribou in both northern and southern British Columbia migrate to higher elevations during the calving season in order to minimize spatial overlap with moose foraging along valley bottoms (Bergerud and Page 1987, Seip 1992). Consistent with the apparent competition hypothesis, this minimizes encounters with both wolves and black bears (Bergerud and Page 1987). Predation risk can influence caribou resource selection differently depending on landscape composition (Wittmer et al. 2007, Fortin et al. 2008), the behaviour and composition of alternate prey and predator communities (Gustine et al. 2006b), and/or differences in how individual woodland caribou perceive risk. Accordingly, resource selection patterns may differ among caribou populations even though the mechanism (i.e., predator avoidance) driving broad-scale patterns of resource selection is the same. For example, woodland caribou inhabiting mountainous regions of British Columbia select for high elevation resource units during the calving/post-calving period (Bergerud and Page 1987, Seip 1992), which might lead one to assume that higher elevations are generally important to woodland caribou during this critical life history stage. However, Latham et al. (2011a) found that female woodland caribou inhabiting a boreal forest ecosystem in northern Alberta strongly select for lowland bog/fen complexes during the calving period, likely to avoid encountering black bears, which selected for upland mixed woods and industrial features. This comparison illustrates how resource selection patterns can vary with resource availability (here the availability of high elevation sites).

Resource availability is linked to how researchers define the spatial and temporal scales of resource selection. Correctly defining the domain of availability is crucial to correctly framing the spatiotemporal scale(s) of a resource selection analysis (Johnson 1980, Boyce et al. 2002), which in turn is critical to making accurate inferences, predictions or management decisions regarding a species' resource use (Turner et al. 1995, Manly et al. 2002, Boyce et al. 2003).Increasingly, researchers are recognizing the value of studying resource selection at multiple spatiotemporal scales. Resource selection is a hierarchical process (Johnson 1980, Schaefer and Messier 1995), with the strength of selection for a resource unit often varying through space and time according to changes in the relevance of limiting factors (Holling 1992, Rettie and Messier 2000). At coarser scales, factors most limiting to fitness may have the greatest influence on resource selection and should continue to affect habitat choices through finer scales of selection until another factor becomes more significant (Rettie and Messier 2000). Woodland caribou are exposed to numerous biophysical factors that vary through space and time (e.g., climatic conditions, seasonal predators, annual vegetation etc.); hence, we can expect the importance of factors to resource selection to also vary through space and time. As mentioned above, predation risk is thought to be a primary limiting factor to woodland caribou at coarser spatial scales (e.g., placement of home range or seasonal range); however, forage availability and accessibility may become more important to resource selection at finer spatial scales (e.g., the food patch; Rettie and Messier 2000, Johnson et al. 2001). In addition, other factors such as insect harassment (Downes et al. 1986, Ion et al. 1989), energetic cost of movement (Johnson et al. 2002, Gustine et al. 2006a) and peaks in natural fire disturbance and/or human activities can become seasonally important at one or more spatial scales. In fact, across spatial scales, there can be considerable temporal variation in the factors affecting woodland caribou resource selection. For example, at the scale of the food patch, changes in snow depth, density and hardness throughout the winter period can affect access to terrestrial lichens (a primary winter food source for caribou; Thomas et al. 1994; Rominger et al. 1996; Thompson et al. 2015), which in turn can affect selection for feeding sites (Johnson et al. 2001). At the scale of the seasonal range, woodland caribou resource selection can vary according to changes in predation pressure from different predators (e.g., black bears (Latham et al. 2011a) and/or wolverines (Gustine at al. 2006b) may have greater influence on resource selection during the calving and summer periods). Clearly, scale is a complex issue, but one that needs to be addressed within the framework of resource selection studies in order to fully understand the mechanisms driving species' distributions and dynamics.

Another consideration for researchers conducting analyses of resource selection is whether to model patterns of resource selection in population (i.e., the mean response of individuals to resources) vs. individual resource selection. Though land managers find it more feasible to manage (and therefore study) wide-ranging species like woodland caribou at the population level (Fortin et al. 2008), population-level patterns don't always capture ecologically significant intraspecific variation in physiology (e.g., reproductive status or sex), personality (e.g., bold vs. shy individuals), access to resources, and overall experience of the landscape (e.g., Bolnick et al. 2003, Boyce et al. 2003, Forester et al. 2009). For example, Latham et al. (2011a) found little spatial overlap between black bears and woodland caribou in northeastern Alberta when they modelled resource selection at the population level; however, when researchers modelled habitat selection at the individual level, they found significant variation in how black bears used resources relative to caribou, which suggests individual caribou experience varying levels of predation risk from black bears within that study area. As discussed in detail by Bolnick et al. (2003, 2011), this sort of individual variation can have significant ecological and evolutionary consequences, which in turn affect species conservation.

Given the complex nature of woodland caribou-environment interactions and the increasing encroachment of humans onto caribou habitat, land managers tasked with conserving woodland caribou face an arduous challenge. Research into understanding how caribou select resources and/or react to industrial disturbances can be used to: (a) identify habitat that needs to be protected or restored in disturbed landscapes in order for woodland caribou to satisfy their life history requirements (e.g., Courbin et al. 2009); and (b) gain a better understanding of how human-driven changes to the landscape affects woodland caribou behaviour and demography (e.g., Hornseth and Rempel 2015). However, analyses of resource selection must be applied at spatiotemporal scales that capture the response of caribou to extrinsic and intrinsic factors governing their dynamics and distributions.

1.2 Saskatchewan Boreal Shield Woodland Caribou Project

In 2012, the Canadian government released *the Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal population, in Canada* (Environment Canada 2012). Recall that boreal woodland caribou (hereafter boreal caribou) are one of six geographically distinct conservation units of forest-dwelling woodland caribou in Canada (green shaded area, Fig.1.1). Endemic to Canada's boreal forests, they typically occur in small, mixed- sex groups at low densities (2-3 individuals per 100km^2, Environment Canada 2012). Unlike other sub-species of caribou (e.g., barren ground caribou [*Rangifer tarandus groenlandicus*] and Peary caribou [*Rangifer tarandus pearyi*]), boreal caribou are somewhat sedentary and inhabit relatively small home ranges (Environment Canada 2012). Nevertheless, local populations require large, continuous tracts of mature conifer forests and muskegs/peatlands in order to satisfy their biological requirements (e.g., foraging, calving, rutting etc.) while still maintaining low enough densities to avoid undue predation risk (Thomas and Gray 2002). These large tracts of habitat provide sufficient surplus area into which boreal caribou can disperse following natural disturbances (Environment Canada 2012), and also serve as refugia for individuals looking to spatially segregate themselves from alternate prey and predators (e.g., James 2004). Where human activities have altered, fragmented or destroyed this habitat, boreal caribou populations are declining (Thomas and Gray 2002, Environment Canada 2008, Environment Canada 2012). As a result, boreal caribou have been listed as Threatened on *Schedule 1* of Canada's Species at Risk Act (SARA), which means they are "likely to become endangered if nothing is done to reverse the factors leading to [their] extirpation and extinction" (Table 5, COSEWIC 2015: 15).

Environment Canada (2008) currently recognizes 57 local populations of boreal caribou (Fig. 1.2), which have been allocated to 51 ranges or management units (Fig. 1.3). After conducting a meta-analysis of study areas across Canada, researchers established a relationship between total disturbance (i.e., natural and anthropogenic) and calf recruitment and then used this relationship to assess the probability that habitat conditions within each management unit could support self-sustaining populations of boreal caribou (Environment Canada 2012: 70-71). According to this assessment, only 14 of the 51 management units were "self-sustaining"; of the remaining 37 units, 26 were listed "not self-sustaining", 10 as "likely not self-sustaining", and one – the SK1 unit encompassing Saskatchewan's Boreal Shield (white polygon, Fig. 1.3) – was listed as "unknown" (Environment Canada 2012). The reason for this last designation is that the levels of natural fire and anthropogenic disturbance in Saskatchewan's Boreal Shield fall outside the range of values used to define the relationship between disturbance and calf recruitment. Therefore, habitat conditions in this region cannot be accurately assessed under the existing disturbance-recruitment model. In fact, when the federal recovery strategy for boreal caribou was published in 2012, there were "no trend data or population data for SK1" (Environment Canada 2012: 70), meaning there was inadequate information to identify critical habitat in the region.

Accordingly, the report's Schedule of Studies (Table 6, Environment Canada 2012: 36) states that the province of Saskatchewan is required to report on population trends and critical caribou habitat by the end of 2016 (Environment Canada 2012).

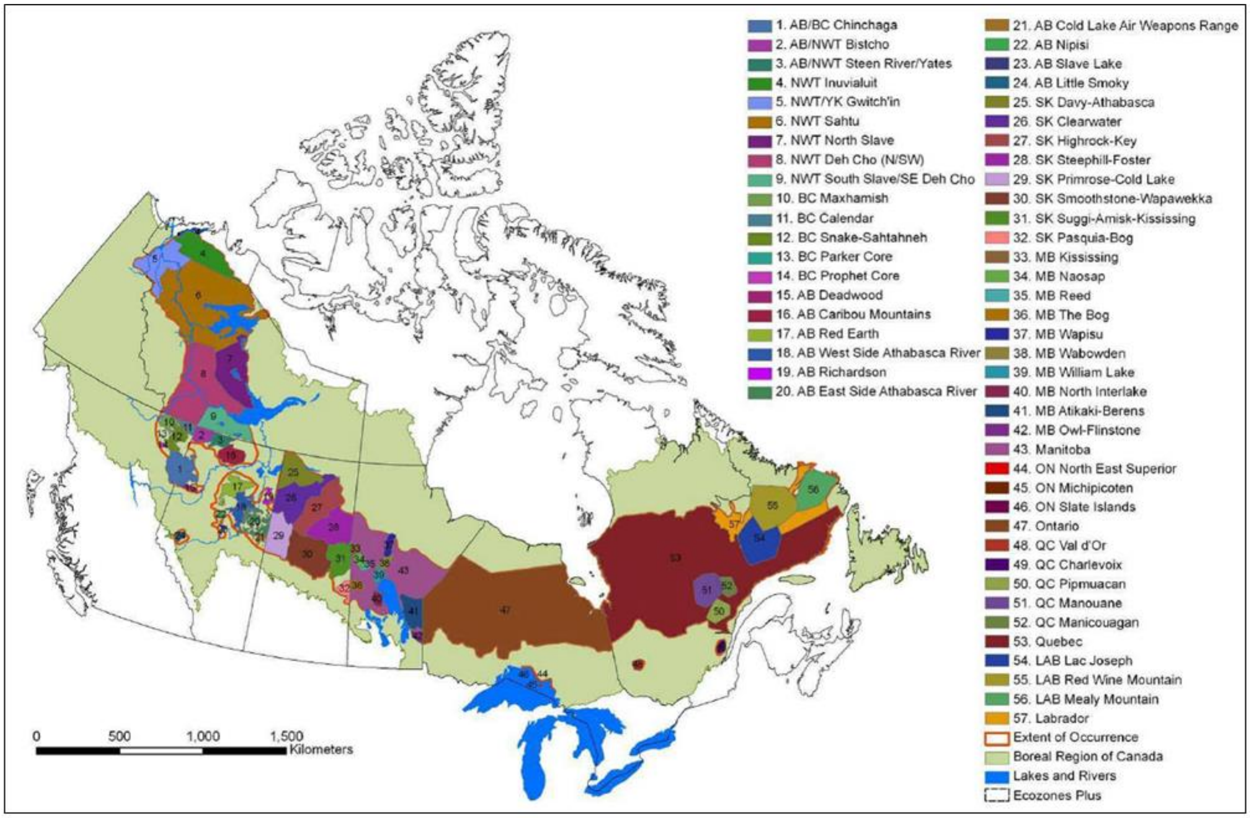


Fig. 1.2: Distribution of the 57 local populations of boreal caribou currently recognized in Canada. Population boundaries that are defined by provincial or territorial boundaries are political artefacts and likely not representative of ecologically relevant population boundaries. [Figure reproduced from Callaghan et al. 2010: 4].

In response to the mandates of the federal recovery strategy (Environment Canada 2012:2, 35-36), the University of Saskatchewan partnered with the Province of Saskatchewan (Ministry of Environment), Environment Canada and Climate Change Canada, and several additional governmental, industrial and academic groups to launch the Saskatchewan Boreal Shield Woodland Caribou Project. The project is using a combination of vegetation surveys, demographic modelling, Aboriginal Traditional Knowledge (ATK), and resource selection studies in order to identify habitat critical to boreal caribou in Saskatchewan's SK1 management unit (white polygon, Fig. 1.3). Between 2013 and 2015, 153 adult, female boreal caribou were fitted with Global Positioning System (GPS) - equipped radio collars (black crosses and yellow and orange bubbles, Fig. 1.4). These collars allow researchers to locate and survey this sample of caribou, as well as remotely track their movements across the landscape. Thirty-seven wolves and (at writing) 3 black bears with similar GPS radio collars (green stars and purple triangles, Fig. 1.4) in order to gain a better understanding of how these predators select resources relative to boreal caribou. An additional 20 black bears will be collared in the spring of 2017. Concurrently, the University of Saskatchewan's Northern Plant Ecology Lab (NPEL) has been conducting intensive summer vegetation surveys to update the province's vegetation layer, which will improve the classification accuracy of the vegetation classes used to define habitat classes for the project's RSFs. This large-scale project offers a good example of the multi-party involvement needed to effectively address boreal caribou conservation. As part of this massive collaboration, my thesis is focused on modelling boreal caribou resource selection in Saskatchewan's Boreal Shield.

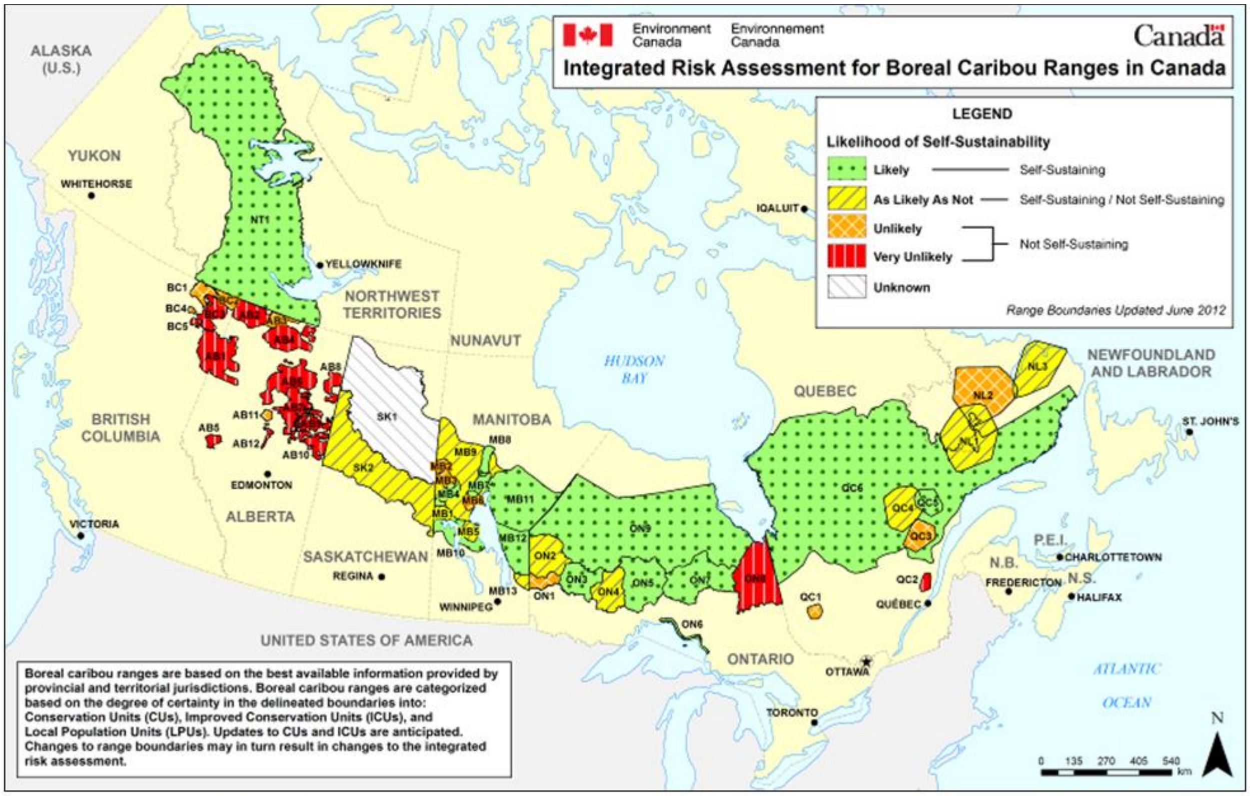


Fig. 1.3: Integrated Risk Assessment for the 51 boreal caribou ranges recognized in Canada. The status of each range denotes its capacity to maintain a self-sustaining population of boreal caribou. [Figure reproduced from the *Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal population, in Canada* (Environment Canada 2012: 8)].

1.3 Thesis Objectives

Relative to other caribou management units, Saskatchewan's SK1 unit encompasses a uniquely pristine and naturally regulated ecosystem. Boreal caribou here are exposed to uncommonly low levels of human activity (< 3% of disturbed habitat is due to humans, Environment Canada 2012) and uncommonly high levels of natural fire disturbance (>55% of disturbed habitat derives from natural forest fires that occurred in the past 40 years, Environment Canada 2012). The region also retains a full complement of native mammals (e.g., moose, wolves, beavers (*Castor Canadensis*) and black bears), and generally lacks invasive mammals (e.g., white-tailed deer and coyotes; Environment Canada 2011). Thus, the SK1 caribou management unit presents an excellent opportunity to study boreal caribou resource selection in conditions approximating those under which caribou and their predators may have evolved. Such information would not only inform the identification of critical habitat, but also provide a baseline of resource selection against which populations in more human-altered landscapes can be compared.

The purpose of my thesis was to characterize boreal caribou resource selection at multiple spatial scales in Saskatchewan's Boreal Shield ecoregion. My specific objectives were to (i) test hypotheses related to how caribou make risk-forage trade-offs between two spatial scales (coarse vs. fine, defined on pp. 55); and (ii) describe spatiotemporal variation in how caribou select resources Saskatchewan's Boreal Shield. Ultimately, the results from my thesis are intended to act as a first step in the identification of critical habitat (defined as habitat that "provides an overall ecological condition that will allow for ongoing recruitment and retirement of habitat cycle" and which is characterized by "biophysical attributes required by boreal caribou to carry out life processes" [Environment Canada 2012: vii]) for boreal caribou in the SK1 management unit. More broadly, this research is intended to improve our understanding of how caribou respond to a high-fire, low-human disturbance regime.

1.4 Thesis Hypotheses

Traditional hypothesis testing in biostatistics involves establishing a null and alternate hypothesis and then using a statistical test or tests to: (a) determine whether there is enough evidence in a sample of data to reject the null hypothesis (frequentist approach) or (b) determine the probability that the given alternate hypothesis is true (Bayesian approach). However, in the context of resource selection modelling, this approach is not very useful. As Cherry (1998) explains, resource selection functions or RSFs (termed "habitat-use-availability models" by Cherry [1998]) assume that organisms are non-randomly distributed with respect to resources; hence, testing whether resource use is non-random is often superfluous because the statistical significance of such a test would only reveal whether this assumption was met. In addition, the statistical significance (i.e., *P*-values) of model predictors are rarely meaningful because they fail to account for ecological interactions between variables and are sensitive to the spatial and/or temporal autocorrelation inherent to most spatial data (Boyce et al. 2002). Instead, researchers studying resource selection are better served by defining multiple alternative hypotheses (i.e., candidate models representing alternate hypotheses about the evolutionary and ecological mechanisms related to a species' resource selection) *a priori* and then applying an information-theoretic method (Anderson et al. 2000) to compare model outputs. This method allows researchers to explore multiple plausible explanations for the observed patterns of selection, and also reduces the bias of the researcher to one result (Chamberlin 1890).

With respect to my thesis, I was interested in quantifying how female caribou select resources in Saskatchewan's Boreal Shield at two spatial scales. Little is known about how boreal caribou behave under the unique disturbance regime and natural conditions of this area, but studies conducted elsewhere suggest that predation risk is limiting to woodland caribou at coarse spatial scales while forage availability and accessibility is more important at finer spatial scales (Rettie and Messier 2000). Therefore, I built two resource selection models (one at the coarse spatial scale and one at the fine spatial scale) for each of six annual seasons using a set of habitat attributes that have been shown to influence predation risk and/or forage availability and accessibility in other study areas (see section *4.3.4*, pp.56 – 61, for a description of the habitat attributes). I generated RSFs using the *R* package `MCMCglmm` (Hadfield 2010), which lacks a robust information criterion by which to compare alternate models (note that although the Deviance Information Criterion (DIC) can be used to compare alternate models run in `MCMCglmm`, its theoretical foundation is still unclear [Plummer 2007, J. Lane, Department of Biology, University of Saskatchewan, *pers. comm.*]). Therefore, instead of building a - set of candidate models for each season and scale, I employed rigorous step-wise selection on a global model (i.e., a model containing all predictor variables that were thought to be important to caribou resource selection in a given season based on review of the literature, see section *4.3.4*, pp.56 for details) to arrive at the top models for each season and scale (*n* = 12 models total). Collectively, these twelve models describe the spatiotemporal variation in factors driving female boreal caribou resource selection in Saskatchewan's Boreal Shield. Since the province of Saskatchewan is committed to "landscape level planning" with respect to managing woodland caribou (Saskatchewan Ministry of Environment 2014), patterns of resource selection observed at the coarse scale may be more useful to land managers, as wide-ranging species such as caribou are more feasibly managed at broader scales (Fortin et al. 2008).

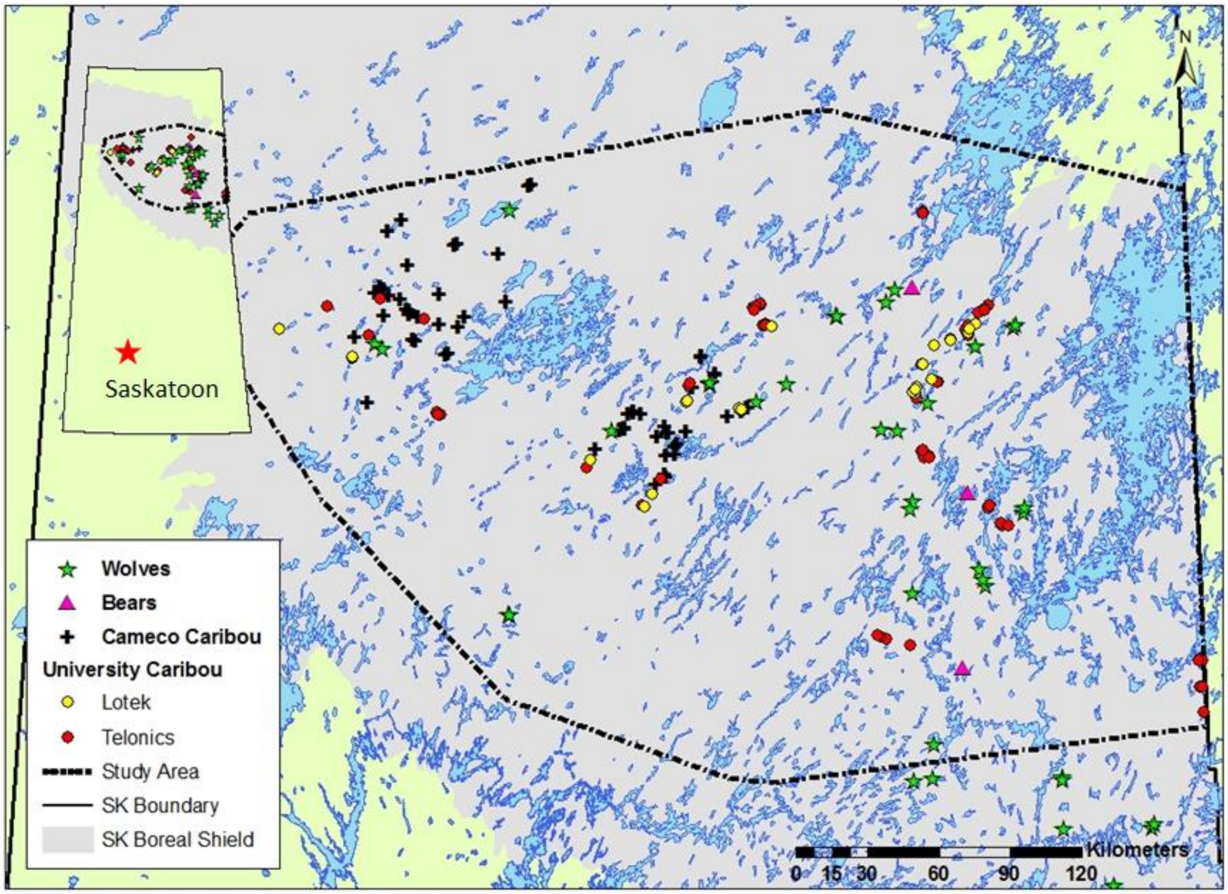


Fig. 1.4: Collaring locations for 153 female woodland caribou, 37 wolves and 3 black bears fit with GPS-capable radio collars between March 2013 and May 2016 in Saskatchewan's Boreal Shield. Caribou were collared in March 2013 (*n* =49), March 2014 (*n* = 101) and March 2015 (*n* = 3). The black crosses (*n* = 59) denote caribou that are being monitored by Cameco Corporation © while the yellow and orange bubbles (*n* = 94) denote caribou that are being monitored by the University of Saskatchewan. More specifically, the yellow bubbles denote caribou fit with *Lotek Wireless Inc. Iridium Track®* GPS collars (*n* = 25) while the orange bubbles denote caribou fit with *Telonics TGW 4680-3 GPS/Argos* collars (*n* =69). The University's collars are divided into the two collar brands in order to show the relative distribution of the two collared populations.

1.5 Thesis Structure

This document was formatted according to the guidelines set forth by the College of Graduate Studies and Research at the University of Saskatchewan. It has been divided into five chapters. Over the first chapter, I introduce the topic of resource selection, provide an overview of resource selection as it relates to woodland caribou, and outline my thesis' objectives. Chapters 2 and 3 are methods chapters detailing the methods used to delineate ecologically meaningful habitat classes (Chapter 2) and seasons (Chapter 3) for boreal caribou in Saskatchewan's Boreal Shield. Chapter 4 is a data-based research chapter focused on resource selection. Chapter 5 represents the conclusion of my thesis in which I briefly summarize the results of my work and discuss its relevance to boreal caribou management in Saskatchewan.

2.0 CHAPTER TWO: DELINEATING ECOLOGICALLY MEANINGFUL HABITAT CLASSES FOR WOODLAND CARIBOU IN SASKATCHEWAN'S BOREAL SHIELD

2.1 Introduction

Resource units, which are often delineated on maps as points or pixels (Manly 2002), can be described as finite spatial units that may be available for an organism to use. Each unit is characterized by an array of abiotic and biotic factors (e.g., temperature, soil composition, vegetation cover, elevation, proximity to roads, etc.). Depending on the species of interest, different factors may have greater influence on resource selection; in addition, the importance of a factor to resource selection may vary across spatiotemporal scales (e.g., Rettie and Messier 2000, Apps et al. 2001, Ciarniello et al. 2007). It is common for researchers to characterize resource units using a set of habitat classes (e.g., forests, swamps, riparian habitats etc.) that occur within their study area (e.g., Rettie et al. 1997, Johnson et al. 2003). These classes, in combination with other biophysical attributes, can then be used as covariates in regression models to formally describe the process of resource selection (e.g., using resource selection functions [RSFs] or resource selection probability functions [RSPFs]; Boyce et al. 2002). Ideally, researchers should delineate habitat classes according to features on the landscape that are ecologically important to the study species (e.g., since seasonal forage is important to woodland caribou, understory characteristics are an important feature of the landscape for boreal woodland caribou [Rettie et al. 1997]). When the results of resource selection studies are intended to guide management decisions, the criteria used to delineate habitats should relate to characteristics of the landscape that can be measured at the spatial and temporal scales at which management is applied.

The Saskatchewan Ministry of Environment's Field Guide to the Ecosites of Saskatchewan's Provincial Forests (hereafter the FEC guide; McLaughlan et al. 2010) defines 27 forestry ecosite classes (hereafter FECs) within Saskatchewan's Boreal Shield. Sites are heterogeneously distributed with varying frequencies throughout the region and are largely distinguished based on floristic properties. Within my study area (denoted by the black dashed line in Fig. 1.4, pp.13), seven of these FECs are either extremely rare (<5 km^2 total area, $n = 4$) or absent ($n = 3$) and hence not very useful for characterizing resource units. The objective of this chapter was to partition the remaining FECs (described in detail in Table A1.1, pp.145) into a parsimonious number of habitat classes that can be distinguished according to features on the landscape (e.g., percent cover of potential forage species, canopy cover etc.) that may govern caribou resource selection at the spatiotemporal scales of my resource selection analyses. I used a combination of multivariate models and ecological interpretation to assign FECs to their final habitat classes. These classes were ultimately used as model covariates to predict the occurrence of female boreal caribou in Saskatchewan's Boreal Shield (Chapter 4, pp. 47).

2.2 Methods

2.2.1 Defining the Clustering Criteria

Predation risk is generally accepted as the primary proximate factor driving woodland caribou habitat selection at coarser spatial and temporal scales (Rettie and Messier 2000, Gustine et al. 2006a), while forage availability and/or accessibility may be more important at finer scales (Johnson et al. 2001). Since I was investigating resource selection at both coarse and fine spatial scales, I grouped FECs according to 13 habitat attributes potentially related to either predation risk (i.e., factors that may mitigate or enhance risk) or forage availability (e.g., abundance of forage species). In other words, I chose attributes that may be important to how a caribou evaluates a habitat in terms of risk and forage opportunities. Values for All habitat attributes were derived from McLaughlan et al.'s (2010) site descriptors and are summarized as follows: **(i)** moisture regime, as defined by the placement of the FEC within an edatopic grid; **(ii)** percent canopy closure, as calculated from the total percent cover of all characteristic tree species; **(iii) – (ix)** percent cover of seven characteristic tree species: jack pine (*Picea banksiana*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*) and tamarack (*Larix laricina*); **(x)** total percent cover of all terricolous lichen species; and, finally, **(xi) –(xiii)** percent cover of three shrub categories: (1) 'alternate shrubs', which included shrubs such as willow (*Salix spp.*) and trembling aspen (*Populus tremuloides*) that are potential forage items for alternate prey species (e.g., moose and beaver); (2) 'berry-bearing shrubs', which included shrubs such as lingonberry (*Vaccinium vitis-idaea*) and blueberry (*Vaccinium myrtilloides*) that have been shown to be important forage for black bears (*Ursus americanus*) during the spring and summer (Baldwin

Table 2.1: Summary of 13 habitat attributes for 20 forestry ecosite classes (FECs) within Saskatchewan's Boreal Shield. The number of sample plots refers to the number of plots used by McLaughlan et al. (2010) to derive values for the site descriptors of each FEC. These site desriptors were then used to derive values for the habitat attributes presented here. (%C) refers to the *weighted* percent cover value, which was calculated by multiplying percent cover values in McLaughlan et al. (2010) by the percent constancy (see section *2.2.1* pp. 15 for a full description of this calculation). The weighted percent cover can be defined as the percent area of ground within a sample plot that is covered or shaded by a species or material. The level 'mod-dry' within the category 'moisture regime' describes FECs that were on the border between moderate and dry grid cells within an edatopic grid. 'Lab. Tea' refers to the shrub Labrador Tea (*Ledum groenlandicum*).

Ecosite Code	# Sample Plots	Moisture Regime	Lichen (%C)	Jack Pine (%C)	Black Spruce (%C)	White Spruce (%C)	Balsam Poplar (% C)	Trembling Aspen (%C)	White Birch (%C)	Tama-rack (%C)	Alternate Shrubs (%C)	Berry Shrubs (%C)	Lab. Tea (%C)	Canopy Closure (%)
BS3	129	Dry	13.00	26.70	5.00	0.00	0.00	0.00	0.00	0.00	0.00	11.50	0.00	31.70
BS4	88	Mod-Dry	7.20	40.00	8.70	0.00	0.00	0.00	0.00	0.00	5.30	14.90	2.80	48.70
BS5	36	Dry	12.30	25.00	4.80	0.00	0.00	0.00	11.00	0.00	5.60	12.10	4.50	40.80
BS6	29	Dry	4.60	27.00	12.50	0.00	0.00	10.00	4.70	0.00	10.80	10.40	2.90	54.20
BS7	28	Dry	41.80	11.10	30.00	0.00	0.00	0.00	0.00	0.00	0.00	9.00	4.10	41.10
BS8	6	Moderate	14.00	11.60	31.00	0.00	0.00	0.00	16.00	0.00	13.70	11.00	6.60	58.60
BS9	81	Dry	10.30	11.60	41.00	0.00	0.00	0.00	0.00	0.00	2.20	7.10	10.20	52.60
BS10	15	Moderate	12.20	6.60	32.00	0.00	0.00	0.00	10.20	0.00	3.20	9.70	8.80	48.80
BS13	25	Dry	5.60	0.00	21.60	0.00	0.00	14.40	29.40	0.00	9.50	14.00	5.30	65.40
BS14	32	Mod-Dry	5.80	0.00	2.40	0.00	0.00	0.00	46.00	0.00	4.80	10.80	8.20	48.40
BS15	38	Dry	3.10	0.00	0.00	0.00	0.00	47.00	8.90	0.00	16.30	13.90	0.00	55.90
BS16	4	Wet	2.20	0.00	30.50	2.50	27.00	0.00	12.80	0.00	34.30	1.00	3.00	72.80
BS17	44	Wet	16.30	0.00	30.00	0.00	0.00	0.00	0.00	0.00	1.60	6.80	3.00	30.00
BS18	33	Wet	6.90	0.00	4.10	0.00	0.00	0.00	0.00	0.00	0.90	0.70	21.30	4.10
BS19	2	Wet	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.00	1.00	0.00
BS20	7	Wet	7.70	0.00	5.20	0.00	0.00	0.00	0.00	0.00	2.00	0.30	3.20	5.20
BS21	2	Wet	0.20	0.00	11.00	0.00	0.00	0.00	5.00	21.00	17.10	0.00	5.00	37.00
BS22	21	Wet	1.00	0.00	0.50	0.00	0.00	0.00	0.00	1.60	16.50	0.00	1.90	2.10
BS23	11	Wet	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	42.00	0.00	0.00	0.00
BS24	10	Wet	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.10	0.00	0.00	0.00

and Bender 2009), but which may also provide winter forage for caribou (Boertje 1984; Thomas et al. 1994); and (3) ‘Labrador tea’ (*Ledum groenlandicum*), which is a potential caribou forage item common to 16 of the 20 FECs. Cover values for each landscape feature are presented in Table 2.1. McLaughlan et al. (2010) describe *percent cover* as the percent area of the ground within a sample plot that is covered or shaded by a species (e.g., tree, shrub, herb etc.) or material (e.g., rock, water, needle litter etc.). In the *FEC guide*, percent cover values reflect the mean percent cover of a species or material calculated across the number of *releves* (sample plots) in which that species or material occurred. For example, the FEC BS3 (McLaughlan et al. 2010: 126-128) has a percent cover value of 10% for black spruce trees; however, because black spruce trees were only recorded in in half of the 129 sample plots used to define BS3, this percent cover value only represents the mean cover of black spruce across 50% of the sample plots. To address this issue, I weighted the percent cover values reported in the *FEC guide* by their corresponding *percent constancy* values, which correspond to the percentage of releves in which a species or material was found. As an example, for the FEC BS3 described above, I multiplied the percent cover value for black spruce (10%) by its percent constancy (0.5 because it occurred in 50% of the sample plots) to get a weighted percent cover value (% C) of 5%. By using the weighted percent cover value, I (a) better captured the importance of each tree, shrub or lichen species to the overall description of each FEC, and (b) made percent cover values somewhat comparable between FECs.

It is important to note that the number of sample plots varied considerably between FECs (*min. = 1 plot, max. = 129 plots,* $\bar{x}$ *= 42 plots*) and were biased towards roads or easy-to-access areas (McLaughlan et al. 2010). Therefore, McLaughlan et al.’s (2010) site descriptors (and by extension the values for the habitat attributes that were used as clustering criteria -) may not accurately represent the true range of conditions possible for each FEC. Researchers in the University of Saskatchewan’s Northern Plant Ecology Lab (NPEL) are currently working on updating the FEC descriptions for Saskatchewan’s Boreal Shield; however, at the time of writing, McLaughlan et al.’s estimates were the best source from which I could derive the 13 FEC attributes described above.

2.2.2 Statistical Analyses

The final grouping of objects in a cluster analysis can be influenced by the choice of clustering method (Legendre and Legendre 1998); therefore it is crucial to select a method that fits with both the structure of the data and the aims of the analysis (Borcard et al. 2011). Since FECs within Saskatchewan's Boreal Shield are hierarchically nested within *ecosections*, which are in turn nested within *ecoregions*, then *ecoprovinces* and finally *ecozones* (see Table 1, McLaughlan et al. 2010: 19), I chose a hierarchical, agglomerative clustering method called Unweighted Pair-Group Method using Arithmetic Averages (UPGMA; Rohlf 1963, Sneath and Sokal 1973) to group the 20 FECs. UPGMA allows an object (here an FEC) to gain membership to a group at a distance equal to the mean of the distance between all of the objects already in the group (Borcard et al. 2011), which offers a nice compromise between single linkage agglomerative clustering (nearest neighbor sorting) and complete linkage agglomerative clustering (furthest neighbor sorting). Its use was justified after a comparison of cophenetic correlations (c.c.), showed that the UPGMA method (c.c. = 0.899) produced a better cluster model than both single linkage clustering (c.c. = 0.770) and complete linkage clustering (c.c. = 0.871), as well two other alternative hierarchical clustering methods: the Ward's Minimum Variance Clustering method (c.c. = 0.795) and Weighted Arithmetic Average Clustering (WPGMA, c.c. = 0.874). The optimal number of clusters (k) was chosen after comparing Mantel's correlation (Mantel 1967) for $k = 1$ to $k = 20$ clusters (a higher correlation indicates a better solution). Classification accuracy was assessed using a silhouette plot, which is a graphical representation of the degree of membership to its cluster. Each bar corresponds to an object's silhouette width, otherwise defined as the average distance between an object and all objects within the cluster. A positive silhouette width indicates an object has likely been classified correctly.

The final UPGMA solution was validated using an unconstrained ordination technique called Nonmetric Multidimensional Scaling (NMDS, Shepard 1962; Kruskal 1964). An NMDS represents the ordered relationships between objects in a reduced number of dimensions (Legendre and Legendre 1998). If the ordination of objects is similar to the clustering of objects, this offers additional support for the cluster solution (Buttigieg and Ramette 2014). I chose a random start for the NMDS, but ran the wrapper `alt.bestnmds` (no. random starts = 50, maximum no. iterations = 100) to double check the final stress values. Code for this wrapper, which is compatible with the function `metaMDS` from *R* package `vegan` (Oksanen et al. 2016a), is available online from Montana State University (http://ecology.msu.montana.edu/labdsv/R/labs/lab9/lab9.html). I selected the optimal number of dimensions (*k*) for the NMDS analysis after graphically comparing stress values from NMDS runs conducted using $k = 1$ through to $k = 10$ dimensions. A Shephard diagram, which is generated by comparing distances among objects in an ordination plot with the original distances in the model's dissimilarity matrix (Borcard et al. 2011), was used to evaluate whether the NMDS ordination adequately represented the relationships between FECs. A model that does a good job of positioning objects in the ordination space should produce a Shepard diagram with a fairly smooth regression line (i.e., few steps) and minimal scatter about that line. I conducted all statistical analyses using open-source *R* statistical software (v.3.3.1, R Core Team 2016).

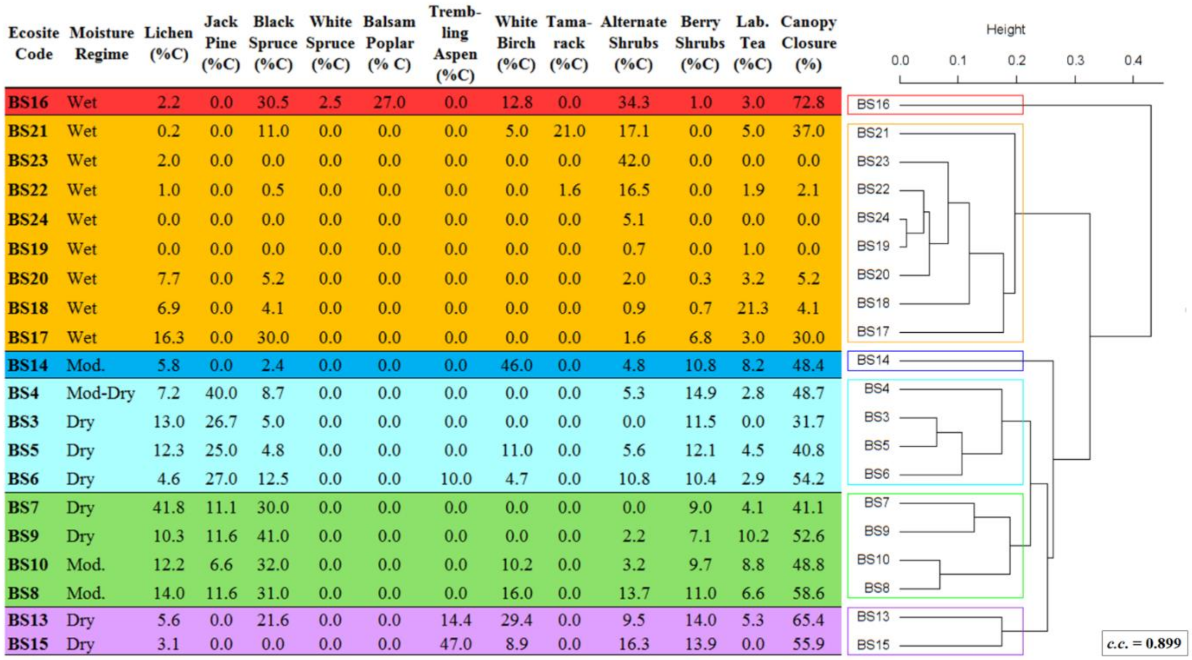
2.2.3 Ecological Interpretation and Final Clustering

After running the UPGMA and NMDS, I critically evaluated discrepancies between the grouping of FECs in the two solutions and then altered the group membership of two FECs in the cluster solution to arrive at an ecologically sensible arrangement of FECs (see section *2.3.4*, pp. 25-28 for a thorough description of this evaluation). Finally, because forest stand age has been shown to be an important driver of boreal caribou habitat selection (e.g., caribou generally select for mature conifer forests and avoiding early successional forests; Metsaranta and Mallory 2007; Hins et al. 2009; Courbin et al. 2009), I partitioned conifer-dominated habitat classes into two broad age categories: mature forests (>40 years post -fire) and young/mid-successional forests (≤40 years post-fire).

2.3 Results

2.3.1 UPGMA Cluster Analysis

Comparison of Mantel's correlation (Mantel 1967) for $k = 1$ to $k = 20$ clusters indicated that the 20 FECs are optimally grouped as 5 habitat classes; however, a comparison of silhouette widths indicated that several FECs were misclassified under this solution. Since the estimate for the Mantel's Correlation was within 0.02 for $k = 3$ to $k = 6$ dimensions, I plotted the silhouette widths for each of these solutions and determined that the 20 FECs were best classified as 6 habitat classes (denoted by the coloured boxes in Fig. 2.1). Moisture regime and the relative percent cover of the seven characteristic tree species appeared to the primary distinguishing attributes between classes. Two FECs – BS14 (blue box, Fig. 2.1) and BS16 (red box, Fig. 2.1) remained independent, likely due to their unique canopy compositions. Specifically, BS16 is dominated by white spruce and balsam poplar while BS14 is dominated by white birch. Most other forested FECs are dominated by either jack pine (*n* = 4, cyan box, Fig.2.1) or black spruce (*n* = 4, green box, Fig. 2.1), although BS13 and BS15 (purple box, Fig.2.1) are characterized by mixed deciduous or mixed deciduous-conifer canopies. The largest cluster (orange box, Fig. 2.1) encompassed eight FECs that can all be described as open (≤ 55% canopy cover, Rettie et al. 1997) wetland habitats. That said, both BS17 and BS21 could be considered unique within the group given their distinct canopy compositions, and, in the case of BS17, its distinct lichen cover. The silhouette widths (Fig. 2.2) for all FECs were positive, which suggests none of the sites were misclassified (note: the silhouette widths for BS14 and BS16 are zero because they are independent; hence, the average distance between them and other members of their respective clusters is zero). However, the small silhouette width for BS17 indicates it has a low degree of membership to the wetland habitat class; hence it may be better classed as a separate group.



Ecosite Code	Moisture Regime	Lichen (%C)	Jack Pine (%C)	Black Spruce (%C)	White Spruce (%C)	Balsam Poplar (% C)	Trembling Aspen (%C)	White Birch (%C)	Tamarack (%C)	Alternate Shrubs (%C)	Berry Shrubs (%C)	Lab. Tea (%C)	Canopy Closure (%)
BS16	Wet	2.2	0.0	30.5	2.5	27.0	0.0	12.8	0.0	34.3	1.0	3.0	72.8
BS21	Wet	0.2	0.0	11.0	0.0	0.0	0.0	5.0	21.0	17.1	0.0	5.0	37.0
BS23	Wet	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	42.0	0.0	0.0	0.0
BS22	Wet	1.0	0.0	0.5	0.0	0.0	0.0	0.0	1.6	16.5	0.0	1.9	2.1
BS24	Wet	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1	0.0	0.0	0.0
BS19	Wet	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	1.0	0.0
BS20	Wet	7.7	0.0	5.2	0.0	0.0	0.0	0.0	0.0	2.0	0.3	3.2	5.2
BS18	Wet	6.9	0.0	4.1	0.0	0.0	0.0	0.0	0.0	0.9	0.7	21.3	4.1
BS17	Wet	16.3	0.0	30.0	0.0	0.0	0.0	0.0	0.0	1.6	6.8	3.0	30.0
BS14	Mod.	5.8	0.0	2.4	0.0	0.0	0.0	46.0	0.0	4.8	10.8	8.2	48.4
BS4	Mod-Dry	7.2	40.0	8.7	0.0	0.0	0.0	0.0	0.0	5.3	14.9	2.8	48.7
BS3	Dry	13.0	26.7	5.0	0.0	0.0	0.0	0.0	0.0	0.0	11.5	0.0	31.7
BS5	Dry	12.3	25.0	4.8	0.0	0.0	0.0	11.0	0.0	5.6	12.1	4.5	40.8
BS6	Dry	4.6	27.0	12.5	0.0	0.0	10.0	4.7	0.0	10.8	10.4	2.9	54.2
BS7	Dry	41.8	11.1	30.0	0.0	0.0	0.0	0.0	0.0	0.0	9.0	4.1	41.1
BS9	Dry	10.3	11.6	41.0	0.0	0.0	0.0	0.0	0.0	2.2	7.1	10.2	52.6
BS10	Mod.	12.2	6.6	32.0	0.0	0.0	0.0	10.2	0.0	3.2	9.7	8.8	48.8
BS8	Mod.	14.0	11.6	31.0	0.0	0.0	0.0	16.0	0.0	13.7	11.0	6.6	58.6
BS13	Dry	5.6	0.0	21.6	0.0	0.0	14.4	29.4	0.0	9.5	14.0	5.3	65.4
BS15	Dry	3.1	0.0	0.0	0.0	0.0	47.0	8.9	0.0	16.3	13.9	0.0	55.9

Fig. 2.1: Final dendogram (right) for the clustering of 20 forestry ecosite classes (FECs) in Saskatchewan's Boreal Shield using the Unweighted Pair-Group Method Arithmetic Averages (UPGMA) clustering method. The coloured boxes represent the optimal number of clusters (*k* = 6) based on a comparison of the Mantel correlation for *k* = 1 to *k* =20 clusters in conjunction with a comparison of silhouette widths for the top four cluster solutions. The *cophenetic correlation (c.c)*, which is a measure of the goodness of fit of the clustering, is presented at the top of the bottom of the dendogram. A summary of the properties of each FEC is provided in the key on the left hand side of the solution. Each row in the table is aligned with its corresponding FEC in the cluster solution and shaded with the colour denoting its membership to a given cluster.

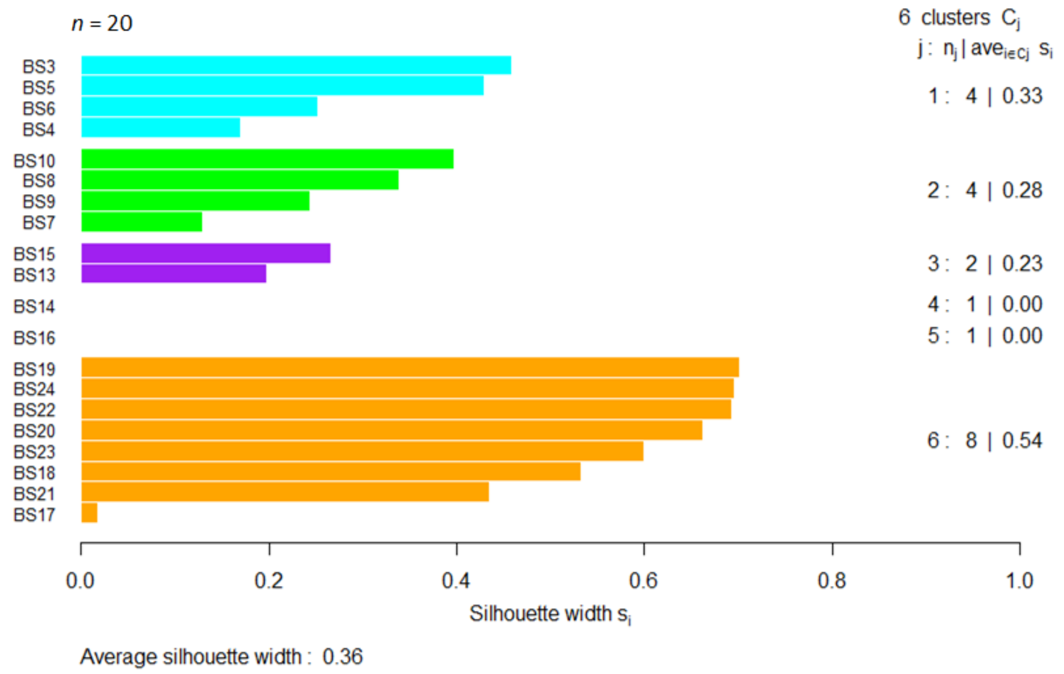


Fig. 2.2: Diagnostic silhouette plot showing the silhouette widths (a measure of the degree of membership of an object to its cluster) for the 20 ecosites. Different colours indicate different clusters. A positive silhouette width indicates an object has been correctly classified. BS14 and BS16 have silhouette widths equal to zero because they are independent classes.

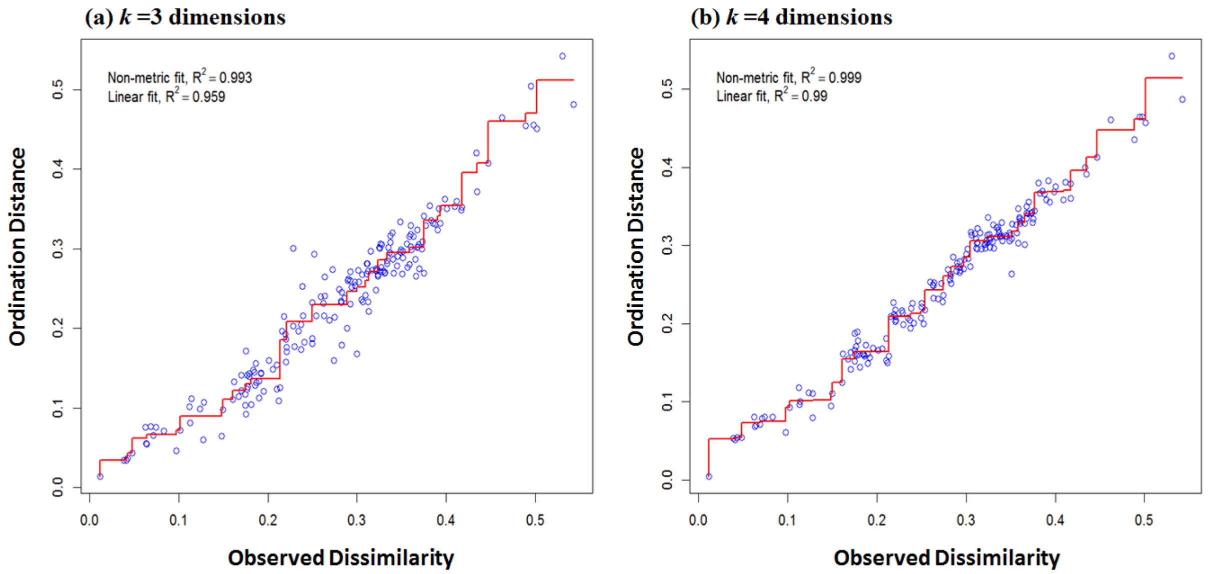


Fig. 2.3: Shepard diagrams comparing the original distances in the dissimilarity matrix to the distances among the 20 FECs in **(a)** 3-dimensional (3D) space and **(b)** 4-dimensional (4D) space. Ideally, the regression line (red line) should be fairly smooth with little scatter about it. The R^2 values in the top left hand corner of the graph represent the model's goodness of fit for a linear regression (*Linear Fit, R^2*) and a non-linear regression (*Non-metric fit, R^2*). Both models appear to do a good job of fitting the data, although the reduced scatter and higher R^2 values for the 4D solution suggests it better represents the ordered relationships between the FECs.

2.3.2 NMDS Ordination Analysis

To validate the UPGMA cluster solution, I applied Nonmetric Multidimensional Scaling (NMDS) to the same dissimilarity matrix used for the cluster analysis. After graphically comparing stress levels calculated for $k = 1$ to $k = 10$ dimensions, I determined that $k = 3$ dimensions ($stress = 0.081$) offered the best compromise between an acceptable level of stress and a minimal number of dimensions (according to Buttigieg and Ramette (2014), stress values ≥ 0.05 and < 0.01 indicate the model does a fair job of fitting the data). Despite this favorable stress value, the Shepard's diagram for the 3-dimensional (3D) NMDS model (Fig. 2.3a) is characterized by a fairly jagged regression line with noticeable scatter above and below it. This suggests that the FECs may be better represented in a greater number of dimensions; however, the linear fit ($R^2 = 0.959$) and the non-metric (non-linear) fit ($R^2 = 0.993$) suggest that the distances between FECs are adequately represented in 3 dimensions. I ran an NMDS with $k = 4$ dimensions in order to compare the diagnostics. The stress value for this model was 0.036, which means it does a good rather than fair job of fitting the data (Buttigieg and Ramette 2014). Compared to the Shepard diagram for the 3D model, the Shepard diagram for the 4-dimensional (4D) model (Fig. 2.3a) had a somewhat smoother regression line with tighter points. That said, an NMDS solutions in four dimensions is incredibly difficult to interpret. Given the moderate difference between the two Shepard diagrams and the fact that the stress value for the 3D model falls within an acceptable range, I chose to continue the analysis with the 3D model.

I used an interactive plot (shown from 3 alternate perspectives in Figure 2.4a, 2.4b and 2.4c) to examine the relative position of the twenty FECs in 3-dimensional space. The solution was rotated using a Principal Components Analysis (PCA; Hotelling 1933) so that the greatest amount of variance is captured along the first axis (i.e., axis NMDS1). The diameters of the black circles indicate how far out of the page the FECs are projected (i.e. the larger the diameter, the closer the FEC is to the reader). With the exception of BS14, BS17 and BS21, the ordination of the FECs aligned fairly well with the UPGMA cluster solution (Figure 2.2a). The incongruity between the relative positions of BS14, BS17 and BS21 in the NMDS solution (Fig. 2a-c) and their relative positions in the UPGMA solution (Fig. 2.1) suggests one or more of these FECs may be misclassified.

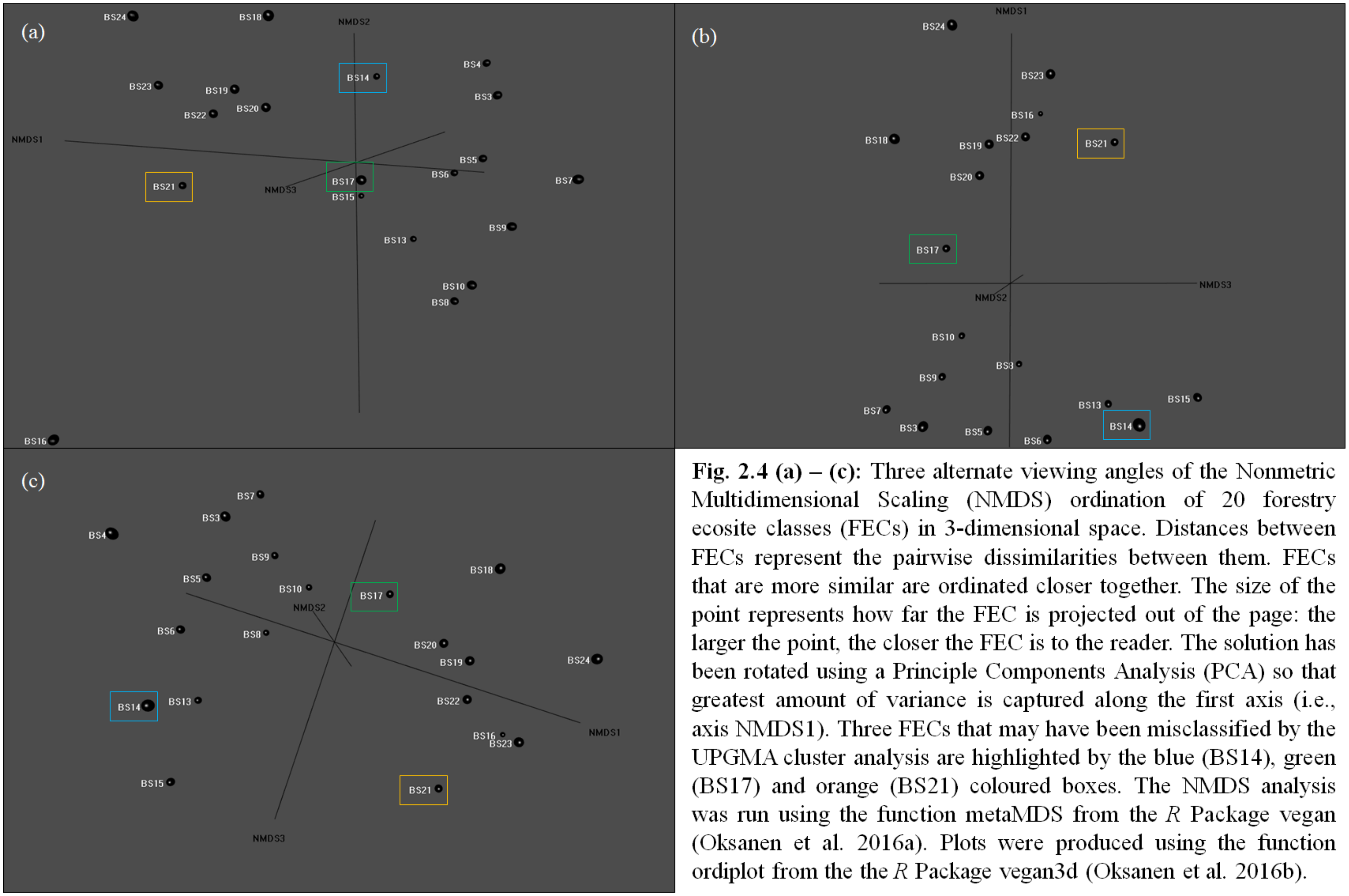


Fig. 2.4 (a) – (c): Three alternate viewing angles of the Nonmetric Multidimensional Scaling (NMDS) ordination of 20 forestry ecosite classes (FECs) in 3-dimensional space. Distances between FECs represent the pairwise dissimilarities between them. FECs that are more similar are ordinated closer together. The size of the point represents how far the FEC is projected out of the page: the larger the point, the closer the FEC is to the reader. The solution has been rotated using a Principle Components Analysis (PCA) so that greatest amount of variance is captured along the first axis (i.e., axis NMDS1). Three FECs that may have been misclassified by the UPGMA cluster analysis are highlighted by the blue (BS14), green (BS17) and orange (BS21) coloured boxes. The NMDS analysis was run using the function metaMDS from the *R* Package vegan (Oksanen et al. 2016a). Plots were produced using the function ordiplot from the the *R* Package vegan3d (Oksanen et al. 2016b).

2.3.4 Ecological Interpretation and Final Clustering

An important step in any ecology-based cluster analysis is assessing whether the final cluster solution makes ecological sense. Looking at the UPGMA cluster solution (Fig. 2.1), there are six broad habitat classes: jack pine-dominated forests (*n* = 4 FECs, cyan box, Fig 2.2a); black spruce-dominated forests (*n* = 4 FECs, green box, Fig. 2.1); mixed canopy forests (*n* = 2 FECs, purple box, Fig. 2.1); white birch-dominated forests (*n* = 1 FEC, blue box, Fig. 2.1); mixed canopy swamps (*n* =1 FEC, red box, Fig. 2.1); and open bogs/fens (*n* = 8 FECs, orange box, Fig. 2.1). A qualitative comparison of the habitat attributes of each FEC (see Table 2.1, pp.17) indicates that most FECs have been logically partitioned into one of these groups; however, there are two FECs—BS17 and BS21—that appear to be misclassified from an ecological perspective. The difference in the relative positions of these FECs in the NMDS solution (Fig. 2.4a-c) vs. the UPGMA solution (Fig. 2.1) offers further support for this observation. Therefore, before dividing up the conifer – dominated classes by age, I critically evaluated the properties of each of these FECs to decide on their final placement in the cluster solution. I did the same for the FEC BS14 due to a similar disparity in its relative positions in the NMDS vs. UPGMA solutions.

According to the final UPGMA solution (Fig. 2.1), BS17 belongs in a cluster with seven other open, wetland habitat types (BS18 – BS24, inclusive); however, its small silhouette width (Fig. 2.2) indicates that BS17 is only marginally similar to the other members of its group. In the NMDS solution (Fig. 2.4a-c), BS17 occurs mid-way between black spruce-dominated sites and wetland sites, which seems to be an accurate representation of its relationship with the two groups. It is an open wetland with low shrub diversity, but it also has a black spruce-dominated canopy and high cover value for lichens that put it on par with the four terrestrial, black spruce-dominated FECs. A comparison of FEC metrics (see Table 2.1, pp. 17) suggests that boreal caribou likely perceive BS17 differently than either class. McLaughlan et al. (2010) describe BS17 as a “very moist, treed bog”, which sets it apart from the four terrestrial FECs. A site’s moisture regime (i.e., wet vs. dry/moderate) can influence the abundance and diversity of grasses, sedges and herbs, all of which may constitute important seasonal forage for boreal caribou (Thomas et al. 1994). These types of vegetation tend to be more numerous in wetlands like BS17 (see Table A1.1, pp.145for summary of FEC characteristics); hence, with respect to seasonal foraging opportunities, a caribou may not perceive BS17 the same way it perceives BS7-BS10. While similar seasonal foraging opportunities may be available in the seven wetland habitats, BS17 may still present a more attractive option because: (a) its black spruce stands may offer refuge from predators; and, (b) it has a relatively high percent cover value for terricolous lichens, which are an important year-round food source for caribou (Environment Canada 2012). During the winter, the difference in canopy closure could constitute another important ecological difference between BS17 and the four terrestrial sites. Snow accumulation tends to be greater in areas with more open canopies. Since snow depth can affect both movement and access to forage (Gustine et al. 2006a), boreal caribou may avoid BS17 sites relative to the other four black spruce-dominated sites during the winter. Given these comparisons, I decided to allocate BS17 to its own habitat class, which I called "black spruce bog".

Like BS17, the FEC BS21 appeared as a distinct class in the NMDS solution but was grouped together with the collection of bogs and fens in the UPGMA solution. While BS21 is classified as a wetland in the *FEC Guide* (McLaughlan et al. 2010), it is unique to the other members of its group in that it supports moderately dense stands of mixed tamarack-black spruce forest (*total canopy cover = 37%*). In fact, it is the only FEC of the 20 FECs considered for this analysis in which tamarack trees occur. The question is: does the addition of tamarack trees to a wetland change how a caribou perceives the risk and foraging opportunities associated with a site? Trees can provide shelter from the elements and may offer cover from predators. In the case of mature conifer forests, they can also support rich communities of terricolous lichens, which are an important year-round food source for boreal caribou (Thomas et al. 1994; Rominger et al. 1996; Thompson et al. 2015). As a component of BS21, tamarack trees likely fill none of these roles. BS21's low percent cover of lichens (*per. cover* = 0.20%) indicates tamarack stands in Saskatchewan's Boreal Shield are generally not associated with terricolous lichens. They may still provide shelter to boreal caribou; however, given BS21's relatively high percent cover of alternate shrubs (*per. cover* = 17.10%), caribou would be better served finding shelter in less risky forests (e.g., those that occur on BS3 or BS7 FECs). Overall, the addition of tamarack stands does not change fact that BS21 – like the other six FECs in its group– is a risky, open wetland with sparse lichen cover. Thus, despite its isolated position in the NMDS solution (Fig. 2.4a-c), I feel justified leaving it in the cluster wetland habitats.

Finally, although the UPGMA solution (Fig. 2.1) partitions the FEC BS14 as its own class, its position in the 3-dimensional space of the NMDS solution suggests it should be grouped with BS13 and BS15. A comparison of the site descriptors for each FEC (see Table 2.1, pp. 17) favors the latter grouping. All three of these FECs are characterized by fairly dense, deciduous-dominated canopies and have similar percent cover values for alternate shrubs, berry-bearing shrubs and lichen. BS14 is unique in that it is the only FEC with a white birch-dominated canopy; however, the fact that a canopy is deciduous-dominated is likely more important to a caribou than the actual species of deciduous tree dominating the canopy [e.g., Hornseth and Rempel 2015]). . This is because, regardless of canopy composition, deciduous-dominated forests in Saskatchewan's Boreal Shield have similar understories (see Table 2.1) , which means caribou likely associate all deciduous forests with similar levels of risk and foraging opportunities. Hence, I grouped BS14 with BS13 and BS15. I defined this triad of FECs as the habitat class "mixed coniferous-deciduous forest". FECs in this class can be described as having either a mixed deciduous or a mixed coniferous-deciduous canopy, but in all cases, one or more deciduous species constitute the dominant tree species.

Table 2.2: Summary of the eight habitat classes used to characterize 30m x 30m resource units in Saskatchewan's Boreal Shield. Each class consists of one or more forestry ecosite clases (FECs) that were grouped together based on 13 habitat attributes related to predation risk and forage availability. Conifer-dominated classes were further partitioned by post-fire age (mature: >40 years post-fire; young/mid-successional: ≤40 years post-fire). **% Area** represents the percent of the land surface area occupied by each class within the study area (black dashed line, Fig. 2.1).

Habitat Class	FEC Constituents	% Area	Brief Description
Mature Jack Pine Forest	BS3, BS4, BS5, BS6	20.3	Jack pine-dominated forests >40 years post-fire; percent cover of terrestrial lichens expected to be higher in mature jack pine forests.
Young/Mid-Succesional Jack Pine Forest	BS3, BS4, BS5, BS6	39.2	Jack pine-dominated forests ≤40 years post-fire.
Mature Black Spruce Forest	BS7, BS8, BS9, BS10	7.1	Black spruce-dominated forests >40 years post-fire; percent cover of terrestrial lichens expected to be higher in mature black spruce forests.
Young/Mid-Succesional Black Spruce Forest	BS7, BS8, BS9, BS10	5.0	Black spruce-dominated forests ≤40 years post-fire.
Mixed Deciduous-Coniferous Forest	BS13, BS14, BS15	5.9	Either mixed deciduous or mixed coniferous-deciduous forest; if the latter, deciduous trees are the dominant species; overstory is relatively dense (total canopy cover >48%).
Mixed Canopy Swamp	BS16	0.2	Dense overstory that tends to be a mix of black spruce and balsam poplar (though can be pure black spruce or pure balsam poplar); relatively high percent cover of risky shrubs (>30%).
Black Spruce Bog	BS17	11.6	Somewhat open, black spruce-dominated canopy; understory dominated by ericaceous shrubs, especially Labrador Tea (*Ledum groenlandicum*). Forest stands tend to be mature (>40 years post-fire).
Open Muskegs	BS18, BS19, BS20, BS21, BS22, BS23, BS24	9.7	Lowland bog or fen habitats with generally low tree and shrub cover; some sites may support tamarack stands or a dense clusters of risky shrubs, such as willows (*Salix* spp.) and alders (*Alnus* spp.).

After reclassifying the FECs BS14 and BS17, the refined UPGMA clusters were as follows: **(i)** jack pine – dominated terrestrial forests (*n* = 4 FECs); **(ii)** black spruce – dominated terrestrial forests (*n* = 4 FECs); **(iii)** mixed coniferous – deciduous forests (*n* = 3 FECs); **(iv)** mixed canopy swamps (n = 1 FEC); **(v)** black spruce bogs (n = 1 FEC); and **(vi)** open bogs and fens, collectively referred to as open muskegs (n = 7 FECs). Because conifer stand age can influence woodland caribou selection of resources (e.g., Metsaranta and Mallory 2007; Hins et al. 2009; Courbin et al. 2009), I further partitioned the jack pine-dominated cluster and the black spruce-dominated cluster into two age categories: mature forest (>40 years post fire) and young/mid-successional forest (≤40 years post fire). I did not partition the black spruce bog cluster into age classes because 93.9% of black spruce bogs in the study area can be classified as mature. The final 8 habitat classes are summarized in Table 2.2 and a map illustrating the distribution of each class across the study area is presented in Fig. 2.5. It should be noted that although the total percent land cover area of the habitat class ‘mixed canopy swamp’ is relatively small (just 0.2%), I still included it in the analysis because it comprised a larger proportion a subset of caribou home ranges in the southeastern section of the study area.

2.4 Discussion

Cluster analyses are useful for identifying discontinuities in ecological data and are best applied when one can justify the need to partition a set of objects into groups (Legendre and Legendre 1998). For researchers studying resource selection, it is common practice to condense available habitat types into a smaller number of habitat classes that can then be used as model covariates (e.g., Rettie and Messier 2000, Houle et al. 2010). Doing so simplifies the modelling process and improves model inference. Given that my study area encompasses 20 common forestry ecosite classes (FECs), it made sense to use a cluster analysis to condense these into a manageable number of habitat classes that could then be used as covariates in a resource selection model. According to a set of 13 habitat attributes derived from site descriptors in Saskatchewan’s *FEC guide* (McLaughlan et al. 2010), the 20 FECs are best grouped as 6 habitat classes (coloured boxes, Fig. 2.1). Overall, the grouping of FECs was ecologically reasonable; however, after comparing the relative positions of BS14, BS17 and BS21 in the UPGMA cluster solution vs. the NMDS solution, I isolated BS17 as a single class and grouped BS14 in with the FECs BS13 and BS15 (see final classes, Table 2.2).

Moisture regime, canopy composition and canopy cover were the primary distinguishing features between the six habitat classes in the original cluster solution (Fig. 2.1). This was likely due to the fact that interdependence between these features caused an inflation of the distances between FECs in the original dissimilarity matrix used for the analysis. For example, different tree species are generally adapted to different environmental conditions (e.g., soil pH and moisture, temperature, light quantity and quality, slope aspect etc.), and therefore tend to have disparate distributions (e.g., black spruce trees primarily grow on wet, organic soils while jack pine trees primarily grow on well-drained, sandy soils [Runesson 2014; http://www.borealforest.org/world/trees.htm]). Accordingly, in an FEC where black spruce is the dominant canopy species (e.g., BS9), percent cover values for other tree species are relatively low or zero (see Table 1); in an FEC where white birch is the dominant canopy species (e.g., BS14), percent cover values for other tree species are also relatively low or zero. When BS9 and BS14 are compared using the clustering algorithm, they are compared based on both the weighted percent cover of black spruce (41.0% vs. 2.4% respectively) and the weighted percent cover of white birch (0.0% vs. 46.0%). These comparisons are treated as independent differences between the two sites (i.e., they are treated as two distinct differences between the sites) when in fact they represent a single difference: the difference in dominant canopy species. As a result, the mean distance between the two FECs (during the first step of the clustering algorithm) or clusters of FECs (during subsequent steps of the algorithm) becomes inflated or exaggerated. One way I could have avoided this exaggeration was by replacing the seven columns of percent cover of canopy species with single categorical variable specifying the dominant tree species.

This issue of redundancy emphasizes a key property of cluster analyses: they are sensitive to the choice of clustering criteria. They are also are inherently subjective because objects are partitioned according to descriptors that are deemed relevant by the researcher. It is therefore crucial to select descriptors (i.e., clustering criteria) that will group objects in a way that is consistent with the goal(s) of the cluster analysis. I clustered FECs using 13 habitat attributes potentially related to caribou predation risk and forage availability because these two ecological factors have been shown to govern caribou resource selection in other (albeit more disturbed) systems (e.g., Rettie and Messier 2000, Bergerud et al. 1990, Johnson et al. 2001). In doing so, I assumed that woodland caribou in Saskatchewan’s Boreal Shield assess habitat suitability according to predation risk and forage availability and that the 13 attributes chosen as clustering criteria were adequate proxies for predation risk and forage availability. One might argue that the classification of FECs could have been improved if percent cover values for grasses, forbs and herbs were included in the clustering criteria, as these are important seasonal forage items for caribou (Thomas et al. 1994, Rettie et al. 1997). That said, Rettie et al. (1997) found a strong relationship between canopy characteristics and understory vegetation in Saskatchewan's Mid-Boreal Upland ecoregion, which led them to suggest that overstory characteristics are sufficient to distinguish between vegetation community types. If this is also true for Saskatchewan's Boreal Shield, then my use of canopy characteristics (e.g., canopy composition and closure) may have been adequate proxies for the availability of understory forage items.

Cluster analyses can be a useful tool for exploring relationships between objects (e.g., habitat classes, organisms, abiotic variables etc.) within a study system. However, because a cluster solution depends on both the clustering method and the information used to group objects, researchers need to be aware of how their choice of methods influences their interpretation of the cluster solution. I used a method appropriate for the data set (i.e., UPGMA), but my cluster analysis may have suffered from: (a) inaccurate measures of the original site descriptors used to derive the 13 habitat attributes used as clustering criteria (see section *2.2.1*, pp. 16 for details); (b) redundancy in the clustering criteria; and (c) a false assumption that woodland caribou in Saskatchewan's Boreal Shield partition habitat according to predation risk and forage availability. If I was not limited to using the FEC classification system – and assuming predation risk and foraging opportunities are indeed important criteria used by caribou to distinguish between habitat types – I would classify vegetation types according to the following attributes: (i) percent cover of terrestrial lichens, which are a key forage item for boreal woodland caribou in other systems (Environment Canada 2012); (ii) a single, categorical descriptor of canopy composition (e.g., black spruce, jack pine, deciduous or mixed deciduous-coniferous), as canopy composition may act as a suitable proxy for understory vegetation communities (Rettie et al. 1997) and, hence, the availability of important seasonal forage such as grasses, forbs and herbs; and (iii) canopy closure, as this attribute influences the amount of cover available for concealment from predators through its effect on light transmission to the forest floor (Lieffers et al. 1999). Provided predictions of canopy closure are accurate and the distributions of lichens and tree species are accurately mapped, this classification scheme has the potential to reduce redundancy in the clustering criteria and improve the overall accuracy of the cluster solution.

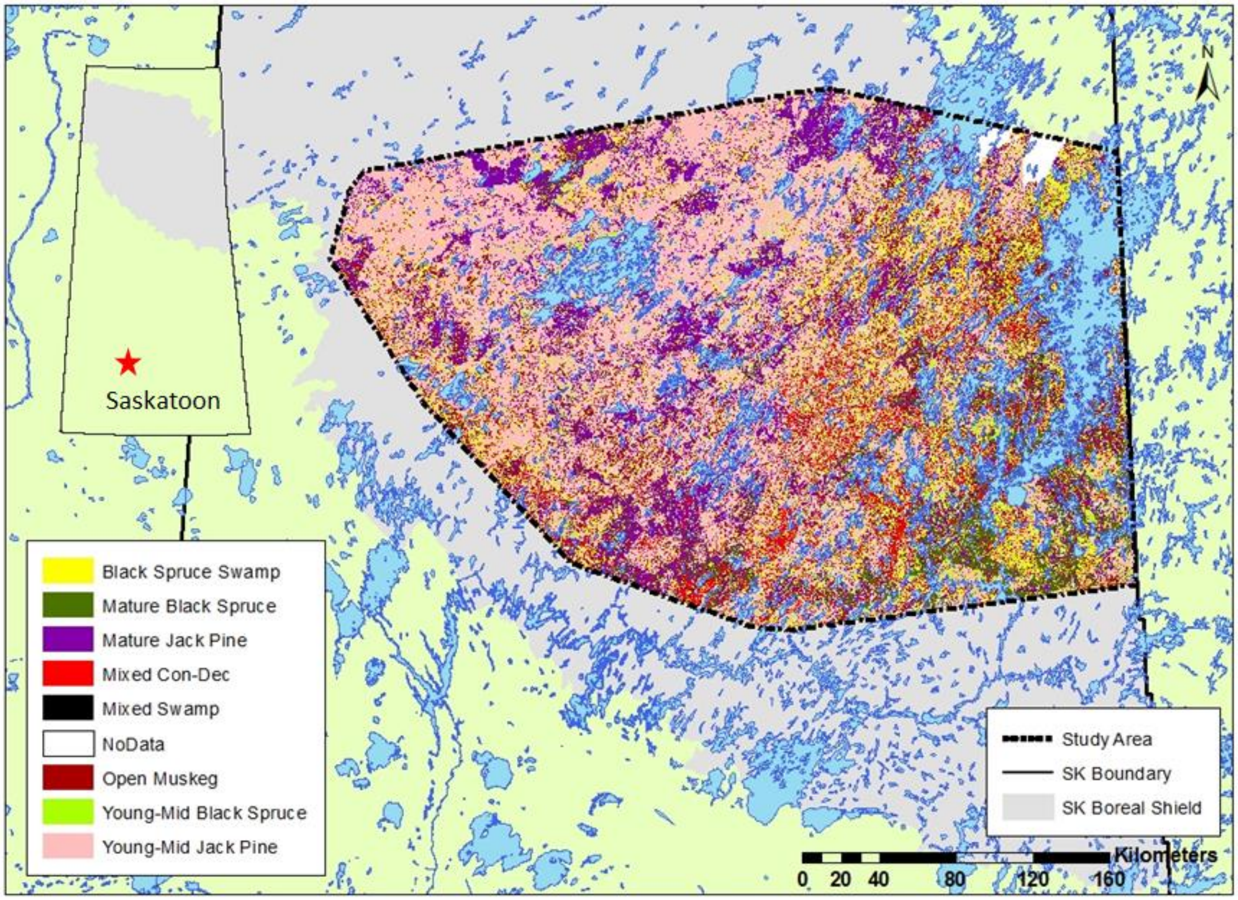


Fig. 2.5: Distribution of the final eight habitat classes used to characterize 30m x 30m resource units within the study area (black dashed line). Habitat classes were delineated by using a combination of multivariate clustering techniques and ecological interpretation to group 20 forestry ecosite classes (FECs) according to 13 habitat attributes related to caribou predation risk and/or forage availability. From the map, it is evident that the most dominant classes are mature jack pine forests (20.3% of total land area) and young to mid-successional jack pine forests (39.2% of total land area). Mixed canopy swamps are the rarest habitat class (0.2% of total land area).

Ultimately, my cluster analysis was meant to inform rather than provide an absolute solution for the grouping of the 20 FECs into a parsimonious set of habitat classes. After critically assessing the placement of FECs in the UPGMA cluster solution and applying an age partition to the two conifer classes, I arrived at a set of eight habitat classes that are ecologically sensible (see Table 2.2, pp. 27). With respect to using these habitat classes as covariates in a resource selection model, I need to be more cautious about interpreting the response of caribou to classes comprised of FECs whose site descriptors (McLaughlan et al. 2010) were derived from only handful of sample plots (e.g., open muskegs and mixed canopy swamps). Conversely, I can be more confident about the response of caribou to jack pine-dominated forests, as the number of sample plots used to derive site descriptors for the four FECs in this class ranged from 29 plots to 129 plots. Future models would benefit from a more accurate classification of habitat types.

The University of Saskatchewan's Northern Plant Ecology Lab (NPEL) is still compiling the data for a final vegetation layer for Saskatchewan's Boreal Shield. During three consecutive summers of vegetation sampling (2014 – 2016), they have made an effort to improve both the distribution and number of sample plots used to derive site descriptors for each FEC. These efforts are intended to improve the accuracy of FEC site descriptions (i.e., they will better reflect the mean state of an FEC), which may affect how FECs are grouped into caribou habitat classes. If the project continues to pursue an FEC classification scheme, I recommend project members use the NPEL's updated description of FECs to derive a new set of habitat classes to use in resource selection models. Whatever the output from this derivation, any resultant conifer-dominated, terrestrial classes should be partitioned into two or more age classes, as stand age is likely an important habitat attribute to woodland caribou (e.g., Metsaranta and Mallory 2007; Hins et al. 2009; Courbin et al. 2009).

3.0 CHAPTER THREE: DELINEATING ECOLOGICALLY MEANINGFUL SEASONS FOR FEMALE WOODLAND CARIBOU IN SASKATCHEWAN'S BOREAL SHIELD

3.1 Introduction

Woodland caribou live in seasonal environments generally characterized by longer winter periods and shorter spring and summer periods (Environment Canada 2012). Accordingly, they experience cyclical changes in weather conditions, forage availability, predation risk (e.g., from bears, which are only active for part of the year), fire disturbance, insect harassment and other factors that may affect how they use space. For example, changes in snow depth, density and hardness can affect where caribou choose to forage during the winter (Johnson et al. 2001), while intense insect harassment can drive caribou to seek refuge in remnant snow patches during the summer (Downes et al. 1986). Woodland caribou also undergo significant physiological changes (e.g., changes in reproductive status and hormone levels) throughout the year that can influence how they behave. For example, during the calving period, female caribou isolate themselves in refuge habitat (e.g., islands or peatlands) in order to minimize predation risk; conversely, during the rut, movement rates increase as bulls, cows and calves congregate into larger groups (Thomas and Gray 2002; Environment Canada 2012). We can reasonably expect that this temporal variation in factors that influence caribou behaviour will generate corresponding temporal variance in caribou resource selection.

Factors governing resource selection can vary both within (i.e., season to season) or between (i.e., year vs. day) temporal scales; therefore, it is crucial to define temporal units of analyses that capture ecologically relevant changes in the ecological processes, interactions and/or physiological conditions that influence an organism's behaviour (e.g., Borger et al. 2006, Basille et al. 2013). In the case of woodland caribou, researchers commonly study resource selection at the seasonal scale because seasons tends to capture a significant amount of the temporal variation in the factors governing caribou behaviour. Caribou seasons have been defined according to calendar dates (i.e., four calendar seasons), snow cover, plant phenology, calving dates, and/or changes in rates of movement (e.g., Rettie and Messier 1998; Gustine et al. 2008; Rudolph and Drapeau 2012, Hornseth and Rempel 2015). Depending on the region and the methods used, the number and length of caribou seasons can vary considerably. For example, Rudolph et al. (2012) used movement rates to delineate seven seasons varying in length from 23 days to 76 days for a population of woodland caribou in James Bay, Quebec; in contrast, Hornseth and Rempel (2015) used calendar dates to define four seasons (spring, summer, fall and winter) ranging in length from 68 days to 113 days for woodland caribou in northeastern Ontario. Even where researchers define the same number of caribou seasons, the length of specific seasons can vary drastically. As an example, both Rettie and Messier (2000) and Ferguson and Elkie (2004) identified five seasons for boreal caribou populations in Saskatchewan's Mid-Boreal Upland ecoregion and northeastern Ontario respectively; however, while Rettie and Messier (2000) defined the post-calving season as a 46-day period extending from 16 May to 30 June, Ferguson and Elkie (2004) defined the post-calving season as a 123-day period extending from 15 July to 14 November. Given regional differences in weather, plant phenology, and caribou migration strategies, as well as the methods used to define seasons, some variation is to be expected. That said, it's imperative that researchers think critically about whether the methods they employ will delineate seasons that are ecologically meaningful to their study population(s).

Vander Wal and Rodgers (2009) argued that modelling changes in movement rates is the most objective method by which to define seasonal boundaries for animal populations. This is because researchers can directly use changes in movement as a robust proxy for animal behaviour rather than having to make assumptions about how variables such as plant phenology and snow depth affect behaviour. The objective of this chapter was to use movement rates to inform the delineation of an ecologically relevant set of annual seasons for female woodland caribou in Saskatchewan's Boreal Shield. Ultimately, these seasons were used as the temporal unit of analysis for my study of caribou resource selection (see Chapter 4, pp. 47).

3.2 Methods

Woodland caribou in Saskatchewan's Boreal Shield are widely distributed and somewhat – but not entirely - sedentary (based on home range size, it appears that some caribou undergo small scale seasonal migrations, see Fig. 4.2, pp. 65). Using movement rates to delineate seasons for such a population can be challenging because: (a) individual movement patterns are often highly variable (e.g., Meuller et al. 2011; Rudolph and Drapeau 2012); and (b) changes in movement rates occur over relatively small spatial scales (Mueller et al. 2011). Van Beest et al. (2013) showed that non-linear generalized additive mixed models (GAMMs) can be effective for modelling changes in movement rates in non-migratory populations of white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus elaphus manitobensis*) in southern Manitoba. Therefore, I employed GAMMs to identify annual, population-level changes in the movement rates of female woodland caribou in Saskatchewan's Boreal Shield.

3.2.1 Generalized Additive Mixed Models

When modelling movement rate over time, it is prudent to only use animals with sets of GPS locations that are similar in size and recorded over a time period of similar length so that all individuals provide equal weight to the analysis (Van Beest et al. 2013). I calculated movement rates using spatial data remotely collected from 68 adult female caribou in Saskatchewan's boreal shield between 18th March, 2014 and 17th March 17, 2016. These 68 individuals represent the subset of the original collared population (*n* = 94; see section *4.3.2*, pp.54-55 for a complete description of collaring procedures) that survived for a full two years; the remaining 26 individuals were excluded from the analysis in order to reduce bias arising from unbalanced sample sizes (though it should be noted that I ran the model with the full data set and got almost identical partition dates). Individual caribou were randomly fitted with either a *Telonics TGW 4680-3* GPS/Argos radio collar with *CR-2A* collar release (Telonics Inc., Mesa, Arizona, USA; *n* = 52) or a *Lotek Wireless Inc. Iridium® Track M 3D* radio collar with a 3-year timed release (Lotek Wireless Inc., Newmarket, Ontario, Canada; *n* = 16 caribou). All collars were programmed to fix a GPS location every five hours, although missed fixes and random switches in recording intervals from 5 to 4 hours and back occurred, which meant intervals between relocations were not always consistent. Therefore, after screening the data for erroneous GPS locations (i.e., locations in Hawaii or Russia); and, in the case of the Lotek collars, 2D fixes (i.e., fixes acquired using just three satellites) or fixes with a Horizontal Dilution of Precision (HDOP) greater than ten (as per Poole, http://www.radioelectronics.com/info/satellite/gps/accuracy-errors-precision.php), I excluded all points less than 4.95 hours or greater than 5.05 hours apart to ensure a uniform step length. This left me with *n* = 44,155 GPS locations for the analysis.

Rather than use movement rates (meters per hour [m/hr]) calculated over individual step lengths (i.e., 5 hour intervals), I chose to use daily movement rates (meters per hour per day [m/hr/day]) as the response variable for my models. This was to account for the fact that the movement rates of large ungulates may significantly increase or decrease *within* seasons in response to short-term human activities or natural disturbances (as discussed by Van Beest et al. 2013: 693). Since these changes in movement usually only last for a couple of hours (Stoen et al. 2010), it made sense to use a coarser resolution of 24 hours in order to dilute the influence of these aberrant movements. Daily movement rates were calculated using the *R* package `adehabitatLT` (v.0.3.20, Calenge 2006), and then natural log-transformed for modelling purposes.

GAMMs were fit using the function `gamm4` from the *R* Package `gamm4` (v.0.2-3, Wood and Scheipl 2014). Unlike Van Beest et al. (2013), I fit the GAMM smoother with the day of the year (1-365 or 1-366 for the leap year) as opposed to Julian Day in order to avoid having to average seasonal boundary dates between the two years. This meant that for each day of the year, there were replicate movement rates per caribou (e.g., for January 1st or day 1, a caribou would contribute a movement rate from 2015 and a movement rate from 2016). The smoother was fit using cyclic cubic splines to: (a) allow individual splines to connect and form a continuous curve; and (b) account for the fact that data collection began on March 18th (day 77) rather than on January 1st (day 1). Animal ID was fit as a random intercept to account for the unbalanced, hierarchical sampling design. Model fit was checked using diagnostic plots provided by the function `gam.check` from the *R* package `gamm4` (v.0.2-3, Wood and Scheipl 2014). I identified seasonal boundaries as the inflection points (i.e., 2nd derivatives) of the model smoother.

3.2.2 Residence Time Analyses

The calving season is arguably the most critical season for woodland caribou because high rates of calf mortality have been associated with significant declines in caribou populations (Culling and Cichowski 2010, Environment Canada 2012, Weir et al. 2014). Accordingly, I conducted Residence Time (RT) analyses (Barraquand and Benhamou 2008) to ensure that the boundaries of the calving/post-calving season encompassed (a) the sample population's range of calving dates, and (b) a sufficient post-calving interval. An RT analysis maps out the amount of time an animal spends in the vicinity (i.e., within a given distance) of successive GPS locations. The residence time associated with a single relocation represents the sum of the *first crossing duration* (which is the sum of the times required to exit a circle of a given radius from its center in the forward and backwards directions [Fauchald and Tverra 2003]) and the passage times that occurred within the radius of this circle before and after the first crossing duration (see

Barraquand and Benhamou 2008: 3340-3342 for an in-depth explanation of the Residence Time method). A visual interpretation of this method is provided in Fig. 3.1.

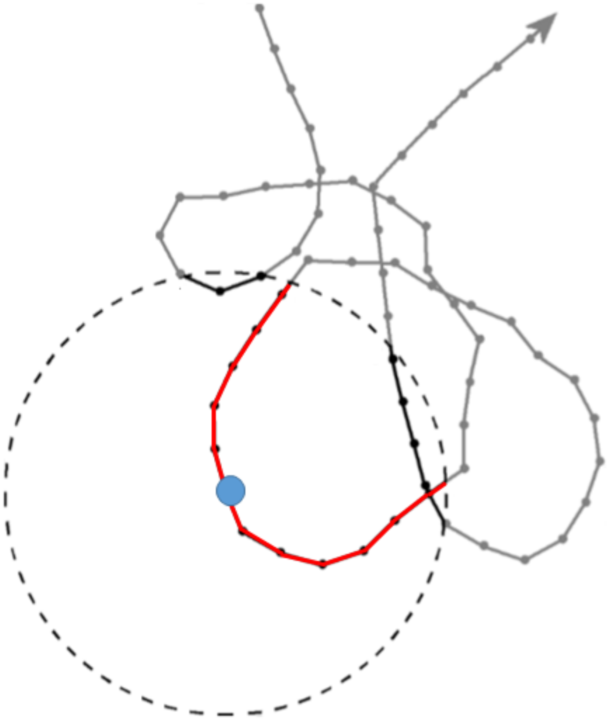


Fig. 3.1: Illustration of Barraquand's and Benhamou's (2008) Residence Time (RT) method (adapted from Barraquand and Benhamou [2008]) . A circle with a pre-defined radius (dashed line) is drawn around a focal GPS location (blue dot). This circle describes the boundary of the patch for which the RT value is calculated. The red line represents the *first crossing duration* (Fauchald and Tverra 2003), which is the time it takes to exit the patch in the forward and backward directions from the focal GPS location. The dark black lines represent additional *passage times,* which are the time intervals the animal spent in the patch before and after the first crossing duration. The grey lines represent the remainder of the animal's trajectory. An RT value is the sum of the first crossing duration and additional passage times; (but note that the additional passage times will only be included in the RT calculation if the intervening time spent outside the circle (i.e., the time it took to traverse the intermediate grey portions of the trajectory) was below some maximum time threshold (*maxt*).

All RT analyses were performed using functions from the *R* package `adehabitatLT` (v.0.3.20, Calenge 2006). For these analyses, I used GPS locations collected between 1st May, 2014 and 1st July, 2014 (*n* = 21,210 points sampled from 92 caribou), and between 1st May, 2015 and 1st July, 2015 (*n* = 17,712 points sampled from 78 caribou). I only retained locations that were >4.95 hours apart, thus setting a minimum step length of 4.95 hours. Coleman et al. (2015) found the most consistent change in RT values when using a 200 meter patch radius. Skatter et al. (2016) also used a 200 meter patch radius when conducting Residence Time analyses for a sample population of caribou around Cree Lake and Key Lake in Saskatchewan's Boreal Shield. Therefore, I set the patch radius for my analyses at 200 meters. I set the maximum time threshold (the maximum time an animal is allowed to spend outside the patch before it is considered to have left the patch [Calenge 2015]) as the time between GPS fixes (i.e., ~5 hours). The longer a caribou remained within a 200 meter radius of a point location, the larger its residence time (RT) value for the patch defined by that 200 meter radius. Caribou were considered as having calved if their peak RT value was greater than 20 hours *and* considerably larger than the average RT value calculated over the time series (as per Coleman et al. 2015). I then used Lavielle's method (Lavielle 1999; Lavielle 2005) to identify the start and end dates of the peak residence time values. As it's generally assumed that caribou are born within 24 hours of the first distinct peak in residence time (Panzacchi et al. 2013), I set the calving date as the start date of the first RT peak.

3.3 Results

3.3.1 Generalized Additive Mixed Modelling

Caribou movement rates varied non-linearly with time (see Fig. 3.2) and so I was able to use second derivatives to identify inflection points (i.e., significant changes in the daily movement rate) along the curve of the model's smoother. In total, there were eight inflection points occurring on days 15 (15th January), 82 (23rd March), 138 (18th May), 179 (28th June), 220 (8th August), 245 (2nd September), 274 (1st October) and 309 (5th November). Not all of these rate changes are obvious in Fig. 3.2, but focusing in on regions adjacent to the inflection points revealed that the smoother's curvature was indeed changing at each point. To check the consistency of these seasonal boundaries across years, I partitioned the data set by year (i.e., year 1 and year 2) and re-ran the model for each year. The resulting smoothers (Fig. 3.3a-b) indicated that inflection points were fairly congruent between years (although changes in daily movement rates appeared to be more pronounced in the smoother fit for the first year of data). Given this congruity, I accepted that, based on movement rates alone, there are eight potential seasons for woodland caribou in Saskatchewan's Boreal Shield (summarized in Table 3.1): *early winter* (5th November – 14th January), *mid-winter* (15th January – 22nd March), *late winter/spring* (23rd March – 17th May), *calving/post-calving* (18th May – 27th June), *summer period 1* (28th June – 7th August), *summer period 2* (8th August – 1st September), *summer period 3* (2nd September – 30th September), and *autumn/rut* (1st October – 4th November).

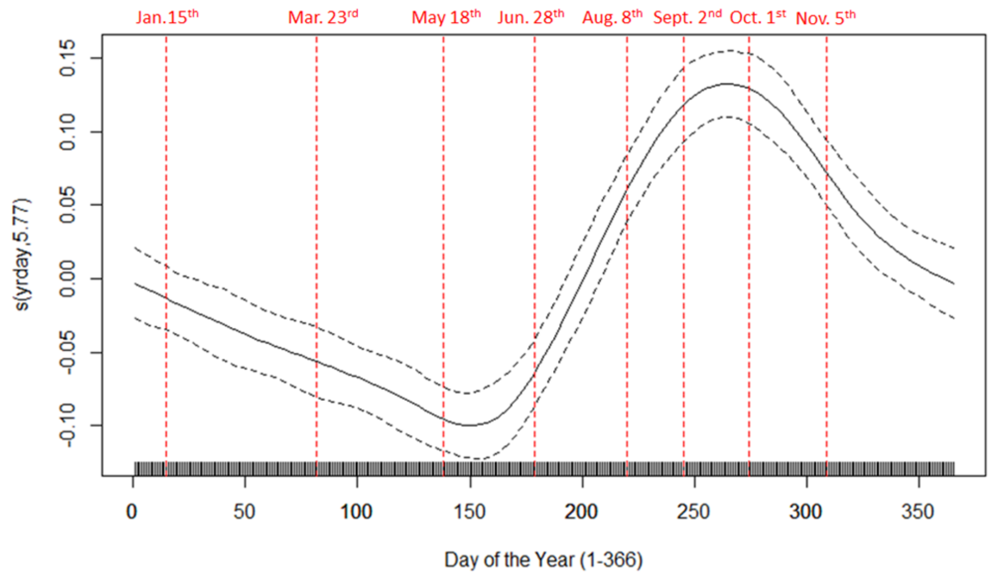
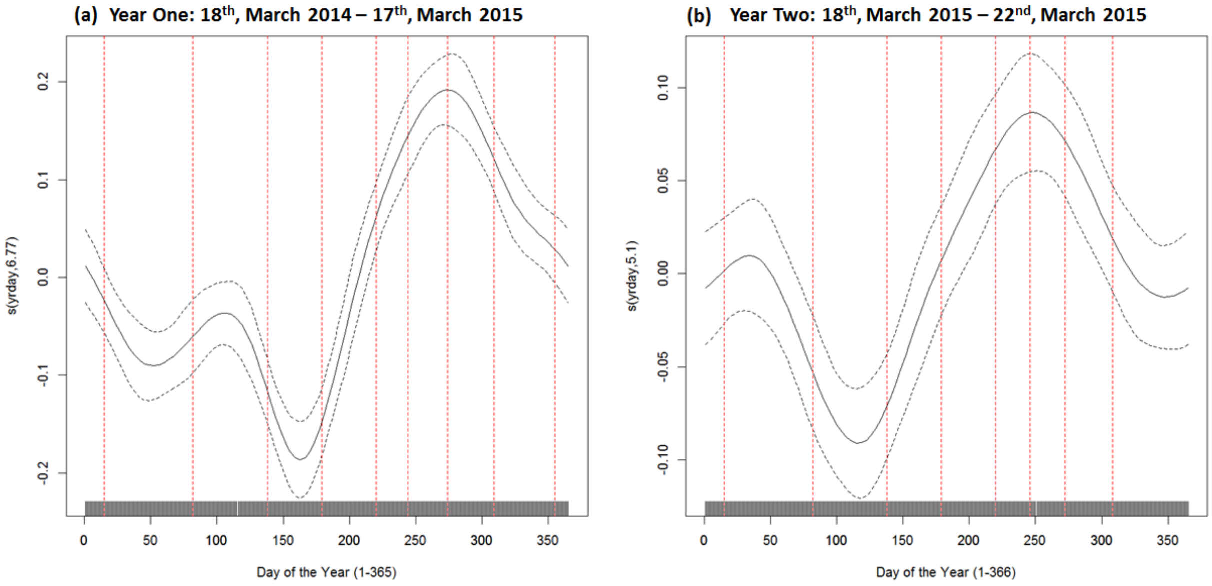


Fig. 3.2: Plot of the smoother from a generalized additive mixed model (GAMM) that fit the natural log of daily movement rates (m/hr/day) for 68 adult female caribou as a function of the day of the year (1-366 days due to a leap year during the two year study period). The solid line is the predicted value of the daily movement rate as a function of the day of the year; the dashed black lines on either side represent upper and lower intervals defined by two times the standard error of the prediction. The units on the y-axis have been scaled to liner units so that the predicted values are centered on zero (this is the default setting for gam objects). The value 5.77 us the estimated degrees of freedom for the model terms. Inflection points (dates where there was a significant change in the daily movement rate) are denoted by the red dashed lines. The small ticks along the bottom illustrate the distribution of data across the sampling period.


(a) Year One: 18th, March 2014 – 17th, March 2015

(b) Year Two: 18th, March 2015 – 22nd, March 2015

Fig. 3.3: Plot of the predicted value for daily movement rate (m/hr/day) as a function of the day of the year (1-365 or 1-366 if a leap year) for **(a)** Year One (18th March, 2014 – 17th March , 2015) and **(b)** Year Two (18th March, 2015 – 17th March 2016). The units of the response have been scaled to liner units so that the predicted values are centered on zero Inflection points (dates where there was a significant change in the daily movement rate) are denoted by the red dashed lines. The small ticks along the bottom illustrate the distribution of data across the sampling period. Though there is noticeable variation in the shape of the smoother between years, the inflection points are almost identical.

Table 3.1: Summary of the 8 annual seasons delineated for woodland caribou in Saskatchewan's Boreal Shield. Seasons were delineated using daily movement rates (m/hr/day) calculated for 68 female caribou over two years.

Season	Abbreviation	Start Date	End Date	No. Days
Early Winter	EW	5th November	14th January	71
Mid-Winter	MW	15th January	22nd March	67*
Late Winter/Spring	LWS	23rd March	17th May	56
Calving/Post-Calving	PC	18th May	27th June	41
Summer 1	S1	28th June	7th August	41
Summer 2	S2	8th August	1st September	25
Summer 3	S3	2nd September	30th September	29
Autumn/Rut	AR	1st October	4th November	35

*68 during a leap year

Table 3.2: Summary of the mean daily movement rate (m/hr/day) for each of the 8 seasons delineated female woodland caribou in Saskatchewan's Boreal Shield. Minimum rates of 0m/hr/day occurred where caribou recorded just two GPS locations (minimum of 4.95 hours apart) within a 24-hour period that occurred at the same coordinates.

Season	No. Relocations	Median	Maximum	Minimum	Mean	Std. Deviation	Std. Error
Early Winter	8959	112.0	2460.1	0.0	161.1	166.6	1.8
Mid-Winter	8265	109.9	2527.9	0.0	156.2	165.1	1.8
Late Winter/Spring	7242	108.9	3013.5	0.4	151.5	157.1	1.8
Calving/Post-Calving	4929	106.6	3547.4	0.0	157.7	172.9	2.5
Summer 1	4476	113.9	2414.8	0.0	161.5	167.1	2.5
Summer 2	2777	126.5	1332.5	1.0	172.0	156.1	3.0
Summer 3	3398	124.8	2474.5	0.6	169.7	166.0	2.8
Autumn/Rut	4109	126.4	2250.0	0.8	174.5	171.7	2.7

Mean daily movement rates for each of these seasons are summarized in Table 3.2. At the population level, the mean daily movement rate peaked during the autumn/rut season ($\bar{x}$ = *174.5 ± 2.7 m/hr/day*) and then declined steadily throughout the three subsequent winter seasons (e.g., early winter, mid-winter and late winter/spring). After reaching a minimum rate during the late winter spring season ($\bar{x}$ = *151.5 ± 1.8 m/hr/day*), it gradually increased throughout the *calving/*post-calving and first two summer seasons before dipping marginally again during the third summer season. The maximum daily movement rate over the two year study period – an epic 3547.4 m/hr/day – was recorded during the calving/post-calving period. This rate can be attributed to a female caribou (id:140123) who undertook a small-scale migration on 23rd May, 2014 just five days before her RT analysis indicated she gave birth to a calf. The second and third fastest movement rates (3013.5 m/hr/day and 2699.5 m/hr/day respectively) were recorded during the late winter/spring season. These maxima suggest that some caribou may undergo small-scale migrations to find suitable calving sites.

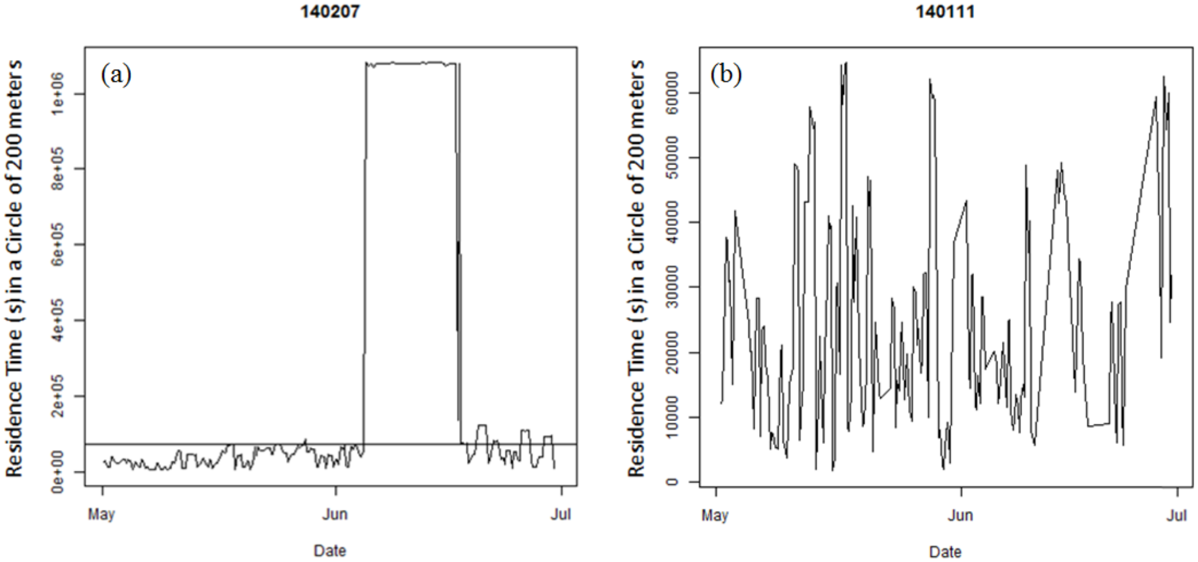


Fig. 3.4: Sample plots of the Residence Times (RT, in seconds) of two adult female caribou within a 200 meter radius patch from May 1st, 2014 – July 1st, 2014. The solid horizontal line in plot **(a)** demarks 20 hours; if a caribou spent more than 20 hours within a 200m radius *and* that RT peak above 20 hours was significantly larger than the average RT peak during the sample period then a caribou was considered to have calved. The caribou in plot **(a)** was assigned a calf in 2014; the caribou in plot **(b)** was not.

3.3.2 Residence Time Analyses

From the Residence Time analyses (see sample plots, Fig. 3.4), I identified 146 calving events over the two year study period (**2014**: 80 events; **2015**: 66 events). A summary of the calving events for the two years is provided in Table A1.2 (pp.146 – 148). The earliest calving event was recorded on 1st May while the latest calving event was recorded on 17th June. The mean calving date over the two year study period was 16th May (± 0.7 days), with the majority of calves (*n* = 108/ 146 calves) born between 10th May and 25th May. For caribou with calving events during the first 3 days of May (*n* = 3), I re-ran the RT analysis using GPS locations recorded between 24th April and 30th June to check that the start date of the peak residence time did not occur earlier than 1st May. In all three cases, it did not. Thus, based on the RT analyses, the calving period for woodland caribou in Saskatchewan's Boreal Shield should extend from 1st May to 17th

June. Looking at the seasonal boundaries delineated by movement rates (Fig. 3.2), the segment extending from 18th May 18th – 28th June comes closest to capturing this period.

3.4 Discussion

According to population-level changes in the movement rates of female caribou, there are eight annual seasons in Saskatchewan's Boreal Shield: *early winter* (5th November – 14th January), *mid-winter* (15th January – 22nd March), *late winter/spring* (23rd March – 17th May), *post-calving* (18th May – 27th June), *summer period 1* (28th June – 7th August), *summer period 2* (8th August – 1st September), *summer period 3* (2nd September – 30th September), and *autumn/rut* (1st October – 4th November). For the most part, these seasons appear to be ecologically sensible, although the RT analyses indicate- that some adjustment may be necessary with respect to the boundary between the late winter/spring and post-calving periods. In addition, it may be more practical from a land manager's point of view to condense the three summer periods into a single season. A critical evaluation of the eight seasons is presented here.

Weather records from eight weather stations in Saskatchewan's Boreal Shield (data available online from the Government of Canada's Environment and Natural Resources branch) indicate that snow begins to accumulate on the ground and daily mean temperatures drop below zero (°C) during the first week of November. In response, boreal caribou are likely settling into early winter habitats (e.g., mature conifer forests with abundant terricolous lichens [Environment Canada 2012]), which would account for the change in daily movement rates denoted by the inflection point on 5th November (Fig. 3.2). By early January, there is a general peak in snow depth throughout Saskatchewan's Boreal Shield, which may impede caribou movement (Johnson et al. 2001, Gustine et al. 2006a), thus resulting in the second inflection point observed on 15th January (Fig. 3.2). As winter progresses, caribou fat and protein reserves become depleted (Adamczewski et al. 1993; Parker et al. 2009) and, in the case of pregnant female caribou, energy allocation to their unborn offspring increases (Adamczewski et al. 1993). Thus, female caribou may further reduce movement during the last few months of winter in order to conserve energy. This behaviour is consistent with the reduced mean daily movement rate observed during the late winter/spring season.

As winter draws to a close, daily movement rates increase as female caribou undergo small-scale migrations towards calving sites. The settling of caribou into calving sites may occur at the inflection point observed on 18th May. However, the RT analyses indicate that some caribou calve as early as 1st May, which means some individuals may begin searching for suitable calving sites during the last week of April. The RT analyses also indicate that 35% of calving events occurred on or after 18th May with the latest potential calving event recorded on 17th June (see Table A1.2, pp.146 – 148, for a summary of calving dates). This means that the calving period defined by the RT analyses is potentially 48 days long, which may be overly long given that caribou generally synchronously mate during a 2-3 week rutting period in late September and/or part of October (e.g., Dauphiné and McClure 1974, Bergerud 1975), and should therefore give birth within a 2-3 week period (assuming a consistent gestation period between females). That said, in some caribou populations, the breeding period is estimated to be longer than 3 weeks (e.g., 4 weeks for caribou in south-central Alaska [Roffler et al. 2002]; and 4 weeks for woodland caribou in northern British Columbia [Gustine and Parker 2008]), which means that the calving period in these populations could also extend over periods longer than 2-3 weeks (although Gustine and Parker (2008) defined the calving period as being only 23 days). The start and end dates of the calving season can also vary, potentially due to changes in environmental conditions, and female age and body condition (Reimers et al. 1983, Adams and Dale 1998). As I did not collect any accurate data on any of these variables, I was not able to test measure the effects of them on calving dates.

Less variable is the length of the gestation period for wild caribou and reindeer, which is known to be longer to be longer than 220 days (e.g., McEwan and Whitehead (1972) reported mean gestation periods of 227 days for both caribou and reindeer; Bergerud et al. (1975) reported a mean gestation period of 229 days; and Messier et al. (1990) report a "typical 230-day gestation period"). If we assume a typical gestation period of 230 days and back track from the earliest calving date (1st May) and latest calving date (17th June), then the breeding season would extend from 13th September – 30th October. This best matches up with the period collectively spaning the third summer period (2nd September – 30th September) and the autumn/rut period (1st October -4th November). Thus, one avenue would have been to condense these two seasons into a general autumn season that is only partially defined by the breeding season. According to the RT analyses, approximately 74% of calving events occurred between 10th May and 25th May. Assuming a 230-day gestation period (Messier et al. 1990), this would correspond to a breeding season spanning 23rd September – 8th October. Accordingly, a potential general autumn season would span 2nd September - 4th November, with a breeding period occurring mid-way through the season. I did not adopt this season for my resource selection analyses (although it may be something to revisit for future analyses).

I found it difficult to make ecological sense of the disparity between the dates of the calving events estimated using the RT analyses and the boundaries of the seasons delineated using population-level movement rates. Given the large size of the sample population's complete range (95,632 km^2), it's plausible that individuals are exposed to varying environmental conditions that cause corresponding local variation in the breeding season, gestation period, and calving dates (e.g., Reimers et al. 1983). It's also equally plausible that the observed Residence Times for some caribou were not associated with a calving event, which means that estimates of calving dates may be inaccurate. Since we currently have little knowledge on the breeding and calving behaviour of caribou in northern Saskatchewan (aside from what is presented here), I decided to adjust the boundaries of the post-calving period to encompass all potential calving events indicated by the RT analyses (i.e., the period spanning 1st May – 17th June). I then added a two-week buffer to the date of the last potential calving event (i.e., June 17th) to allow for a full 2 week post-calving period for all individuals in the sample population. The result was a new calving/post-calving season extending from 1st May to 30th June, which may be best described as a season encompassing caribou arrival at calving sites, calving events, and the post-calving period. I did not change the dates of the autumn/rut season,

The final set of seasons to consider are the three summer seasons. The inflection points on 8th August and 2nd September create three short summer seasons collectively spanning 28th June to 30th September (see Fig. 3.2). During this three-month period, there may be a lot of variation in caribou behaviour due to differences in reproductive status, exposure to forest fires and predation risk from black bears (*Ursus americanus*). Accordingly, these inflection points could be the result of extreme behaviour from a few individuals. However, the fact that these inflection points were almost identical between the two years (see Fig. 3.3a-b) suggests that these inflection points *do* mark important, consistent changes in caribou behaviour. The first 'mini' season (July 28th – August 7th) may encompass a short migratory period during which female caribou that isolated themselves for the calving/post-calving season are condensing back into larger social groups. Similarly, the third mini season (September 8th – September 30th) could encompass a period during which caribou are moving into fall habitats and forming reproductive units (i.e., harems of females overseen by a single male). The critical question is: *will female caribou resource use change markedly between these three mini summer seasons?* Using plant phenology, snow cover and calving dates as criteria, Rettie and Messier (2000) defined the summer season for boreal woodland caribou in Saskatchewan's Boreal Plains ecoregion as a period extending from 1st July to 15th September. This season overlaps quite well with the time interval collectively defined by the three summer seasons delineated here. Therefore, in the interest of delineating a parsimonious number of seasons, I decided to condense the three summer periods into a single summer season spanning 1st July – 30th September.

Ultimately, I arrived at a set of six annual seasons, defined as follows: **Early Winter** (*EW*, 5th November – 14th January); **Mid-Winter** (*MW*, 15th January – 22nd March); L**ate Winter/Spring** (*LWS*, 23rd March – 30th April); **Calving/Post-Calving (***CPC*, 1st May – 30th June); **Summer** (*S*, 1st July – 30th September); and **Autumn/Rut** (*AR*, 1st October – 4th November). These seasons (summarized in Table 3.3) were used to define the temporal units of my resource selection analyses (see Chapter 4, pp.47).

3.5 Conclusion

Using movement rates to delineating biological seasons for non-migratory or widely dispersed populations can be challenging because individual movement rates in these populations are often highly variable (e.g., Rudolph and Drapeau 2012), and changes in movement rates tend to occur over relatively small scales (Meuller et al. 2011). The sample population used for this analysis (*n* = 68 caribou) is distributed across a 95,632 km^2 area and, according to trajectory analyses conducted by Debeffe and McLoughlin (2016; *unpublished data*), may adopt varying life history strategies with respect to migration. Specifically, one-third of the entire collared population (*n* = 94 caribou) were classified as migrants while the remaining two-thirds were either partially migratory or residents. Hence, it is reasonable to expect that individual movement rates are quite variable across Saskatchewan's Boreal Shield.

Where movement rates are variable, seasons defined using population-level movement rates may not be ecologically meaningful for individuals (Rudolph and Drapeau 2012). In fact, even within individuals, there can be a great deal of variation in the timing of seasonal events from year to year (Ferguson and Elkie 2004, Rudolph and Drapeau 2012). Given the large size of my study area (95,632 km^2) and the fact that individuals may have highly variable movement strategies (as evidenced by a trajectory analysis conducted on the population by Debeffe and McLoughlin [2016, *unpublished*]), seasons defined using population-level movement rates may not be ecologically meaningful to individual caribou. Though I did use the six seasons defined here for my resource selection analyses, the delineation of seasons in Saskatchewan's Boreal Shield needs to be revisited for future analyses. One approach may be to use individual seasonal boundaries in order to capture local variation in seasonal migration, climate and plant phenology. Whatever the approach, researchers need to think critically about whether the resultant seasons make ecological sense.

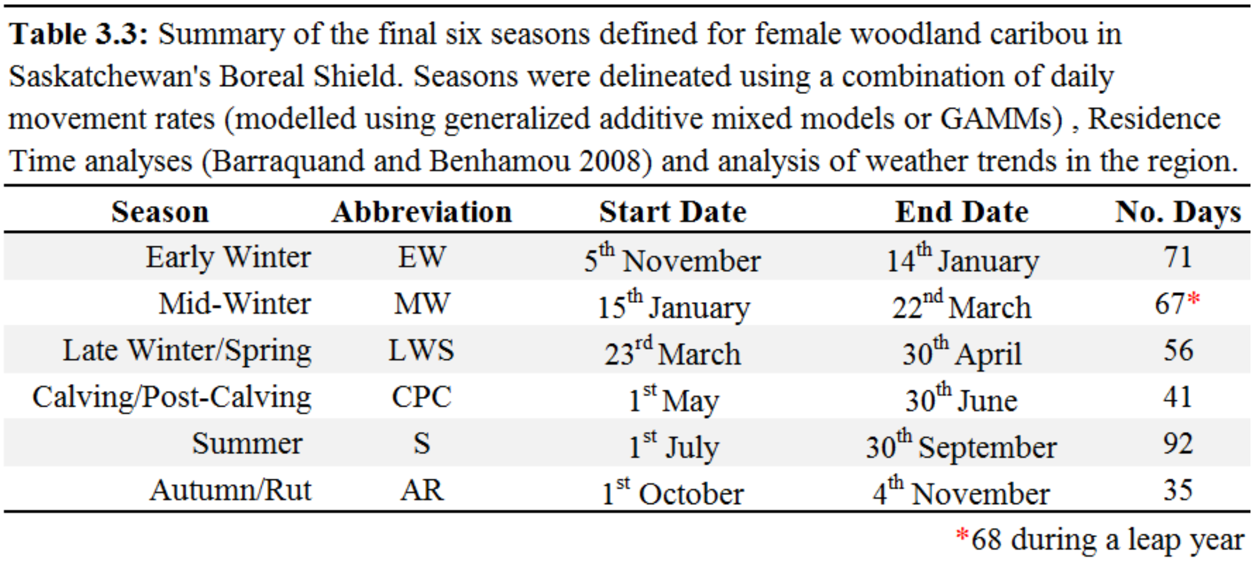


Table 3.3: Summary of the final six seasons defined for female woodland caribou in Saskatchewan's Boreal Shield. Seasons were delineated using a combination of daily movement rates (modelled using generalized additive mixed models or GAMMs) , Residence Time analyses (Barraquand and Benhamou 2008) and analysis of weather trends in the region.

Season	Abbreviation	Start Date	End Date	No. Days
Early Winter	EW	5th November	14th January	71
Mid-Winter	MW	15th January	22nd March	67*
Late Winter/Spring	LWS	23rd March	30th April	56
Calving/Post-Calving	CPC	1st May	30th June	41
Summer	S	1st July	30th September	92
Autumn/Rut	AR	1st October	4th November	35

*68 during a leap year

4.0 CHAPTER 4: MULTISCALE RESOURCE SELECTION BY BOREAL WOODLAND CARIBOU IN SASKATCHEWAN'S BOREAL SHIELD

4.1 Introduction

Resource selection functions (RSFs), which are functions proportional to a species' probability of occurrence (Boyce et al. 2002), are commonly used to map the distribution and abundance of organisms (Manly et al. 2002, Johnson et al 2004, Boyce et al. 2006), as well as gain insight into predator-prey dynamics (Latham et al. 2011a, Gervasi et al. 2013), sympatric species' interactions (van Beest et al. 2014), migratory behaviour (Saher and Schmiegelow 2005, Lendrum et al. 2012), and other ecological processes and interactions that influence life history strategies. Because they offer a spatially-explicit, reproducible method for quantifying resource selection (Boyce et al. 2002, Johnson et al. 2004a), RSFs are an attractive option for land managers looking to understand and characterize the long-term resource requirements of a threatened or endangered species.

In wildlife ecology, RSFs are typically generated by using logistic regression to compare the abiotic and/or biotic attributes of a set of locations known to be used by a species to a set of locations that are potentially available to that species (i.e., use-availability design, Manly et al. 2002). They are defined by the following fixed-effects, exponential equation:

$$w(x) = \exp\left(\beta_1 x_1 + \beta_2 x_2 + \ldots\ldots \beta_k x_k\right) \qquad [4.1]$$

where $w(x)$ is the relative probability of a species' occurrence in a given resource unit; β_0 is the model intercept, and β_1, β_2, …..β_k are the model coefficients (i.e., slopes) for the model covariates, x_1, x_2……x_k. The model covariates represent the suite of abiotic (e.g., elevation, slope, temperature etc.) and biotic (e.g., predation risk, vegetation cover etc.) factors that influence the probability that an animal will use a resource unit.. An RSF equation can be used to define the probability of occurrence in a given resource unit (e.g., points or pixels in space) within the study area by inputting the values of the model covariates (x_1, x_2……x_k) for that unit into the RSF equation.

Wildlife telemetry data (e.g., GPS data from radio-collared animals) are often used to derive the coefficients for RSFs. When dealing with this sort of spatial data, researchers need to be cognizant of several things. First, the data are inherently hierarchical; that is, point locations are clustered within collared animals and may be further clustered within family groups or sub-populations etc. Thus, points recorded from a single animal are not independent of one another, and depending on a species' social structure, may not be independent of conspecifics. Second, points within individuals may be spatially and temporally auto-correlated depending on the time between fixes (Fieberg et al. 2010), which, like the first point, violates the assumption of independence underlying the modelling techniques used to generate RSFs (Manly et al. 2002). Finally, samples of points drawn from individuals are often unbalanced due to differences in the number of successful fixes between individuals over a given time period (as is true for the telemetry data used in this study).

Generalized Linear Mixed Models (GLMMs) offer the statistical framework to address some of these issues through the inclusion of random intercepts and random slopes (Gillies et al. 2006). Briefly, a random intercept allows the magnitude of the response to vary between individuals, while a random slope allows the effect of a covariate to vary between individuals (Gillies et al. 2006). For the purpose of generating RSFs, GLMMs are often structured as logit models of the form:

$$g(x) = \ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = \beta_0 + \beta_1 x_{1ij} + \ldots + \beta_n x_{nij} + \gamma_{nj} x_{nj} + \gamma_{0j} \qquad [4.2]$$

where *g(x)* is a binomial response comparing a set of used points to a set of unused or available points (Manly et al. 2002); ln[π(x)/1-π(x)] is the logit-link function, which relates the binomial response to the linear predictor on the right side of the equation; β_0 is the model's global intercept; β_1, β_2, …..β_n are the model coefficients (i.e., slopes) for the covariates x_1, x_2……x_n; $\gamma_{nj}x_{nj}$ is the random slope term in which γ_{nj} represents the random coefficient of variable x_n for the individual or group *j* (Gillies et al. 2006); and γ_{0j} is the random intercept term, which represents the difference between the intercept for the individual or group *j* and the mean (global) intercept (Gillies et al. 2006). The beta –coefficients (e.g., β_1…..β_n) derived from a GLMM become the model coefficients for the RSF (e.g., β_1…..β_k).

Resource selection functions are intimately tied to species' evolutionary life histories because organisms select resources in order to maximize their fitness under current biological conditions (Fretwell and Lucas 1969). Accordingly, RSFs can provide insight into the ecological *trade-offs* (e.g., trade-offs between growth, maintenance and reproduction; Gadgil and Bossert

1970, Stearns 1989) governing animal behaviour through time and space. In its most general sense, an ecological trade-off can be described as a negative interaction between two traits, in which one trait cannot functionally increase without the other decreasing due to the fact that organisms have a finite amount of energy, time and/or space (Garland Jr. 2014). Common examples include the trade-off between the size and number of offspring (e.g., the quality-quantity trade-off; Stearns 1992, Roff 1992), the trade-off between the age and size of an organism at sexual maturity (Roff 2001), and the trade-off between immune response and reproductive effort (reviewed in Zuk and Stoehr 2002). RSFs are most useful for modelling trade-offs related to predation risk and access to forage. By understanding the role this ecological trade-off plays in governing resource selection, land managers can gain a better sense of which areas to set aside so that threatened or endangered populations have sufficient resources to meet their life history requirements.

Ungulate species like boreal caribou are simultaneously prey and predators (to plants) and therefore must trade-off avoiding predators with gaining access to energy (Festa-Bianchet 1988, Fryxell et al. 1988). This risk-forage tradeoff can occur across multiple spatiotemporal scales (Lima and Zollner 1996), and can manifest as various behavioural changes, including changes in habitat choice, movement patterns (e.g., migration can allow ungulates to escape predation; Fryxell et al. 1988), intraspecific associations (e.g., animals in larger groups may face reduced predation risk but increased intraspecific competition for food; Bertram 1978), and levels of vigilance (Houston et al. 1993). As the direct energetic cost of avoiding predators may be greater at finer scales (Houston et al. 1993, Brown and Kotler 2004), it may be more beneficial for ungulates to adopt a strategy by which they avoid predators at coarser scales and focus on foraging at finer scales. In other words, they may benefit by trading off predation risk and foraging opportunities *between* spatiotemporal scales. However, ungulates have also been shown to make risk-forage trade-offs *within the same* scale (e.g., moose in Quebec, Canada (Dussault et al. 2005) and non-migratory elk in Banff National Park, Canada [Hebblewhite and Merrill 2009]), which suggests that the nature of risk-forage trade-offs is more complex. Indeed, risk-forage trade-offs for ungulates can vary both within and between scales according to behavioural state (e.g., migratory vs. non-migratory individuals, [Hebblewhite and Merrill 2009]), variation in abiotic conditions (e.g., snow depth, [Johnson et al. 2001]), and heterogeneity in predator distributions (e.g., absence vs. presence of a predator in a system, [Hernandez and Laundre 2005]). Thus, although predation risk may be an important driver of ungulate behaviour at coarser spatiotemporal scales (Houston et al. 1993), the relative importance of predation risk vs. foraging may vary across spatiotemporal scales, leading to differences in the behaviour of individuals, populations and/or species.

Boreal caribou typically occur at low densities, which is generally thought to be an anti-predator strategy (i.e., it is harder for a predator to locate small groups of caribou in the boreal forest than vast herds, [Environment Canada 2012]). This behaviour suggests that predation risk is limiting to boreal caribou at coarser spatial scales, which is consistent with the hypothesis that ungulate species initially focus on predator avoidance at broader spatial and temporal scales (e.g., Rettie and Messier 2000). As discussed in Chapter 1 (see pp. 6), forage availability and accessibility may exert greater influence on boreal caribou behaviour at finer spatiotemporal scales (e.g., at the level of the food patch [Johnson et al. 2001]).

The objective of this chapter was to quantify resource selection by female boreal caribou in Saskatchewan's Boreal shield at two spatial scales and across six seasons (delineated in Chapter 3, pp.33) in order to test hypotheses related to the importance of predation risk vs. foraging at multiple spatiotemporal scales. Ultimately, my goals were to: (a) test whether risk-forage trade-offs occurred between or within spatial scales; and (b) build a set of resource selection functions that are useful to researchers and land managers looking to identify critical habitat for woodland caribou in Saskatchewan's Boreal Shield.

4.2 Hypotheses and Predictions

Hypothesis 1: Predation risk has been shown to be a primary factor governing coarse-scale resource selection by woodland caribou in other systems (e.g., Rettie and Messier 2000); however, little is known about how predation risk influences caribou resource selection in a system with a high fire – low anthropogenic disturbance regime like the one observed in Saskatchewan's Boreal Shield. A key property of resource selection is that it is a hierarchical process (Johnson 1980, Wiens 1989, Schaefer and Messier 1995), and it is widely posited that factors most limiting to a species (e.g., a factors that set the position of a population's equilibrium [Sinclair 1991]) will be the most important determinants of resource selection at coarser spatiotemporal scales (Holling 1992, Rettie and Messier 2000). There is considerable evidence that predation can be limiting to ungulate species (e.g., moose [reviewed in

Ballenberghe and Ballard 1994], roe deer [Melis et al. 2009, 2010], and caribou (as reviewed in Seip 1991]), although the role of predation as a limiting factor to ungulate species can vary depending on the relative body sizes of the predator and prey species (Sinclair et al. 2003), environmental productivity (Melis et al. 2009, 2010), the numerical response of the predator species to the prey species (e.g., when a numerical response is absent, the influence of predation may be weak, [Boutin 1992]), as well as other ecological factors (see Gervasi et al. 2012: 444). Predation may also share a limiting role with density-dependent factors (e.g., lynx predation and the density of roe deer both seem to influence roe deer population dynamics in Sweden [Andrèn and Liberg 2015]), which can further complicate the study of predator-prey interactions. However, given that (a) predation has been shown to be limiting to ungulate species across a variety of landscapes (e.g., Seip 1991, Ballenberghe and Ballard 1994); and (b) limiting factors are posited to influence resource selection at coarser spatiotemporal scales (Rettie and Messier 2000), it is reasonable to expect that predation influences coarse-scale caribou resource selection in Saskatchewan's Boreal Shield. Therefore, I hypothesize that woodland caribou in Saskatchewan's Boreal Shield will select for resource units that *minimize* predation risk (either through direct or indirect effects on risk) at the coarse spatial scale for all seasons.

Prediction 1: At the coarse spatial scale, female boreal caribou will select for mature conifer-dominated forests during autumn and the three winter seasons, and black spruce bogs during the calving/post-calving and summer seasons because both of these habitat classes may offer refuge from predators. They will consistently avoid young/mid-successional forest and deciduous-dominated forests, as these may be preferred habitat for alternate prey (e.g., moose [Seip 1992, Dussault et al. 2005, Jacqmain et al. 2008]). Caribou will also avoid linear features as these features may carry a higher level of real or perceived predation risk from wolves, (James and Stuart-Smith 2000, Oberg 2001, DeCesare et al. 2012; though it should be noted that more robust analyses are needed to link increased predation on caribou to linear features [Mcloughlin et al. 2016, in review]).

Hypothesis 2: At finer spatial scales, caribou resource selection patterns may be better explained by forage availability (e.g., Bergerud et al. 1990, Johnson et al. 2001). Little is known about the foraging dynamics of woodland caribou in Saskatchewan's Boreal Shield. Assuming that access to forage also becomes more important at finer scales in this study system, then female caribou should show strongest selection for model covariates that are associated with seasonal foraging opportunities.

Prediction 2a: During the calving/post-calving, summer and autumn/rut seasons, female woodland caribou will show the strongest selection (relative to all other habitat types) for open muskegs and black spruce bogs because these habitats support seasonal abundances of shrubs, grasses, sedges and herbs. These food items are relatively rich in nitrogen and other nutrients that female caribou require in order to maintain lactation and build body condition before the lean winter months (Klein et al. 1990, Johnstone et al. 1999).

Prediction 2b: During the early winter and mid-winter seasons, caribou will show stronger selection for mature jack pine-dominated and black spruce-dominated forests. These habitat classes have some of the highest percent cover values for lichens (see Table 2.1, pp. 17), which are a staple winter food source for woodland caribou (Thomas et al. 1994; Rominger et al. 1996; Thompson et al. 2015).

Prediction 2c: The late winter/spring season is a nutritionally stressful period for female caribou. Fat reserves built up during the previous summer and autumn seasons have been exhausted (Adamczewski et al. 1993; Parker et al. 2009), but energy expenditure is increasing because (a) females are migrating to calving sites; and (b) females are allocating a greater proportion of resources to their unborn offspring (Adamczewski et al. 1993). Therefore, I predict that female caribou will select for mature conifer forests and black spruce bogs. The former may be more important earlier in the season because mature conifer stands are generally a reliable source of carbohydrate-rich lichens while the latter may be important later in the season because black spruce bogs may support spring forage (in addition to being a source of terrestrial lichens), as well as provide suitable calving habitat.

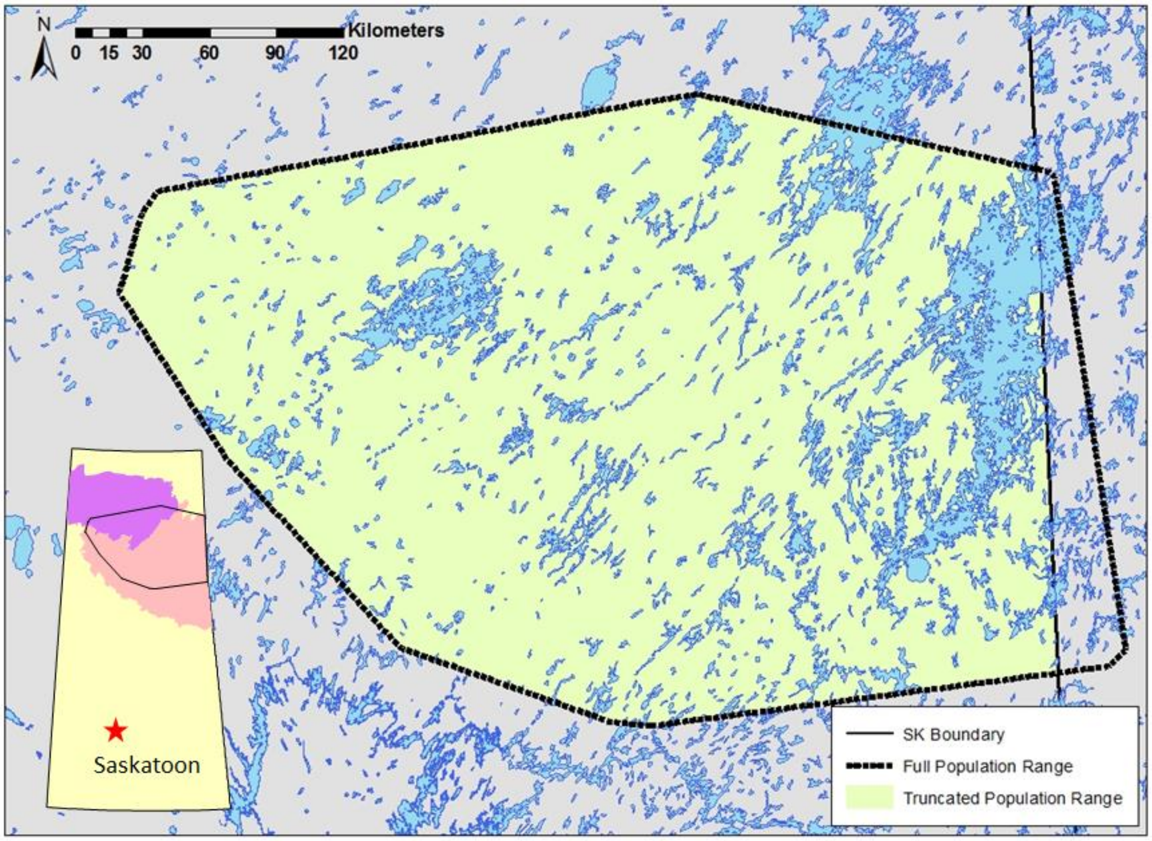


Fig. 4.1: The complete population range (dashed line) and truncated population range (green polygon) calculated over two years (23rd March, 2014 – 22nd, March 2016) for 94 female woodland caribou in Saskatchewan’s Boreal Shield. Ranges were delineated using 100% Minimum Convex Polygons (MCPs, Mohr 1974) buffered by an average daily step length of 1 km. The complete population range covers an area of 95, 632km^2 while the truncated range covers an area of 91, 238km^2. The coloured polygons in the inset denote the two ecoregions encompassed by the population range: the Athabasca Plains Ecoregion (purple) and the Churchill River Upland Ecoregion (pink).

4.3 Methods

4.3.1 Study Area

The study area (Fig. 4.1) was defined as the area of Saskatchewan’s Boreal Shield encompassed by the population range of a sample of 94 adult, female caribou (see sections *4.3.2* and *4.3.3*, pp. 54 and pp. 55 for details regarding the sample population and range delineation). It lies north of the Churchill River, extending between 55°44’N and 58°17’N and between -101°48’W and -108°43’W. Roughly two-thirds of the area falls within the Churchill River Upland Ecoregion, with the remaining third falls within the Athabasca Plains Ecoregion (see inset, Fig. 4.1, pp. 53).

The Churchill River Upland Ecoregion is underlain by Precambrian crystalline bedrock and its thinner, acidic soils support stands of jack pine (*Picea banksiana*), black spruce (*Picea mariana*), and mixed deciduous forests, especially along the southern edges (Secoy 2006). The terrain in this ecoregion tends to be more rugged than in the Athabasca Plains Ecoregion, which is characterized by networks of sandy glacial deposits, moraines and eskers (Secoy 2006). Jack pine forests are dominant in this Athabasca Plains Ecoregion, as they are well-suited to its sandy soils. The overall climate is harsh, with long, cold winters and short, humid summers.

4.3.2 Telemetry Data

In March 2014, 94 adult, female caribou in Saskatchewan's Boreal Shield were fitted with Global Positioning System (GPS) - equipped radio collars (see Fig. 1.4, pp. 13, for collaring locations). Animals were captured and handled according to the procedures outlined in the University of Saskatchewan's animal care protocol No. 20130127. Each caribou was randomly assigned either a *Telonics TGW 4680-3* GPS/Argos radio collar with *CR-2A* collar release (Telonics Inc., Mesa, Arizona, USA; *n* = 69 caribou) or a *Lotek Wireless Inc. Iridium® Track M 3D* radio collar with a 3-year timed release (Lotek Wireless Inc., Newmarket, Ontario, Canada; *n* = 25 caribou). Collars were programmed to fix a location every 5 hours; however, due to differences in the number of failed fixes per animal and random shifts in the recording intervals (e.g., from 5 hours to 4 hours and back), time intervals between points were irregular and individual sample sizes were unbalanced.

Two of the original 94 caribou (AID no.140158 and 140209) died within a month of being collared and were therefore censored from the data set. I used GPS locations collected from the remaining 92 collared animals over a two-year period spanning 23rd March, 2014 – 22nd March, 2016 to develop resource selection functions (RSFs). A total of 230, 686 GPS locations were recorded from these 92 caribou over this two-year period. Before beginning my analyses, I discarded all erroneous fixes (e.g., GPS locations in Hawaii or Russia, *n* = 102 points); fixes that occurred in pixels denoted as 'water' (*n* = 3,937 points) or rare habitat types (e.g., sand dunes or white spruce-dominated habitats, *n* = 10 points); fixes that occurred outside the extent of the vegetation layer or outside the provincial boundary (*n* = 4,075 points); duplicate fixes (*n* = 40); and, for the Lotek collars, all 2D fixes (*n* = 111 points) and fixes with a horizontal dilution of precision (HDOP) greater than 10 (as per Poole, http://www.radioelectronics.com/info/satellite/-

gps/accuracy-errors-precision.php ; *n* = 242 points). I further excluded all fixes that occurred less than five hours apart (*n* = 16,701 points) to set a minimum bound on the level of temporal autocorrelation between fixes. At the coarse scale of selection, I removed all GPS points that fell outside the 95% contours of individual home ranges (*n* = 10,778 points), while at the fine scale, I removed all points that fell outside the 95% contours of individual annual seasonal ranges (*n* = 11,131 points; see section *4.3.3*, pp. 55, for a more details regarding range delineation). For each season, I then excluded all individuals with fewer fixes than the total number of days encompassed by that season. As an example, I removed caribou 140105 from the fine scale summer models because she only had 54 points remaining for this season after I cleaned the data. In order to have been included in this analysis, she would have needed to have a minimum of 92 points (i.e., 92 points for 92 days of summer). This screening process ensured a ratio of 1 point per day per season for all caribou in the models. After this extensive vetting of the data, I was left with *n* = 194,713 GPS locations for the coarse scale analyses and *n* = 194, 312 GPS locations for the fine scale analyses.

4.3.3 Range Delineation

Resource selection can be quantified by using logistic regression to compare used resource units (defined by survey data or GPS point locations from radio-collared animals) to available resource units, which are often defined as a sample of randomly generated points within the "domain of availability" (e.g., home range, seasonal range, food patch etc., Manly et al. 2002). Resource selection patterns may change with the spatial scale(s) at which used and available points are sampled; therefore, it is useful to define multiple scales over which to examine resource selection in order to better understand how an animal interacts with its environment (Rettie and Messier 2000, Mayor 2009)I chose two spatial scales over which to model resource selection by female woodland caribou in Saskatchewan's Boreal Shield. The first was a coarse spatial scale defined by the collared caribou's population range and the second was a fine spatial scale defined by 1 kilometer buffers around individual GPS locations. I chose a radius of one kilometer, as this was the mean daily step length of the sample population (*n* = 92 caribou). This meant that for each season at the coarse scale, I was modelled the factors that influenced the placement of seasonal ranges within the population range. At the fine scale, I modelled the factors that influenced the selection of resource patches (e.g., for foraging, resting, travelling etc.).

For the coarse scale analyses, used points were sampled from within individual home ranges (Fig. 4.2), which were delineated as 95% utilization distributions (UDs, van Winkle 1975) based on two years of data. An equal number of random points (n = 194, 713 points) were sampled within the population range, which was defined by a 100% Minimum Convex Polygon (MCP, Mohr 1974) buffered by the average daily step length of one kilometer and then truncated at the eastern border of Saskatchewan (green polygon, Fig. 4.1). The MCP was generated using ArcGIS® software (v.10.2.1). For the fine scale analyses, used points were sampled from within annual seasonal ranges (95% utilization distributions based on *one year* of data) and corresponding random points (n = 194, 312 points) were sampled from within one kilometer buffers drawn around each telemetry location.

Utilization distributions were estimated in the *R* program (R Core Team 2016) using a fixed kernel density estimator (KDE) with a plug-in bandwidth ($h_{\text{plug-in}}$), which greatly improved the accuracy (i.e., the fit of the range boundaries to the distribution of points) of range estimation over other choices of smoother (e.g., h_{ref} and h_{LSCV}). Code to estimate the plug-in bandwidth was provided by the Walter Applied Spatial Ecology Laboratory at Pennsylvania State University (Penn State 2016). I chose to delineate range boundaries at the 95% UD contour to account for the fact that some collared caribou made brief, infrequent forays outside their typical ranges. By excluding 5% of the utilization distribution, I aimed to remove these aberrant points and thereby avoid overestimating the size of each home or seasonal range. I also calculated 50% utilization distributions to delineate core areas of home ranges in order to qualitatively compare core vs. home range sizes. Annual seasonal range sizes (e.g., seasonal ranges for year 1 and year 2) were compared using a Kruskal-Wallis Test (Kruskal and Wallis 1952) in conjunction with Dunn's Multiple Comparison Test (Dunn 1964).

4.3.4 Model Covariates

Depending on the spatiotemporal scale of analysis, the factors governing the selection of resource units by woodland caribou can vary (e.g., Rettie and Messier 2000, Gustine et al. 2006a, Leblond 2011). Therefore, it was important that I characterized resource units using a set of habitat attributes that have the potential to influence caribou behaviour at the coarse and/or fine scale(s) defined for this study. I defined resource units as 30 meter by 30 meter pixels of land within Saskatchewan’s Boreal Shield as this was the resolution of most of the data rasters available for the area. I then selected the following habitat attributes by which to characterize resource units: elevation (m), slope (degrees), heat load index; mean daily temperature (°C), mean daily snow depth (cm), habitat class (*n* =8, see Table 2.2, pp.27), proximity (m) to the nearest linear feature (e.g., major road, trail, geophysical survey line, fire break etc.), and reproductive status (i.e., presence of a calf). All of these variables have the potential to influence caribou behaviour and thus, risk-forage trade-offs, at the two spatial scales of my analyses. I used a combination of ArcGIS 10.2.1® software (v.10.2.1) and *R* statistical software (R Core Team 2016) to extract values for each attribute to each used and available point.

4.3.4.1 Topographical Variables

Elevation and slope values were extracted from raster layers derived from a digital elevation model (DEM) in ArcGIS®. Heat load index, which is a unit-less index comparing the relative amount of heat received at a location (here, a 30m x 30m resource unit) based on its slope, aspect and latitude, was calculated using the coefficients defined for equation 2 in McCune and Keon (2002: 605). Because heat load index is derived from a measure of slope (in radians), the two attributes are non-linearly related; however, I decided to include both slope (in degrees) and heat load index as covariates in my resource selection models because, although they can both indirectly influence caribou behaviour through their impacts on vegetation communities, they may also influence caribou behaviour via independent mechanisms. Specifically, the steepness of a slope may affect predation risk independent of heat load index while heat load index may affect forage availability independent of the steepness of a slope (e.g., in the northern hemisphere, south-facing slopes receive more sunlight and so support drought-resistant vegetation and fewer trees; while north-facing slopes retain more moisture and are cooler and more humid [Maren et al. 2015]).

4.3.4.2 Climate-Related Variables

Mean daily temperatures (^{o}C) and snow depths (cm) were calculated using historical weather records from the following six weather stations in Saskatchewan's Boreal shield: Cigar Lake Mine (station id: 4061629), Collins Bay (station id: 4061629), Island Falls (station id: 4063605), Key Lake Mine (station id: 4063755), La Ronge (station id: 4064149) and Southend (station id: 406755). Historical records were obtained online through the Government of Canada's Environment and Natural Resources Branch (http://climate.weather.gc.ca/). I assigned mean daily temperature and snow depth values to each used and available point using weather records from the nearest weather station (i.e., each point was assigned a temperature and snow depth value from the weather station that it was closest to). Mean daily snow depth was excluded from the global model for the summer and autumn/rut seasons because the mean daily snow depth was 0 meters for the entire summer season and all but the last week of the autumn/rut season.

4.3.4.3 Habitat Classes

Habitat classes were derived from a forestry ecosite class (FEC) layer provided by Dr. Kunwar Singh and his colleagues in the University of Saskatchewan's Northern Plant Ecology Lab (NPEL). I initially derived six major habitat classes (see Chapter 2, pp. 15 - 32 for a detailed description of how FECs were condensed into a these six classes), and then partitioned the black sprue-dominated and jack-pine dominated habitat classes into two age categories: mature forests (>40 years post fire) and young/mid-successional forests (≤40 years post fire). To do this, I used forest fire records to estimate the time since the most recent fire (in years) for each 30 meter x 30 meter pixel of jack pine or black spruce forest in Saskatchewan's Boreal Shield.

Saskatchewan's forest fire season officially begins on 1st April and runs until 31st October, although fires can also occur outside this period (see *Appendix B - Prevention and Prearedness Plan*, http://www.environment.gov.sk.ca/firesmart). Since I used caribou relocation data collected between 23rd March 2014 – 22nd March 2016, I had relocation data spanning two official fire seasons (e.g., season 1: 1st April, 2014 – 31st October, 2014; and season 2: 1st April, 2015 – 31st October 2015). During a fire season, natural forest fires can reset the 'time since last fire' of a pixel of habitat to zero; alternatively, the age (in years) of a pixel can increase during a fire season. For example, if a fire last burned through a pixel of conifer forest on 1st May, 1975, then during the 2016 fire season, that pixel would turn 41 years old on 1st May, 2016. In other words, for the first two months of the 2016 fires season, that pixel would be 40 years old (or classified as young to mid-successional forest) and for the last five months of the fire season, it would be 41 years old (or classified as mature forest). For most forest fires in the fire data base – which was provided to the project by Gigi Pitoello (Saskatchewan Ministry of Environment) and which contained data for fires spanning 1945 to 2015 – only the year of each fire polygon was provided. This meant that I could not accurately estimate the day during a fire season when the ‘time since last fire’ was either reset or increased for each pixel of conifer forest that occurred within a historical fire polygon (i.e., a burned area mapped from 1945 – 2015). Accordingly, I set 1st July as the date on which the age of habitat pixels could either reset or increase. I chose this date because it occurs near the mid-point of the official fire season and, hence, approximates the mean date of a fire event. It also aligns nicely with the end of the post-calving/calving period.

By setting 1st July as the date when the age of a habitat pixel could change, I effectively partitioned the year into two halves: during the first half (1st January – 30th June), a pixel of conifer forest was assigned an age value from the previous year’s fire season (i.e., the age it turned on 1st July from the previous year); during the second half of the year (1st July – 31st December), a pixel of conifer forest was assigned an age value from the current year’s fire season (i.e., the age it turned on 1st July of the current year). This meant that all caribou relocations recorded between 23rd March, 2014 and 30th June, 2014 occurred in habitat pixels with age values assigned from the 2013 fire season. Similarly, all caribou relocations recorded between 1st July, 2014 and 30th June, 2015 occurred in habitat pixels with age values assigned from the 2014 fire season, while all caribou relocations recorded between 1st July, 2015 and 22nd March, 2016 occurred in habitat pixels with age values assigned from the 2015 fire season. Where points occurred in conifer forests, I used the associated age value to classify the forest as either mature (>40 years post-fire) or young to mid-successional (≤40 years post-fire). Where points occurred in another habitat class (e.g., black spruce bogs or deciduous-dominated forests), I ignored the age value. An in-depth description of the data and the methods used to assign age values to individual pixels of conifer forest is provided in Appendix 2.

For modelling purposes, individual habitat classes were coded as columns of 0s and 1s with a '1' indicating the point was located in that habitat class and a '0' indicating the point was not. This allowed me to remove insignificant habitat classes from the model. I used selection ratios

(Manly et al. 2002) to assign a reference habitat class to each scale and season of selection: the habitat class with the selection ratio closest to one was designated as the reference category because a value of one indicates that a class is neither selected for nor avoided (Manly et al. 2002). A summary of the reference habitat classes for each scale and season is provided in Table A1.3 (pp.148).

4.3.4.4 Proximity to Linear Features

The proximity to linear features was measured as the Euclidean distance (in meters) between a point location and the edge of the nearest linear feature. Linear features included major roads (e.g., all-season highways), minor roads (e.g., all-season roads providing access to mine sites and communities), municipal roads (e.g., roads within and around residential areas), winter roads, fire breaks, electrical utility corridors, trails, and geophysical survey lines. An updated layer of these features was provided by Shawn Francis from S. Francis Consulting Inc. (Drumheller, Alberta, Canada) and Brent Bitter, Jackie O'Neil and Andrea Penner from the Saskatchewan Ministry of Environment. Within this layer, linear features were buffered according to their average width. For example, the Department of Transportation estimates the average width of a road to be 60m (30m buffer on either side of the road's center line representing the maximum road allowance, including ditches). This buffer does not include the somewhat arbitrary human zone of influence (a 500 meter buffer) defined in the federal recovery strategy (Environment Canada 2012). I decided not to add this 500 meter buffer to linear features because, given that it is somewhat arbitrary, it may overestimate the amount of functional habitat lost due to caribou avoidance of human disturbance. Thus, the proximity to linear features variable in my models describes the Euclidean distance between a point location and the unbuffered edge (based on average width) of the linear feature. A summary of the types of linear features and the methods used to derive them is provided in Appendix 3 (pp. 153).

4.3.4.5 Reproductive Status

I assigned a reproductive status ('calf-yes' or 'calf-no') to each caribou based on a combination of Residence Time analyses (Barraquand and Benhamou 2008; see Chapter 3, pp.36-38 regarding the methodology) and cow/calf surveys conducted in March 2015 and March

2016. Results from the Residence Time analyses were used to assign reproductive status during the calving/post-calving period while results from the March surveys were used to assign reproductive status in other seasons (i.e., if a cow was recorded with a calf during the March 2015, it was designated as having a calf in the previous summer, autumn/rut, early winter and mid-winter; if it was not, then it was designated as not having a calf for these four seasons). Our cow: calf surveys over two years revealed that female caribou generally occur in small, mixed-sex groups during March (*min*. = 1 caribou, *max*. = 12 caribou, $\bar{x}$ = 5 caribou; *n* = 133 groups over two years). Due to the small number of individuals in a group, it was usually fairly easy to identify males, females and calves and then assign individual calves to cows (as calves are generally thought to follow their mothers during chase events [H. Skatter, Omnia Ecological Services (Calgary, Alberta)], *pers. comm.*). That said, there was still potential for error for misreporting the reproductive status of a collared cow where the cow: calf ratio in a group was greater than one because a calf may have been observed following an individual other than its mother. As this error was difficult to quantify, I did not explicitly account for it when modelling resource selection. Calf mortality is generally high during the first six weeks post-partum (Gustine et al. 2006b, Pinard et al. 2012) so I assumed that all caribou observed without a calf during the March surveys lost it by the end of the calving/post-calving season (i.e., by 30th June). Available points took on the reproductive status of their corresponding used points. Note that I did not include reproductive status as a covariate in the models for the late winter/spring season because surviving calves are approximately 10 months old by this season and likely both physically and mentally weaned from their mothers (Lavigueur and Barrette 1992). Thus, their influence on their mothers' behaviour is likely to be minimal.

All model covariates were screened for multicollinearity using methods outlined in Zurr (2010). As recommended by Gelman (2008), all continuous variables were scaled by centering them to 0 and then dividing through by 2 standard deviations using the `rescale` function from the *R* package `arm` (v.1.8-6, Gelman and Su 2015). Dividing through by two standard deviations as opposed to one makes the scaled continuous predictors directly comparable to unscaled binary predictors in the model (e.g., habitat classes and reproductive status).

4.3.5 Statistical Analyses

Generalized Linear Mixed Models (GLMMs) offer a powerful statistical framework within which to model complex ecological relationships because they allow the inclusion of random intercept and slope terms (see Gillies et al. 2006). I employed GLMMs to model resource selection by female woodland caribou in Saskatchewan's Boreal Shield and included individual animal id (AID) as a random intercept in order to account for the hierarchical, unbalanced sampling of GPS point locations from the collared population of boreal caribou (*n* = 92 caribou). Given the heterogeneity in both the availability of different habitat classes and the levels of natural and anthropogenic disturbance throughout the study area, it would have been sensible to include one or more random slopes as well. Specifically, I would have liked to include a random slope for the model covariate 'proximity to linear feature' in order to account for the differential exposure of caribou to linear disturbances in Saskatchewan's Boreal Shield. However, the processing power required to get my random slope models to converge in the time frame allotted for this thesis was beyond the capability of both my lab computer and the research computer available to me through the University of Saskatchewan's High Performance Computing Center (HPCC).

There are numerous packages available in the *R* statistical program (R Core Team 2016) that can be used to fit a GLMM (e.g., `nlme`, `lme4`, `glmmADMB`, `glmm`, `MASS`, `MCMCglmm` etc.). Though technically challenging and computationally expensive, the package `MCMCglmm` (Hadfield 2010) is becoming popular among ecologists because its Bayesian framework allows for a more accurate estimation of model parameters (Hadfield 2015, but see Li et al. 2011 regarding large binomial and ordinal data sets), and it can better handle the inclusion of random effects (Hadfield 2015). Because I was experiencing convergence issues running mixed-effects models in other packages, I adopted the `MCMCglmm` approach.

Before running a model in `MCMCglmm`, one must specify an appropriate prior distribution for the model. The prior distribution expresses current beliefs about what values are most likely for an uncertain parameter, θ (e.g., a model coefficient in an RSF). It is combined with the probability distribution of new data (e.g., the set of used and available points) to produce a posterior distribution representing the updated beliefs about what values are most likely for θ (Gelman 2002). In `MCMCglmm`, a prior can include 3 elements: the R structure (for residual variance), the G structure (for random effects) and the B structure (for fixed effects). For binomial data with single observations per trial (as is the case with my data), the R structure is not identifiable and is therefore fixed to 1 (Hadfield 2015). The G structure is a list containing values for the expected (co)variances (`V`) and degree of belief parameter (`nu`) for the inverse-Wishart prior (the default prior distribution for variance-covariance matrices in `MCMCglmm`), as well as values for the mean vector (`alpha.mu`) and covariance matrix (`alpha.V`) of the redundant working parameters (Hadfield 2015). The B structure is a list containing the expected value (`mu`) for the mean of a parameter and a (co)variance matrix (`V`) representing the strength of belief in the prior for the fixed effects (which is specified as a normal prior by default in `MCMCglmm`). The default values of `mu` and `V` for the B structure are 0 and $I*1\mathrm{e}^{10}$ (where I is an identity matrix of the appropriate dimensions) respectively. These values specify a prior with zero mean and high variance, which is generally considered reasonable for a fixed effects prior (Hadfield 2015) and so most people (including myself) retain the default B structure when constructing priors in `MCMCglmm`. Hadfield (2015) recommends using weakly informative, parameter expanded priors when modelling a binomial response in order to prevent the Monte Carlo Markov Chain from getting stuck at values close to zero. For these models, the alpha.V component of the G structure becomes non-zero, which allows for prior specifications from a non-central, scaled F-distribution (Gelman 2006). For my models, I initially used an uninformative, parameter-expanded prior of the form:

```
prior = list (R=list(V=1,fix=1),B=list(mu=0,V=1e+10)              [4.3]
              G=list(G1=list(V=1,nu=0.002,alpha.mu=0,alpha.V=1000)))
```

I then modified it to test for model sensitivity to prior specification. Specifically, I changed the value of `nu`, which is the degree of belief in the inverse-Wishart for the model variance (Hadfield 2015), from 0.002 to 0.2.

For each season, I split the data into a training set and a validation set. The training set consisted of all caribou fit with the Telonics (Telonics Inc., Mesa, Arizona, USA) radio-collars (up to n = 68 caribou); it was used to train the models for each season and scale. The validation set consisted of all caribou fit with the Lotek (Lotek Wireless Inc., Newmarket, Ontario, Canada) radio-collars (up to n = 24 caribou); it was used to validate the model. If the coefficients from the validation model fell within the 95% credible intervals of the corresponding coefficients from the training model, this implied that the posterior means estimated for the training model were well representative of both the direction and magnitude of the response of female caribou to that covariate (see section *4.4.3*, pp. 91, for an in-depth description of how model and individual covariate comparisons were scored).

For each season and scale, I employed step-wise, backwards model selection on a global model containing all relevant model covariates (up to 15 depending on the season) in order to arrive at a final top model. At each step of the selection process, model fit was evaluated using the following diagnostic tools: (a) trace plots, which show coefficient estimates after each iteration (should resemble white noise with few major spikes); (b) density plots, which show the posterior distribution of each model parameter (should resemble a normal distribution); (c) autocorrelation between iterations (<0.05 is considered good, Hadfield 2015); and (d) the Highest Probability Density (HPD) intervals for each coefficient. Coefficients with HPD intervals (also referred to as '95% credible intervals') overlapping zero were deemed uninformative and removed from the model. Model convergence was primarily assessed using the Heidelberger-Welch test for convergence (Heidelberger and Welch 1983); however, because Heidelberger and Welch (1981) caution against using this method too frequently due to problems that arise with sequential testing, I used Geweke's convergence diagnostic (Geweke 1992) as a secondary check for convergence and also employed Gelman and Rubin's convergence diagnostic (Gelman and Rubin 1992) to check the mixing of chains between different runs of the same model. All diagnostics were run using functions available in the *R* package `coda` (v.0.18-1, Plummer et al. 2006). I accepted a model as the 'top' model when all of the diagnostics were acceptable and none of the HPD intervals overlapped zero.

All models were run with a minimum effective sample size of 1000 and a *burnin* value at least equal to 10% of the total number of model iterations. For example, if I ran a model for 1,100,000 iterations, I would sample (at most) every 1000 iterations and discard the initial 100,000 iterations as the burnin period. The burnin period represents the number of iterations that need to pass before one can be sure that the coefficient estimates are independent of the initial parametrization (see Hadfield 2015:22 for further details). One can use the function `raferty.diag` from the *R* package `coda` (Plummer et al. 2006) to calculate the appropriate burnin value, although 10% is usually considered sufficient (Dr. J. Lane, Department of Biology, University of Saskatchewan, *pers. comm.*).

4.4 Results

4.4.1 Range Analyses

4.4.1.1 Population Range

The range of my collared caribou was defined using a 100% Minimum Convex Polygon (MCP) buffered by a mean daily step length of one kilometer. The full range (black dashed line, Fig. 4.1) had a total area of 95,632 km^2 while the truncated range (i.e., truncated at the Saskatchewan – Manitoba border, green polygon, Fig. 4.1) had a total area of 91,238 km^2. Available points for the coarse-scale analyses were sampled from within the truncated range because the spatial layers used to derive values for elevation, slope, heat load index and habitat class didn't extend past Saskatchewan's eastern border.

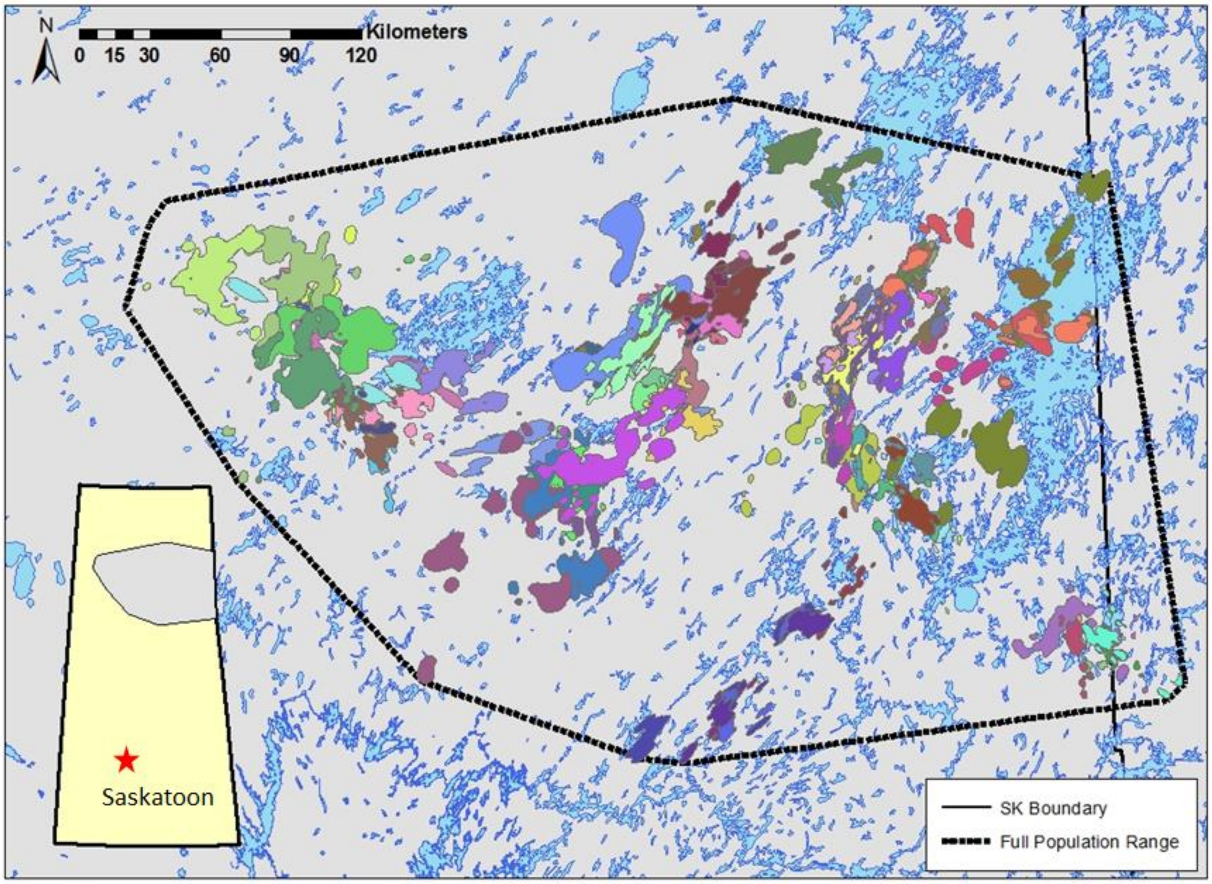


Fig. 4.2: Home ranges for 92 female woodland caribou in Saskatchewan's Boreal Shield. Ranges were delineated as 95% utilization distributions (UDs, van Winkle 1975) using up to two years of GPS point locations recorded from individual caribou. Excluding ranges belonging to caribou that did not survive for the full two years ($n = 24$), mean range size was 435.2 +/- 34.3 km^2.

4.4.1.2 Home Ranges

Individual home ranges (Fig. 4.2), which were defined as 95% utilization distributions (UDs, van Winkle 1975) based on up to two years of GPS locations, varied in size from 16.2 km^2 to 1363.9 km^2, with a mean size (± standard error) of 406.7 ± 30.6 km^2. This value is based on the home ranges of all 92 radio-collared caribou used to generate my models; however, 24 of these individuals died before the end of the second study year so their ranges were smaller (e.g., caribou 140146 only survived until 28th May, 2014 so her range was only 16.2 km^2). Excluding these caribou, the mean home range size for females that survived a full two years was 435.2 ± 34.3 km^2. Core ranges (defined as 50% UDs) were considerably smaller. For the entire collared population (n = 92 animals), the mean core size was 53.2 +/- 4.2 km2; for the subset that survived the full two years (n = 68 animals), the mean core size was 57.7 +/- 4.5 km2. A summary of individual home and core range sizes is presented in Table A1.4 (pp.149).

Variation in home range sizes may be indicative of differences in local migratory behaviour. I explored whether linear features influenced the distribution of individual caribou by regressing home range size against the density of linear features (km/km^2) in an area and found no significant correlation between the two ($R^2 = 0.02$, F(1, 90) = 1.71, p = 0.19). This was not surprising given that: (a) the overall density of linear features in Saskatchewan’s Boreal Shield is very low (0.1 km/km^2), and (b) the majority of linear features (~88.8%) that have been mapped in the region are geophysical survey lines and trails, both of which may be permeable to boreal caribou due to their minimal vehicle traffic and low impact on the landscape (e.g., Curatolo and Murphy 2002, Dyer et al. 2002). Home range sizes appear to be slightly smaller in the eastern half of the province (see Fig. 4.2, pp.65) so I regressed home range size against each animal’s median location (calculated for the period they were tracked) to investigate whether home range size followed a latitudinal or longitudinal gradient. Though there was no statistically significant correlation between home range size and latitude ($R^2 = 0.04$, F(1, 90) = 3.67, p = 0.06); there was a statistically significant correlation between home range size and longitude ($R^2 = 0.11$, F(1, 90) = 11.26, p = 0.001). Specifically, home range sizes were significantly smaller in the eastern half of the study area.

4.4.1.3 Seasonal Ranges

For each collared caribou, seasonal ranges were defined on an annual basis using 95% UDs. A total of 959 individual seasonal ranges were defined over the two year study period (23rd March, 2014 – 22nd March 2016). Excluding ranges belonging to caribou who died, dropped their collars or went offline prior to the end of a season (*n* = 13), mean range sizes pooled over the two years were as follows (mean ± standard error, *n* = sample size): **early winter** (267.9 ± 16.3 km^2, *n* = 149*)*; **mid-winter** (106.5 ± 7.0 km^2, *n* = 147 ranges); l**ate winter/spring** (101.4 ± 11.4 km^2, *n* = 170 ranges); **calving/post-calving** (80.9 ± 7.8 km^2, *n* = 167 ranges); **summer** (80.3 ± 5.6 km^2, *n* = 158 ranges); and **autumn/rut** (67.0 ± 5.2 km^2, *n* = 155 ranges).

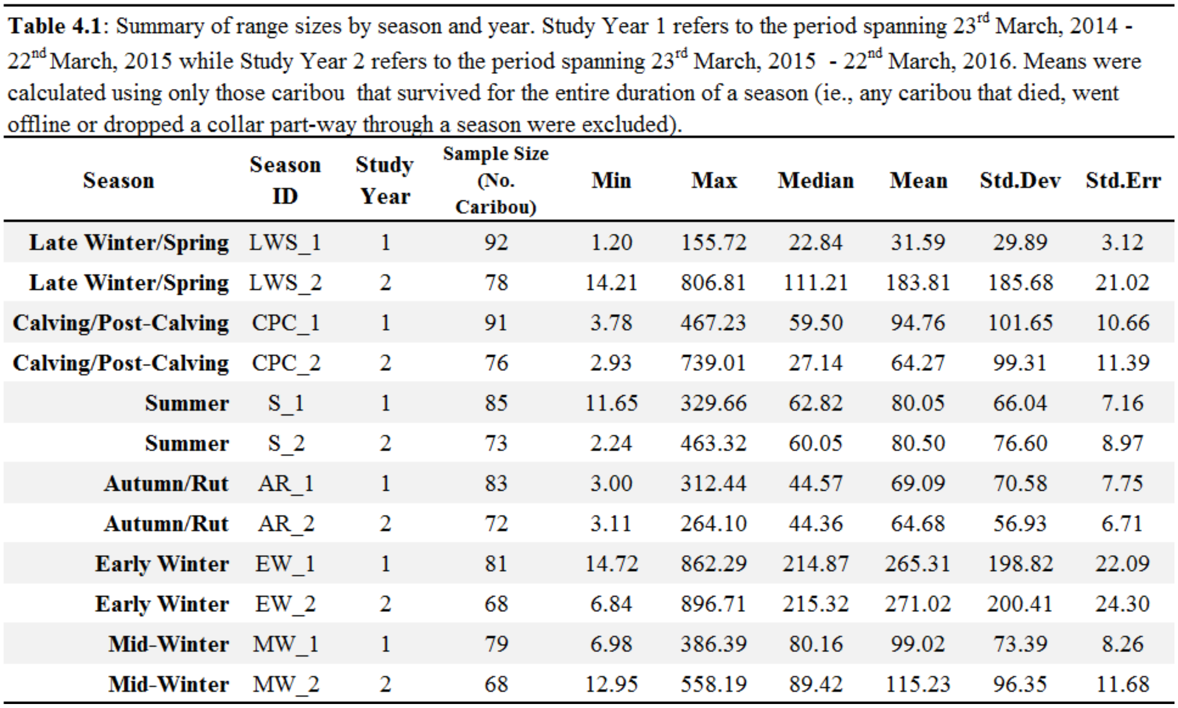


Table 4.1: Summary of range sizes by season and year. Study Year 1 refers to the period spanning 23rd March, 2014 - 22nd March, 2015 while Study Year 2 refers to the period spanning 23rd March, 2015 - 22nd March, 2016. Means were calculated using only those caribou that survived for the entire duration of a season (ie., any caribou that died, went offline or dropped a collar part-way through a season were excluded).

Season	Season ID	Study Year	Sample Size (No. Caribou)	Min	Max	Median	Mean	Std.Dev	Std.Err
Late Winter/Spring	LWS_1	1	92	1.20	155.72	22.84	31.59	29.89	3.12
Late Winter/Spring	LWS_2	2	78	14.21	806.81	111.21	183.81	185.68	21.02
Calving/Post-Calving	CPC_1	1	91	3.78	467.23	59.50	94.76	101.65	10.66
Calving/Post-Calving	CPC_2	2	76	2.93	739.01	27.14	64.27	99.31	11.39
Summer	S_1	1	85	11.65	329.66	62.82	80.05	66.04	7.16
Summer	S_2	2	73	2.24	463.32	60.05	80.50	76.60	8.97
Autumn/Rut	AR_1	1	83	3.00	312.44	44.57	69.09	70.58	7.75
Autumn/Rut	AR_2	2	72	3.11	264.10	44.36	64.68	56.93	6.71
Early Winter	EW_1	1	81	14.72	862.29	214.87	265.31	198.82	22.09
Early Winter	EW_2	2	68	6.84	896.71	215.32	271.02	200.41	24.30
Mid-Winter	MW_1	1	79	6.98	386.39	80.16	99.02	73.39	8.26
Mid-Winter	MW_2	2	68	12.95	558.19	89.42	115.23	96.35	11.68

Partitioning the seasonal ranges by year (e.g., Summer_Range_Year1, Summer_Range_Year2 etc.), there were noticeable differences in mean range sizes both within and among seasons over the two year study period (see summary of range sizes in Table 4.1). A Kruskal-Wallis Test (Kruskal and Wallis 1952) indicated that at α = 0.95, there was a significant difference between the mean range size of at least one of the twelve partitioned seasons (*Kruskal-Wallis* $\chi^2 = 287.3, p<0.001$). According to Dunn's Multiple Comparison Test (see summary of Dunn's z-test statistics, Table 4.2), the mean range size for the first late winter/spring season was significantly smaller than all other seasons, except for the second calving/post-calving season (see Fig. 4.3). There were also significant differences between (a) the mean range sizes of the two early winter seasons and all other seasons, except for the second late winter/spring season; (b) the mean range size for the second late winter/spring season and all other seasons except for the two mid-winter seasons; and (c) the mean range size for the second mid-winter season and both autumn/rut seasons, the second calving/post-calving season and the first late winter/spring season. Mean ranges sizes calculated for the first mid-winter season and all autumn/rut, summer and calving/post-calving seasons were not significantly different.

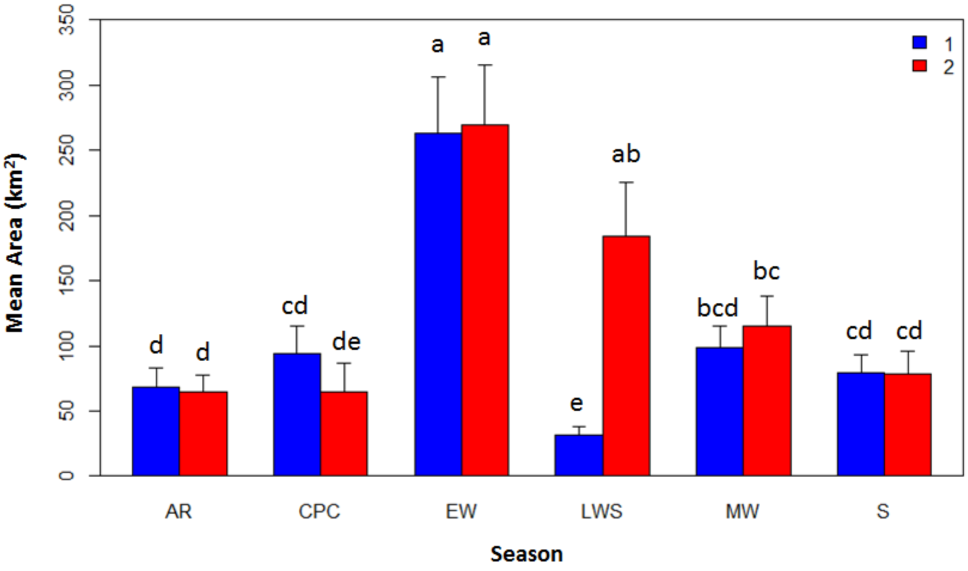
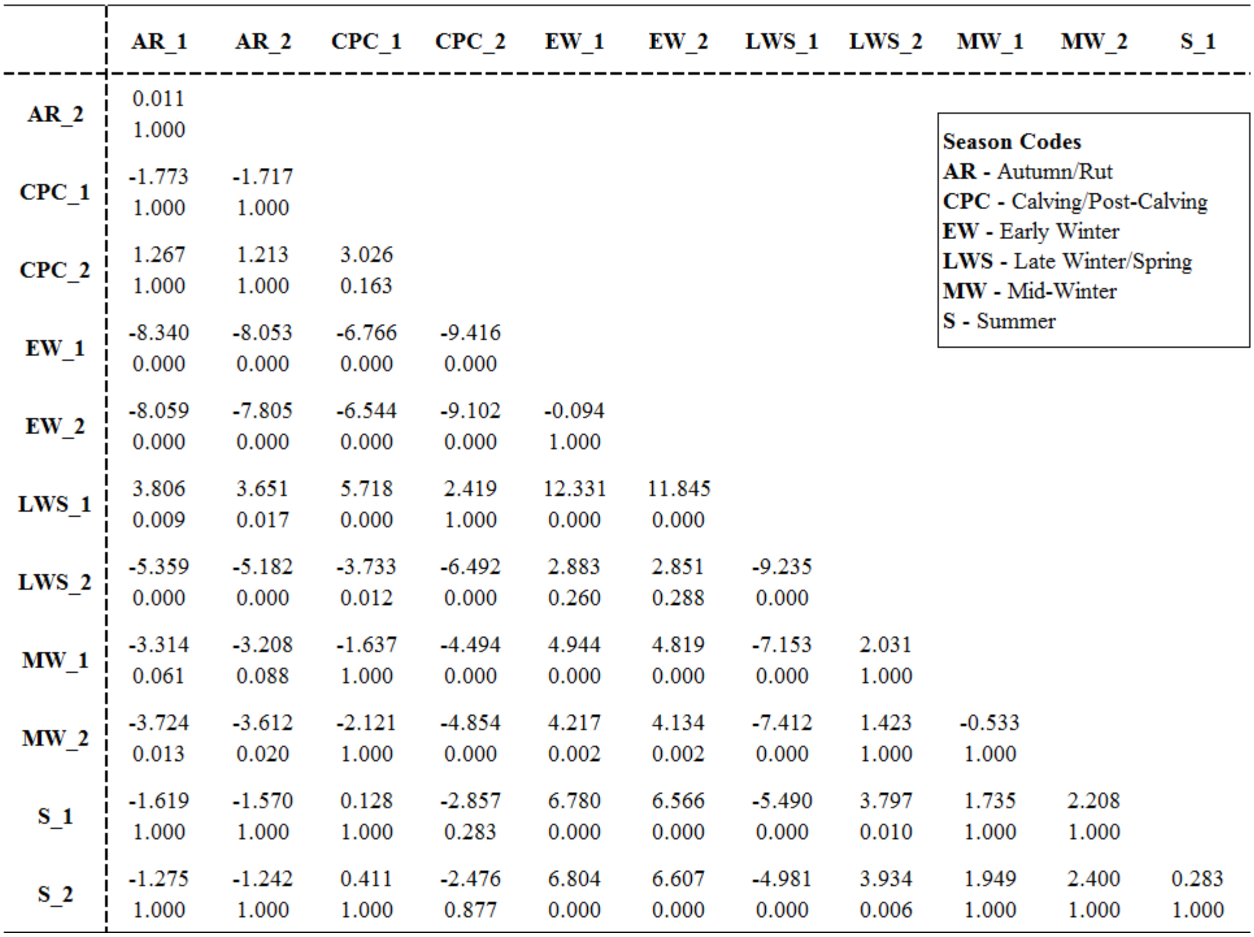


Fig. 4.3: Mean annual range sizes (with standard error bars) for each of six seasons by study year (Year 1 [blue] or Year 2 [red]). A Kruskal-Wallis Test (i.e., a non-parametric one-way ANOVA; Kruskal and Wallis 1952) was used to compare mean range sizes between seasons and years (*Kruskal-Wallis* χ^2 *= 287.3, df = 11, p<0.001*). Pairwise comparisons were made using Dunn's Multiple Comparison Test (Dunn 1964) with Bonferroni adjusted p-values. Bars with the same lower case letters above them are not significantly different from one another.

Within seasons, the only significant difference in mean range size between Year 1 (23rd March, 2014 – 22nd March, 2015) and Year 2 (23rd March, 2015 – 22nd March, 2016) occurred between the annual late winter/spring (LWS) seasons (Dunn's pairwise z-statistic = -9.235, $p < 0.001$). The mean range size for the second year (183.8 ± 21.0 km^2, $n = 92$) was almost six times larger than for the first year (31.5 ± 3.1 km^2, $n = 78$); similarly, the median for the second year (111.2 km^2) was almost five times larger than for the first year (22.8 km^2). These differences suggest that caribou were migrating over larger distances in the second year. In fact, only seven of the seventy-eight caribou who survived for two full LWS seasons recorded a decrease in range size from year one to year two. The remaining 71 caribou recorded a mean increase in LWS range size of 168.0 ± 20.3 km^2; the median increase in LWS range size was 95.1 km^2.

Table 4.2: Summary of Dunn's (1964) z-statistics for pairwise comparisons between mean seasonal range sizes split by season (n = 6) and year (n = 2). Columns and rows are labelled using range ids corresponding to each season and year. The letters represent season codes (see legend) while the numbers indicate the year (either 1 or 2). The upper number for each pairwise comparison is Dunn's z-statistic. The lower numbers are the p-values adjusted using Bonferroni's correction. Mean range sizes were considered to be significantly different if $p < 0.05$.



	AR_1	**AR_2**	**CPC_1**	**CPC_2**	**EW_1**	**EW_2**	**LWS_1**	**LWS_2**	**MW_1**	**MW_2**	**S_1**
AR_2	0.011 1.000										
CPC_1	-1.773 1.000	-1.717 1.000									
CPC_2	1.267 1.000	1.213 1.000	3.026 0.163								
EW_1	-8.340 0.000	-8.053 0.000	-6.766 0.000	-9.416 0.000							
EW_2	-8.059 0.000	-7.805 0.000	-6.544 0.000	-9.102 0.000	-0.094 1.000						
LWS_1	3.806 0.009	3.651 0.017	5.718 0.000	2.419 1.000	12.331 0.000	11.845 0.000					
LWS_2	-5.359 0.000	-5.182 0.000	-3.733 0.012	-6.492 0.000	2.883 0.260	2.851 0.288	-9.235 0.000				
MW_1	-3.314 0.061	-3.208 0.088	-1.637 1.000	-4.494 0.000	4.944 0.000	4.819 0.000	-7.153 0.000	2.031 1.000			
MW_2	-3.724 0.013	-3.612 0.020	-2.121 1.000	-4.854 0.000	4.217 0.002	4.134 0.002	-7.412 0.000	1.423 1.000	-0.533 1.000		
S_1	-1.619 1.000	-1.570 1.000	0.128 1.000	-2.857 0.283	6.780 0.000	6.566 0.000	-5.490 0.000	3.797 0.010	1.735 1.000	2.208 1.000	
S_2	-1.275 1.000	-1.242 1.000	0.411 1.000	-2.476 0.877	6.804 0.000	6.607 0.000	-4.981 0.000	3.934 0.006	1.949 1.000	2.400 1.000	0.283 1.000

Season Codes
AR - Autumn/Rut
CPC - Calving/Post-Calving
EW - Early Winter
LWS - Late Winter/Spring
MW - Mid-Winter
S - Summer

4.4.2 Resource Selection Analyses

Top models for each season and scale are presented in Table 4.3. Model coefficients for these models were generated using logistic regression, which means that the linearized relationship between the response (i.e. used vs. available) and the model covariates was fit in a non-linear fashion (Zurr et al. 2007). This affects how model coefficients are interpreted. With respect to continuous covariates (e.g., elevation, temperature, slope etc.), model coefficients are estimates of how the log (base e) of the odds ratio changes with a one unit increase in these variables. For example, if the coefficient for the variable “elevation” was –1.3, this indicates that for every 1 unit increase in elevation, the log of the odds ratio changes by -1.3. To convert this into a more intuitive odds ratio (i.e., p/1-p where p is the probability of success (which for this study is the probability of a point being used)), one must raise e to the power of the *absolute value* of the logistic coefficient (Zuur et al. 2007). For the elevation coefficient in this example, the odds ratio would be $e^{1.3}$ or 0.27. In other words, for every one unit increase in elevation, a caribou is 3.7 times less likely to occur in a resource unit. In general, where a coefficient for a continuous variable is negative, this indicates a caribou will be less likely to occur in a resource unit. Where a coefficient is positive, this indicates that a caribou will be more likely to occur in a resource unit.

In contrast, categorical variables (e.g., habitat classes and reproductive status) are interpreted relative to a reference category. If all habitat classes were included in the top model, then the model coefficients for each habitat class were interpreted relative to a reference habitat class (which was set as the class with a selection ratio (Manly et al. 2002) closest to one). As an example, all eight habitat classes were included in the top model for coarse scale resource selection during the calving/post-calving season (see Table 4.3). The estimate of the posterior mean (i.e. coefficient) for black spruce bogs was 0.55, which means that if we sampled a random point within the study area, the log of the odds of it being a used point would increase by 0.55 if it was sampled from within a black spruce bog compared to if it was sampled within the reference habitat class (which was mature jack pine-dominated forest). If, however, some of the habitat classes were excluded from the top model, then the model coefficients for the remaining classes would be interpreted as the log-odds of a point being a used point relative to an available point in the same habitat class. For example, only five of the eight habitat classes were retained in the top, coarse-scale model for the autumn/rut season (see Table 4.3). The model coefficient for the variable “black spruce bog” was 0.19, which means that if we randomly sampled a point in a black spruce bog, the log odds of that point being a used point would be 0.19 times higher than if it were an available point. With respect to the model covariate ‘reproductive status’, the

Table 4.3: Summary of the top models describing female woodland caribou resource selection in Saskatchewan's Boreal Shield for six seasons at two spatial scales: a coarse scale defined as the sample population's range and a fine scale defined as one kilometer buffers around individual GPS locations. Models were fit using the R© package MCMCglmm (Hadfield 2015). Within this framework, resource selection was modelled using generalized linear mixed models (GLMMs), with individual animal IDs (AID) set as the random intercept. Top models were derived by employing step-wise, backwards selection on a global model containing 14 or 15 fixed covariates depending on the season. The number of caribou represent the sub-sample of adult, female caribou wearing *Telonics* © radio collars that were used to train the model. The number of individual ranges represent the number of home ranges (delineated using two years of data) or annual seasonal ranges from which used points were sampled. Home ranges were used for the coarse scale models while annual seasonal ranges were used for the fine scale models. The effective sample size is the number of iterations out of the total no. of iterations (*nitt*) used to estimate model coefficients. A red asterisk (*) denotes a reference habitat class. These classes are only relevant to models for which all eight habitat classes were retained in the top model. The legend to the right of this table can be used to decipher the abbreviations for each habitat class, as well as the other model variables.

Season	Scale	No. GPS Locations (Used + Available Points)	Sample Size (No. Caribou)	No. Individual Ranges (Home or Seasonal)	No. Model Iterations (*nitt*)	Effective Sample Size	No. Fixed Co-variates	Top Model
Late Winter/Spring	Coarse	34,878	68	68	2,200,000	4,000	10	UseAv~Elevation+Slope+LinDist+SnowDepth+JPMat+JPYM+ BSMat+ BSYM+MixCD+Mswamp, random = AID
Late Winter/Spring	Fine	34,980	68	120	4,400,000	8,000	8	UseAv~Elevation+LinDist+SnowDepth+JPMat+JPYM+BSMat+ BSBog+ Muskeg, random = AID
Calving/Post-Calving	Coarse	51,494	67	67	1,500,000	3,000	12	UseAv~Elevation+Slope+LinDist+Calf+JPYM+BSMat+BSYM+ MixCD+ BSBog+Mswamp+Muskeg+JPMat*, random = AID
Calving/Post-Calving	Fine	50,534	67	121	4,400,000	8,000	11	UseAv~Elevation+Slope+HeatLoad+LinDist+Calf+JPMat+JPYM+ BSMat+ MixCD+BSBog+Muskeg, random = AID
Summer	Coarse	61,232	64	64	3,300,000	6,000	9	UseAv~Elevation+Slope+LinDist+JPYM+BSMat+BSYM+MixCD + BSBog+Mswamp, random = AID
Summer	Fine	59,482	64	117	5,500,000	10,000	8	UseAv~Slope+HeatLoad+LinDist+BSMat+JPYM+BSYM+ MixCD+ Mswamp, random = AID
Autumn/Rut	Coarse	24,966	60	60	2,750,000	5,000	9	UseAv~Elevation+Slope+LinDist+Temp+JPYM+BSYM+MixCD+ BSBog+Mswamp, random = AID
Autumn/Rut	Fine	24,406	60	110	8,800,000	16,000	8	UseAv~Elevation+Slope+JPMat+JPYM+BSMat+BSYM+BSBog+ Muskeg, random = AID
Early Winter	Coarse	54,914	58	58	2,200,000	4,000	12	UseAv~Elevation+Slope+HeatLoad+LinDist+JPYM+BSYM+ MixCD+ BSBog+Mswamp+Muskeg+JPMat+BSMat*, random = AID
Early Winter	Fine	57,350	58	108	5,000,000	10,000	11	UseAv~Slope+HeatLoad+LinDist+temp+snow+JPMat+JPYM+ BSYM+ MixCD+BSBog+Mswamp, random =AID
Mid-Winter	Coarse	48,558	57	57	2,200,000	4,000	12	UseAv~Elevation+Slope+HeatLoad+LinDist+temp+Calf+JPMat+ JPYM+ BSYM+MixCD+BSBog+Mswamp, random = AID
Mid-Winter	Fine	48,686	57	107	4,400,000	8,000	8	UseAv~Elevation+Slope+LinDist+JPMat+JPYM+BSMat+BSBog+ Muskeg, random = AID

Model Abbreviations

UseAv = binomial response
LinDist = proximity to linear features (m)
Calf = reproductive status (yes = with calf; no = no calf)
JPMat = mature jack pine-dominated forests
JPYM = young to mid-successional jack pine-dominated forests
BSMat = mature black spruce-dominated forests
BSYM = young to mid-successional black spruce-dominated forests
MixCD = mixed coniferous-deciduous forests
BSBog = black spruce bogs
Mswamp = mixed canopy swamps
Muskeg = open muskegs

reference category was always ‘Calf-No’ (i.e., caribou without calves). Accordingly, the value of the coefficient for this variable represents the difference in the log-odds of a point being used vs. available for caribou with calves relative to caribou without calves. Essentially, when reproductive status is included in the model, I interpreted this to mean that having a calf caused a significance difference in how female woodland caribou selected resources in Saskatchewan’s Boreal Shield.

For reference, the terms “weak (avoidance or selection)” and “slightly (more or less) likely” refer to covariates with |posterior means| < 0.10 while the terms “strong (avoidance or selection)” and “much (more or less) likely” refer to covariates with |posterior means| > 1.50. These thresholds are somewhat arbitrary, but were chosen because they fit with the distribution of the absolute values for posterior means across the twelve top models. A summary of general trends of selection and avoidance are presented in Table 4.4.

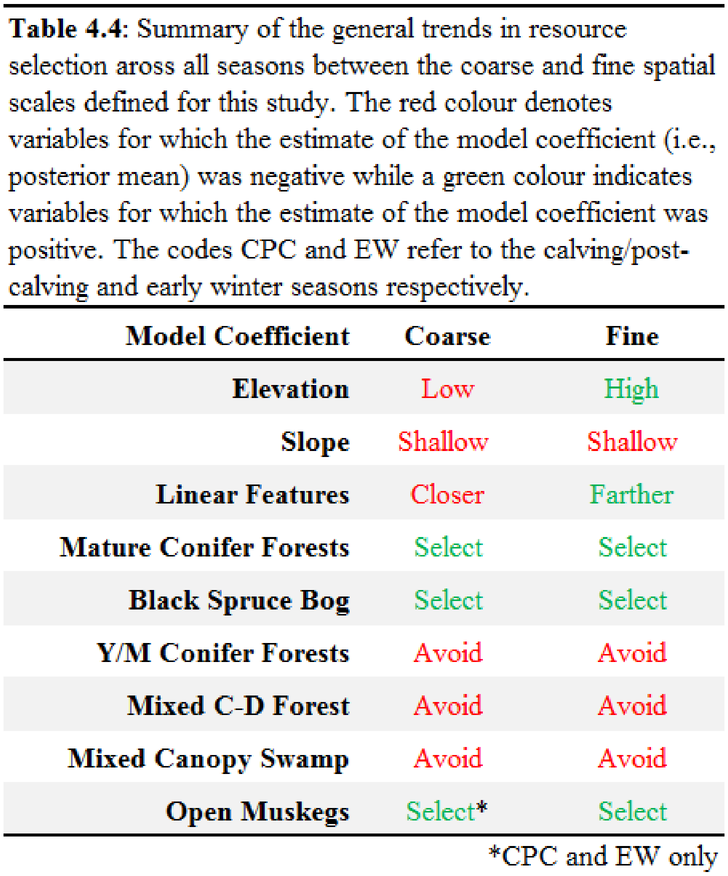


Table 4.4: Summary of the general trends in resource selection aross all seasons between the coarse and fine spatial scales defined for this study. The red colour denotes variables for which the estimate of the model coefficient (i.e., posterior mean) was negative while a green colour indicates variables for which the estimate of the model coefficient was positive. The codes CPC and EW refer to the calving/post-calving and early winter seasons respectively.

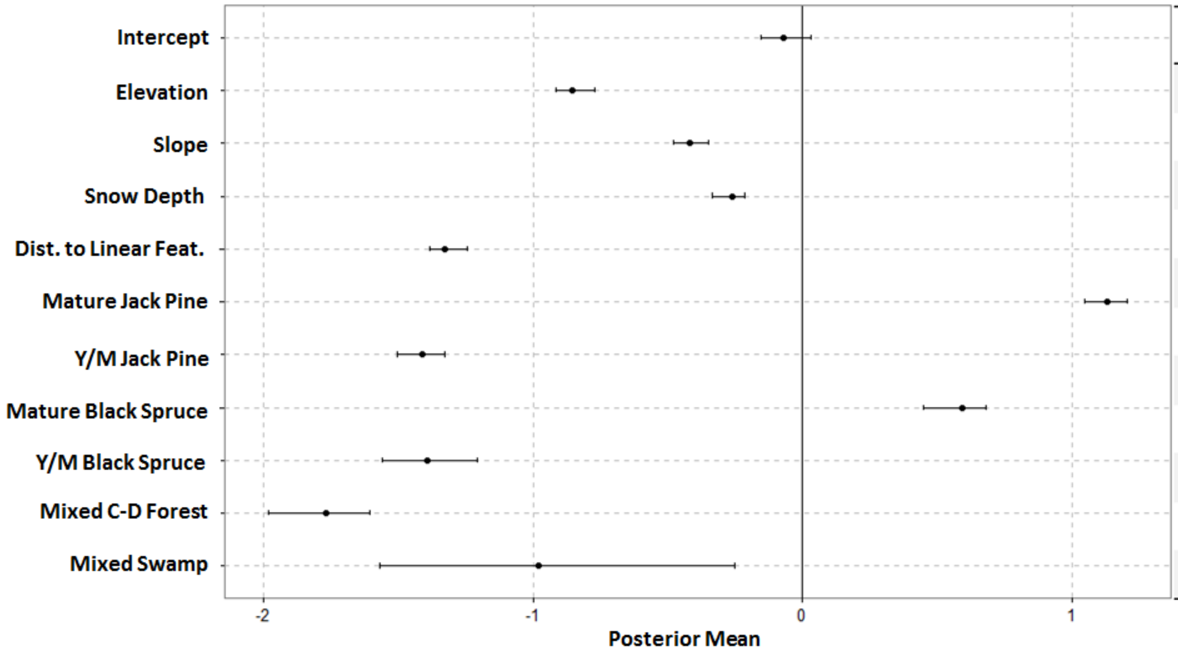
Model Coefficient	Coarse	Fine
Elevation	Low	High
Slope	Shallow	Shallow
Linear Features	Closer	Farther
Mature Conifer Forests	Select	Select
Black Spruce Bog	Select	Select
Y/M Conifer Forests	Avoid	Avoid
Mixed C-D Forest	Avoid	Avoid
Mixed Canopy Swamp	Avoid	Avoid
Open Muskegs	Select*	Select

*CPC and EW only

4.4.2.1 Late Winter/Spring Season

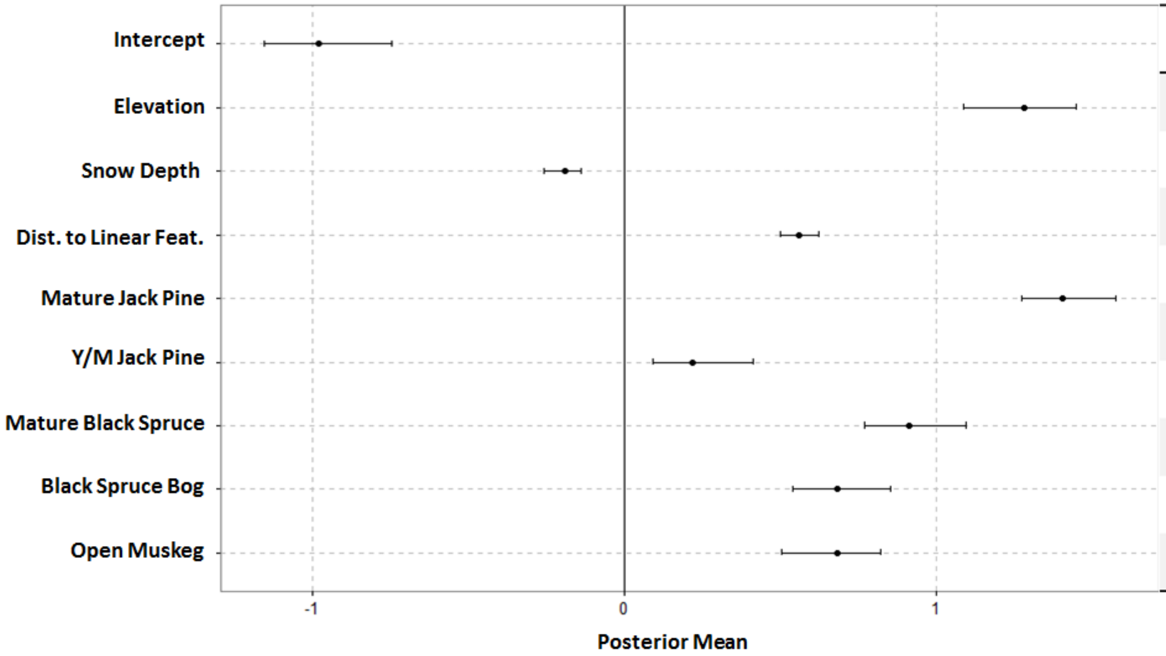
At the coarse scale level of selection (i.e., the population range), I used 17,439 GPS locations recorded from 68 adult female caribou over two late winter/spring seasons to generate my models. After backwards selection on a global model containing 14 fixed covariates, I arrived at a top model consisting of ten covariates (see Table 4.3). Coefficients from this model (Fig. 4.4) indicate that female caribou were more likely to occur at lower elevations on shallower slopes and in areas with shallower snow depths. They were also more likely to be found in resource units that were closer to linear features. With respect to habitat classes, female caribou avoided young to mid- successional jack pine-dominated forests (hereafter 'YM jack pine forests'), young to mid-successional black spruce-dominated forests (hereafter 'YM black spruce forests) and swamps with mixed canopies (although there was considerable variation in the response to this last habitat class) mixed deciduous-coniferous forests (i.e., |posterior mean| for this habitat class was >1.50). They selected for mature black spruce- dominated forests (hereafter 'mature black spruce forests') and mature jack pine-dominated forests (hereafter 'mature jack pine forests'). The global intercept for this model overlapped zero; however, I did not suppress it because in doing so I would have made the assumption that the response is zero if all of the predictors are zero, which is likely untrue for this system.

At the fine scale level of selection (i.e., one kilometer patches around used GPS locations), models were generated using 17,490 GPS locations (*n* = 68 caribou) spread across 166 individual caribou seasons. Model coefficients for the top model are presented in Fig. 4.5. Although caribou continued to select for resource units with shallower snow depths, they were more likely to be found at higher elevations and farther from linear features. They continued to select for mature conifer-dominated forests (i.e., jack pine and black spruce forests >40 years old), and additionally selected for black spruce bogs, open muskegs and YM jack pine forests.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.07	-0.16	0.03
Elevation (m)	-0.85	-0.91	-0.77
Slope (deg.)	-0.42	-0.48	-0.35
Snow Depth (cm)	-0.26	-0.34	-0.22
Dist. to Linear Feat. (m)	-1.33	-1.38	-1.25
Mature Jack Pine	1.13	1.04	1.20
Young-Mid Jack Pine	-1.41	-1.50	-1.33
Mature Black Spruce	0.59	0.45	0.68
Young-Mid Black Spruce	-1.39	-1.56	-1.21
Mixed Coniferous-Decid.	-1.77	-1.98	-1.61
Mixed Canopy Swamp	-0.98	-1.57	-0.25

Fig. 4.4: Plot of the posterior means and 95% credible intervals for the 10 fixed covariates retained in the top resource selection model for the late winter/spring season (23rd March – 30th April) at the coarse spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 68 adult female woodland caribou (n = 17,439 GPS locations). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 4,000 iterations (*total iterations* = 2,200,000; *sampling interval* = 500 iterations; *burnin* = 200,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table. Although the credible interval for the global intercept overlapped zero, I did not suppress it because this would mean making the likely false assumption that when all model predictors are zero, the response would also be zero.



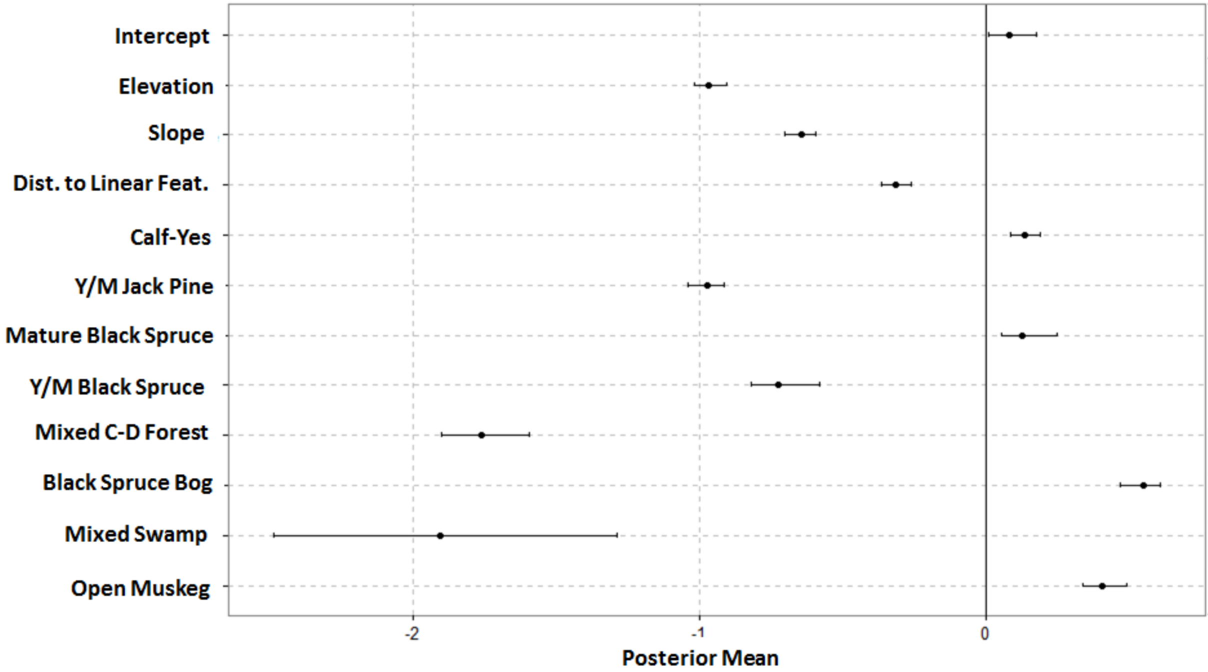
Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.98	-1.16	-0.75
Elevation (m)	1.28	1.09	1.45
Snow Depth (cm)	-0.19	-0.26	-0.14
Dist. to Linear Feat. (m)	0.56	0.50	0.62
Mature Jack Pine	1.41	1.28	1.58
Young-Mid Jack Pine	0.22	0.09	0.41
Mature Black Spruce	0.91	0.77	1.10
Black Spruce Bog	0.68	0.54	0.85
Open Muskeg	0.68	0.50	0.82

Fig. 4.5: Plot of the posterior means and 95% credible intervals for the 8 fixed covariates retained in the top resource selection model for the late winter/spring season (23rd March – 30th April) at the fine spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 68 adult female woodland caribou (*n* = 17,490 GPS locations distributed across 120 individual caribou seasons). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 8,000 iterations (*total iterations* = 4,400,000; *sampling interval* = 500 iterations; *burnin* = 400,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.

4.4.2.2 Calving/Post-Calving Season

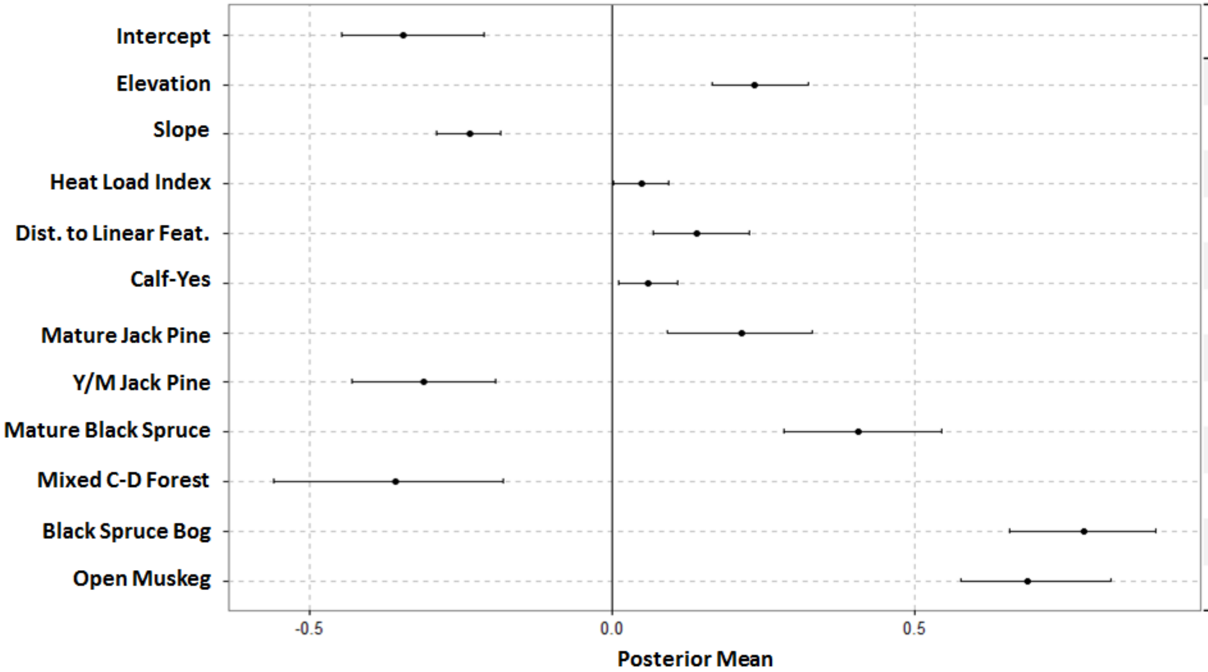
To model coarse scale resource selection during the Calving/Post-Calving (CPC) season, I used 25,747 GPS points recorded from 67 adult female caribou over two consecutive CPC seasons. Eleven of the 15 covariates originally included in the global model were retained in the top model for this season (see Table 4.3). Model coefficients (Fig. 4.6) indicate that female caribou were more likely to be found at lower elevations, on shallower slopes and closer to linear features at the coarse spatial scale. With respect to habitat classes, all eight were included in the top model, which means model coefficients for these variables must be interpreted relative to a reference habitat class. For the CPC season, this was mature jack pine forests. Relative to this class, caribou avoided young to mid-successional conifer – dominated forests (i.e., jack pine and black sprue forests ≤40 years old), and strongly avoided mixed coniferous-deciduous forests and mixed canopy swamps. As was observed during the late winter/spring season, there was considerable variation in the degree of avoidance of this latter habitat class. Female caribou selected for mature black spruce forests, black spruce bogs and open muskegs relative to mature jack pine forests. Finally, there was a small but significant difference in resource selection between females with calves and those without calves.

At the fine scale level of selection, models were generated using 25,267 GPS points distributed across 167 individual caribou seasons (*n* = 67 caribou). According to the top model (see Table 4.3 and Fig. 4.7), female caribou were still more likely to occur on shallower slopes, but switched from being more likely to occur at lower elevations and in closer proximity to linear features to being more likely to occur at higher elevation and farther from linear features. There was also weak selection (i.e., |posterior mean| <0.10) for resource units with a higher heat load index, which suggests caribou were more likely to be found in areas with greater sun exposure (i.e., on south-facing slopes). With respect to habitat classes, female caribou continued to avoid YM jack pine forests and mixed coniferous-deciduous forests and select for mature black spruce forests, black spruce bogs and open muskegs. The presence of a calf continued to have a small but significant effect on resource selection at the fine spatial scale.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.08	0.01	0.17
Elevation (m)	-0.97	-1.02	-0.90
Slope (deg.)	-0.65	-0.70	-0.59
Dist. to Linear Feat. (m)	-0.32	-0.37	-0.26
Calf -Yes	0.14	0.09	0.19
Young-Mid Jack Pine	-0.97	-1.04	-0.92
Mature Black Spruce	0.13	0.05	0.24
Young-Mid Black Spruce	-0.72	-0.82	-0.58
Mixed Coniferous-Decid.	-1.76	-1.90	-1.59
Black Spruce Bog	0.55	0.47	0.61
Mixed Canopy Swamp	-1.90	-2.49	-1.29
Open Muskeg	0.40	0.34	0.49

Fig. 4.6: Plot of the posterior means and 95% credible intervals for the 12 fixed covariates retained in the top resource selection model for the calving/post-calving season (1st May– 30th June) at the coarse spatial scale. Note that the 12th covariate (the habitat class mature jack pine – dominated forest) has been incorporated into the global intercept. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 67 adult female woodland caribou (*n* = 25,747 GPS locations). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 3,000 iterations (*total iterations* = 1,500,000; *sampling interval* = 500 iterations; *burnin* = 150,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). The variable 'Calf-Yes' represents a binomial covariate (Yes/No) describing the reproductive status of individual caribou. The reference category for this covariate is 'Calf-No' (i.e., caribou without calves); hence, the coefficient for 'Calf-Yes' (i.e., caribou with calves) is interpreted relative to this reference category. As all eight habitat classes were included in the top model, coefficients for the seven classes shown in the above figure are interpreted relative to the reference habitat class, which is mature jack pine – dominated forests. Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.



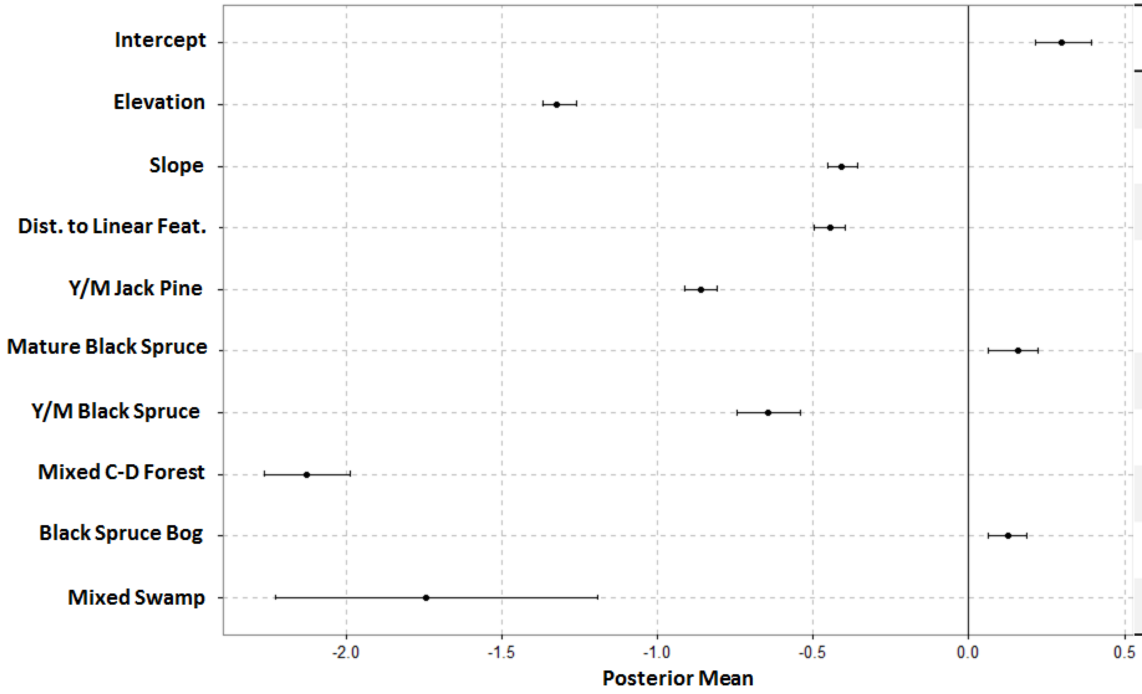
Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.35	-0.45	-0.21
Elevation (m)	0.24	0.17	0.33
Slope (deg.)	-0.24	-0.29	-0.18
Heat Load Index	0.05	0.00	0.09
Dist. to Linear Feat. (m)	0.14	0.07	0.23
Calf -Yes	0.06	0.01	0.11
Mature Jack Pine	0.21	0.09	0.33
Young-Mid Jack Pine	-0.31	-0.43	-0.19
Mature Black Spruce	0.41	0.28	0.54
Mixed Coniferous-Decid.	-0.36	-0.56	-0.18
Black Spruce Bog	0.78	0.66	0.90
Open Muskeg	0.69	0.58	0.82

Fig. 4.7: Plot of the posterior means and 95% credible intervals for the 11 fixed covariates retained in the top resource selection model for the calving/post-calving season (1st May– 30th June) at the fine spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 67 adult female woodland caribou (*n* = 25,267 GPS points distributed across 121 individual caribou seasons over two years). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 8,000 iterations (*total iterations* = 4,400,000; *sampling interval* = 500 iterations; *burnin* = 400,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). The variable 'Calf-Yes' represents a binomial covariate (Yes/No) describing the reproductive status of individual caribou. The reference category for this covariate is 'Calf-No' (i.e., caribou without calves); hence, the coefficient for 'Calf-Yes' (i.e., caribou with calves) is interpreted relative to this reference category. Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.

4.4.2.3 Summer Season

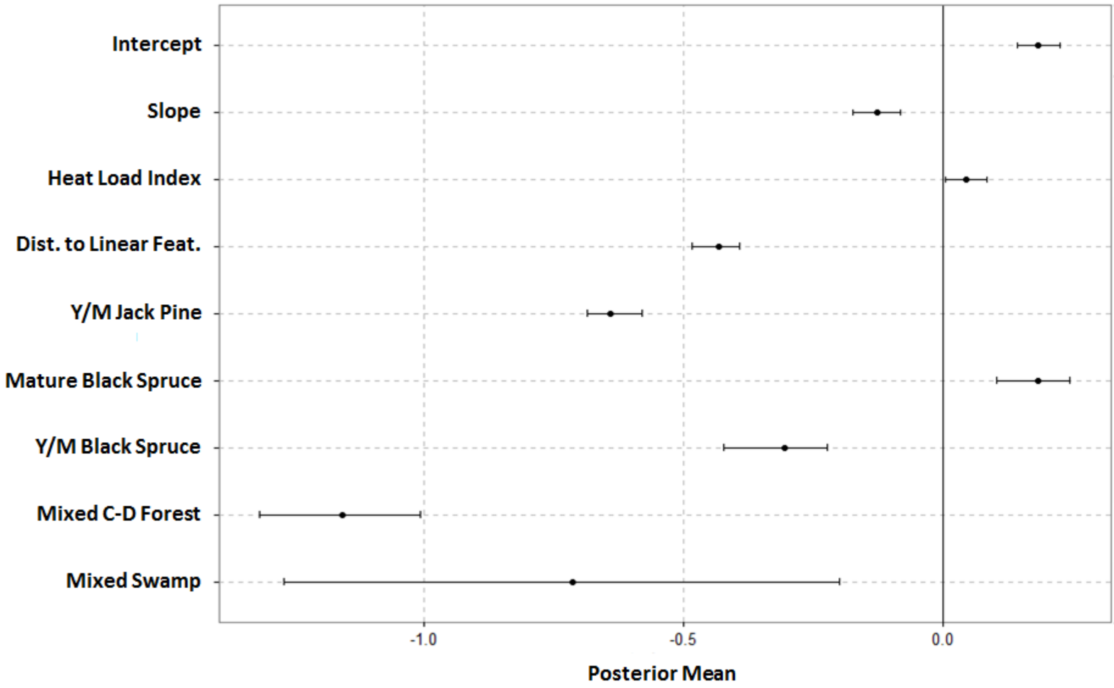
At the coarse spatial scale, resource selection models for the summer season were generated using 30,616 GPS locations recorded from 64 adult female caribou over two summers. After backwards model selection on a global model containing 14 covariates, I arrived at a top model containing nine covariates (see Table 4.3 and Fig. 4.8). As was the case in late winter/spring and calving/post-calving seasons, female caribou were more likely to be found at lower elevations, on shallower slopes and closer to linear features during the summer season. They selected for mature black spruce forests and black spruce bogs, but avoided young to mid-successional conifer-dominated forests, and strongly avoided mixed coniferous-deciduous forest and mixed canopy swamps (albeit with considerable variation in the strength of avoidance for this latter habitat class). Reproductive status (i.e., the presence of a calf) was no longer an important predictor of caribou resource selection.

Models at the fine scale level of selection were generated using 29,741 GPS recorded over 117 individual caribou seasons. The top model contained 8 of the original 14 covariates included in the global model. Elevation was excluded from this model, which suggests elevation is not an important predictor of how female caribou select resources at finer spatial scales during the summer season. Model coefficients (see Fig. 4.9) indicate that caribou were more likely to be found on shallower slopes and slightly more likely to be found in resource units with a higher heat load index. As was the case at the coarse spatial scale, they were more likely to select for resource units that were in closer proximity to linear features. They continued to avoid young to mid-successional conifer-dominated forests, mixed coniferous-deciduous forests and mixed canopy swamps, although the avoidance wasn’t as strong compared to the coarse spatial scale for the last two classes. The also continued to select for mature black spruce forests.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.30	0.22	0.39
Elevation (m)	-1.32	-1.37	-1.26
Slope (deg.)	-0.41	-0.45	-0.36
Dist. to Linear Feat. (m)	-0.45	-0.50	-0.40
Young-Mid Jack Pine	-0.86	-0.91	-0.81
Mature Black Spruce	0.16	0.06	0.22
Young-Mid Black Spruce	-0.65	-0.74	-0.54
Mixed Coniferous-Decid.	-2.13	-2.26	-1.99
Black Spruce Bog	0.12	0.06	0.19
Mixed Canopy Swamp	-1.74	-2.23	-1.19

Fig. 4.8: Plot of the posterior means and 95% credible intervals for the 9 fixed covariates retained in the top resource selection model for the summer season (1st July– 30th September) at the coarse spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 64 adult female woodland caribou (*n* = 30,616 GPS locations). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 6,000 iterations (*total iterations* = 3,300,000; *sampling interval* = 500 iterations; *burnin* = 300,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.



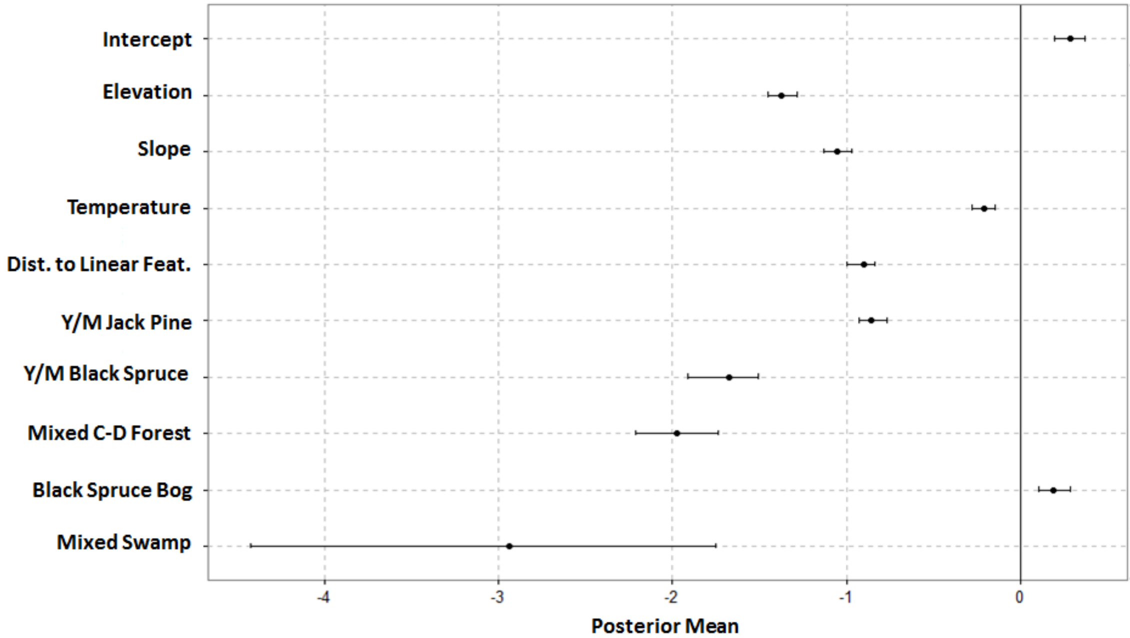
Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.18	0.14	0.23
Slope (deg.)	-0.13	-0.17	-0.08
Heat Load Index	0.04	0.01	0.09
Dist. to Linear Feat. (m)	-0.43	-0.48	-0.39
Young-Mid Jack Pine	-0.64	-0.69	-0.58
Mature Black Spruce	0.18	0.10	0.25
Young-Mid Black Spruce	-0.31	-0.42	-0.22
Mixed Coniferous-Decid.	-1.16	-1.32	-1.01
Mixed Canopy Swamp	-0.71	-1.27	-0.20

Fig. 4.9: Plot of the posterior means and 95% credible intervals for the 8 fixed covariates retained in the top resource selection model for the summer season (1st July– 30th September) at the fine spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 64 adult female woodland caribou (*n* = 29,714 GPS locations distributed across 121 individual caribou seasons over two years). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 10,000 iterations (*total iterations* = 5,500,000; *sampling interval* = 500 iterations; *burnin* = 500,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.

4.4.2.4 Autumn/Rut Season

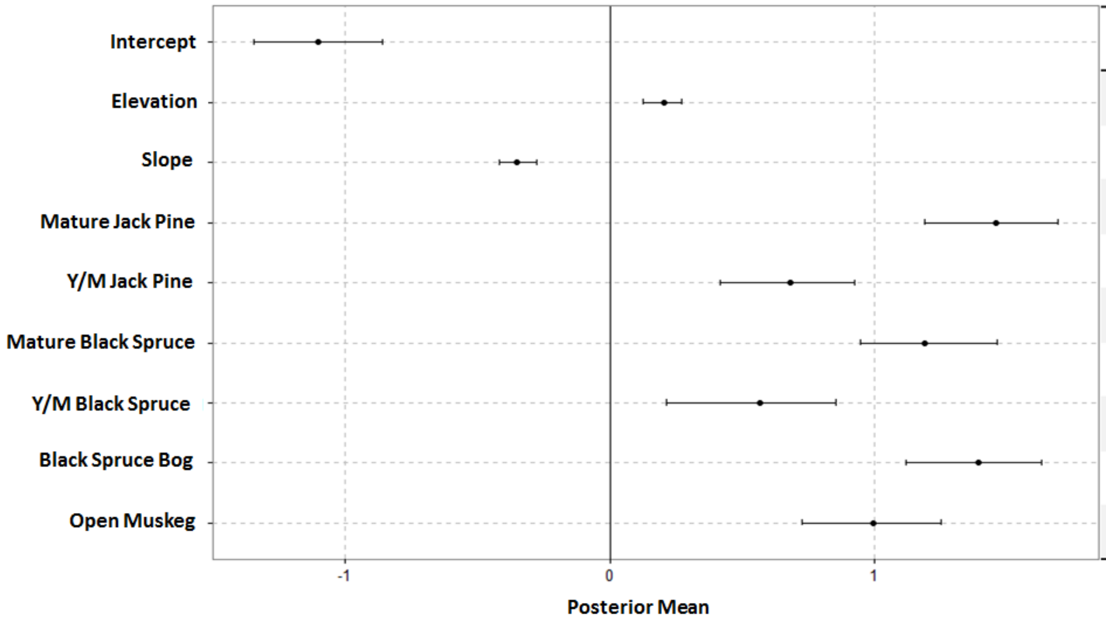
I used 12,483 GPS locations collected from 60 adult female caribou over two autumn/rut seasons to generate models at the coarse spatial scale. Model coefficients for the top model are presented in Fig. 4.10. Consistent with the three previous seasons, caribou were more likely to be found at lower elevations, on shallower slopes and closer to linear feature. For the first time, temperature had a small, but significant effect on how female caribou select resources; specifically, caribou were more likely to be found in regions with slightly cooler temperatures. They avoided YM jack pine forests, and strongly avoided YM black spruce forests, mixed coniferous-deciduous forests, and mixed canopy swamps (albeit with large variation in the response to this last habitat class). The only habitat class that was selected for was black spruce bogs.

At the fine spatial scale, I used 12,203 GPS points distributed over 110 individual caribou seasons (*n* = 60 caribou) to generate my models. The top model retained 8 of the original 14 covariates included in the global model (see Table 4.3 and Fig. 4.11). According to this model, female caribou continued to occur on shallower slopes (though the response was weak), but switched from being more likely to occur at lower elevations to being more likely to occur at higher elevations. With respect to habitat classes, they selected for all conifer-dominated habitat classes (i.e., mature and young to mid-successional forests), open muskegs, and black spruce bogs. Of these, caribou showed the strongest selection for mature black spruce forests and black spruce bogs. It should be noted that the three tests used to check the convergence of model chains for this model reported conflicting results. Specifically, the Heidelberger-Welch test (Heidelberger and Welch 1983) and Geweke's diagnostic (Geweke 1992) indicated that many of the random effects (i.e., individual caribou) did not converge while the Gelman and Rubin's diagnostic (Gelman and Rubin 1992) indicated that these chains did converge. In addition, the posterior distributions for individual caribou (*n* = 60) were steeply curved and centered on zero, which indicates that the random intercept was not explaining much variation in the data. Increasing the number of model iterations did not improve the shape of these curves (I ran the model for up to 8,800,000 iterations), nor did it extinguish the issues with convergence. However, because: (a) the mixing of chains between independent models was excellent; (b) the autocorrelation between samples was well below the threshold of 0.05; and (c) the model was not sensitive to prior specification, I accepted the top model presented in Table 4.3 and Fig. 4.11, while acknowledging that results from this model need to be interpreted with caution.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.29	0.19	0.37
Elevation (m)	-1.37	-1.45	-1.28
Slope (deg.)	-1.05	-1.13	-0.97
Temperature (°C)	-0.21	-0.28	-0.15
Dist. to Linear Feat. (m)	-0.90	-1.00	-0.84
Young-Mid Jack Pine	-0.86	-0.93	-0.76
Young-Mid Black Spruce	-1.68	-1.91	-1.51
Mixed Coniferous-Decid.	-1.98	-2.21	-1.74
Black Spruce Bog	0.19	0.10	0.28
Mixed Canopy Swamp	-2.94	-4.43	-1.75

Fig. 4.10: Plot of the posterior means and 95% credible intervals for the 9 fixed covariates retained in the top resource selection model for the autumn/rut season (1st October– 4th November) at the coarse spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 60 adult female woodland caribou (n = 12,483 GPS locations). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 5,000 iterations (*total iterations* = 2,750,000; *sampling interval* = 500 iterations; *burnin* = 250,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-1.10	-1.35	-0.86
Elevation (m)	0.20	0.12	0.27
Slope (deg.)	-0.35	-0.42	-0.28
Mature Jack Pine	1.46	1.19	1.69
Young-Mid Jack Pine	0.68	0.42	0.92
Mature Black Spruce	1.19	0.94	1.46
Young-Mid Black Spruce	0.56	0.21	0.85
Black Spruce Bog	1.39	1.12	1.63
Open Muskeg	0.99	0.73	1.25

Fig. 4.11: Plot of the posterior means and 95% credible intervals for the 8 fixed covariates retained in the top resource selection model for the autumn/rut season (1st October– 4th November) at the fine spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 60 adult female woodland caribou (*n* = 12,203 GPS locations distributed across 110 individual caribou seasons over two years). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 16,000 iterations (*total iterations* = 8,800,000; *sampling interval* = 500 iterations; *burnin* = 800,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table. Note that for this model, there were conflicting diagnostics with regards to the convergence of several of the random chains (i.e., individual caribou) so results from this model should be interpreted cautiously.

4.4.2.5 Early Winter Season

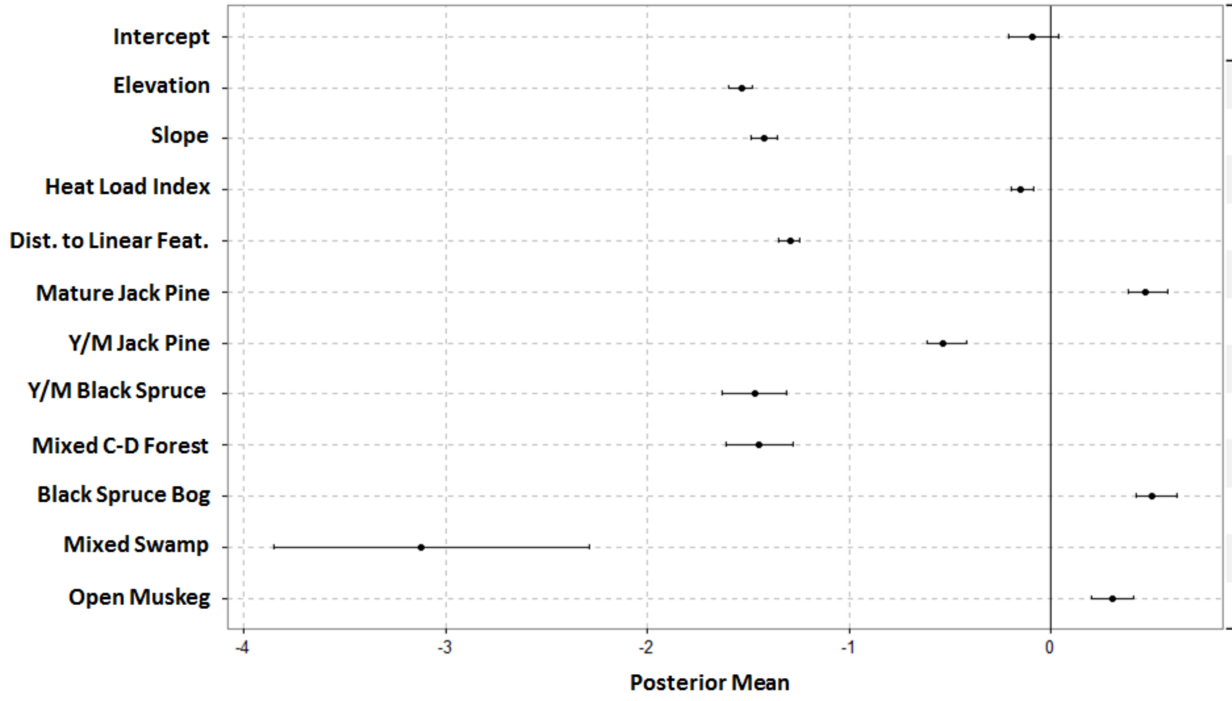
To generate models at the coarse spatial scale for the early winter season, I used 27,457 GPS locations recorded from 58 adult female caribou over two consecutive early winter seasons. After performing backwards selection on a global model containing 15 fixed covariates, I arrived at a top model containing 11 of these covariates (see Table 4.3 and Fig. 4.12). This model indicates that female caribou were much more likely to be found at lower elevations and more likely to be found in resource units with shallower slopes, lower values for heat load index, and in closer proximity to linear features. Aside from the inclusion of heat load index, this pattern mimics the general patterns observed in the four previous seasons. All eight habitat classes were included in the top model, which means model coefficients for these covariates must be interpreted relative to a reference class. For this scale and season, the reference class was mature black spruce forest. Relative to this type of forest, caribou avoided young to mid – successional conifer-dominated forests and mixed coniferous-deciduous forests, and strongly avoided mixed canopy swamps (although there was substantial variation in the response to this last habitat class). They selected for mature jack pine forests, black spruce bogs and open muskegs. As was the case with the coarse-scale model for the late winter/spring season, the global intercept for this model overlapped zero; however, I did not suppress it for the same reason it was not suppressed for that model: doing so would have meant assuming that the response is zero if all of the model predictors are zero, which is likely untrue for this system.

I used 28,675 GPS locations (*n* = 58 caribou) distributed over 108 individual caribou seasons to generate models for the early winter season at the fine spatial scale. The top model (see Table 4.3 and Fig. 4.14) contained 11 of the original 15 fixed covariates included in the global model. Unlike at the coarse spatial scale, elevation was not an important predictor of caribou resource selection at this scale and caribou were more likely to be found further from linear features rather than closer; however, they continued to be more likely to occur on shallower slopes and in resource units with lower values for heat load index (although the estimate of the posterior mean for this latter variable (-0.08) indicates that caribou were only slightly more likely to occur in units with lower heat load indexes). They were also slightly more likely to occur in areas with warmer temperatures and deeper snow. With respect to habitat classes, caribou selected for mature jack pine forests and black spruce bogs, but avoided young to mid-successional conifer-dominated forests and mixed coniferous-deciduous forests. They strongly avoided swamps with mixed canopies. Consistent with all previous models in which mixed canopy swamps have been included, there was a substantially large 95% credible interval around the estimate of the posterior mean for this class.

4.4.2.6 Mid-Winter Season

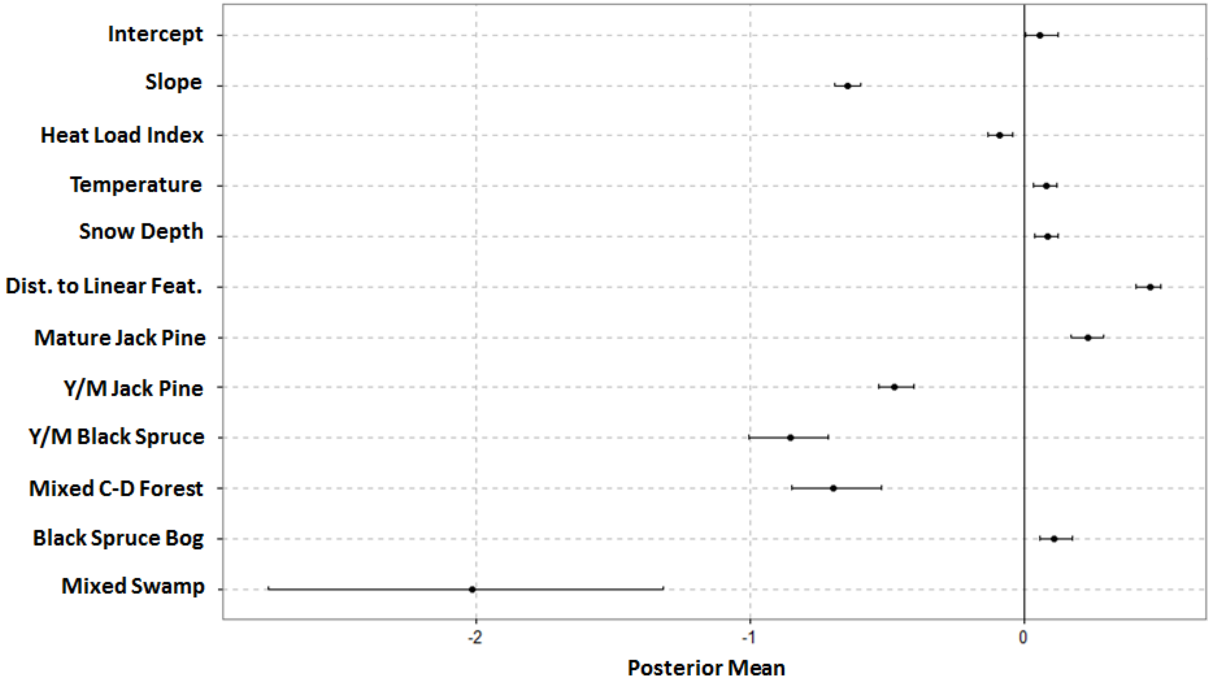
At the coarse scale level of selection, I used 24,279 GPS locations recorded from 57 adult female caribou over two mid-winter seasons to generate my models. After backwards selection on a global model containing 15 fixed covariates, I arrived at a top model consisting of 12 covariates (see Table 4.3). Model coefficients from this model (Fig. 4.14) indicate that female caribou were more likely to be found at lower elevations, on shallower slopes, in closer proximity to linear features, as well as in resource units with lower values for heat load index. This pattern is consistent with the pattern described for coarse scale resource selection during early winter. However, unlike during the early winter, caribou were slightly more likely to be found in resource units characterized by cooler temperatures. With respect to habitat classes, caribou avoided YM jack pine forests and mixed canopy swamps (albeit with characteristic variation for the latter class), and strongly avoided YM black spruce forests and mixed coniferous-deciduous forests. As was the case at the coarse spatial scale for early winter, caribou selected for mature jack pine forests and black spruce bogs. Surprisingly, the presence of a calf had a small influence (posterior mean = 0.09) on how female caribou selected resources during the mid – winter season at the coarse spatial scale.

At the fine spatial scale, models were generated using 24,343 GPS locations (*n* = 68 caribou) sampled from 120 individual caribou seasons. The top model contained just 8 of the original 15 fixed covariates included in the global model (see Fig. 4.15). Coefficients from this model indicate that caribou continued to be more likely to occur on shallower slopes; however, they switched from being more likely to occur at lower elevations and in closer proximity to linear features to being more likely to occur at higher elevations and further from linear features. Like the autumn/rut season at the fine spatial scale, caribou selected for all of the habitat classes that were included in the top model (here, five classes). Specifically, they selected for all conifer-dominated forests, black spruce bogs, and open muskegs. Of these, they showed the strongest selection for mature jack pine forests (posterior mean = 1.31). At this spatial scale, reproductive status was no longer an important predictor of caribou habitat selection.



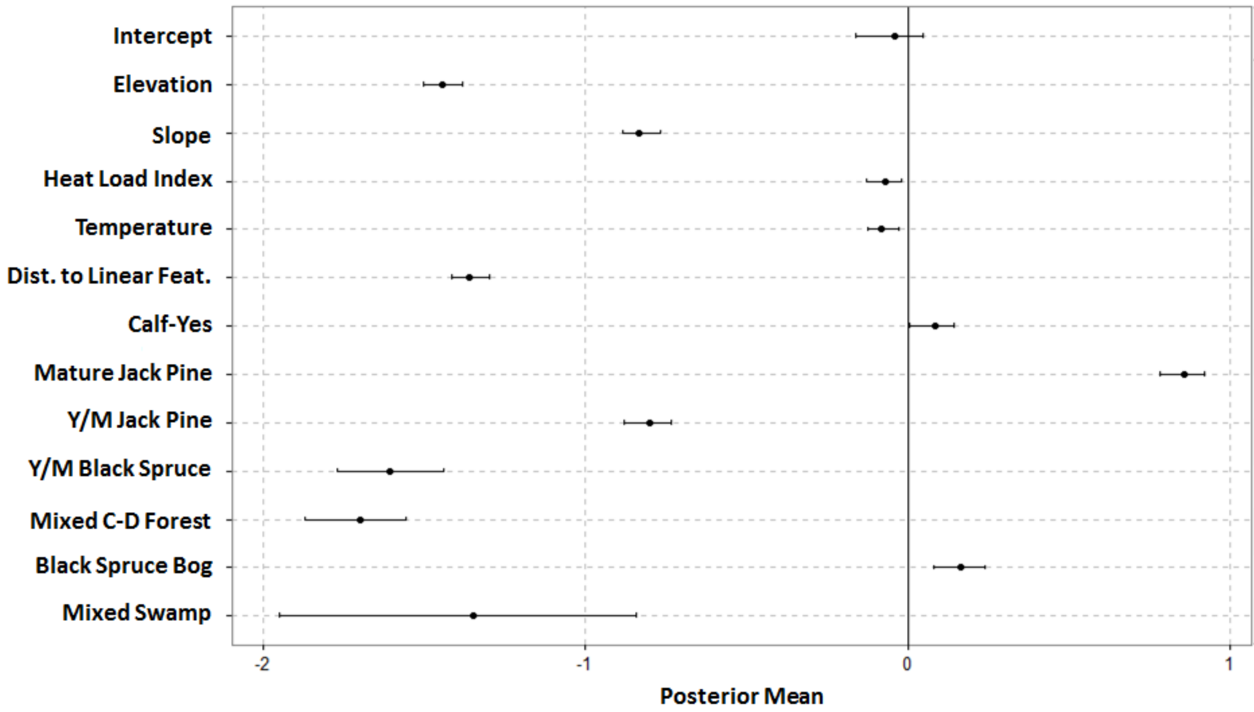
Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.09	-0.21	0.04
Elevation (m)	-1.53	-1.60	-1.48
Slope (deg.)	-1.42	-1.49	-1.36
Heat Load Index	-0.15	-0.20	-0.09
Dist. to Linear Feat. (m)	-1.29	-1.35	-1.24
Mature Jack Pine	0.47	0.38	0.57
Young-Mid Jack Pine	-0.54	-0.61	-0.42
Young-Mid Black Spruce	-1.47	-1.63	-1.31
Mixed Coniferous-Decid.	-1.45	-1.61	-1.28
Black Spruce Bog	0.50	0.42	0.62
Mixed Canopy Swamp	-3.12	-3.85	-2.29
Open Muskegs	0.30	0.20	0.41

Fig. 4.12: Plot of the posterior means and 95% credible intervals for the 12 fixed covariates retained in the top resource selection model for the early winter season (5th November– 14th January) at the coarse spatial scale. Note that the 12th covariate (the habitat class mature black spruce– dominated forest) has been incorporated into the global intercept. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 58 adult female woodland caribou (n = 27,457 GPS locations). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 4,000 iterations (*total iterations* = 2,200,000; *sampling interval* = 500 iterations; *burnin* = 200,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). As all eight habitat classes were included in the top model, coefficients for the seven classes shown in the above figure are interpreted relative to the reference habitat class, which is mature black spruce– dominated forests. Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.



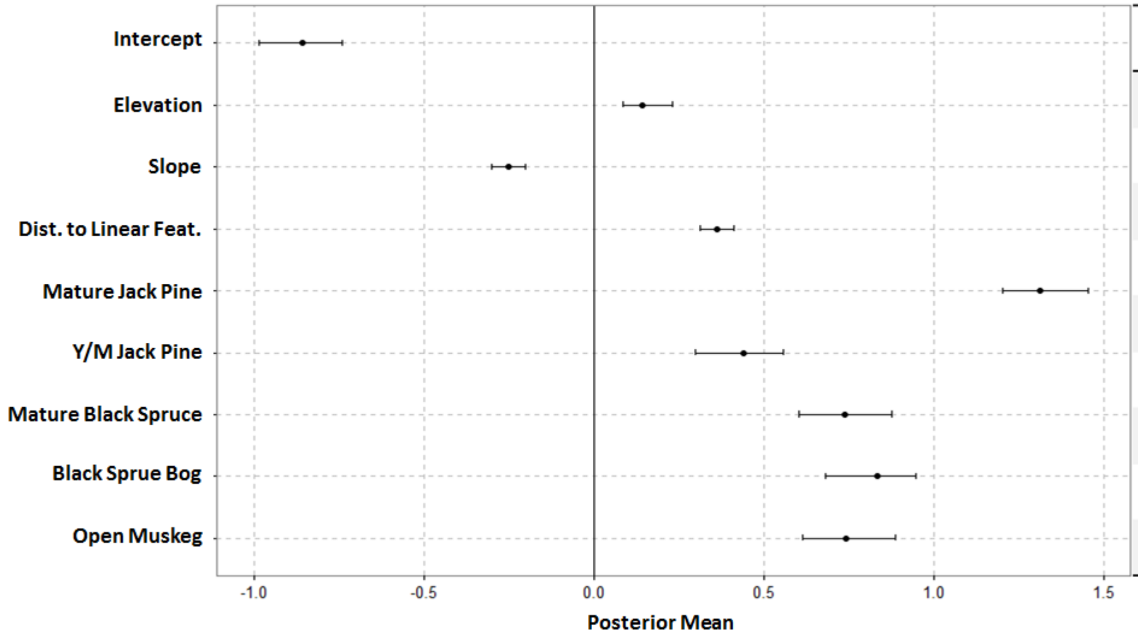
Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.06	0.00	0.12
Slope (deg.)	-0.64	-0.69	-0.59
Heat Load Index	-0.09	-0.13	-0.04
Temperature (°C)	0.08	0.04	0.12
Snow Depth (cm)	0.09	0.04	0.12
Dist. to Linear Feat. (m)	0.46	0.41	0.50
Mature Jack Pine	0.24	0.17	0.29
Young-Mid Jack Pine	-0.47	-0.53	-0.40
Young-Mid Black Spruce	-0.85	-1.00	-0.72
Mixed Coniferous-Decid.	-0.70	-0.85	-0.52
Black Spruce Bog	0.11	0.06	0.18
Mixed Canopy Swamp	-2.02	-2.76	-1.32

Fig. 4.13: Plot of the posterior means and 95% credible intervals for the 11 fixed covariates retained in the top resource selection model for the early winter season (5th November– 14th January) at the fine spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 58 adult female woodland caribou (*n* = 28,675 GPS locations distributed across 108 individual caribou seasons over two years). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 10,000 iterations (*total iterations* = 5,500,000; *sampling interval* = 500 iterations; *burnin* = 500,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.04	-0.16	0.05
Elevation (m)	-1.44	-1.50	-1.38
Slope (deg.)	-0.83	-0.88	-0.77
Heat Load Index	-0.07	-0.13	-0.02
Temperature (°C)	-0.08	-0.12	-0.03
Dist. to Linear Feat. (m)	-1.36	-1.41	-1.30
Calf-Yes	0.09	0.01	0.14
Mature Jack Pine	0.86	0.78	0.92
Young-Mid Jack Pine	-0.80	-0.88	-0.73
Young-Mid Black Spruce	-1.61	-1.77	-1.44
Mixed Coniferous-Decid.	-1.70	-1.87	-1.55
Black Spruce Bog	0.16	0.08	0.24
Mixed Canopy Swamp	-1.35	-1.95	-0.84

Fig. 4.14: Plot of the posterior means and 95% credible intervals for the 12 fixed covariates retained in the top resource selection model for the mid-winter season (15th January– 22nd March) at the coarse spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 57 adult female woodland caribou (*n* = 24,279 GPS locations). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 4,000 iterations (*total iterations* = 2,200,000; *sampling interval* = 500 iterations; *burnin* = 200,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). The variable 'Calf-Yes' represents a binomial covariate (Yes/No) describing the reproductive status of individual caribou. The reference category for this covariate is 'Calf-No' (i.e., caribou without calves); hence, the coefficient for 'Calf-Yes' (i.e., caribou with calves) is interpreted relative to this reference category. Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table. Note that the credible interval for the global intercept overlaps zero, but I did not suppress it because in doing so, I would have been making the likely false assumption that the response is zero if all predictors are zero.



Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.86	-0.99	-0.74
Elevation (m)	0.14	0.08	0.23
Slope (deg.)	-0.25	-0.30	-0.20
Dist. to Linear Feat. (m)	0.36	0.31	0.41
Mature Jack Pine	1.31	1.20	1.45
Young-Mid Jack Pine	0.44	0.30	0.56
Mature Black Spruce	0.74	0.60	0.88
Black Spruce Bogs	0.83	0.68	0.95
Open Musekgs	0.74	0.61	0.88

Fig. 4.15: Plot of the posterior means and 95% credible intervals for the 8 fixed covariates retained in the top resource selection model for the mid-winter season (15th January– 22nd March) at the fine spatial scale. The model was fit in the R© Package *MCMCglmm* (Hadfield 2015) using a training set of 57 adult female woodland caribou (*n* = 24,343GPS locations distributed across 107 individual caribou seasons over two years). Individual animal ids (AIDs) were set as the random intercept to control for unbalanced sample sizes and the fact that repeated measures were taken from each caribou. The effective sample size for the model was 8,000 iterations (*total iterations* = 4,400,000; *sampling interval* = 500 iterations; *burnin* = 400,000 iterations). Because the model was fit using logistic regression, coefficients are interpreted in terms of the log-odds of a successful response (i.e., a point being used). Estimates of the posterior means (i.e., model coefficients) and their corresponding upper and lower credible intervals (C.I.s) are provided in the adjacent table.

4.4.3 Model Validation

To validate the top model for each season and scale (*n* = 12 total), I re-ran each model using subsets of female caribou (see Table 4.5) fit with Lotek brand radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada). I then compared patterns observed in the top models (i.e., those trained using the sample of caribou fit with Telonics brand radio-collars (Telonics Inc., Mesa, Arizona, USA); *n* = 68) to the patterns observed in the validation models. Where a covariate from a validation model fell outside the credible interval for the trained covariate, and/or its own credible interval overlapped zero, the interpretation of this covariate was limited to the sample used to train the model (hereafter 'Telonics caribou'). If the posterior mean for a covariate from a validation model fell within the 95% credible interval of the posterior mean for that same covariate in the corresponding training model (or vice-versa), this suggested that the covariate was a consistent predictor of caribou resource selection in Saskatchewan's Boreal Shield (i.e., both the magnitude and direction of the response to that covariate were consistent between the two collared populations). However, if the posterior mean for a covariate from a validation model had the same sign but considerably different magnitude (i.e., the difference in the estimates of the coefficients was large enough that the estimate for one covariate fell outside the 95% credible interval surrounding the estimate of the other coefficient) than the posterior mean for the corresponding trained covariate (e.g., see the comparison for the covariate 'Slope' in Fig. 4.16), this was more suggestive of a general trend in the response to that covariate. Note that the values of coefficients across all training and validation models ranged from -3.1 to 2.0, which means that where coefficients between training and validation models showed the same general trend (i.e., same sign), the difference between the coefficient values was always less than 3. In fact, the largest difference between a pair of coefficients that were classified as showing the same general trend was 1.413, which was recorded as the difference in the positive response of Telonics and Lotek caribou to open muskegs during the early winter season at the coarse spatial scale. I have no knowledge whether a difference of this magnitude represents a significant difference in the response of a caribou to a given covariate. Hence, the phrase 'same general trend' should only be interpreted as describing a general response (i.e., selection or avoidance) to a covariate.

It is also important to note that the posterior means for covariates in a validation model may not represent the estimates that would be found in the true top model for the sample of caribou fit with Lotek collars (hereafter ‘Lotek caribou’). That is, one or more covariates may be missing or need to be removed from the validation model before it could be considered a top model (i.e., a model with good diagnostics containing all covariates whose HPD (credible) intervals do not overlap zero). In addition, because the 95% credible intervals were of varying size for different covariates (e.g., the intervals for elevation tended to be small while those for mixed canopy swamp tended to be large), it was more likely for the posterior means of some of the covariates in the validation models to fall within the 95% credible intervals of their corresponding covariates in the training models. Therefore, the main goal of this validation exercise was to identify trends in the data, rather than make rigorous comparisons between the values for each covariate.

Table 4.5: Summary of the number of GPS locations (equal number of used + available points) and individual home or seasonal ranges used to fit the validation models for each season and spatial scale (coarse vs. fine). Used points were sampled from within home ranges at the coarse spatial scale and annual seasons ranges at the fine spatial scale. Models were generated using sub-samples of adult, female caribou fit with Lotek brand radio collars (recorded in the column 'sample size').

Season	Spatial Scale	No. GPS Locations (Used + Available Points)	Sample Size	No. Individual Ranges (Home or Seasonal)
Late Winter/Spring	Coarse	12,990	24	24
Late Winter/Spring	Fine	13,188	24	46
Calving/Post-Calving	Coarse	21,356	24	24
Calving/Post-Calving	Fine	20,822	24	46
Summer	Coarse	30,458	23	23
Summer	Fine	29,588	23	45
Autumn/Rut	Coarse	10,810	23	23
Autumn/Rut	Fine	10,684	23	42
Early Winter	Coarse	18,776	22	22
Early Winter	Fine	20,010	22	39
Mid-Winter	Coarse	18,994	22	22
Mid-Winter	Fine	18,894	22	38

I used *percent congruency* to compare individual covariates among models generated with the two sets of data For reference, the term “congruent” refers to any comparison for which the 95% credible interval of a covariate in the validation model did not overlap zero and the posterior mean for that covariate fell within the 95% credible interval of the same covariate in the corresponding training model (e.g., see the comparison for the covariate ‘Snow Depth’ in Fig. 4.16); The term “percent congruency” describes the percentage of total covariate comparisons that were consistent (either within a covariate or between models). As an example, the covariate elevation was included in ten of the twelve top models, which means it was included in ten validation models. After comparing estimates of the posterior mean for elevation between these ten model pairs, I found that only one comparison was consistent (i.e., the posterior mean of elevation in the validation model fell within the 95% credible interval elevation in the corresponding training model); two comparisons showed the same general trend (i.e., the posterior means had the same sign but did not fall within one another’s 95% credible intervals); four comparisons showed an opposing trend (i.e., one posterior mean was negative while the other was positive); and three comparisons were not relevant (i.e., the 95% credible interval for elevation overlapped zero in the validation model). The percent congruency for elevation was calculated as the sum of the number of consistent comparisons ($n = 1$) divided by the total number of comparisons ($n = 10$), then multiplied by 100%. Thus, the percent congruency for the covariate elevation was (1/10)*100% = 10%. Detailed summaries of covariate comparisons by season and scale and by individual covariates and by are presented in Tables 4.5 and 4.6 respectively.

None of the validation models were one hundred percent congruent with their corresponding training models, although many of the training and validation models described similar general trends in patterns of resource selection (see Fig. 4.16 – 4.27 and Table 4.6). The highest percent (p.c.) congruency occurred during the autumn/rut season at the fine spatial scale (p.c. = 87.5%), while the lowest percent congruency occurred during the early winter seasons at the coarse spatial scale (p.c. = 9.1%). The mean percent congruency (+/- standard error) was 40.7 ± 19.3%, which suggests that inferences made regarding caribou resource selection in Saskatchewan’s Boreal Shield may be limited to the sample population (i.e., the Telonics caribou). Partitioning the models by scale, the mean percent congruency for comparisons made at the coarse scale was 32.9 ± 13.9% while the mean percent congruency for comparisons made at the fine scale was 70.3 ± 21.8%. These values suggest that resource selection patterns at the fine spatial scale are generally more consistent across populations of woodland caribou in Saskatchewan’s Boreal Shield.

Table 4.6: Summary of covariate comparisons between the top (i.e., training) models and validation models by season and scale. If the posterior mean for a covariate in a validation model fell within the 95% credible interval of that same covariate in the corresponding training model, the covariate was classified as a **consistent predictor** (i.e., the two posterior means had the same sign and similar magnitude). If the posterior mean for a covariate in the validation model had the same sign as the corresponding trained covariate, it was classified as showing the **same general trend**. Conversely, if the posterior mean for a covariate in the validation model had the opposite sign as the corresponding trained covariate, it was classified as showing an **opposing trend**. If the 95% credible of a covariate in a validation model overlapped zero, it was classified as **not relevant**. The percent congruney for a covariate was calculated by dividing the number of consitent predictor by the total number of comparisons for that covariate and then multiplying the quotient by 100%.

Season	Spatial Scale	Consistent Predictor	Same General Trend	Opposing Trend	Not Relevant	Percent Congruency
Late Winter/Spring	Coarse	4	3	0	3	40.0
Late Winter/Spring	Fine	3	1	0	4	37.5
Calving/Post-Calving	Coarse	5	4	2	0	45.5
Calving/Post-Calving	Fine	6	0	0	5	54.5
Summer	Coarse	3	4	1	1	33.3
Summer	Fine	4	2	0	2	50.0
Autumn/Rut	Coarse	4	4	1	0	44.4
Autumn/Rut	Fine	7	1	0	0	87.5
Early Winter	Coarse	1	7	1	2	9.1
Early Winter	Fine	4	4	1	2	36.4
Mid-Winter	Coarse	3	7	0	2	25.0
Mid-Winter	Fine	2	4	1	1	25.0
	TOTAL	**46**	**41**	**7**	**22**	

A total of 116 comparisons were made between the individual covariates of validation and training models (intercept comparisons excluded, see Table 4.7). Of these, 46 covariates came out as consistent predictors; 41 covariates came out as showing a general trend in resource selection, had the same sign as the corresponding training covariates); 7 covariates came out as having an opposing trend (i.e., posterior means had the opposite sign); and 22 covariates were not comparable (i.e., the 95% credible intervals of the validation covariates overlapped zero). Interestingly, of the seven covariate comparisons that showed opposing trends, four of them were for the covariate elevation. At the coarse spatial scale for the autumn/rut (Fig. 4.22), calving/post-calving (Fig. 4.18), and summer (Fig. 4.20) seasons, Lotek caribou were more likely to be found at higher elevations while Telonics caribou were more likely to be found at lower elevations. Conversely, at the fine spatial scale for the mid-winter season (Fig. 4.27), Lotek caribou were more likely to be found at lower elevations while Telonics caribou were more likely to be found at higher elevations. Even where the posterior mean for elevation in a validation model had the same sign as the posterior mean for elevation in the corresponding training model (and for which the 95% credible interval did *not* overlap zero), there was only one instance (the fine scale model for the autumn/rut season, Fig. 4.23) where the posterior mean from the validation model fell inside the 95% credible interval for elevation in the training model. For the other two instances, there were relatively large differences in the estimates of the posterior mean for elevation between the training and validation models. Specifically, Telonics caribou had a stronger response to an increase in elevation relative to the Lotek caribou during both the early winter and mid-winter seasons at the coarse spatial scale (see Fig. 4.24 and 4.26). Together, these observations suggest that elevation is not a consistent predictor of how female woodland caribou select habitat in Saskatchewan's Boreal Shield. In fact, of all the covariate comparisons, it had the lowest percent congruency (p.c. = 30%, see Table 4.7 for details).

With respect to the eight habitat classes, congruity between the posterior means in the validation vs. training models was generally high (mean p.c. = 78.4 ± 7%). The posterior means for mature jack pine – dominated forests and black spruce bogs were 100% congruous, which suggests that the general response (i.e., selection or avoidance) of female caribou to these two habitats is fairly predictable across all seasons and spatial scales. In contrast, the responses of female caribou to mature black spruce forests and mixed canopy swamps may be less predictable. Both of these habitats recorded a 50% congruency, which means that only half of the comparisons for these two covariates could be classified as being consistent or showing the same general trend. Of all the habitat classes, mixed coniferous-deciduous forests recorded the highest percentage (66%) of consistent comparisons. This suggests that both the magnitude and direction of the response of female caribou to mixed coniferous – deciduous forests is fairly predictable across populations. Overall, the top models for each season and scale (presented in Fig. 4.5 – 4.16) seem to do a reasonable job of describing patterns of selection and avoidance for different habitat classes in Saskatchewan's Boreal Shield.

Table 4.7: Summary of covariate comparisons between the top (i.e., training) models and validation models . If the posterior mean for a covariate in a validation model fell within the 95% credible interval of that same covariate in the corresponding training model, the covariate was classified as a **consistent predictor**. If the posterior mean for a covariate in the validation model had the same sign as the corresponding trained covariate, it was classified as showing the **same general trend**. Conversely, if the posterior mean for a covariate in the validation model had the opposite sign as the corresponding trained covariate, it was classified as showing an **opposing trend**. If the 95% credible of a covariate in a validation model overlapped zero, it was classified as **not relevant**. The percent congrunecy for a covariate was calculated by dividing the consitent predictor by the total number of comparisons for that covariate and then multiplying the quotient by 100%.

Model Covariate	Consistent Predictor	Same General Trend	Opposing Trend	Not Relevant	Percent Congruency
Elevation	1	2	4	3	10.0
Slope	6	5	0	0	54.5
Heat Load Index	2	0	0	3	40.0
Temperature	1	2	0	0	33.3
Snow Depth	1	1	1	0	33.3
Dist. to Lin. Feat.	2	7	0	2	18.2
Calf-Yes	1	0	0	2	33.3
Mature Jack Pine	5	3	0	0	62.5
Y/M Jack Pine	5	5	1	1	41.7
Mature Black Spruce	3	1	1	3	37.5
Y/M Black Spruce	3	4	0	2	33.3
Mixed C-D Forest	6	2	0	1	66.7
Black Spruce Bog	4	6	0	0	40.0
Mixed Swamp	4	0	0	4	50.0
Open Muskeg	2	3	0	1	33.3
TOTAL	**46**	**41**	**7**	**22**	

In general, this validation exercise has shown that my top models are fairly representative how female woodland caribou select resource units in Saskatchewan's Boreal Shield, particularly at the coarse spatial scale. As the percent congruity was 100% for the covariates slope, temperature, mature jack pine – dominated forests and black spruce bogs, we can have the greatest confidence in extrapolating inferences made about how these four covariates influence caribou resource selection across the study area. Conversely, we can be less confident in how reproductive status, elevation, heat load index, mature black spruce forests and mixed canopy swamps influences caribou resource selection outside the sample of Telonics caribou.

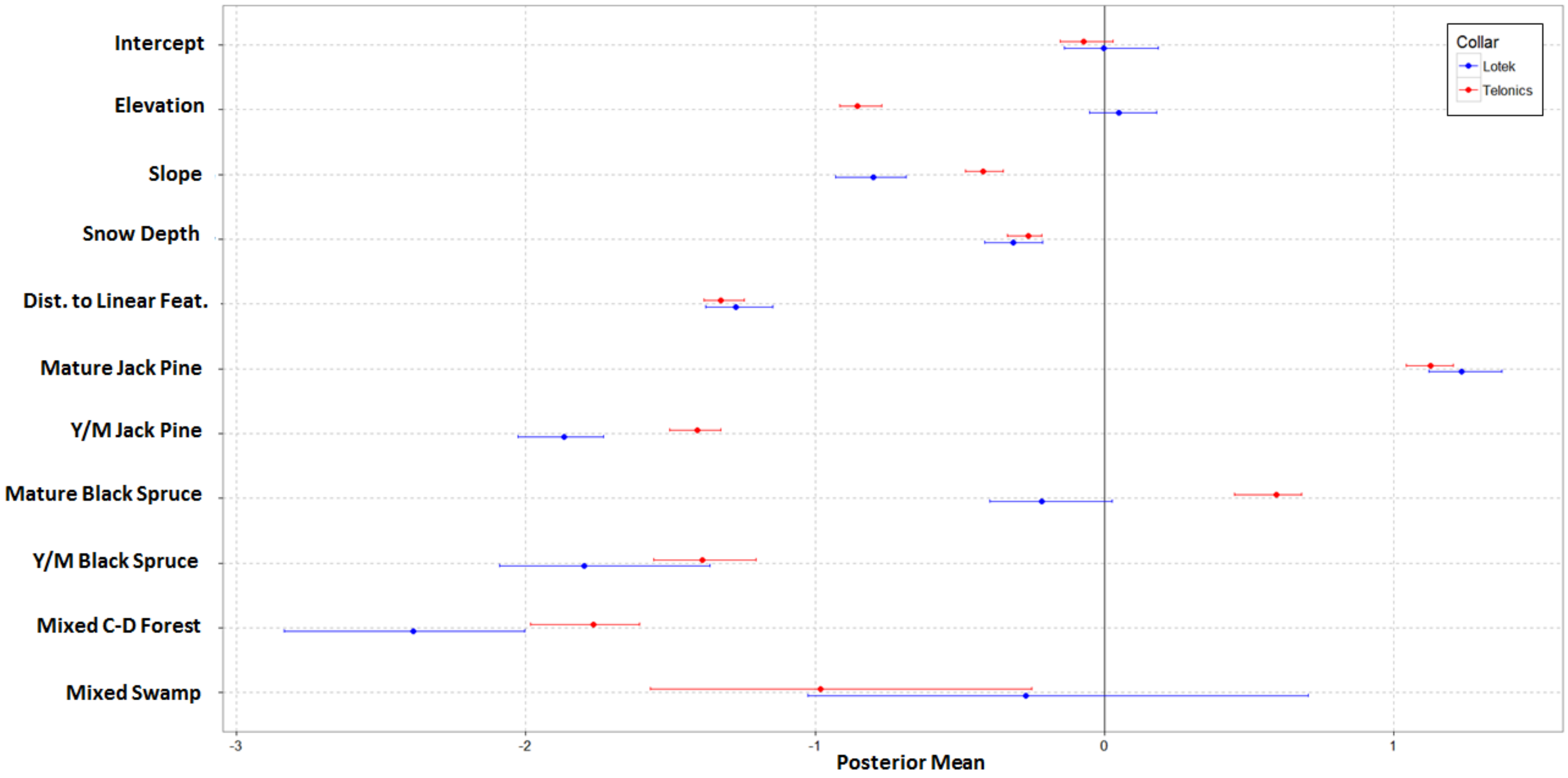


Fig. 4.16: Comparison between the top model (red) and validation model (blue) for the late winter/spring (LWS) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 17,439 GPS locations recorded from 68 individuals over two LWS seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 6,495 GPS locations recorded from 24 individuals over two LWS seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

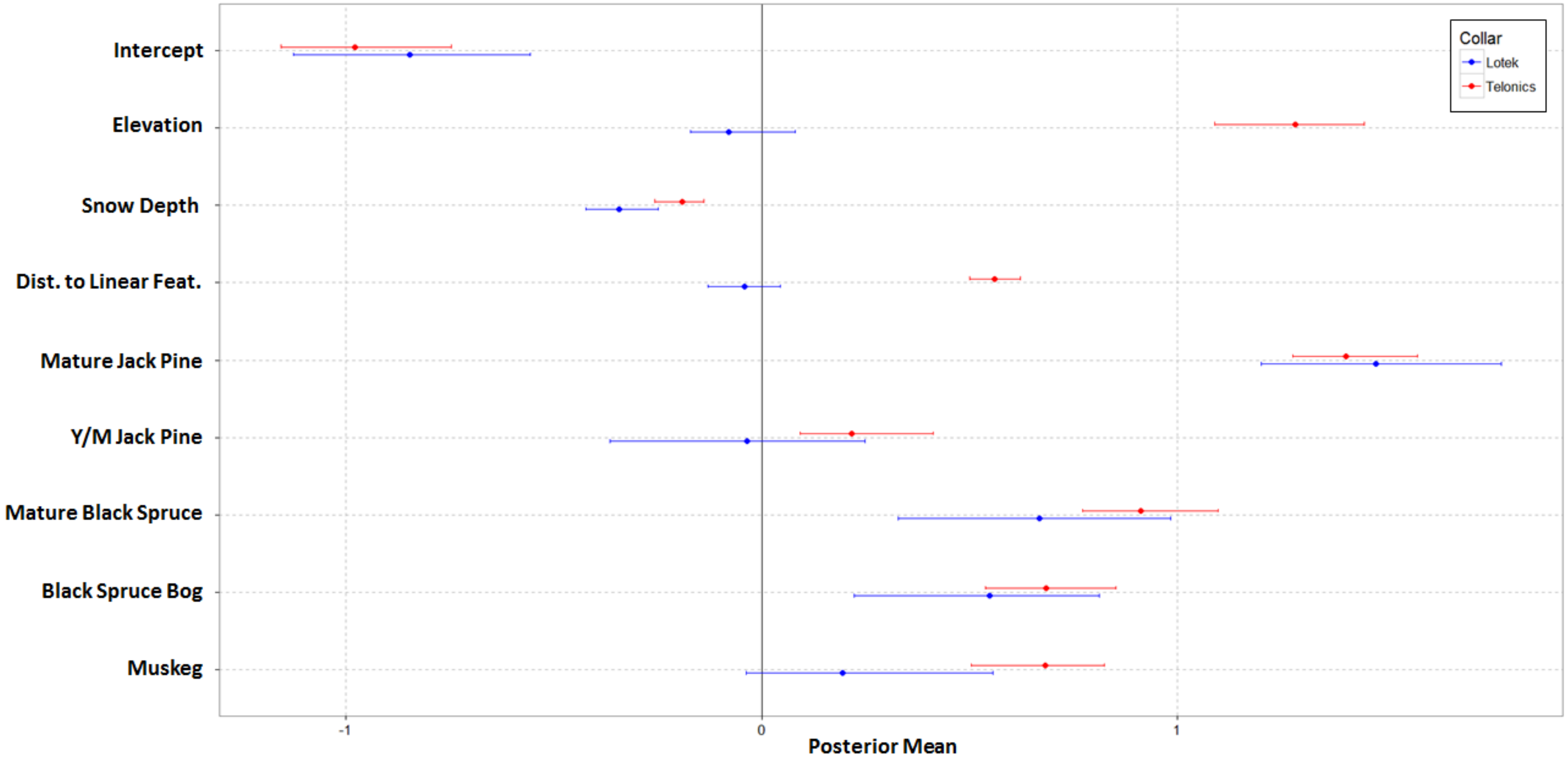


Fig. 4.17: Comparison between the top model (red) and validation model (blue) for the late winter/spring (LWS) season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 17,490 GPS locations recorded from 68 individuals over two LWS seasons) and validated using a sample of female woodland caribou fit with *Lotek* ® GPS collars (n = 6,594 GPS locations recorded from 24 individuals over two LWS seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

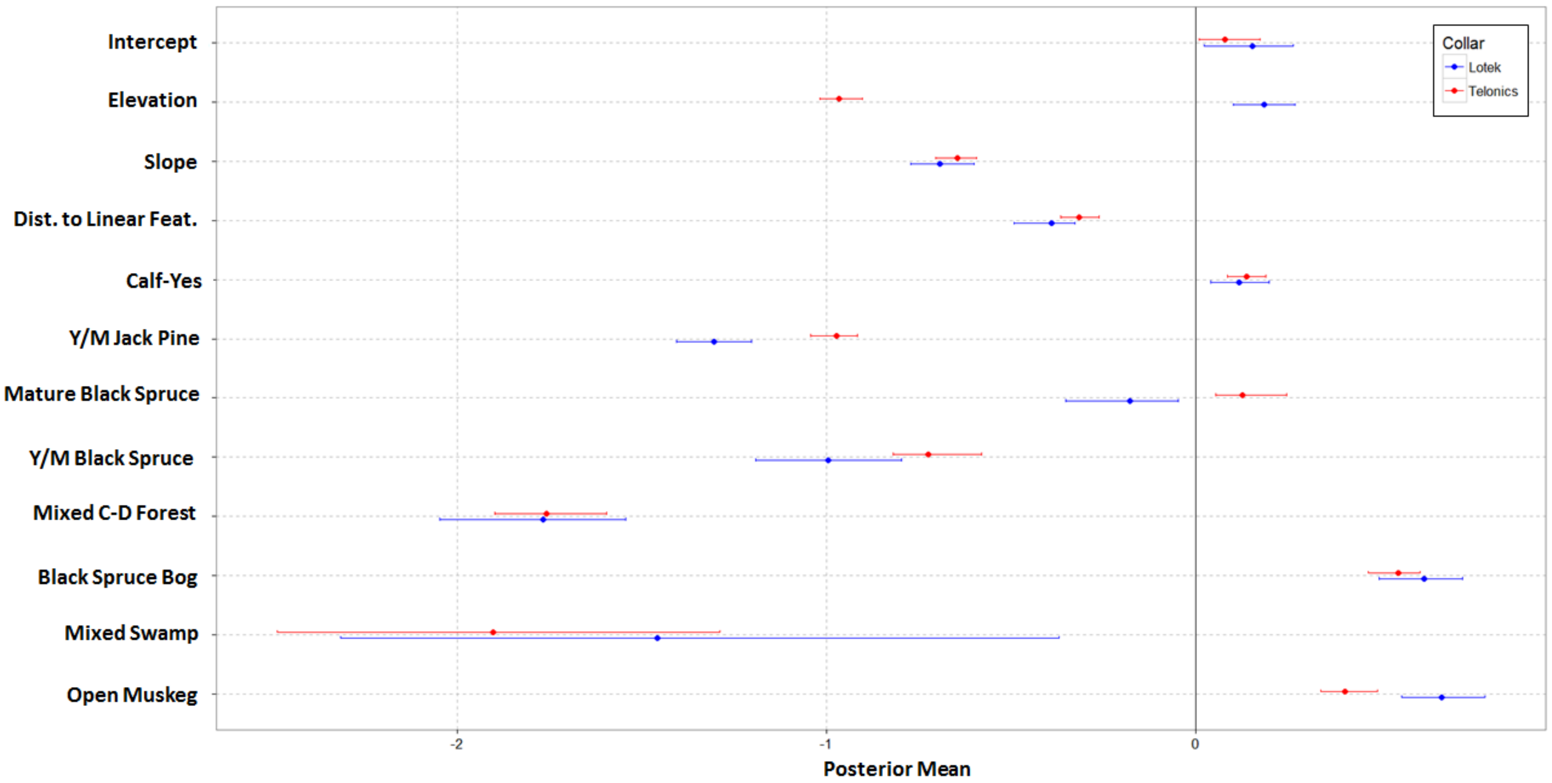


Fig. 4.18: Comparison between the top model (red) and validation model (blue) for the calving/post-calving (CPC) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 25,747 GPS locations recorded from 67 individuals over two CPC seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 10,678 GPS locations recorded from 24 individuals over two CPC seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability). Because all eight habitat classes were included in the top model, the reference habitat class of mature jack pine – dominated forest has been incorporated into the global intercept. The posterior means for the remaining seven habitat classes are interpreted relative to this reference class.

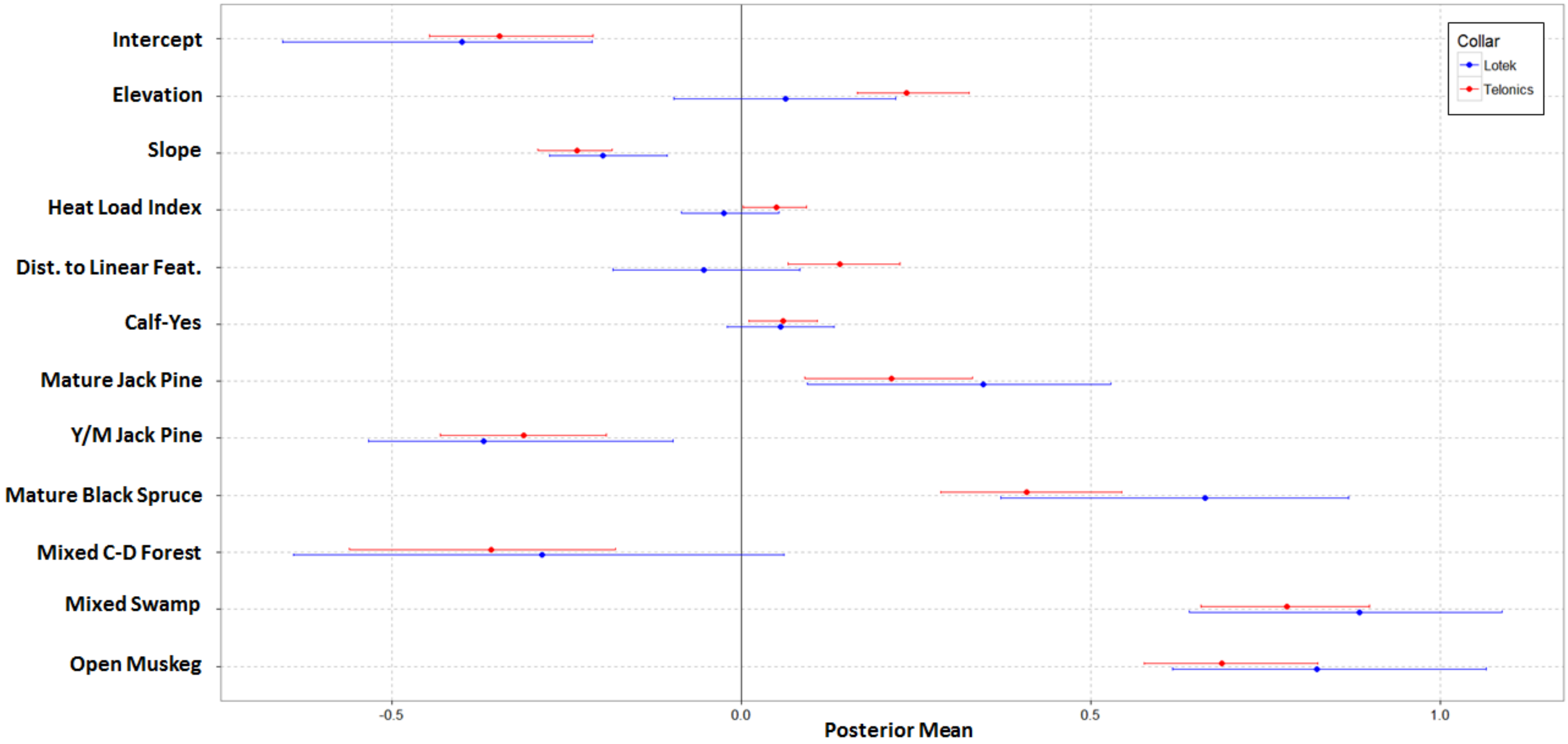


Fig. 4.19: Comparison between the top model (red) and validation model (blue) for the calving/post-calving (CPC) season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 17,439 GPS locations recorded from 67 individuals over two CPC seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 10,411 GPS locations recorded from 24 individuals over two CPC seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

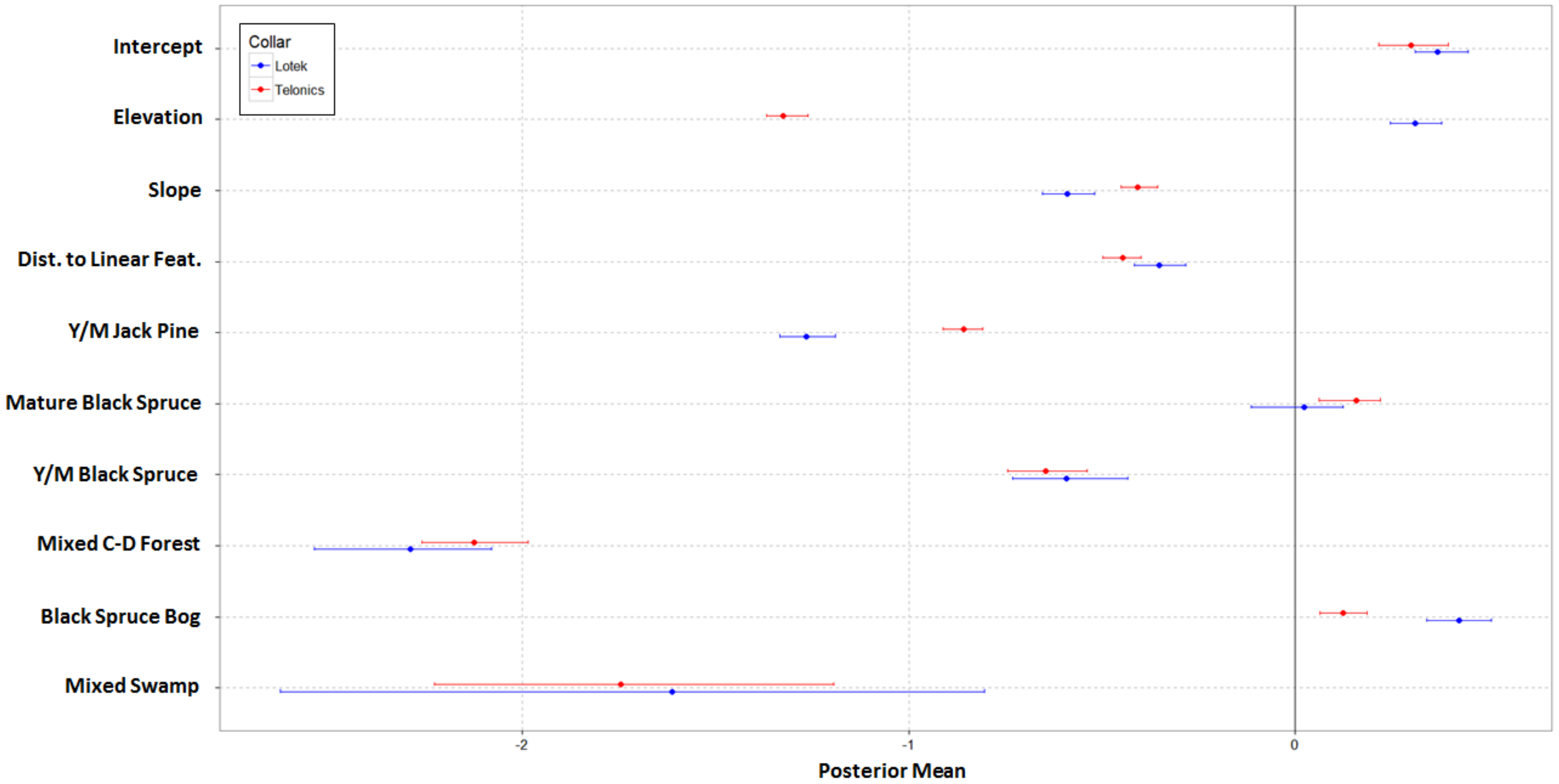


Fig. 4.20: Comparison between the top model (red) and validation model (blue) for the summer season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars ($n = 30{,}616$ GPS locations recorded from 64 individuals over two summer seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars ($n = 15{,}229$ GPS locations recorded from 23 individuals over two summer seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

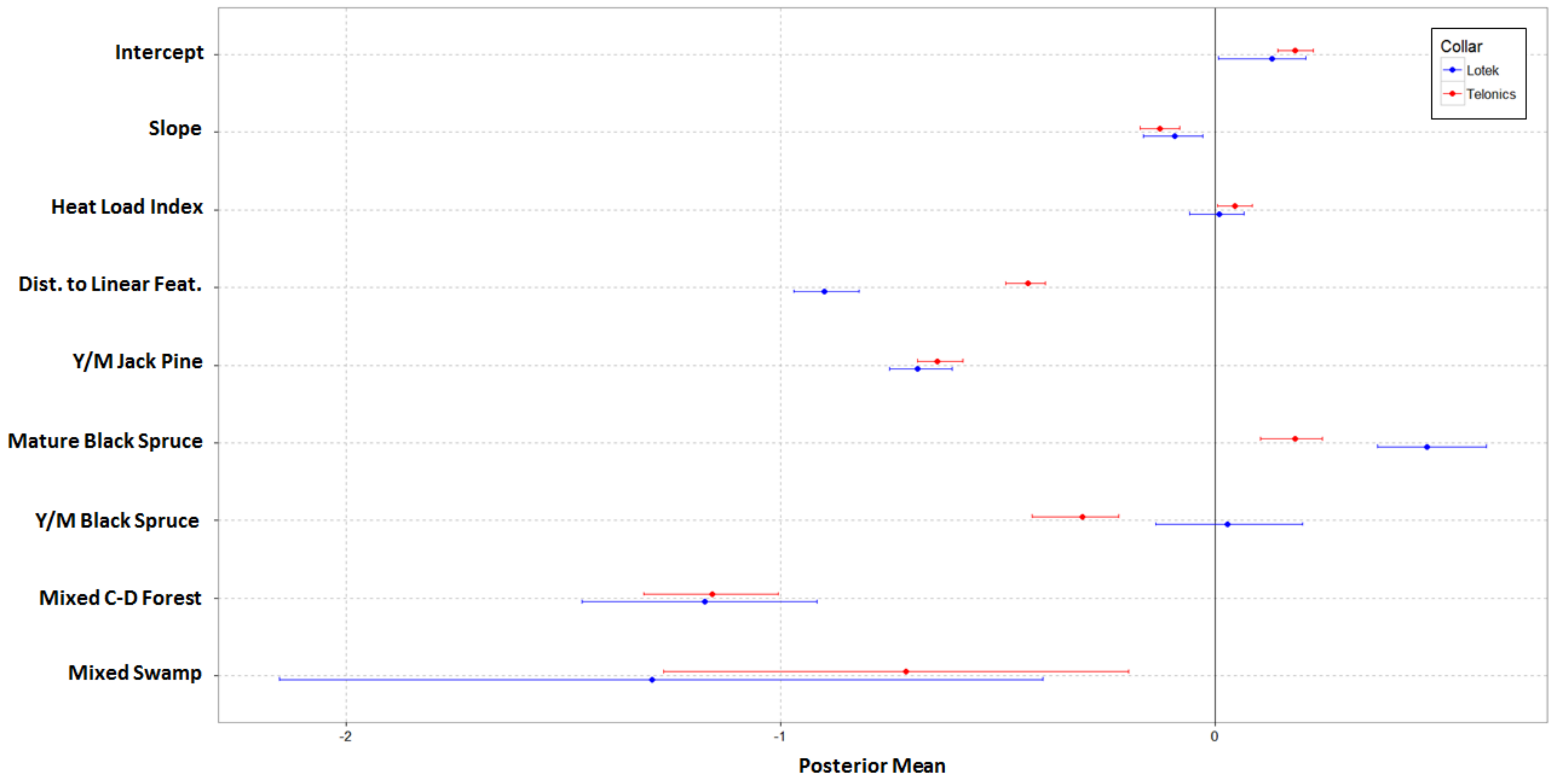


Fig. 4.21: Comparison between the top model (red) and the validation model (blue) for the summer season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars ($n = 29{,}741$ GPS locations recorded from 64 individuals over two summer seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars ($n = 14{,}794$ GPS locations recorded from 23 individuals over two summer seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

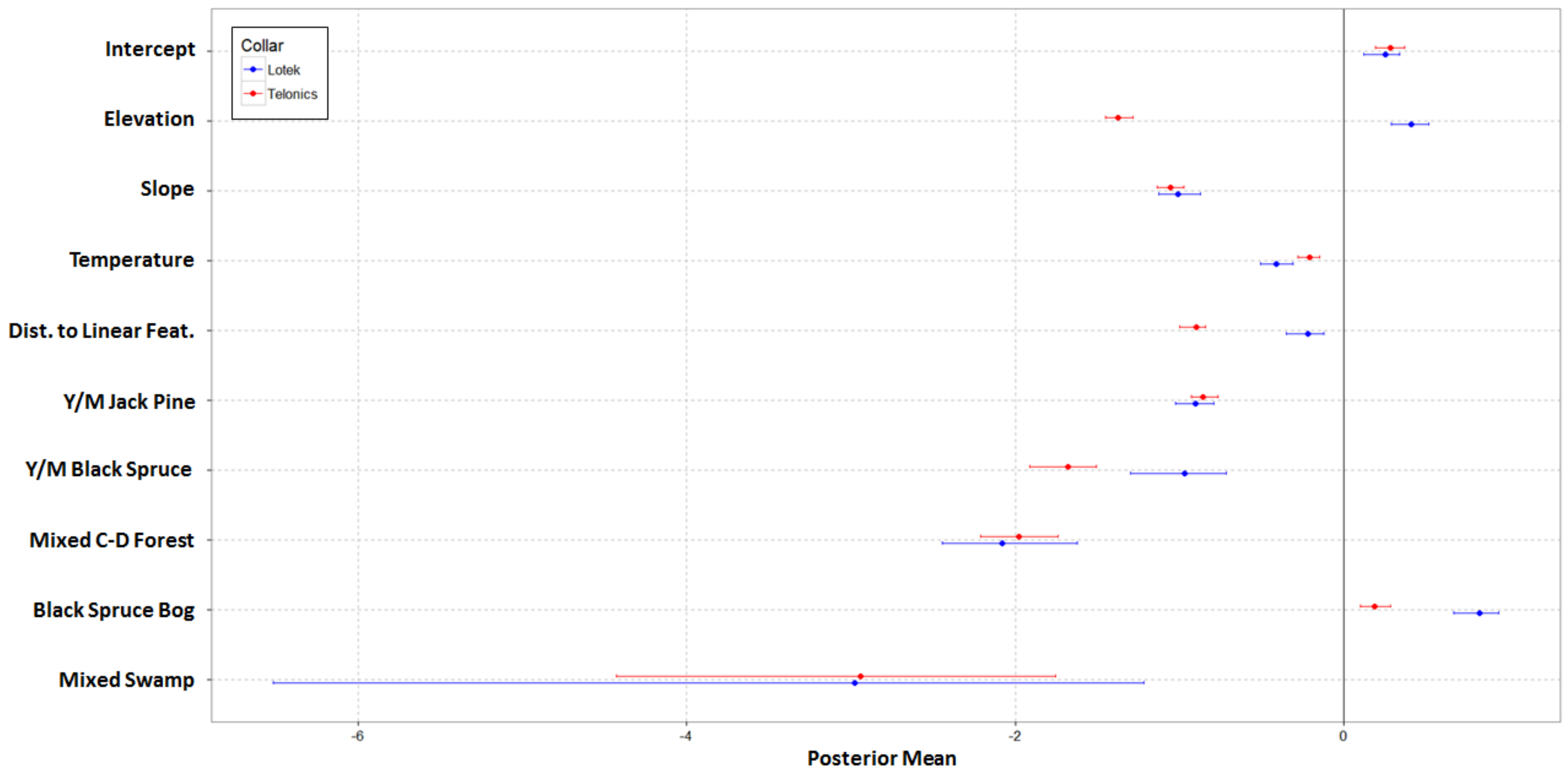


Fig. 4.22: Comparison between the top model (red) and the validation model (blue) for the autumn/rut (AR) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 12,483 GPS locations recorded from 60 individuals over two AR seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 5,405 GPS locations recorded from 23 individuals over two AR seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

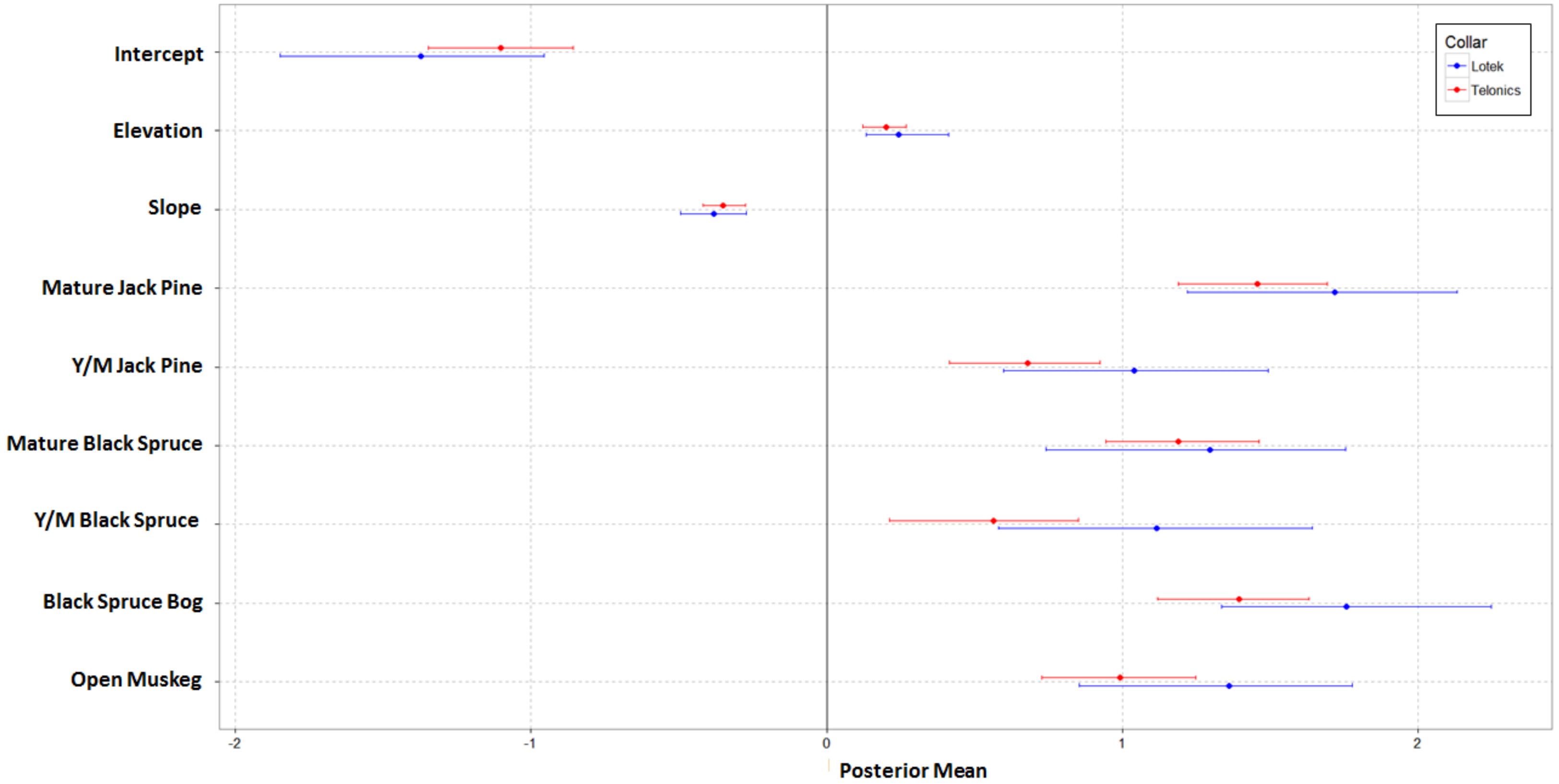


Fig. 4.23: Comparison between the top model (red) and the validation model (blue) for the autumn/rut (AR) season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 12,203 GPS locations recorded from 60 individuals over two AR seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 5,342 GPS locations recorded from 23 individuals over two AR seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

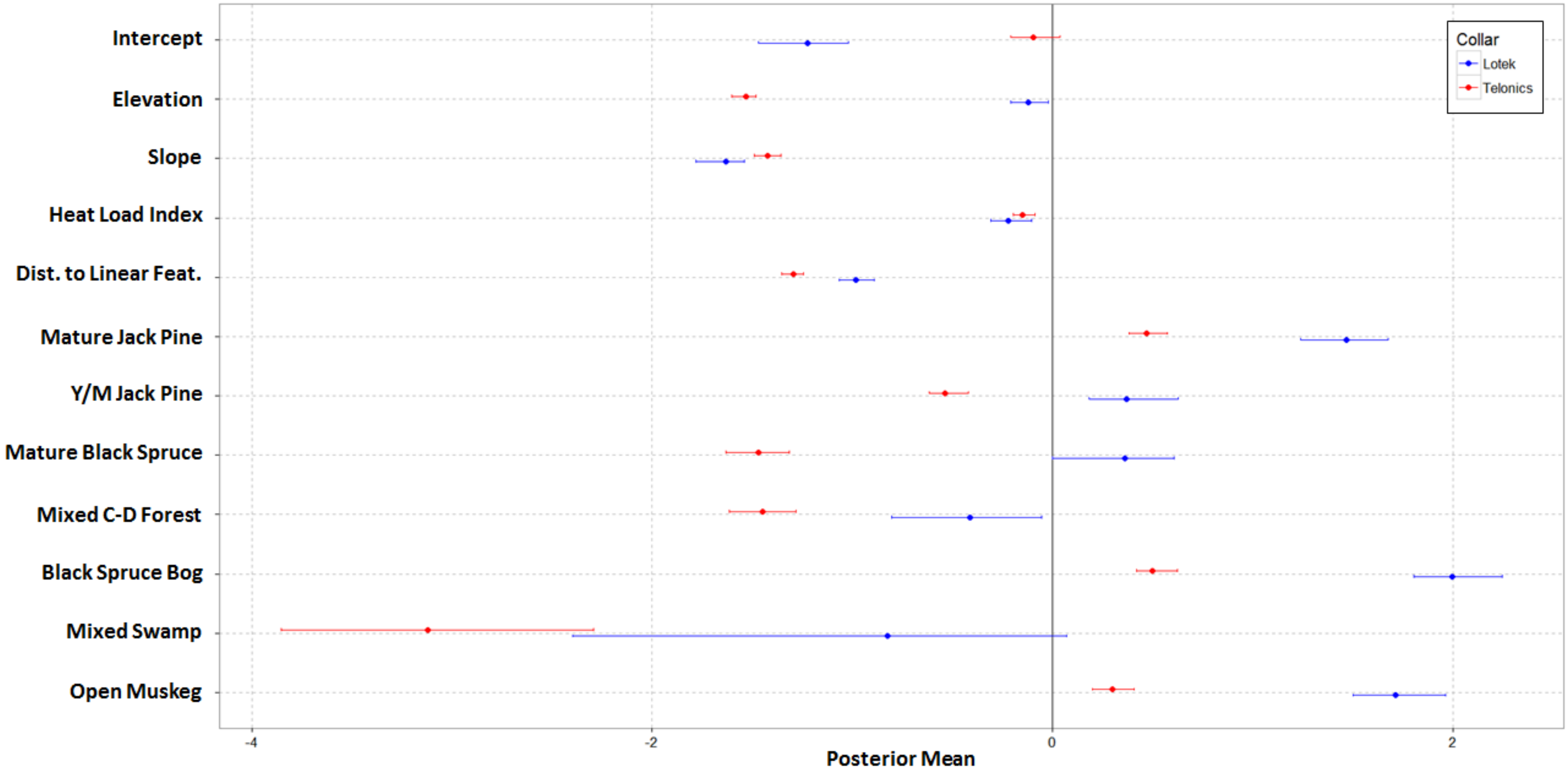


Fig. 4.24: Comparison between the top model (red) and the validation model (blue) for the early winter (EW) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (*n* = 27,457 GPS locations recorded from 58 individuals over two EW seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (*n* = 9,388 GPS locations recorded from 22 individuals over two EW seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability). Because all eight habitat classes were included in the top model, the reference habitat class of mature black spruce– dominated forest has been incorporated into the global intercept. The posterior means for the remaining seven habitat classes are interpreted relative to this reference class.

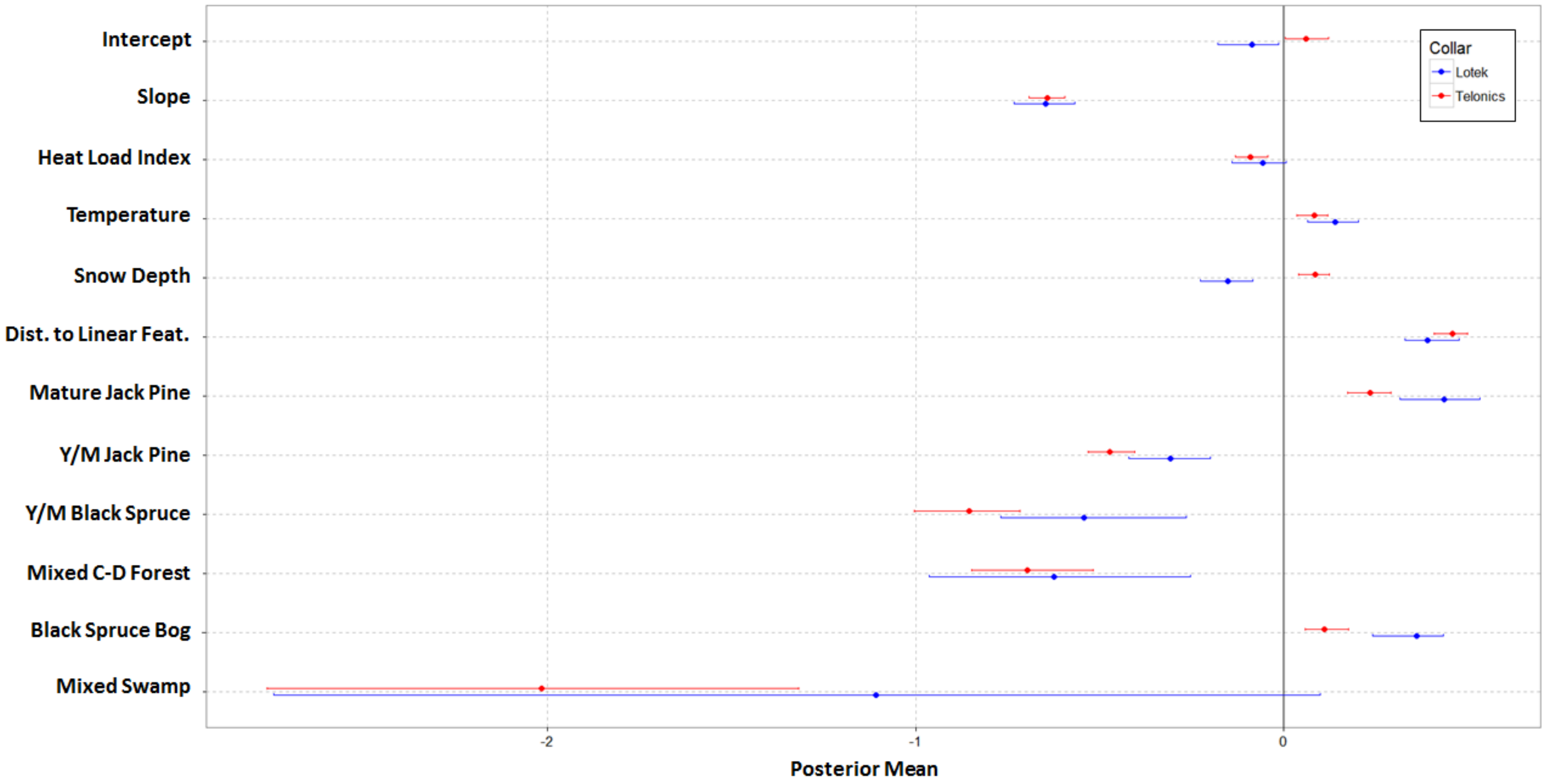


Fig. 4.25: Comparison between the top model (red) and the validation model (blue) for the early winter (EW) season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 28,675 GPS locations recorded from 58 individuals over two EW seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 10,005 GPS locations recorded from 22 individuals over two EW seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

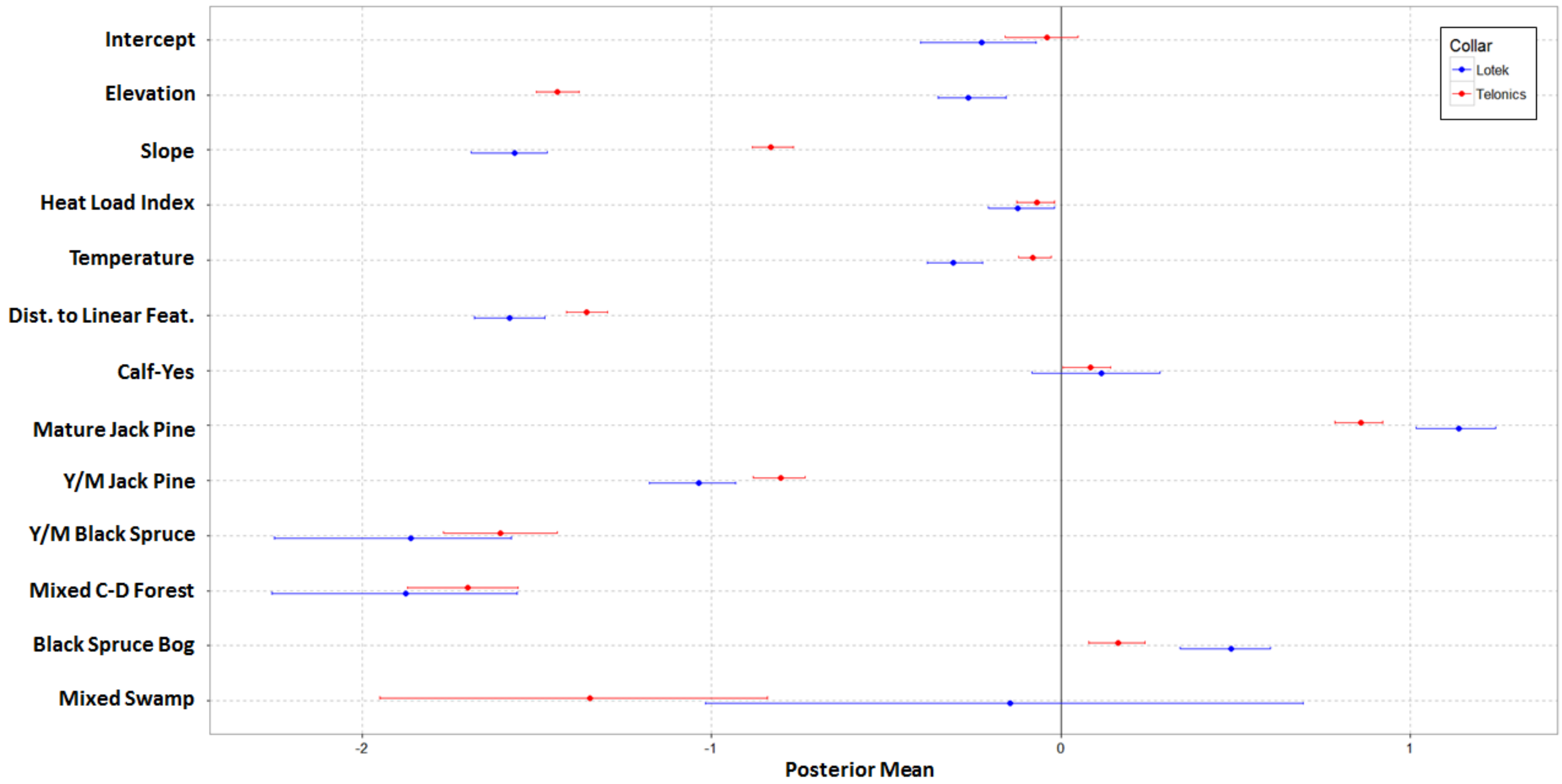


Fig. 4.26: Comparison between the top model (red) and the validation model (blue) for the mid-winter (MW) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 24,279 GPS locations recorded from 57 individuals over two MW seasons) and validated using a sample of female woodland caribou fit with *Lotek* ® GPS collars (n = 9,497 GPS locations recorded from 22 individuals over two MW seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

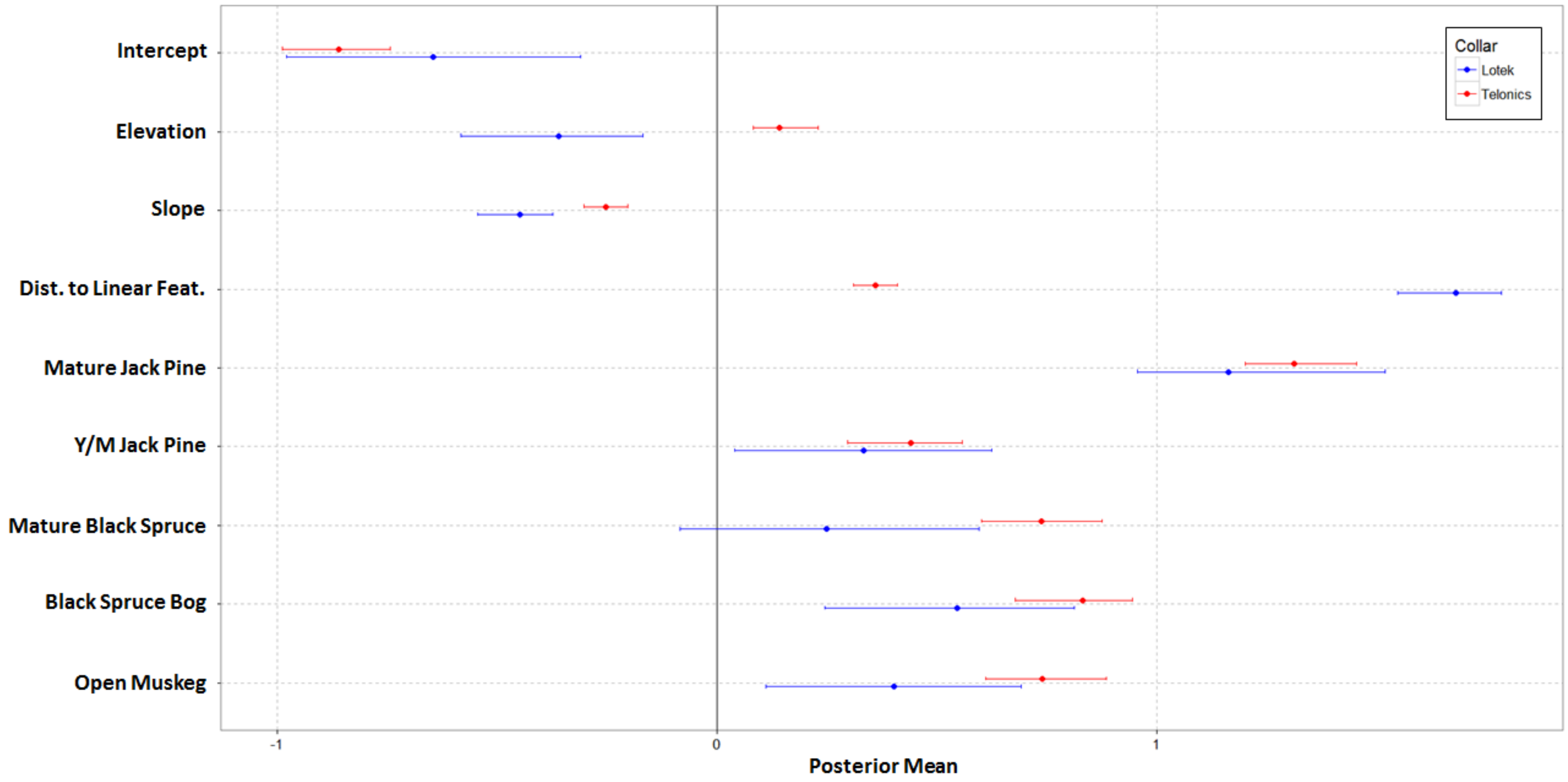


Fig. 4.27: Comparison between the top model (red) and the validation model (blue) for the mid-winter (MW) season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 24,343 GPS locations recorded from 57 individuals over two MW seasons) and validated using a sample of female woodland caribou fit with *Lotek*® GPS collars (n = 9,447 GPS locations recorded from 22 individuals over two MW seasons). The points denote estimates of the posterior means for each covariate while the error bars on either side of the points are the 95% credible intervals (i.e., the range of values on the posterior probability distributions for each covariate that capture 95% of the probability).

4.5 Discussion

4.5.1 Home Range Analysis

Powell and Mitchell (2012) describe an organism's home range as "the part of an animal's cognitive map of its environment that it chooses to keep updated". In other words, home ranges are not static but instead have fluid borders that expand and contract depending on changes in both the environment and how the animal perceives its environment. For my study, I defined a home range as the space required by an individual to satisfy its life history requirements (e.g., foraging, mating, calving, etc.) over the period it was alive or tracked during my two year study. With respect to the sample of caribou that survived for the full two years (n = 68 of the 92 collared animals used for my resource selection study), there was considerable variation in individual home range size, but much less variation in individual core range size. This pattern alludes to differences in local migratory behaviour.

Migration is a form of movement distinct from other forms of movement (e.g., post-natal dispersal) that allows animals to exploit temporarily available resources (Dingle and Drake 2007). Where migratory strategies differ, this may be indicative that individuals experience different levels of spatiotemporal variation in resources, predation pressure, and/or other drivers of migration. Alternatively, individuals may be limited in their movements by natural or anthropogenic barriers (e.g., roads with moderate vehicle traffic acted as semi-permeable barriers to boreal caribou in northeastern Alberta, [Dyer et al. 2002]) and/or density-dependence (Lundberg 1987, Kaitala et al. 1993). In Saskatchewan's Boreal Shield, variation in migratory behaviour may be due to one or more of these factors. The region encompasses a vast area (>180, 000 km^2) of heterogeneously distributed habitat types, variable fire disturbance, variable local densities of linear features and potentially heterogeneous distributions of predators and alternate prey animals; therefore, it is reasonable to expect that individual boreal caribou might be exposed to varying suites of factors that promote or minimize migratory behaviour.

Home range sizes were significantly smaller in the eastern half of the study area, which suggests that processes influencing local migratory behaviour are variable across the study area. Specifically, resources may become more patchily distributed moving east to west across the study area (which may promote migration [Dingle and Drake 2007]) or caribou densities may increase moving west to east across the study area (which may constrain migration [Lundberg

1987, Kaitala et al. 1993]). Since individual movement patterns can affect individual fitness, which in turn can have ramifications for population-level dynamics (Gaillard et al. 2010), a more rigorous exploration of the relationship between home range size and biophysical attributes would be beneficial to our understanding of what drives female woodland caribou space-use patterns in Saskatchewan's Boreal Shield.

4.5.2 Seasonal Range Analysis

A seasonal range is a spatial subset of an organism's home range that encompass a suite of biophysical attributes needed to meet that organism's biological needs over a smaller temporal scale. To ensure that the seasonal ranges were defined over time periods that are ecologically relevant to female woodland caribou in Saskatchewan's Boreal Shield, I used a combination of movement analyses, calving dates and climate data to partition the year into six seasons (see Chapter 3, pp.33). I calculated ranges on an annual basis so that caribou who survived the full two years had a total of 12 seasonal ranges (i.e., 2 ranges per season). As at the home range scale, there was considerable variation in seasonal range sizes over the study period (23rd March, 2014–22nd March, 2016). Overall, ranges were largest in the early winter (EW) season and in the late winter/spring (LWS) season during the second year, which makes biological sense given that boreal caribou have been shown to migrate between summer and winter habitats (e.g., Brown et al. 2003, Ferguson and Elkie 2004). Ranges tended to be smaller in the calving/post-calving (CPC), summer (S) and autumn/rut (AR) seasons, which is generally consistent with trends observed in other populations (e.g., Rettie and Messier 2001, Brown et al. 2003, Ferguson and Elkie 2004).

Surprisingly, the mean LWS range size for the first year (i.e., 2014) was significantly smaller than all other annual ranges, except for the CPC season in year 2 (i.e., 2015). This may point to variation in when caribou migrate to calving sites. Differences in mean range sizes were compared using *P*-values that were adjusted using the Bonferroni correction (Bonferroni 1935) which is an ultra-conservative method by which to test significance (see Table 4.2, pp. 69 for summary of adjusted *P*-values). When I compared mean range sizes using less conservative, unadjusted *P*-values, I found that, in addition to the significant difference between LWS range sizes in year one and year two, there was also a significant difference in CPC range sizes between the two years ($Z = 3.026$, $p = 0.002$). Specifically, LWS ranges were significantly smaller in the first year while CPC ranges were significantly smaller in the second year. In other words, a significant expansion in mean LWS range size was followed by a significant contraction in mean CPC range size. This relationship may be mediated by annual differences in the onset of migration to calving sites. We could reasonably expect that an earlier migration would cause an increase in LWS range size (and a corresponding decrease in CPC range size) because the LWS range would encompasses the migration route. However, if migration occurred at a later date, the migration route might overlap the two seasons, in which case we would observe a decrease in LWS range size and an increase in CPC range size. I compared the timing of individual calving events over the two years and found that the mean calving date for the second year (12th May ± ~1 day) was a full week earlier than the mean calving date for the first year (19th May +/- ~1 day). This suggests that female caribou arrived at calving sites earlier during the second year; hence LWS ranges were larger and CPC ranges were smaller.

As discussed in section *4.5.1* (pp.109), variation in migration (and therefore range sizes) can be due to an array of abiotic and biotic factors. In this instance, one could argue that temporal variation in migration to calving sites may be confounded by variation in the number of caribou that were pregnant each year. However, caribou pregnancy rates are usually quite high (e.g., pregnancy rates for populations of caribou in central Quebec have been estimated to be near 100% [Courtois et al. 2007]), and the pregnancy rate for our collared caribou in 2014 (estimated from an analysis of the progesterone concentrations in blood samples drawn from caribou at the time of capture) was 0.932 [95% CI: 0.875–0.978]). Hence, it is unlikely that differences in pregnancy rates accounted for much variation in migratory behaviour. Other factors such as fire disturbance, weather-related variables (i.e., temperature and snow-depth) and predation risk may play a more important role in guiding the migratory behaviour of female caribou in Saskatchewan’s Boreal Shield. Given the importance of calf survival to caribou population dynamics (Culling and Cichowski 2010, Environment Canada 2012, Weir et al. 2014), gaining a better understanding of what drives variation in caribou migration to calving sites, as well as how this variation may affect female reproductive success, will improve our understanding of both caribou demography and resource selection. Therefore, a more rigorous exploration of caribou migratory behaviour—especially between winter and calving sites—would be beneficial to the caribou range planning efforts in Saskatchewan’s Boreal Shield.

4.5.3 Resource Selection Analyses

Trade-offs between acquiring food and avoiding predators are important to many species' survival strategies (Lima and Dill 1990). The dynamics of risk-forage trade-offs can vary across spatiotemporal scales according to changes in the relevance of predation risk vs. forage availability as limiting factors (e.g., Rettie and Messier 2000), as well as within the same scale according to changes in levels of forage availability and predation risk at that scale (e.g., Fraser and Huntingford 1986, Lima and Dill 1990, Dussault et al. 2005). With respect to boreal caribou, predation risk is generally thought to have a greater influence on caribou resource selection at coarser spatial scales (e.g., home range or seasonal range; Ferguson et al. 1988, Rettie and Messier 2000, Gustine et al. 2006a), while forage availability is thought to become increasingly important at finer spatial scales (e.g., the food patch; Johnson et al. 2001). In other words, risk-forage trade-offs may be more prominent across spatial scales. I used resource selection functions (RSFs) to quantify resource selection by female boreal caribou across six seasons and at two spatial scales (i.e., coarse vs. fine) in order to test the relative influence of predation risk vs. forage availability on caribou behaviour through time and space. Consistent with Rettie and Messier (2000), I expected that predator avoidance would be the primary factor driving caribou resource selection at the coarse spatial scale while forage availability would better explain selection patterns observed at the fine spatial scale.

Resource selection patterns varied between seasons and within seasons across the two spatial scales. In general, there was greater inter-seasonal variation in patterns observed at the fine spatial scale. Results from my coarse scale analyses are consistent with the hypothesis that predation risk is a primary factor limiting how boreal caribou select resources at the coarse spatial scale while results from my fine scale analyses suggest that predation risk continues to govern caribou behaviour at the fine spatial scale. I did not observed a prominent risk-forage trade-off between the two spatial scales, but there was evidence to suggest that risk-forage trade-offs occur at the fine spatial scale for some seasons.. An in-depth review of the resource selection patterns as they relate to predation risk and forage availability is presented here.

4.5.3.1 Topographical Variables

Topographical features such as elevation and slope vary in how they influence the selection of resources by woodland caribou both within and between spatiotemporal scales (Jones et al. 2006). In some populations, woodland caribou have been shown to select for lowland habitats that facilitate spatial segregation from alternate prey species and predators (e.g., James et al. 2004, Latham et al. 2011a). In other populations, higher elevation habitats are used for the same purpose (Bergerud and Page 1987, Seip 1992). Similarly, caribou in different populations have been shown to select for resource units that varied significantly in steepness (Gustine et al. 2008). The steepness of slope may be especially important during the calving period at fine spatial scales, as females have shown a preference for level calving sites in some populations (Bergerud and Page 1987, Barten et al. 2001). In Saskatchewan's Boreal Shield, little is known about how predators (e.g., wolves and black bears) and alternate prey (e.g., moose) respond to elevation and slope; therefore it is not possible to draw empirical conclusions about the role of these variables in mitigating direct and indirect predation risk. However, results from my study show that, at the coarse spatial scale, female boreal caribou are more likely to occur at lower elevations and on shallower slopes across all seasons. Such a strong pattern suggests that both covariates are tied to a primary factor (potentially predation risk [e.g., Rettie and Messier 2000]) governing caribou resource selection at the coarse spatial scale.

At the fine spatial scale, female caribou continued to be more likely to occur on shallower slopes in all seasons except during the late winter/spring (for which it was not an important predictor of resource selection); however, they switched from being more likely to occur at lower elevations to being more likely to occur at higher elevations in all seasons except for early winter and summer (for which it was excluded from the top models). This switch from low to high elevations between scales may be indicative of a continued response to predation risk in some seasons. For example, during the calving/post-calving season, female caribou selected for black spruce bogs at both the coarse and fine spatial scales. Bogs have been shown to mitigate predation risk in some systems (e.g., James et al. 2004, Latham et al. 2011a); therefore, caribou may have selected for black spruce bogs at the coarse scale as a predator-avoidance tactic. Because bogs are typically lowland habitats, selecting for them may have increased the likelihood that caribou occurred at lower elevations at the coarse spatial scale. At the fine spatial scale, female caribou may have been more likely to occur at higher elevations within black spruce bogs because these offer a better vantage point from which they can scan for predators (e.g., Gustine et al. 2006b). In other words, predation risk may have still been an important factor driving caribou resource selection at the fine spatial scale. For the same proximal reason (i.e., predation risk), caribou may have continued to select for shallower slopes at finer scales because it may be easier to outrun a predator on a shallower gradient.

In addition to slope and elevation, I included heat load index as a topographical variable in my resource selection models. Heat load is derived from transformations of slope, aspect and latitude and reaches a maximum on southwest facing slopes and a minimum on northeast facing slopes. Since the aspect of a slope is related to soil temperature, soil moisture content, and other factors that can affect the net primary productivity and composition of vegetation communities (Waugh 2002: 305), I included heat load index as a model covariate as it may capture the response of caribou to the topographical effects of slope aspect. More specifically, I was looking to see whether caribou were more likely to be found on warmer, drier southwest-facing slopes or on cooler, wetter northeast-facing slopes. At the coarse spatial scale, caribou were marginally more likely to occur on northeast-facing slopes during the early and mid-winter seasons. At the fine spatial scale, caribou were slightly more likely to occur on northeast-facing slopes during the early winter season and slightly more likely to occur on southwest-facing slopes during the summer and calving-post-calving seasons.

During the winter seasons, selection for northeast-facing slopes may be tied to the impact aspect has on forage availability and predation risk via its effects on snow depth, density and hardness. North-facing slopes typically have deeper, less stable snow packs because they don’t receive sufficient sunshine for the snow to melt and condense into a more solid layer (National Avalanche Center, http://www.fsavalanche.org/aspect/). Deep snow can influence the selection of food patches (e.g., caribou are more likely to crater for terricolous lichens in areas with shallower snow [Johnson et al. 2001, Kinley et al. 2003, Johnson et al. 2004b]); however, caribou may still select for northeast-facing slopes (and therefore areas with potentially deeper snow depending on tree cover) because their longer legs and broader feet may give them an advantage over wolves when running through deep snow (Telfer and Kelsall 1984, but see review in Bergerud et al. 2007: 406-410). This may represent a risk-forage trade-off within spatial scales. Alternately, selection for north-facing slopes may be tied to the strong selection for mature jack pine forests, which tend to occur on north-facing slopes in Saskatchewan’s

Boreal Shield (Acton et al. 1998). Due to their denser canopies, mature conifer forests are subject to less snow accumulation; thus, selection for north-facing slopes may actually be tied to selection for areas with shallower snow depth and, accordingly, easier access to forage (e.g., Parker et al. 2007, Courbin et al. 2009). Heat load index proved to be a difficult variable to interpret. I used it as a proxy for slope aspect; however, it may have been more prudent to just use aspect because: (a) this would have guarded against any confounding effects the non-linear relationship between slope and heat load index had on resource selection; and (b) made the models more comparable to other studies of caribou resource selection (e.g., Poole et al. 2000, Gustine et al. 2006a and Jones et al. 2006 all included aspect in their resource selection studies).

4.5.3.2 Climate Variables

Snow depth has been shown to influence caribou diets and choice of feeding sites through its effects on forage availability and accessibility (Adamczewski et al. 1988, Rominger and Oldemeyer 1990, Johnson et al. 2001), and may also hinder caribou locomotion if it is too deep (e.g., Henshaw 1968) or too soft (e.g.,Adamczewski 1988). Under some conditions, deep snow may also increase predation risk from wolves (see review in Bergerud et al. 2007:406-410), although lower adult caribou mortality during the winter vs. the summer (e.g., McLoughlin et al. 2003) suggests caribou gain an advantage over wolves during the winter. Given the importance of snow depth in other systems (Adamczewski et al. 1988, Rominger and Oldemeyer 1990, Johnson et al. 2001, Kinley et al. 2003, Johnson et al. 2004b), I expected snow depth to come out as a significant predictor of caribou resource selection during the winter seasons, especially at the fine spatial scale. However, snow depth was only included in top models for the late winter/spring season (coarse and fine scale) and the early winter (fine scale). During the late winter/spring season, female caribou were more likely to select for areas with shallower snow depth, a pattern which is generally linked to the fact that shallower snow facilitates easier access to terricolous lichens (Johnson et al. 2001, 2004b). Conversely, caribou were more likely to occur in areas with deeper snow during the early winter and at the fine spatial scale, which seems puzzling given they were also more likely to occur on south-facing slopes (south-facing slope tend to accumulate less snow than north-facing slopes [National Avalanche Center, http://www.fsavalanche.org/aspect/). However, consider that while values for mean daily snow depth were extrapolated across the study area from just six weather stations, the building blocks of the heat load index (e.g., slope, aspect and latitude) were derived from raster layers comprised of 30 m × 30 m pixels. Clearly, heat load index is capturing environmental changes at a much finer resolution than snow depth, which makes it difficult to reconcile the values for these covariates. In the future, it would be better practice to use values for snow depth that were measured at a resolution more relevant to the fine spatial scale.

Temperature has been shown to significantly affect the activity budgets (e.g., resting, travelling, foraging) of caribou (Morschel and Klein 1997), as well as the timing of key forage species in the spring (Russell et al. 1993). Accordingly, temperature has the potential to affect caribou resource selection at both the coarse scale (e.g. via direct and plant-meditated impacts on the onset and speed of migration) and at the fine scale (via impacts on the rates of foraging, Morschel and Klein 1997). At the coarse spatial scale, female caribou were more likely to occur in resource units with cooler mean daily temperatures during the autumn/rut and mid-winter seasons (though only slightly more likely for the latter). At the fine spatial scale, they were more likely to occur in units with slightly higher mean daily temperatures during the early winter season. With respect to the coarse scale, I investigated whether the fact that caribou are more likely to be occur in resource units with cooler temperatures was tied to latitudinal shifts in the placement of seasonal ranges (i.e., since temperature tends to decrease moving towards the poles, placing seasonal ranges further north may result in coarse scale selection for units with cooler temperatures because a greater number of available points are likely sampled south of the range). To do this, I visually compared the relative placement of all seasonal ranges along the y-axis, but found no discernible trends in range placement from one season to the next. In other words, autumn and mid-winter ranges did not appear to occur further north than other seasonal ranges. As with snow depth, the effects of temperature were likely muted due to the coarse resolution of the data. It may be prudent to discard snow depth and temperature as covariates in future models, unless more accurate measures of these two variables become available.

4.5.3.3 Proximity to Linear Features

Wolves have been shown to not only select for linear features (e.g., Latham et al. 2011b), but also move up to three times faster along them than in natural forest (Dickie et al. 2016). In contrast, woodland caribou tend to avoid linear features, (e.g., James and Stuart-Smith 2000, Oberg 2001, DeCesare et al. 2012), possibly because they carry a higher predation risk than other landscape features. Accordingly, I predicted that female boreal caribou would avoid linear features at the coarse spatial scale as a predator avoidance tactic.

Contrary to this prediction, female caribou were more likely to occur in closer proximity linear features across all seasons at the coarse spatial scale. There are several possible explanations for this pattern. First, over 50% of linear features in the study area are constructed through or adjacent to habitat types that were selected for by caribou (e.g., mature black spruce forests and black spruce bogs), which means that caribou may be selecting for linear features by proxy. Specifically, I inspected the distribution of linear features across the study area and found that although roads rarely intersect black spruce bogs (total area of intersection = 0.12%), they commonly run through mature black spruce forests (total area of intersection = 23.5%) and over pixels denoted as being water (total area of intersection = 27%). Since black spruce bogs have high spatial correlation with water, roads, trails and other linear features are commonly constructed adjacent to this habitat class. It is important to note here that, contrary to what one might predict, most linear features that were constructed over pixels of water were not designated as all-season roads. This raises some concern as to the accuracy of the classification of water pixels on the original FEC map. . A second hypothesis is that linear features in Saskatchewan's Boreal Shield do not carry the same level of risk observed in other systems. Wolves may use linear features differently in this region or occur at densities that are too low to allow for regular association with them. From preliminary GPS-collar data for 18 established territories, we recently documented wolf home range sizes in the Saskatchewan's Boreal Shield to average >2,600 km² (*n* = 18; wolves in packs with at least one full year of data; T. Perry, University of Saskatchewan, *pers. comm.*). These territories are 2.5× larger than territories recorded for wolves in other boreal caribou ranges, including west-central Alberta where average pack home range size was 937 km^2 (Kuzyk 2002). As there is an expected strong, negative relationship between density and territory size for carnivores (reviewed in McLoughlin and Ferguson 2000), this suggests that wolf densities are relatively low in the study area. Hence, they may not use linear features regularly. Further, since 96.9% of linear features in the study area are low impact geophysical survey lines and trails with minimal vehicle traffic, human-caused mortality associated with linear features is likely low. Finally, it is possible that sampling of caribou was biased towards individuals occurring near roads, as our fuel caches were principally accessed near roads for logistical reasons.

The response of caribou to linear features was more variable at the fine spatial scale. During the calving/post-calving and three winter seasons, caribou were more likely to be found farther from linear features; however, during the summer season, they continued to select for resource units that were in closer proximity to these features. Linear features were not a significant predictor of caribou resource selection during the autumn/rut season. The fact that boreal caribou shifted their response in four of the seasons suggests linear features are associated with some degree of risk. As an example, caribou selected for mature conifer-dominated forests (e.g., jack pine and black spruce forests >40 years old), black sprue bogs and open muskegs during the calving/post-calving season. The latter two habitats may facilitate spatial segregation from predators and alternate prey species (e.g., James et al. 2004, Latham et al. 2011a), and all three may provide seasonal forage to support lactation (Thomas et al. 1994); therefore, it makes sense that caribou positioned their seasonal ranges over these habitat classes. However, in doing so, caribou were also selecting for linear features by proxy (as discussed on pp. 117). Now consider the shift to avoiding linear features at the fine spatial scale. This suggests that when choosing patches within seasonal ranges, female caribou opt for sites that are further from linear features, possibly as a predator avoidance tactic. This response is reminiscent of the response observed for elevation (see section *4.5.3.1*, pp.113-114), and may offer additional support for the hypothesis that predation risk is an important limiting factor at both the coarse and fine spatial scales for the calving/post-calving season.

4.5.3.4 Reproductive Status

Female caribou with calves (hereafter CWC) may behave differently than female caribou without calves (hereafter CNC) because: (a) they incur greater energetic costs associated with lactation (Chan-McLeod et al. 1994), and (b) they are tasked with minimizing predation risk to their vulnerable offspring. Research has shown that during calving and post calving periods, CWC generally spatially segregate from predators and alternate prey species in order to minimize predation risk to their offspring (e.g., Bergerud and Page 1987, Pinard et al. 2012). They may also undertake local migrations to find patches of high quality forage during peak lactation (Gustine et al. 2006b). These behaviours illustrate the strong influence that calves can have on their mothers during the calving and post-calving periods. But what about the effect of calves outside these periods? Caribou calves can remain with their mothers for almost a year (Lavigeur and Barrette 1992), which suggests that some degree of dependence exists between neonates and adult caribou beyond the calving period. Indeed, Lavigeur and Barrette's (1992) work suggests calves are not behaviourally weaned from their mothers until approximately 160 days post-partum, meaning calves still rely on 'parental advice' well into the winter. To explore whether calves influence female caribou resource selection outside the calving and post/calving period, I included a variable for reproductive status (i.e., with calf or without calf) for all models (except those for the late winter/spring season, as calves are ~10 months old by this point and likely behaviourally weaned from their mothers [Lavigueur and Barrette 1992]).

Results indicate that caribou neonates had a significant (albeit small) effect on female caribou resource selection during the calving/post-calving season at both spatial scales. Outside the calving season, the presence of a calf was only weakly significant during the mid-winter season at the coarse spatial scale. The absence of a calf effect in most seasons is not surprising. Reimers (1983) showed that milk production in female caribou declines sharply approximately four weeks post-partum, which means calves may become nutritionally independent from their mothers at around one months of age (though note that they are still behaviourally dependent on their mothers [Lavigeur and Barrette's 1992]). Around that same time, CWC are suffering from a deficiency in fat deposition relative to CNC (Chan-McLeod et at. 1999). Since autumn body condition may significantly impact a female caribou's reproductive success in the following year (Cameron et al. 1993), female caribou likely relax their risk-averse behaviour in order to focus on building up sufficient protein and fat stores for the winter. Thus, as calves become more independent, the behaviour of CWC likely converges with the behaviour of CNC (assuming equal predation risk and access to forage). Hence, with the exception of the mid-winter season at the coarse scale, resource selection was not significantly affected by the presence of a calf outside the calving/post-calving season.

4.5.3.5 Habitat Classes

At the coarse spatial scale and across all seasons, caribou avoided mixed coniferous-deciduous forests, young to mid-successional conifer forests (e.g., jack pine and black spruce forests ≤40 years old), and mixed canopy swamps (albeit with a lot of variation in the response to this last habitat class). These patterns are strongly indicative of predator avoidance via spatial segregation from alternate prey (e.g., moose) and predators (e.g., wolves). Moose generally select for mature deciduous forests, young coniferous forests, mixed coniferous-deciduous forests, and riparian habitats (Seip 1992, Courtois et al. 2002., Dussault et al. 2005, Jacqmain et al. 2008), although they may also select for mature conifer forests as a thermoregulatory behaviour (Dussault et al. 2004). Since moose seem to be the primary prey of wolves in wolf-moose-caribou systems (Seip 1992, James et al. 2004), the avoidance of moose habitats in our system suggests caribou are spatially segregating themselves from moose in order to minimize apparent competition (i.e., predation from wolves mediated by the presence of moose). At the fine spatial scale, responses to potential moose habitat were variable across seasons, although caribou continued to avoid mixed canopy swamps and mixed coniferous-deciduous forests whenever they were included in a top model. Interestingly, YM jack pine forests were selected for during the autumn/rut, mid-winter and late winter/spring seasons. This is the most abundant habitat class within the study area (percent cover of land area = 39.2%) and so selection for this habitat may be an artefact of caribou having to traverse these younger forests as they move between forage sites and/or winter and summer habitats.

Mature conifer-dominated forests (e.g., jack pine or black spruce forests >40 years old) and black spruce bogs were commonly selected for at both the coarse and fine spatial scales, although the relative importance of each class varied between seasons. In general, mature jack pine forests were more important (i.e., had relatively larger, positive estimates for the posterior mean) during the three winter seasons while mature black spruce forests were more important during the calving/post-calving and summer seasons. Black spruce bogs were consistently important in all models for which they were included (note that this class was excluded from the coarse-scale model for the late winter/spring season and the fine scale model for the summer season). These patterns indicate that mature conifer forests and black spruce bogs are generally important habitats for caribou at both coarse and fine spatial scales, likely because they jointly provide refuge from predators, shelter from the elements and seasonal foraging opportunities (Environment Canada 2012).

Open muskegs were only included in six of the twelve top models, but were selected for in every case. In Saskatchewan's Boreal Shield, muskegs can be described as wetland habitats (e.g., bogs and fens) with sparse tree cover and varying abundances of herbs, grasses, forbs and sedges (see Table A1.1, pp.145, and also McLaughlan et al. 2010). Depending on the time of year and the behaviour of alternate prey species, muskegs may be associated with varying levels of risk and forage. During the winter, snow accumulation may be greater in muskegs due to the open canopy (although it may also be shallower in areas where strong winds cause the snow to drift up against the edges [Davies et al. 1991:160]). Thus, depending on the depth, density and hardness of the snow, moving through and foraging in muskegs during the winter period can be energetically costly (Henshaw 1968, Rominger and Oldemeyer 1990, Johnson et al. 2001). Conversely, if snow depths are shallower, it may be beneficial to forage in muskegs because: (a) they support high cover values of *Ledum* spp. (Labrador Tea), which may be minor, but important winter food item (Thomas et al. 1994); and (b) the open habitat allows them to detect predators from afar. During the spring and summer, muskegs support nutrient-dense gramminoids (e.g., grasses and sedges), willows (*Salix* spp.) and other plants that may be important forage items for woodland caribou looking to replenish fat and protein stores after the long winter (Thomas et al. 1994). However, some of these plants may also be important forage items for moose (Timmerman and McNicol 1988, Shipley 2010), in which case foraging in muskegs may increase predation risk (from wolves) to caribou via the mechanism of apparent competition (Holt 1977). At the same time, selection of muskegs during the calving/post-calving may minimize encounters with bears (e.g., Latham et al. 2011b), thus reducing predation risk from bears. Thus, selection for muskegs may represent a trade-off between risk from different predators (e.g., caribou may be "caught between Scylla and Charybdis" during the calving/post-calving and summer seasons [Leblond et al. 2016]).

Caribou in this study selected for muskegs during the calving/post-calving season (coarse and fine scale), early winter (coarse), late winter/spring (fine), autumn/rut (fine) and mid-winter (fine). Selection for muskegs at both the coarse and fine scale during the calving post-calving season suggests muskegs serve a dual purpose during this season: at the coarse scale, selection of muskegs may facilitate the spatial segregation from black bears while at the fine spatial scale, muskegs may provide critical seasonal forage. Caribou may minimize apparent competition with moose by using islands of mature conifer forests within muskegs as refugia. Since bears are hibernating during the mid-winter and most of the late winter/spring season, fine scale selection for muskegs during these periods may be linked to foraging opportunities (provided the snow is not too deep). Alternatively, caribou may use these habitats for thermoregulation on warmer, sunnier days (*pers. obs*). With respect to the early winter season, caribou may select for muskegs at the coarse scale to improve predator detection and/or minimize overlap with moose (e.g., James et al. 2004). Finally, it is challenging to make inferences about the fine scale benefits of muskegs during the autumn/rut season because caribou selected for juxtaposing habitat classes at this scale. Specifically, caribou were more likely to occur in mature conifer-dominated forests, young to mid-successional conifer-dominated forests, muskegs and black spruce bogs. This pattern may be linked to greater sporadic movement associated with the annual caribou rut. The rut is a dynamic period characterized by frequent duels between males and high rates of movement (e.g., mean daily movement rates for our study population were highest during the autumn/rut season; see section *3.3.1*, pp. 38-40). Accordingly, female caribou may be cycling through the habitats that are available to them at the fine scale due to the behaviour of the males.

4.5.4 Model Performance

Resource selection functions (RSFs) are routinely used to predict species' resource use and spatial distributions, often for the purpose of informing land management practices (e.g., James and Stuart-Smith 2000, Johnson et al. 2004a, Courtois et al. 2007, Courbin et al. 2009, Polfus et al. 2011). However, due to spatiotemporal variability in animal behaviour and environmental conditions, an RSF may break down when applied to geographic areas, time periods and/or populations other than those used to generate the model (Boyce et al. 2002), Thus, it is important to validate an RSF with an independent data set in order to assess its utility to land managers through space and time. I used a sample of twenty-four caribou fit with Lotek Wireless Inc. Iridium® Track M 3D radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) to validate my top models for each season and scale. Though this sample was not spatially or temporally independent from the sample used to train my models (*n* = 68 caribou fit with *Telonics TGW 4680-3* GPS/Argos radio-collars [Telonics Inc., Mesa, Arizona, USA]), the two populations (hereafter 'Telonics' and 'Lotek' caribou) could be considered functionally different due to potential differences in the accuracies of their collars in different habitat types. Given this point, it may have been more prudent to randomly sub-sample a validation set from the full sample population (*n* = 92 caribou) so that both the training and validation data were characterized by the similar errors in fix accuracy.

Predictive power was evaluated by comparing the posterior means of covariates in corresponding training and validation models. If the posterior mean of a covariate from one model occurred inside the 95% confidence interval of the other model, then that covariate was considered to be a consistent predictor of female caribou resource selection in Saskatchewan's Boreal Shield. Only 40% of the comparisons made between covariates were consistent; however, many of the trends observed in the training models were echoed in the validation models (i.e., the signs of the covariates' posterior means were the same but value of the posterior mean of one coefficient fell outside the 95% credible interval for the second coefficient). I scored training models according to their percent congruency (p.c.), which was the percentage of covariate comparisons between training and validation models that were consistent (see section *4.4.3*, pp.91-108, for details). The fine-scale model for the autumn/rut season recorded the highest percent congruency while the coarse-scale model- for early winter season had the lowest percent congruency. The mean percent congruency was below 50%, which means that aside from the fine-scale model for the autumn/rut season, inferences from the top models may be better limited to the sample population of Telonics caribou. In other words, the utility of the remaining models to land managers may be limited. That said, the general trends of selection and avoidance between models were similar. Therefore, we can make inferences about the general response of caribou in Saskatchewan's Boreal Shield to a particular coefficient (i.e., they select or avoid it); however we cannot be confident in making inferences about the strength of the response outside the sample of Telonics caribou.

With respect to individual covariates, comparisons between the posterior means for slope, mature jack pine forests and mixed coniferous-deciduous forests were over 50% congruous. Thus, we can have greater confidence in inferences made about the influence these variables have on how caribou select resources in Saskatchewan's Boreal Shield. .. In contrast, coefficient comparisons made between r the remaining 12 covariates were less ≤50% congruous. Accordingly, inferences made regarding the influence of these variables on caribou resource selection may be limited to the sample of Telonics caribou. Overall, top models were fairly representative of general trends in caribou resource selection, but may be less useful for making accurate predictions about the magnitude of the response of caribou to habitat attributes in Saskatchewan's Boreal Shield.

The poor predictive power of some covariates (e.g., elevation, mature black spruce forest, etc.) may be due to the fact that (a) the domain of availability was poorly defined at the coarse scale of analysis; and (b) habitat attributes were heterogeneously distributed between the Telonics and Lotek caribou such that the two populations had different domains of availability for these habitat attributes. One of the key assumptions of a resource selection function is that all habitat attributes are encountered with equal probability by all organisms within the domain of the study (Boyce 1999, Manly 2002). In other words, all resource units should be equally available to all organisms. This assumption is not met at the coarse scale of the analysis. Available points for each individual were randomly sampled from within the population range. If I had sampled available points from within individual home ranges, this would have established more realistic domains of availability for each caribou. With respect to habitat attributes, Telonics and Lotek caribou did not have access to the same range of values for elevation or the same densities of mature black spruce forests. In addition, the density of linear features in individual home ranges varied from 0 km/km^2 to 1.74 km/km^2. In general, caribou located in the western half of the study area were exposed to higher densities of linear features. Due to time constraints and a lack of sufficient computing power, I was unable to use random slopes (Gillies et al. 2006) to explicitly model this differential exposure (and thus potentially different response) of caribou to linear features However, given that linear features are potentially risky features (e.g., James and Stuart-Smith 2000, Oberg 2001, DeCesare et al. 2012) caribou exposed to higher densities of linear features may engage in different strategies to trade off access to forage with risk avoidance. Thus, it would be prudent to include a random slope for proximity (or density) of linear features in future models.

4.6 Conclusion

Overall, patterns of resource selection were similar between the coarse and fine spatial scales defined for this study (see summary of general patterns, Table 4.4, pp. 72), with some notable exceptions (e.g., changes in the response to elevation and linear features). Where patterns of resource selection are similar between scales, this suggests that the processes governing resource selection are the same or only change monotonically between scales (Wiens 1989). In other words, the coarse and fine spatial scales defined for this study likely occur within the same domain of selection (Wiens 1989). Based on the discussion presented above, results from this study support the hypothesis that predator avoidance is a primary factor driving resource selection at coarse spatial scales, and also suggests that predator avoidance continues to influence resource selection at finer scales. That is, resource selection at the coarse scale did not entirely free caribou from predation risk at the fine scale. Accordingly, I did not observe a strong trend in risk-forage trade-offs between spatial scales. During the autumn season, risk-forage trade-offs were harder to characterize, possibly due to the fact that caribou behaviour during this period is dominated by reproductive behaviour (i.e. searching for a mate and mating). I used proxies for predation risk and forage availability/accessibility in order to investigate multi-scale trade-offs between gaining access to forage and avoiding predators. In doing so, I had to make assumptions about how these proxies influenced the behavioural strategies adopted by female boreal caribou to make risk-forage trade-offs. A more objective approach would be to directly quantify forage availability (e.g., through remote sensing technologies [Pettorelli et al. 2005]) and predation risk (e.g., by deriving a spatial continuum of risk from measures of predators' habitat use [e.g., Hebblewhite and Merrill 2009]). Researchers with the University of Saskatchewan's Animal Population Ecology Lab (APEL) are currently working on building resource selection functions for wolves (*Canis lup*us) and black bears (*Ursus americanus*) in Saskatchewan's Boreal Shield using GPS data collected from radio-collared animals. Concurrently, the university's Northern Plant Ecology Lab (NPEL) is mapping the distribution of terricolous lichens using a combination of remote sensing and vegetation sampling throughout the Boreal Shield. Once these projects are complete, researchers will have the tools necessary to objectively quantify predation risk and forage availability. At that time, I strongly recommend that researchers update the models presented here with this new information.

Organisms often have to trade off gaining access to forage with avoiding predators in order to maximize their fitness (Lima and Dill 1990). These risk-forage trade-offs can vary across spatiotemporal scales (Lima and Zollner 1996), and there may be benefits for some species in avoiding risk at coarser scales so they can focus on foraging at finer scales (Brown and Kotler 2004). Rettie and Messier (2000) found that resource selection by woodland caribou in central Saskatchewan was limited by predation at a coarse spatial scale (seasonal range) and better explained by forage availability at a fine spatial scale (area inside a 1-km buffer around telemetry locations). Caribou in Rettie and Messier's (2000) system appeared to make a distinct risk-forage trade-off between scales; however this between-scale trade-off was less evident in my study. Results showed that while predation risk appears to be a primary factor limiting caribou resource selection at coarser spatial scales, it may also continue to govern selection at finer spatial scales. In other words, resource selection at the coarse spatial scales did not always free up caribou to focus on foraging at fine spatial scale. Resource selection patterns also suggested that caribou may make risk-forage trade-offs within both coarse and fine spatial scales, which suggests that caribou can reduce predation risk by making strategic habitat choices within the same scale. Johnson et al. (2001) theorized that because caribou show enormous behavioural and physiological plasticity, they are not limited to one behavioural strategy when it comes to making risk-forage trade-offs; instead, they adopt different behavioural strategies depending on environmental conditions (e.g., levels of risk, climate, forage availability etc.) and their own physiological needs. Results from this study are consistent with this theory: female caribou in Saskatchewan’s Boreal Shield can make risk-forage trade-offs both within and between spatial scales according to their needs and current environmental conditions.

5.0 CHAPTER FIVE: GENERAL CONCLUSION

5.1 Review

Resource selection functions (RSFs) can be used to quantify animal-environment interactions underlying species distributions across multiple scales (e.g., Rettie and Messier 2000, Gustine et al. 2006a, DeCesare et al. 2012). As a conservation tool, they can be used to map species probability of occurrence within management units, thus providing land managers with important information as to which habitats species select to fulfill their life history requirements. However, because the factors governing a species' resource selection can vary over spatiotemporal scales (Johnson 1980, Manly 2002, Boyce 2006), it is important that RSFs are generated over scales that capture the responses of animals to their environment (Wiens 1989). Otherwise, RSFs may yield inaccurate predictions about a species' resource use (Turner et al. 1995, Manly et al. 2002). Often, modelling resource selection at multiple spatial scales can reveal important variation in animal-environment interactions through space and time (e.g., Rettie and Messier 2000, Apps et al. 2001, Boyce et al. 2003).

My ultimate objective was to characterize seasonal resource selection by female woodland caribou in Saskatchewan's Boreal Shield at two spatial scales (coarse vs. fine), in order to provide insight into the factors governing the distribution of caribou in this region. The coarse scale was defined at the level of the population range so patterns observed at this scale offered insight into which factors govern the placement of caribou seasonal ranges within the study area. The fine spatial scale was defined as 1-km buffers around individual GPS points remotely collected from radio-collared caribou; patterns observed at this scale offered insight into which factors might govern the selection of patches (e.g., for foraging, resting or travelling) within seasonal ranges.

Results suggest that predator avoidance is a primary factor driving caribou selection of resources at the coarse spatial scale, and may also continue to drive selection at the fine scale, especially during the calving/post-calving season. At the coarse spatial scale, females generally selected for mature conifer-dominated forest (e.g., jack pine or black spruce forests >40 years old) and black spruce bogs and avoided young to mid-successional conifer forests (e.g., jack pine or black spruce forests ≤40 years old), mixed coniferous-deciduous forest and mixed canopy swamps (although the response to this latter habitat class is likely spurious given the low probability that caribou encounter it). Patterns at the fine scale were more variable, but, in general, caribou continued to select for mature conifer-dominated forests and/or black spruce bogs and avoid mixed coniferous-deciduous forests and mixed canopy swamps at the fine scale. Open muskegs were important caribou calving habitat at both spatial scales. Caribou selected for linear features at the coarse scale of the analysis, but then avoided them at the fine scale of analysis. Selection for this feature at the coarse scale may have been due to the spatial correlation between linear features and selected caribou habitat (i.e., in selecting for mature black spruce forests and black spruce bogs, caribou may have been selecting for linear features by proxy). At the fine scale, avoidance of linear features may be indicative of a strategy to minimize predation risk (assuming that linear features are risky). A robust analysis is needed to properly quantify the relationship between caribou predation risk and linear features.

5.2 Model Utility

Analyses of individual home and seasonal ranges suggested that there is considerable variation in space use by individual caribou. Results from the top resource selection models for each seasons and scale suggest that mature, conifer-dominated forests, black spruce bogs and, in some seasons, open muskegs, are important habitat for woodland caribou in Saskatchewan's Boreal Shield. Together, these patterns suggest that caribou require large tracts of these three habitat types in order to fulfill their life history requirements. But are the results presented here useful to land managers? In general, patterns observed at coarser scales are more useful to land managers because it is more feasible to manage landscapes at broader scales (Fortin et al. 2008). The model validation exercise revealed that, although top models at the coarse scale may adequately describe general trends in caribou resource selection (i.e., selection or avoidance of a given habitat attribute), inferences about the relative strength of selection or avoidance of given habitat attributes may be limited to the sample population used to train the models (i.e., the sample of caribou fitted with Telonics brand (Mesa, Arizona, USA) collars, $n = 68$ animals). In other words, the models presented in this thesis may not be useful for informing land management decisions.

The lack of model utility was likely due, in part, to a misspecification of the domain of availability at the coarse scale (i.e., available points should have been sampled from within individual home ranges). There are also issues with the accuracy of the FEC classification scheme, the delineation of seasons and some of the model variables that should be addressed as this project moves forward. First, the descriptions for many FECs are likely inaccurate due to small sample sizes and the fact that sampling sites were biased to being near roads or in easy-to-access areas (McLaughlan et al, 2010). The Northern Plant Ecology Lab (NPEL) is currently working to improve the accuracy of the FEC classification scheme through robust sampling across gradients of natural and human disturbance within the Boreal Shield. Once they have updated the site descriptions (i.e., descriptions of moisture regime, dominant overstory and understory vegetation, moisture regime etc.), habitat types should be updated to reflect this new knowledge. Second, using population-level movement rates to define seasons may have diluted important individual variation in seasonal movements and access to seasonal forage. Since management decisions are made over broader time scales than a season, defining a set of population-level seasons is not necessary from a land manager's perspective. Accordingly, it would be useful to define individual seasons for caribou per year to better capture local mating, calving and migratory behaviour. Finally, measures of snow depth and temperature were too coarse for the scales defined in this thesis. In addition, the habitat class 'mixed canopy swamps' may have been too rare on the landscape to justify including it as a covariate. These variables should be removed from future models, or, in the case of snow depth and temperature, measured at a scale that aligns with the scale of the study. Even then, one must be careful that measurements are accurate.

As a final point, it is important that land managers recognize that the boundaries of Saskatchewan's Boreal Shield are political artefacts, rather than ecologically meaningful delineators of local caribou populations. The shield encompasses an area that is approximately 187,238 km^2 and includes two distinct ecoregions that are characterized by different topography and abundances of habitat types. Accordingly, the suite of habitat attributes available to individuals in the two regions are different. Given that caribou can only make decisions about resources that are available to them, we could reasonably expect that resource selection patterns between caribou to vary across the Boreal Shield. Thus, the SK1 Caribou Administrative Unit (i.e., the boreal shield) may be better managed as a series of smaller units that better capture important local variation in behaviour. To capture this variation, I recommend finding an ecologically sensible method by which to cluster collared individuals (e.g., along gradients of resource availability [Fortin et al. 2008] or by partitioning animals according to median locations [Schaefer et al. 2001]) and then investigating resource selection patterns within smaller (but still feasibly manageable) populations of caribou. Models derived from this approach may have greater predictive power through space and time, which is especially important given the frequency natural fires in this system (>55% of area is estimated to have burned in the past 40 years [Environment Canada 2012]).

5.3 Concluding Remarks

The University of Saskatchewan is currently spear-heading several projects in Saskatchewan's Boreal shield that are aimed at improving the models presented in this thesis. Researchers in the university's Animal Population Ecology Lab (APEL) are working to describe caribou population dynamics and define resource selection functions for caribou predators (e.g., wolves and bears), while researchers in the university's Northern Plant Ecology Lab (NPEL) are mapping the distribution of terrestrial lichens in Saskatchewan's Boreal Shield. Once these projects are complete, researchers will be able to directly quantify caribou predation risk and the availability of key caribou forage in Saskatchewan's Boreal Shield, as well as tie patterns of caribou resource selection to caribou survival. This will be an exciting time for researchers as they fit all of the pieces of the caribou puzzle together. The methods and models presented in this thesis provide a good starting point for researchers looking to build the final models that will inform the identification of critical woodland caribou habitat in Saskatchewan's Boreal Shield; however, several issues need to be addressed so that future models can be confidently applied to management decisions.

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7.0 APPENDIX ONE: ADDITIONAL DATA TABLES

Table A1.1: Descriptions of twenty forestry ecosite classes (FECs) that occur in Saskatchewan's Boreal Shield. Descriptions were summarized directly from The Saskatchewan Ministry of Environment's *Field Guide to the Ecosites of Saskatchewan's Provincial Forests* (McLaughlan et al. 2010). Shrubs are defined as being less than 2m in height (McLaughlan et al. 2010).

FEC Code	# sample plots	Full Name	Ecosite Description
BS3	129	Jack pine/blueberry/lichen: moderately fresh sand	Overstory is dominated by jack pine; *approximately 75% of BS3 ecosites are pure jack pine*. The understory is relatively sparse and herbs are virtually absent. The forest floor is characteristically covered with reindeer lichens, with some Schreber's moss. Needle litter cover is significant. *Lichen species diversity is high*. Soils are deep sands.
BS4	88	Jack pine - black spruce/feathermoss: moderately dry sand	Overstory dominated by jack pine and black spruce; *however, ~60% of the sites are pure jack pine*. The understory consists primarily of ericaceous shrubs and green alder. The forest floor is predominantly a mixture of needle litter and Schreber's moss. Soils tend to be sandy loams.
BS5	36	Jack pine-white birch/feathermoss: moderately dry sand	Overstory is predominantly jack pine but may have substantial proportions of white birch and/or black spruce. The shrub layer is mostly ericaceous shrubs and green alder, with occassional willow and trembling aspen. The extensive leaf litter found on the forest floor is characteristic of this ecosite.
BS6	29	Jack pine -trembling aspen/green alder; moderately fresh loamy sand	Overstory has variable composition of trembling aspen in combination with jack pine. Black spruce and/or white birch are commonly found in both the overstory and understory. Eericaceous shrubs, green alder, and willow are also found in the understory. The leaf litter is relatively dense.
BS7	28	Black spruce/blueberry/lichen: moderately dry sand	Overstory is usually black spruce dominated and may be mixed with subdominant or codominant jack pine. The shrub layer generally consists of ericaceous shrubs, advanced-growth black spruce and the occasional willow or green alder. Herbs are sporadically distributed and the *dominant ground cover is reindeer lichen.*
BS8	6	Black spruce-white birch/lichen: moderately dry sandy loam	Overstory is typically black spruce dominated, often with locally abundant jack pine and white birch. The understory is composed of ericaceous shrubs, green alder and willow, sometimes with considerable black spruce advanced growth. Lacks a herbaceous layer, but typically has low cover-high diversity moss and lichen layer. Leaf litter usuallly
BS9	81	Black spruce-jack pine/ feather moss: moderately fresh sandy loam	Overstory predominantly pure black spruce or black spruce dominated.These ecosites tend to have high stem density and closed canopy conditions. Ericaceous shrubs and green alder are present on the site but herbaceous cover is low. One of the distinguishing features of this ecosite is the nearly continuous carpet of Schreber's moss.
BS10	15	Black spruce-white birch/feather moss: fresh sand	Sites tend to be dominated by black spruce. Jack pine and/or white birch may also be found in the overstory and the understory is composed of scattered ericaceous shrubs and the occasional willow. Schreber's moss is common as an extensive forest floor covering.
BS13	25	White birch-black spruce-trembling aspen: moderately fresh sand	White birch and black spruce occur in the overstory ~70 % of the time; however, birch and trembling aspen or black spruce and trembling aspen canopy combinations are also possible. Ericaceous shrubs, green alder, low bush-cranberry, and willow are characteristic understory species. The herb layer is relatively abundant; moss cover is patchy.
BS14	32	White birch/ligonberry-Labrador tea: moderately dry sand	*Overstory usually pure or nearly pure white birch,* but can contain black spruce, white spruce, jack pine, or trembling aspen. The understory is mostly ericaceous shrubs and scattered green alder. A moderate herbaceous layer can usually be observed in combination with patches of Schreber's moss and scattered lichens. Substantial leaf litter.
BS15	38	Trembling aspen-white birch/green alder; moderately fresh loamy sand	*Overstory is pure or nearly pure trembling aspen* with white birch sometimes present in small amounts. Approximately 10% of BS15 ecosites may include black and/or white spruce, jack pine, or balsam poplar in the overstory. The understory of BS15 ecosites is relatively rich with a variety of both shrub and herb species. Moss and lichen cover is low.
BS16	4	Black spruce/balsam poplar/river alder swamp: very moist mesic organic	Overstory can be nearly pure black spruce or pure balsam poplar and may have scattered white birch. River alder, willows and low bush-cranberry are common in the understory as are sedges and a variety of moisture loving or moisture tolerant herbaceous species. While Sphagnum will be the dominant moss, feathermoss is also frequently encountered.
BS17	44	Black spruce treed bog: very moist mesic organic	Consistently have a somewhat open canopy of all-aged black spruce. Tamarack may also occur on about 20% of the sites but with relatively little cover. The understory is largely ericaceous shrubs (mostly Labrador tea) and the ground cover is represented by an even distribution of Sphagnum and Schreber's moss.
BS18	33	Labrador tea shrubby bog: moderately wet mesic organic	Dominated by a variety of ericaceous shrubs, notably leatherleaf and Labrador tea. Occasionally, black spruce, tamarack or even jack pine can occur in tree form (i.e. >2 m), but the cover is usually low (i.e., <10%). Shrubby bogs tend to have a greater proportion of Sphagnum moss than would be found on treed bogs.
BS19	2	Graminoid Bog: very wet humic organic	Dominated by sedges and other graminoids in association with Sphagnum moss. They typically lack any substantial tree or shrub cover and can occur on mineral or organic substrates.
BS20	7	Open bog: moderately wet fibric organic	Dominated by Sphagnum moss (and a low cover of scattered Schreber's moss) and have low cover values of trees, shrubs and herbs. They are typically associated with organic soils.
BS21	2	Tamarack treed fen: Wet fibric organic	Tamarack is the predominant tree species, though black spruce and white birch may occurr. It is not uncommon for treed fens to have a water table at or near the surface.
BS22	21	Leatherleaf shrubby poor fen: very wet fibric organic	Leatherleaf, willow, and dwarf birch are the dominant shrub species; however, scattered tamarack or black spruce may also occur. Sedges are the dominant species in the herbaceous layer and Sphagnummosses are abundant. The substrate for these ecosites is usually organic although a mineral substrate is also possible.
BS23	11	Willow shrubby rich fen: wet fibric organic	*Have a characteristically high cover value of willow*. River alder, skunk and wild red current, dwarf birch, red-osier dogwood, and sweet gale are other common shrubs. Grasses tend to be more common than sedges. More commonly associated with a mineral soil substrate but will also occur on an organic substrate.
BS24	10	Graminoid fen: very wet humic organic	Has various sedge species and sometimes marsh reed grasses, but generally lacks trees and shrubs. Sphagnummoss is the most common moss. Usually has water at or near the surface, which accounts for the presence of bladderwort, a carnivorous aquatic plant. Usually associated with organic soils, but can also occur with mineral substrates.

Table A1.2: Summary of (a) individual calving dates for the 2014 and 2015 calving periods for 92 female boreal caribou, which were derived from Residence Time analyses (Barraquand and Benhamou 2008); and (b) the results from cow:calf surveys conducted during March 2015 and March 2016. n/a values for the cow:calf surveys denote caribou who were either dead, offline or not found during the survey.

Animal ID	Calving Event 2014?	Est. Calving Date (yyyy-mm-dd)	March 2015 Survey: with Calf?	Calving Event 2015?	Est. Calving Date (yyyy-mm-dd)	March 2016 Survey: with Calf?
140100	Yes	2014-05-15	n/a	n/a	n/a	n/a
140101	Yes	2014-06-08	No	Yes	2015-05-24	Yes
140102	Yes	2014-05-24	Yes	Yes	2015-05-30	No
140103	Yes	2014-05-24	No	Yes	2015-05-08	Yes
140104	Yes	2014-05-19	No	Yes	2015-05-15	Yes
140105	Yes	2014-05-14	Yes	Yes	2015-05-12	No
140106	Yes	2014-05-13	No	Yes	2015-05-17	Yes
140107	Yes	2014-06-17	No	Yes	2015-05-16	Yes
140108	Yes	2014-05-10	No	Yes	2015-05-11	Yes
140109	Yes	2014-05-18	Yes	Yes	2015-05-15	Yes
140111	No	n/a	n/a	n/a	n/a	n/a
140112	Yes	2014-05-26	Yes	Yes	2015-05-15	Yes
140113	Yes	2014-05-21	No	Yes	2015-05-14	No
140114	Yes	2014-05-19	No	Yes	2015-05-16	No
140115	Yes	2014-05-12	Yes	Yes	2015-05-11	No
140116	Yes	2014-05-15	No	Yes	2015-05-18	No
140117	Yes	2014-05-19	No	Yes	2015-05-11	No
140118	Yes	2014-05-20	No	Yes	2015-05-18	n/a
140119	Yes	2014-05-09	No	Yes	2015-05-06	Yes
140120	Yes	2014-05-13	No	Yes	2015-05-06	No
140121	Yes	2014-05-16	No	Yes	2015-05-08	Yes
140122	No	n/a	No	Yes	2015-05-04	No
140123	Yes	2014-05-28	No	Yes	2015-05-04	No
140124	No	n/a	No	No	n/a	No
140125	Yes	2014-05-14	Yes	No	n/a	n/a
140126	Yes	2014-05-14	No	Yes	2015-05-13	No
140127	Yes	2014-05-10	Yes	Yes	2015-05-12	No
140128	Yes	2014-06-01	No	Yes	2015-05-02	n/a
140129	Yes	2014-05-17	No	Yes	2015-05-12	No
140130	Yes	2014-05-15	Yes	Yes	2015-05-06	No
140131	Yes	2014-05-23	No	Yes	2015-05-12	No
140132	Yes	2014-05-25	No	Yes	2015-05-14	Yes
140133	Yes	2014-05-10	Yes	Yes	2015-05-07	Yes
140134	Yes	2014-06-15	Yes	No	n/a	No
140135	Yes	2014-05-10	No	Yes	2015-05-07	Yes
140140	Yes	2014-05-28	Yes	Yes	2015-05-11	No
140141	Yes	2014-05-15	No	Yes	2015-05-10	No

140142	No	n/a	No	No	n/a	No
140143	Yes	2014-05-15	No	Yes	2015-05-10	Yes
140144	No	n/a	No	No	n/a	No
140145	No	n/a	No	Yes	2015-05-15	No
140146	Yes	2014-05-10	n/a	n/a	n/a	n/a
140147	Yes	2014-05-25	No	Yes	2015-05-19	No
140148	Yes	2014-05-14	No	Yes	2015-05-05	No
140149	Yes	2014-05-12	n/a	n/a	n/a	n/a
140150	Yes	2014-05-13	No	Yes	2015-05-15	No
140151	Yes	2014-05-23	No	Yes	2015-05-17	No
140152	Yes	2014-05-14	n/a	n/a	n/a	n/a
140153	Yes	2014-05-22	Yes	No	n/a	n/a
140154	Yes	2014-05-15	No	Yes	2015-05-01	No
140155	Yes	2014-05-21	n/a	n/a	n/a	n/a
140156	Yes	2014-05-25	No	Yes	2015-05-18	No
140157	Yes	2014-05-11	No	Yes	2015-05-04	No
140159	Yes	2014-05-17	No	Yes	2015-05-20	Yes
140160	No	n/a	No	n/a	n/a	n/a
140161	Yes	2014-05-25	No	Yes	2015-05-06	No
140162	Yes	2014-05-24	n/a	n/a	n/a	n/a
140163	Yes	2014-05-20	No	Yes	2015-05-05	Yes
140164	Yes	2014-05-11	Yes	No	n/a	No
140165	Yes	2014-05-14	Yes	Yes	2015-05-06	No
140166	Yes	2014-05-11	n/a	n/a	n/a	n/a
140167	No	n/a	No	No	n/a	No
140168	Yes	2014-05-11	No	Yes	2015-05-06	No
140169	Yes	2014-06-10	Yes	Yes	2015-05-23	No
140170	Yes	2014-05-04	n/a	n/a	n/a	n/a
140171	Yes	2014-05-24	n/a	n/a	n/a	n/a
140175	Yes	2014-05-15	n/a	n/a	n/a	n/a
140176	Yes	2014-05-25	No	Yes	2015-05-14	Yes
140200	Yes	2014-05-29	n/a	n/a	n/a	n/a
140201	Yes	2014-05-15	No	Yes	2015-05-21	n/a
140202	No	n/a	No	Yes	2015-05-13	No
140203	Yes	2014-06-08	No	Yes	2015-05-11	No
140204	Yes	2014-05-20	No	Yes	2015-05-25	No
140205	Yes	2014-05-16	No	Yes	2015-05-05	No
140206	No	n/a	No	Yes	2015-05-12	No
140207	Yes	2014-06-05	n/a	n/a	n/a	n/a
140208	Yes	2014-05-23	No	Yes	2015-05-17	n/a
140210	Yes	2014-05-14	No	No	n/a	No
140211	Yes	2014-05-03	No	Yes	2015-05-08	No
140212	No	n/a	No	No	n/a	No

140213	Yes	2014-05-15	Yes	Yes	2015-05-10	No
140214	Yes	2014-05-23	No	Yes	2015-05-08	No
140215	Yes	2014-05-16	Yes	No	n/a	No
140216	Yes	2014-05-20	Yes	Yes	2015-05-16	n/a
140217	Yes	2014-05-23	No	Yes	2015-05-10	No
140218	Yes	2014-05-26	No	Yes	2015-05-17	Yes
140219	Yes	2014-05-17	No	Yes	2015-05-12	n/a
140220	Yes	2014-05-27	No	No	n/a	No
140221	Yes	2014-05-13	Yes	Yes	2015-05-10	n/a
140222	Yes	2014-05-16	No	Yes	2015-05-12	No
140223	Yes	2014-05-21	No	Yes	2015-05-19	n/a
140224	No	n/a	No	Yes	2015-06-16	No

Table A1.3: Summary of the reference habitat classes used for each global resource selection model. Reference classes were assigned by comparing selection ratios (Manly et al. 2002) between habitat classes for each season and scale. The habitat class with the selection ratio closest to one was designated as the reference class.

Season	Scale	Reference Habitat Class
Late Winter/Spring	Coarse	Open Muskegs
Late Winter/Spring	Fine	Mixed Canopy Swamps
Calving/Post-Calving	Coarse	Mature Jack Pine Forest
Calving/Post-Calving	Fine	Mature Black Spruce Forest
Summer	Coarse	Mature Jack Pine Forest
Summer	Fine	YM Black Spruce Forest
Autumn/Rut	Coarse	Mature Black Spruce Forest
Autumn/Rut	Fine	Open Muskegs
Early Winter	Coarse	Mature Black Spruce Forest
Early Winter	Fine	Open Muskegs
Mid-Winter	Coarse	Mature Black Spruce Forest
Mid-Winter	Fine	Black Spruce Bogs

Table A1.4: Summary of home range areas and core range areas for 92 female woodland caribou fit with radio-collars in Saskatchewan's Boreal Shield. Home ranges were delineated as a 95% utlization distributions (UDs, Van Winkle 1975) while core ranges were delineated as 50% utilization distributions. Kernels were estimated using a plug-in bandwidth. Ranges were estimated using up to two years of spatial data remotely collected from individual caribou. A "Yes" in the column 'Two Years?' means that individual survived for the full two years of sampling; a "No" indicates the animal died, went offline or dropped its collar before the end of the sampling period.

AID	No. Fixes	Core Range Size (km^2)	Home Range Size (km^2)	Two Years?	AID	No. Fixes	Core Range Size (km^2)	Home Range Size (km^2)	Two Years?	AID	No. Fixes	Core Range Size (km^2)	Home Range Size (km^2)	Two Years?
140100	987	11.80	126.98	No	140132	2529	19.20	205.88	Yes	140168	2951	77.03	484.72	Yes
140101	2977	76.14	584.09	Yes	140133	2776	32.65	207.49	Yes	140169	2817	61.34	406.18	Yes
140102	2004	15.76	142.31	Yes	140134	2915	32.37	226.36	Yes	140170	507	9.22	68.16	No
140103	2779	30.06	208.44	Yes	140135	3014	32.55	288.36	Yes	140171	917	193.07	1354.14	No
140104	2974	68.20	417.85	Yes	140140	2297	140.80	963.61	Yes	140175	571	28.02	253.51	No
140105	2549	17.53	90.17	Yes	140141	2897	106.57	618.20	Yes	140176	2325	42.57	289.48	Yes
140106	2304	8.47	76.54	Yes	140142	2643	41.67	311.97	Yes	140200	949	41.38	500.63	No
140107	2772	30.86	175.72	Yes	140143	2883	76.90	728.73	Yes	140201	2037	30.51	204.83	No
140108	2724	13.22	166.49	Yes	140144	2036	103.57	509.88	Yes	140202	2888	163.46	1363.87	Yes
140109	2928	48.10	402.71	Yes	140145	2241	73.00	520.56	Yes	140203	2915	47.99	522.92	Yes
140111	601	10.91	122.42	No	140146	300	1.84	16.23	No	140204	2909	45.62	351.99	Yes
140112	2473	19.68	135.38	Yes	140147	3103	45.69	260.28	Yes	140205	2891	25.29	240.09	Yes
140113	2191	22.86	145.86	Yes	140148	3056	43.98	345.90	Yes	140206	2893	54.79	734.08	Yes
140114	2410	19.80	134.48	Yes	140149	714	45.42	372.85	No	140207	476	2.52	46.68	No
140115	3007	17.68	157.60	Yes	140150	2681	71.78	601.36	Yes	140208	2159	21.42	206.70	No
140116	2265	58.64	340.68	Yes	140151	2782	68.34	479.91	Yes	140210	2910	32.45	437.91	Yes
140117	1676	20.51	135.79	Yes	140152	780	22.01	151.80	No	140211	2918	84.88	647.67	Yes
140118	2019	16.93	120.85	No	140153	1673	47.15	376.79	No	140212	2892	109.98	720.08	Yes
140119	2385	35.42	299.47	Yes	140154	2918	29.63	237.43	Yes	140213	2919	109.02	826.37	Yes
140120	1826	19.51	184.45	Yes	140155	349	18.68	167.83	No	140214	2825	67.87	509.52	Yes
140121	2672	130.67	1200.77	Yes	140156	2525	74.93	706.98	Yes	140215	2910	35.36	213.57	Yes
140122	2407	53.46	351.19	Yes	140157	2875	67.31	465.21	Yes	140216	2204	12.54	115.35	No
140123	3114	13.98	135.69	Yes	140159	3222	26.88	255.07	Yes	140217	2890	40.61	307.30	Yes
140124	2458	40.63	225.93	Yes	140160	1371	154.86	1109.82	No	140218	2913	89.73	516.26	Yes
140125	2419	55.31	355.34	No	140161	2907	91.78	640.92	Yes	140219	2070	20.54	219.98	No
140126	2660	148.20	1040.92	Yes	140162	1206	42.02	261.07	No	140220	2892	26.48	214.67	Yes
140127	3064	125.06	904.16	Yes	140163	2702	100.48	919.26	Yes	140221	2247	39.45	352.66	No
140128	1315	63.11	535.64	No	140164	2514	42.05	365.92	Yes	140222	2922	18.39	113.48	Yes
140129	2840	44.07	314.02	Yes	140165	2519	92.66	619.46	Yes	140223	2452	60.84	473.96	No
140130	2504	51.97	456.27	Yes	140166	517	21.87	306.62	No	140224	2868	135.62	945.08	Yes
140131	1895	37.85	308.09	Yes	140167	2953	74.36	537.68	Yes					

8.0 APPENDIX 2: FIRE RASTER CREATION

Summary of the process behind the creation of the fire rasters that were used to assign black spruce-dominated and jack-pine dominated forests to mature (>40 years post-fire) and young to mid-successional (YM; ≤40 years post-fire) age classes.

Fire data (fire polygons and residual patches) from the years 1988 – 2014 were provided by Omnia Ecological Services (Omnia Ecological Services, Calgary, Alberta, Canada), while fire data from the years 1945 – 1947 and 2015 (fire polygons only) were provided by Gigi Pitoello from the Fish and Wildlife Branch of the Saskatchewan Ministry of Environment. Al

NOTE: ArcGIS tools are highlighted in **blue.** Attribute table headers are bolded in **red**. Command pathways and expressions are in **green**. Explanations are *italicized*. The term 'working title" just refers to the arbitrary name I assigned to each layer.

A. Initial Fire Layer Creation:

A.1: 1988-2014 fire data

1. Import all individual layers (e.g., **E-BS-burn-1988-hab-final_region.shp**) from the HABTECH 2015 folder **E-BS_Digitized Burns** – *this is one of the folders provided by Omnia Ecological Services; it contains the outline of all of the fire polygons.*

2. **Merge** all of the E-BS layers. Some of the fire polygons are not closed so they need to be repaired. Use the tool **Repair Geometry**.

3. **Dissolve** the merged E-BS layer, using the column **Year** as the priority. This means that whenever the year differs between two overlapping layers, the most recent Year value is ascribed to the area of overlap.

4. **Export** the new layer into a geodatabase. To do this, simply right click on the layer in the Table of Contents and select **Data -> Export Data…..**

   OUTPUT FROM A.1: a merged layer with all of the fires from 1988-2014.

A.2: 1945 – 1987 and 2015 fire data

*In order to add the fires from 1945-1987 and 2015 to the layer created in step 3, you need to work with another fire layer (titled **Fire_1945_2015**). This layer does not have residuals or water accounted for.*

5. Import the layer **Fire_1945_2015** into ArcGIS.

6. **Dissolve** the layer **Fire_1945_2015**, using the column **Year** as the priority (as above).

7. Extract all fire polygons from the dissolved layer with a **Year** value less than 1988 or greater than 2014. Use the tool **Select by Attribute**; specify the selection type as NEW SELECTION and the condition as **Year** > 0 or **Year**<=1987 or **Year**=2015. Right click on the **Fire_1945_2015** layer in the Table of Contents and choose **Selection->Create Layer from Selected Features**.

8. Export the new layer into the same geodatabase used in step 4. In this geodatabase, you should now have the following feature class layers:
    a. fire polygons from 1988-2014 (residuals and water NOT yet excluded)
    b. fire polygons from 1945-1987 and 2015

A.3: Combining the two fire layers

9. **Merge** the two fire polygon layers. **Dissolve** this merged layer, using the column **Year** as the priority (as above). Make sure to save all new layers into the geodatabase!

10. Use the tool **Polygon to Raster** to convert the merged and dissolved fire polygon layer from step 8 into a raster. You should now have a raster with all fires spanning 1945 – 2015 (working layer name: **Fire_Polygons**).

B. Excluding Residual Patches (the patches in fire polygons not consumed by fire):

11. Import all individual layers (e.g., **Threshold BS-Burn 1992_region.shp**) from the HABTECH 2015 folder **Threshold BS-Burns(1)**.

12. **Merge** all of the Threshold Layers. **Dissolve** this merged layer, using the column **Year** as the priority (as above).

13. Extract the residual portions of the above dissolved layer using the tool **Select by Attribute**; specify the selection type as NEW SELECTION and the condition as **Landcover_**= ‘Residual’. Right click on the dissolved layer in the table of contents and then choose **Selection->Create Layer from Selected Features**. You should end up with a layer containing the outline of all of the residuals.

14. There is a possibility that some of the residual patches may have been burned over by fires in later years. For example, a residual patch in 1988 may have been burned over by a fire in 1997. This needs to be accounted for.

15. Use the tool **Raster Calculator** to subtract the **Fire_Polygons** raster from the **Residuals** raster. This creates a new layer (working title: **Raster_Fire_Sub**) with positive and negative values for each pixel.

NOTE: When digitizing the fire polygons, the crew from HABTECH used Landsat images spanning (mostly) 5 year intervals (see the HABTECH methods PDF provided with the fire layers). This means that within those 5 year periods, we cannot be sure which residuals were burned over. Therefore, we want to exclude all residual patches from the ***Raster_Fire_Sub Layer*** *that have a value > -5 (i.e., there is less than 5 years between the residual patch and the overlaying fire).*

16. Use the tool **Extract by Attributes** to extract all pixels from the **Raster_Fire_Sub** layer with a value less than or equal to -5 (i.e., want to exclude all pixels with a value > -5). This creates a new raster layer (working title: **Residual Mask**).

17. Use the tool **Extract by Mask** to extract all pixels from the **Residuals** raster that fall within the extent of the **Residual Mask** layer. This is the final residual layer (working title: **Residual_Final**).

1. Use the **Raster Calculator** to exclude all of the residual patches from the **Fire_Polygons** raster; use the expression: SetNull(~IsNull(**Residual_Final**), **Fire_Polygons**). This results in a new fire raster without the residuals (working title: **Fire_No_Resid**)

C. Excluding Water Patches

NOTE: For this task, I used the water pixels extracted from Dr. Kunwar Singh's and Jonathan Henkelman's vegetation layer (working title: ***Veg_Water_Only1****)*

2. As above, use the **Raster Calculator** to exclude all of the water patches from the **Fire_No_Resid** raster; use the expression: SetNull(~IsNull(**Veg_Water_Only1**), **Fire_No_Resid**). This results in a new fire raster that has both the residuals and water excluded (working title: **Fire_Final_1**)

3. **Clip** the **Fire_Final_1** raster to the boundary of the SK1 region. Make sure that the extent of the clipped raster = the extent of the boundary of the SK1 region polygon. [NOTE: the clip tool for rasters can be found under **Data Management Tools -> Raster -> Raster Processing -> Clip**]**. The result is the fire layer Fire_1945-2015_NR_SK11.**

9.0 APPENDIX THREE: ANTHROPOGENIC DISTURBANCE MAPPING

Anthropogenic Disturbance Mapping for the SK1 Caribou Administration Unit

DRAFT Methods and Feature Codes, Version 1.0

Updated: June 01, 2016

Prepared by:
Shawn Francis, S. Francis Consulting Inc., and
Brent Bitter, Jackie O'Neil and Andrea Penner, Saskatchewan Ministry of Environment

1. Overview

This document describes version 1.0 human feature (disturbance) mapping for the SK1 Caribou Administration Unit in northern Saskatchewan (*Figure 1*). Linear features (roads, trails and cutlines) and areal features (settlements, mine sites, gravel pits, airfields, and similar) have been mapped separately. Future changes should be anticipated as better information becomes available and users identify potential errors or revisions that would increase the utility of the mapping for different applications.

2. Methods

The SK1 human disturbance mapping project was initiated in 2012. Saskatchewan Ministry of Environment staff and contractors, and University of Regina students, all contributed to data capture. A number of different sources and vintages of satellite and orthophoto imagery have been utilized to develop the human feature mapping. <u>Where ever possible, human disturbances and features have been interpreted and digitized at a scale of 1:5,000</u>. A more detailed methodology document will be developed at a future date.

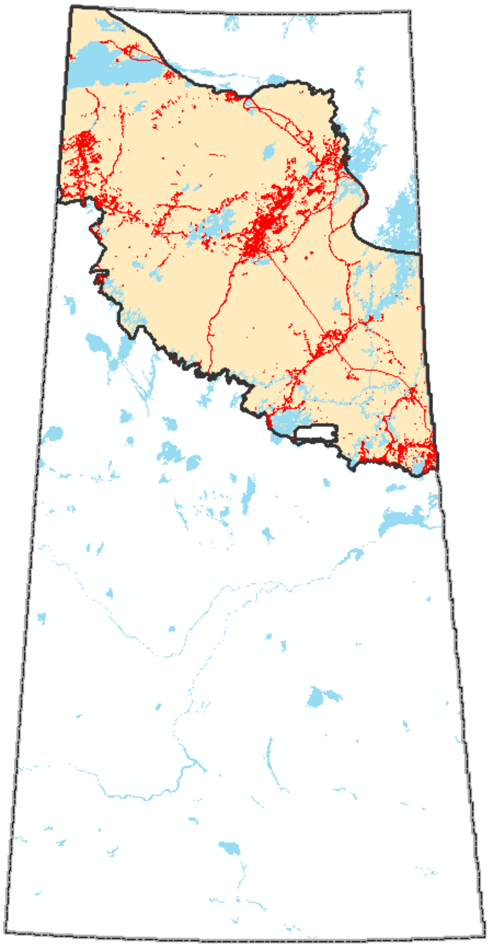

Figure 1. SK1 Caribou Administration Unit in northern Saskatchewan

3. Anthropogenic Feature Codes and Definitions

The DISTURBANC field contains anthropogenic feature codes. Feature codes and names for the linear and area features are listed in the following tables.

A3.1 Linear Features

File: \linear **\SK1_Anthro_Linear_v1.shp**
\SK1_Anthro_Linear_DirectFT_v1.shp

CODE	NAME	AVERAGE WIDTH (m)	DESCRIPTION	NOTES
EUC	Electrical Utility Corridor	30	Major electrical transmission and distribution lines and their associated cleared right-of-way.	New feature code; previously classed as TRN and TRA
FIR	Fire Break	20	Human-created linear clearings in forested areas around human settlements or structures for the purpose of fire protection.	Fire break widths are variable. In the future, this feature class may be better represented as an area feature class.
GEO	Geophysical Survey Line (Cutline)	2	Straight narrow clearings in forested areas for the purpose of surveying or mineral and oil and gas exploration. May occur in regular grid patterns. GEO can be differentiated from trails and rough roads, as those features are typically curvilinear.	GEO class includes previous CUT features.
MJR	Major Road	60	Major all-season roads. In SK1, most MJR are the main gravel surface north-south highways, but also includes large access roads to mine sites and communities. This feature class was originally considered as all-season paved roads (primary and secondary paved provincial high speed highways, > 80km/hr), but the MJR concept has been modified to fit the SK1 situation.	In the future MJR should utilize the Primary roads from the CARTO CLASS attributes from the TRANSPORTATION.Roadseg linear shapefile. A major road is generally considered a paved road with ditches but in SK1 MJR are generally gravel roads with ditches. Referring to the above mentioned shapefile would help classify the roads more consistently in this dataset.
MNR	Minor Road	44	Minor all-season roads. In SK1, MNR are located around, and provide access to, some mine sites and communities. Generally considered gravel roads with noticeable ditches. MNR would typically have lower amounts of traffic than MJR	MNR is considered a gravel road with noticeable ditches visible from FlySask Imagery. In the future MNR should utilize the Secondary roads from the CARTO CLASS attributes from the TRANSPORTATION.Roadseg linear shapefile.
MUR	Municipal Road	20	Roads within and around residential areas, villages, towns, and cities.	MUR was added to differentiate between roads within and outside of built-up areas. Previously classed as MUN.
TRL	Trail	12	A linear transportation feature suitable for travel by motorized off-road vehicles. Generally considered any rough road that is not a Major or Minor Road. This includes forestry and ATV trails but they are smaller and narrower in size. Trails may or may not have ditches.	In the future, it may be useful to separate out large trails with obvious vehicle tracks and smaller trails only accessible by quads, snowmobile, or similar.
UNK	Unknown Linear Feature	12	Any unknown linear disturbance that does not fit into any other categories, or was unknown to the interpreter.	
WTR	Winter Road	12	A rough road or trail that is only usable under frozen conditions. Some winter roads utilize frozen water bodies (e.g., winter road to Uranium City).	This is a new feature class that was not included in previous versions of the mapping.

3.2 Areal Features

File: \areal**SK1_Anthro_Area_v1.shp**

CODE	NAME	DESCRIPTION	NOTES
AGR	Agricultural Region	Large land areas that have been cleared for cultivation or grazing. AGR is the dominant land cover in southern and central Saskatchewan but only occurs in the very southern fringe of SK1.	
AIR	Airstrip	Paved or unpaved runways suitable for use by fixed-wing aircraft. A large number of AIR features are located in SK1 near communities, camps and mine sites.	Many AIR features were originally mapped as linear features; these were buffered by 50m (100m average width), added to area AIR features, and then deleted from the linear feature file. In the future, AIR mapping could be improved by utilizing NAV Canada locations of all airstrips and aerodromes.
BLT	Built-up Area	Built-up (developed) areas, usually within and around towns and villages. Includes residential and commercial buildings and related infrastructure.	BLT includes the (MUN, previously termed residential, RES) and unknown buildings (UNB) classes from previous schema.
CMP	Camp	Commercial and recreational camps and lodges (includes mineral exploration/mining camps). Most camps are comprised of two or more buildings clustered together in a remote area, and if on a shoreline, usually have at least one dock structure.	
HAR	Forest Harvest Blocks (i.e., Cutblock)	Clear cut areas resulting from forest harvesting. HAR features are represented by the Forest Management Branch forest harvest database (Forestry.Actual_Harvest.gdb). Only harvest blocks between the years 1975-2015 were included.	Forest harvest areas were previously digitized by interpreters. This method was inaccurate and duplicated work completed by the Forest Management Branch. Forest harvest blocks were previously termed CUT (Cutblock).
HYD	Hydro Dams or Water Control Structures	Hydroelectricity dams and associated power generation facilities, or water control structures	

CODE	NAME	DESCRIPTION	NOTES
		New feature class	
IND	Industrial Areas	General industrial land use features (parking areas, storage buildings, etc.). In SK1 IND is typically associated with Mine Sites (MIN).	IND was originally intended to be used in area 'zoned for industrial land use'. However, broadening this category to general industrial use appears to fit the SK1 situation more accurately.
LFS	Landfill Site	Any site used for the disposal and burial of residential or industrial waste material (not TLP).	
MIN	Mine Site	Location of mineral or coal extraction, including major structures, clearings and facilities (tailings ponds are classified separately).	The major mining pit and associated facilities have been classified as MIN; associated storage buildings, clearings, etc. are classed as IND.
OTH	Other	Areal features that were able to be identified, but for which no category exists (look under field named "DATA_SOURC" for reference).	
PIT	Gravel Pit	Any excavation site or pit used for the extraction of aggregate (gravel, sand or rock).	
REC	Recreational Area	Camping or other recreational facilities located within a designated park boundary.	
TLP	Tailings Pond	Ponds (natural or man-made) or containment facilities for the storage of mining waste rock and fluids. Associated with Mine Sites (MIN)	
UNK	Unknown Areal Feature	Any unknown areal disturbance that does not fit into any of the other categories, or was unknown to the interpreter.	In the future some features can likely be classified into existing categories.
WSL	Waste Sewage Lagoon	Municipal waste stabilization lagoon used for sewage treatment.	