Population dynamics and critical habitat of woodland caribou in the Saskatchewan Boreal Shield

Interim Project Report, 2013–2016

Department of Biology

University of Saskatchewan

UNIVERSITY OF SASKATCHEWAN

November 18, 2016

Status of Woodland Caribou in the Saskatchewan Boreal Shield

ABOUT THIS REPORT

PDM

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TABLE OF CONTENTS

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1.0 EXECUTIVE SUMMARY

In 2013, the University of Saskatchewan, in collaboration with a consortium of industry and government partners, launched a multi-faceted research program on the population dynamics and critical habitat of woodland caribou in the Saskatchewan Boreal Shield (the SK1 caribou administrative unit). Our main goal has been to increase our understanding of how caribou are responding to natural and anthropogenic disturbance, predators in the region, and how we might define the amount, location, and type of critical habitat available to woodland caribou. This report presents an update on our research with respect to caribou population dynamics, mapping of caribou habitat, estimating critical habitat for caribou, and preliminary data on predator ecology for the Saskatchewan Boreal Shield to October, 2016. Our project continues until December, 2018, and we will produce a final report on items presented in this report at that time.

In consideration of all data available at the time of writing, we have come to the following preliminary conclusions with respect to the population status and trend of woodland caribou of the Saskatchewan Boreal Shield: (1) the population occupies some of the most pristine habitat available to non-migratory, forest-dwelling caribou in Canada, with very low levels of anthropogenic disturbance; (2) although being subject to large fires in the past 40 years, the SK1 unit retains large tracts of high-quality habitat available for woodland caribou, with half (50.1%) of the land area characterized by >40 year-old pine and black spruce forests, and black spruce bogs and open muskegs that positively predicted caribou probability of occurrence at a broad scale; (3) selected habitat supports some of the highest densities currently observed for non-migratory, boreal caribou in mainland Canada, which we estimate at 36.9 caribou/1000 km^2 (95% CI: 26.7–47.2 caribou/1000 km^2) or approximately 3380 caribou in our collaring study area, and what we expect to be around 5000 caribou across the Saskatchewan Boreal Shield; (4) at the same time, wolf densities in the region are likely low (based on estimates of ungulate prey biomass and home range sizes [e.g., territories of wolves are on average 3.5× as large as found in other caribou ranges; densities of the only other alternate ungulate prey in the system, moose, are recorded as being among the lowest in the boreal forests of North America]); and (5) hunting pressure by humans on woodland caribou in the region is also very low. We believe that, collectively, these conditions resulted in our finding that: (6) the population is presently characterized by high adult female survival rates (>0.90) and moderate-low recruitment (≈0.20 calves per 100 females in March), but yet high pregnancy rates (≈0.90); (7) these traits are suggestive of a large herbivore population that may be experiencing density-related constraints on further population growth, but not so much as to result in phasic population decline; and (8) the standing age- and sex-structure, combined with known survival rates and reproductive data, indicates a stable to slightly increasing population over the recent past and as a future projection (e.g., if we considered the chance that the population might decline to 90% of its current population size over the next 20 years, we observed that 24% of simulations resulted in this

outcome and 76% did not; alternatively, when we projected the likelihood of at least a 10% population increase from current size, 57% of simulations presented this outcome).

In terms the amount, location, and type of critical habitat available to woodland caribou in the Saskatchewan Boreal Shield, habitat classes selected by collared caribou included mature stands of jack pine- and black spruce-dominated forest, black spruce bog, and open muskeg. Other habitat types, including young and mid-successional jack pine and black-spruce forest, mixed-wood forests of various ages, white spruce forests of various ages, and mixed-wood canopy swamps were not good predictors of caribou occurrence. Caribou did not consistently avoid anthropogenic (linear) features on the landscape, and in fact caribou were shown to select for linear features in all seasons at the broad scale. This response to linear features may reflect a lack of predation or hunting risk associated with these lines as compared to other jurisdictions, given the low density of predators in the area and density of lines that are an order of magnitude less (at 0.1 km/km^2) than where linear features have been shown to affect caribou movements. Preliminary estimates of lichen forage availability within the amounts and types of vegetation associations selected by woodland caribou did not appear to be limiting. Our finding that approximately half of the available vegetation associations were mature forests selected by caribou was expected and reflects the natural fire cycle in the region (which is approximately 100 years).

We believe that one of the great values of our research may be in describing the dynamics of a woodland caribou population in a region that has changed little from historic conditions, i.e., the conditions in which the species originally evolved. As such, our data on woodland caribou of the Saskatchewan Boreal Shield may now serve as a 'benchmark' for the study and conservation of other caribou populations. We believe that the initial conclusion that the caribou population in the SK1 unit should not be self-sustaining, based on the disturbance threshold outlined in the federal *Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada*, is incorrect with what we currently know about the population and how it responds to available habitat. Rather, the best available evidence suggests that the status of woodland caribou in the Saskatchewan Boreal Shield is one of a large and self-sustaining population, perhaps one of the most secure populations of boreal caribou in Canada. Our final analysis and report on the population dynamics and critical habitat of caribou in the Saskatchewan Boreal Shield is scheduled for December 31, 2018.

2.0 INTRODUCTION

In 2013, in collaboration with our industry and government partners, the University of Saskatchewan launched to multi-faceted research program on the population dynamics and critical habitat of woodland caribou in the Saskatchewan Boreal Shield (Fig. 2.1). When we initiated this project, we knew little about the population dynamics of woodland (boreal) caribou (*Rangifer tarandus caribou*, hereafter 'caribou') in areas of relatively high natural disturbance but low human activity. Almost all research on caribou—a Threatened species listed on Schedule 1 of the Canada *Species at Risk Act* (SARA)—had been directed at highly modified landscapes where forestry and oil and gas projects contribute to the majority of the disturbance footprint (Environment Canada 2011, 2012). However, for caribou of the Saskatchewan Boreal Shield (the 'SK1' caribou administrative unit [187,000 km^2] as delineated in the October 2012 federal *Recovery Strategy for the Woodland Caribou, Boreal Population, in Canada* [Environment Canada 2012]), anthropogenic contributions to cumulative effects are minor compared with natural disturbance from fire. The SK1 range is noted for its short fire-return interval (BQCMB 1994; Parisien et al. 2004) with 55% of the region having been mapped as burned in the past 40 years[1]; while at the same time only 3% of the area occurs within 500 m of industrial features (e.g., roads, transmission lines, settlements, mines [Environment Canada 2012]).

In comparison, percentage area burned (<40 years old) and buffered by industry (500 m) averages 16.7 ± 15.7 [2.2] and 33.3 ± 26.6 [3.7] ($\bar{x} \pm 1$ SD [SE]), respectively, across all caribou ranges in Canada (data in Environment Canada 2012).

The SK1 unit also stands out as an 'intact' ecosystem: all of the expected predators (e.g., wolves [*Canis lupus*], black bears [*Ursus americanus*]) and alternate prey (moose [*Alces alces*], beaver [*Castor canadensis*]) occur, but without the invasive species
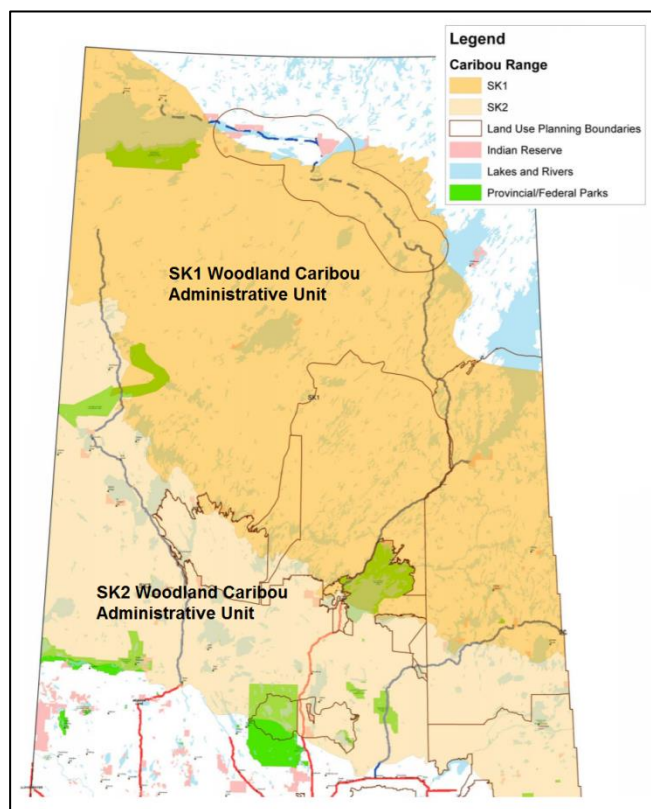
Fig. 2.1: Woodland Caribou Administrative Units in northern Saskatchewan, Canada.

[1]Using different methods compared to how fire data were initially provided by the Saskatchewan Ministry of Environment, Kansas et al. (2016) showed that this is likely an overestimate as a result of including post-fire residuals and water bodies as burned habitat.

(e.g., coyotes [*Canis latrans*], white-tailed deer [*Odocoileus virginianus*]) known from more southern ranges (e.g., Latham et al. 2011; Environment Canada 2011, 2012; McLoughlin et al. 2016). Initiating research on the ecology of SK1 caribou presented an opportunity to study woodland caribou in a region little modified by humans where historically natural processes dominate—the conditions in which the species evolved.

The special nature of the Saskatchewan Boreal Shield was highlighted in the federal *Recovery Strategy* (Environment Canada [2012]; Figs. 2.2–2.4). In this document, Environment Canada assigned status and identified critical habitat for caribou ranges nation-wide but noted that: "[…] northern Saskatchewan's Boreal Shield range (SK1) represent[s] a unique situation that falls outside the range of variability observed in the data that informed the disturbance model used by Environment Canada (2011) [p. 4]." Consequently, a status of 'unknown' was applied to the SK1 unit for both population viability (self-sustainability) and critical habitat. SK1 was the only range of 51 in Canada to be classed as data deficient in the *Recovery Strategy* (Figs. 2.3 and 2.4). Environment Canada identified December 2016 as the SARA-mandated deadline by which at least preliminary data on population dynamics and critical habitat for caribou in the range is needed; it is the only schedule of required studies in the *Recovery Strategy*. Acquiring this information is not only a priority for the federal government and researchers interested in how woodland caribou populations might function as part of a largely intact, natural system; but also the people that live and work in Saskatchewan. In the absence of information, communities and companies in the Boreal Shield region face regulatory delays and costs to investment with respect to future development, and little guidance as to how their activities must be mitigated to allow for acceptable practices under the Canada *Species at Risk Act* (SARA). Of particular concern are implications for developing access and infrastructure (roads, transmission lines) for northern communities and sustainably developing the region's mineral resources.

Table 6. Schedule of studies required to complete the identification of critical habitat in the Boreal Shield range (SK1) in northern Saskatchewan.

Description of Activity	Rationale	Timeline
Collect population information (size, trend, etc.) for a minimum of 2 years in SK1 where population condition is unknown.	The effect of a high fire and very low anthropogenic disturbance habitat condition on the SK1 local population is unknown. These activities will provide the necessary information to identify critical habitat.	Population data collected and critical habitat identified for SK1 by end of 2016.
Update disturbance model in Environment Canada's Scientific Assessment (2011b) by including population information for SK1 to incorporate situations of high fire and very low anthropogenic disturbance.		
Identification of critical habitat in SK1.		

Fig. 2.2: Reproduction of Table 6 of the October 2012 federal *Recovery Strategy for the Woodland Caribou, Boreal Population, in Canada* (Environment Canada 2012: p. 36), outlining a schedule of studies required to complete the identification of critical habitat in the Boreal Shield (SK1) Caribou Administrative Unit of northern Saskatchewan.
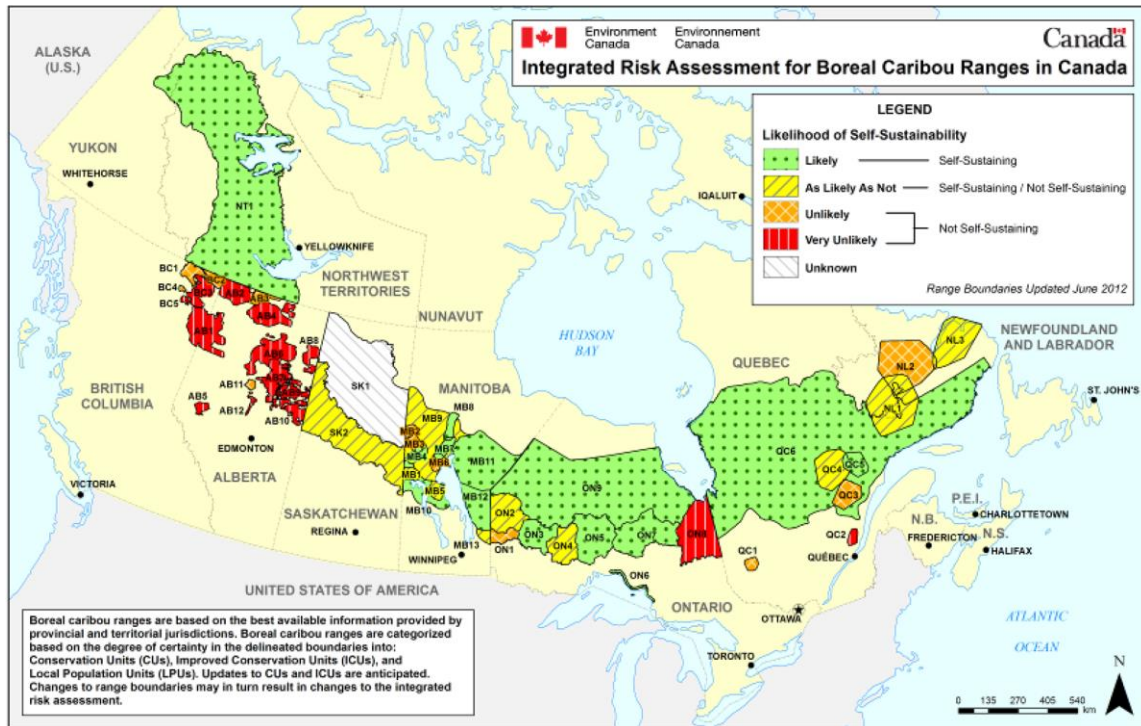
Fig. 2.3: Integrated risk assessment for boreal caribou ranges in the October 2012 federal *Recovery Strategy for the Woodland Caribou, Boreal Population, in Canada* (Environment Canada 2012: p. 8). Lack of data for the Boreal Shield (SK1) Caribou Administrative Unit of northern Saskatchewan precluded inclusion in the assessment model.
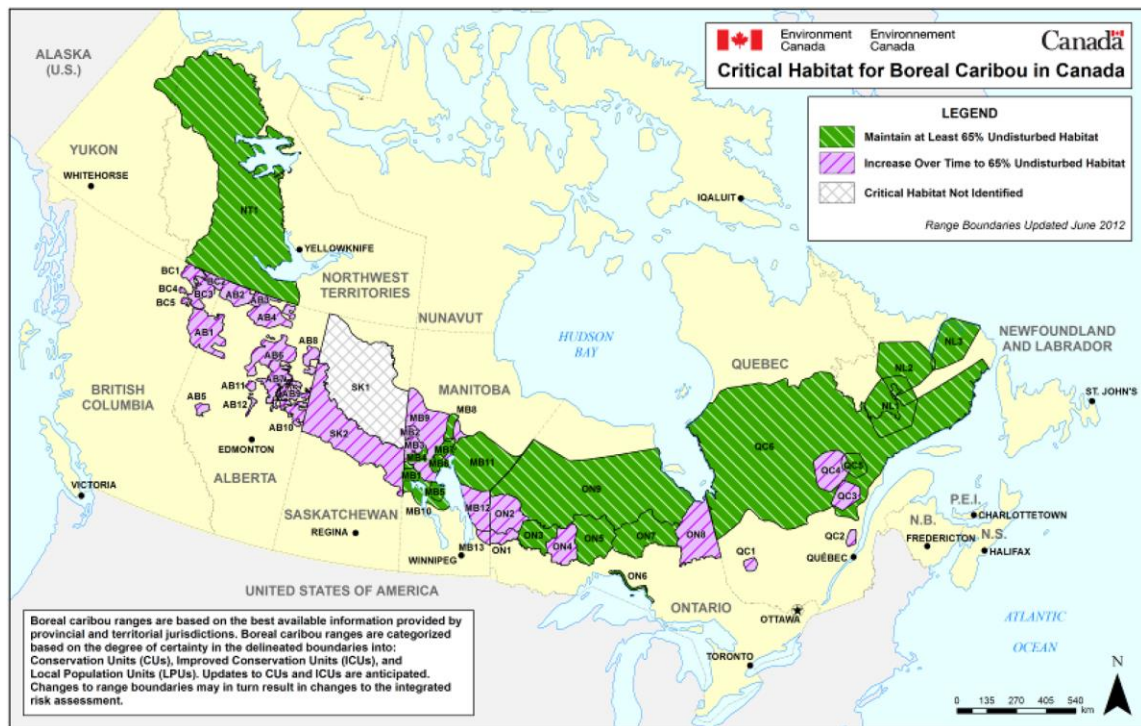
Fig. 2.4: Critical habitat assessment for boreal caribou ranges in the October 2012 federal *Recovery Strategy for the Woodland Caribou, Boreal Population, in Canada* (Environment Canada 2012: p. 33). Lack of data for the Boreal Shield (SK1) Caribou Administrative Unit of northern Saskatchewan precluded estimation of critical habitat.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

We initiated our project on caribou of the SK1 unit to address information gaps about caribou habitat and population dynamics closely aligned with information required by Environment and Climate Change Canada (ECCC) as part of the federal *Recovery Strategy* for boreal caribou (Fig. 2). With the above in mind, we have been pursuing a 5-year, comprehensive research plan founded in basic and applied ecology to study woodland caribou habitat in the Saskatchewan Boreal Shield, the population and behavioural ecology of caribou, and that of their natural predators including wolves and black bears. Our main goal has been to increase our understanding of how caribou populations respond to natural disturbances and low levels of anthropogenic disturbance, and how we might define the amount, location, and type critical caribou habitat. This report presents interim results for our project.

Section 3.0 identifies status, trend, and density (population size) for the SK1 caribou population at the time of writing. *Section 4.0* presents our analysis of critical habitat for caribou by identifying location, amount, and type of habitat that can best predict probability of occurrence of caribou. *Section 5.0* addresses our understanding of predators in the Saskatchewan Boreal Shield, including preliminary analyses of wolf ecology and plans for initiating research on the ecology of black bears in the region. By December, 2018, we will be in a position to more fully report on caribou population dynamics including status, trend, and population size; movements and habitat use of wolves and black bears in relation to caribou, and relative densities of these predators and alternate prey (moose); and present an updated and ground-truthed digital habitat map and interpretation of successional dynamics of habitat and caribou forage resources. Further, we will also be able to directly define 'critical habitat' according to the legal definition as it exists in the SARA (S.2[1]): "[…] habitat that is necessary for the survival or recovery of a listed wildlife species […]." For the latter, we will be directly relating survival and reproduction of tracked caribou and use their use of habitat features, and that of their predators, to predict those aspects of habitat that are most critical for survival and reproduction.

Our research is structured to comprise part of a larger directed-studies program for caribou in the province by the Saskatchewan Ministry of Environment and the Saskatchewan Woodland Caribou Technical Committee. Our focus is on work conducted through the western scientific tradition. We do not detail results of the ongoing community engagement process nor complementary Aboriginal Traditional Knowledge study that is also being conducted by the Saskatchewan Ministry of Environment and partners at the University of Saskatchewan.

3.0 STATUS AND TREND OF SK1 CARIBOU

Woodland caribou of the Saskatchewan Boreal Shield comprise one of the last remaining caribou populations in Canada that exists largely in the same state as it has historically. Caribou in the region occupy their normal extent of distribution (the fourth-largest range of 51 in Canada [COSEWIC 2014]); habitat disturbance is almost entirely driven by lightning-caused fire (only 6.1% of fires are human-caused compared to 52.5% of fires in the Saskatchewan Boreal Plain [Parisien et al. 2004]); hunting pressure is very low (*Section 3.2*); and only naturally occurring predators and alternate ungulate prey inhabit the area (wolves, black bears, moose). Very few woodland caribou populations in Canada can be characterized by these same conditions. No population has the juxtaposition of high-fire, low anthropogenic disturbance to the same extent as found in SK1 (see Table F-1 of Environment Canada [2012]). Whereas some ranges might have as low anthropogenic disturbance as has the SK1 unit, e.g., ranges in Labrador, heavy hunting compromises the viability of several of these populations (COSEWIC 2014). Other ranges may have as high fire disturbance, but there anthropogenic disturbance also dominates.

The unique conditions of the Saskatchewan Boreal Shield presented us with an opportunity to identify several ecological 'benchmarks' with respect to what we might historically have expected for the dynamics of a large woodland caribou population, including: (1) natural rates of survival and reproduction (pregnancy rates, productivity, recruitment) and population trend (which may be density-dependent; see Gaillard et al. [1998] for a review of what is expected for large herbivore populations); (2) resulting population age- and sex-structure; (3) regional-specific densities of caribou, predators (wolves and black bears), and alternate prey (moose); and (4) probabilities of extinction based on stochastic population projections. In practical terms, by identifying these benchmarks for SK1 caribou our aim was to both understand and inform as to how disturbance modelling as part of the federal *Recovery Strategy* (Environment Canada 2012) might predict status and trend of caribou populations when given novel data, particularly data collected under expected historic or 'baseline' conditions.

Population data on caribou (and densities of moose) are presented in this section. Interim data on predators (wolves and black bears) are presented in *Section 5.0*; however, these data are also discussed in the context of caribou population dynamics in *Section 3.4*. We analyze movements of SK1 caribou, including their responses to disturbance, habitat selection, and how these movements define critical habitat by predicting probability of occurrence in *Section 4.0*. From these data (*Section 4.0*) we identify the amount, type, and location of critical habitat in the Saskatchewan Boreal Shield. We also discuss how the amount and type of critical habitat available to caribou can explain dynamics of the SK1 population in *Section 3.4*.

3.0.1 HYPOTHESES AND PREDICTIONS

At the outset of our work, given the high amount of natural disturbance in the Saskatchewan Boreal Shield (55% of habitat was mapped as burned in the past 40 years [but see Kansas et al. 2016]); 3% of habitat was located within 500 m of an industrial feature [Environment Canada 2011, 2012]), initial projections for this population were dire. Although this level of disturbance might have been expected for the region (99–104 year fire-return interval for the Saskatchewan Boreal Shield *vs*. 263–288 years for the Saskatchewan Boreal Plain [Parisien et al. 2004]), the population was initially estimated as 'unlikely' to be self-sustaining (Environment Canada 2011). Presently, the *Recovery Strategy* identifies <35% disturbed habitat (equating natural with anthropogenic footprints) as a management threshold presenting a 60% probability for a local population of caribou to be self-sustaining (Environment Canada 2012: p. vii).

Where disturbance occurs in caribou habitat, it has been generally hypothesized that increases in the abundance of alternate prey like deer or moose (which favour early seral stages) may lead to increases in predator (principally wolf) numbers, which can then have a negative, consumptive effect on caribou through incremental increases on (principally calf) predation (Seip 1992; Wittmer et al. 2005; Serrouya et al. 2015). In the context of human modifications to landscapes that improve conditions for ungulate herbivores like moose or colonizing deer, this has been termed 'habitat-mediated apparent competition' (Hervieux et al. 2014): increasing alternate prey densities have a decreasing effect on caribou, similar to what might occur if alternate prey and caribou directly compete for space or resources (the competition is 'apparent', but not direct). Habitat-mediated apparent competition represents a special form of predator-mediated indirect effects of humans on caribou and is often cited as one of the most important reasons for why caribou populations may be in decline in areas subject to high levels of anthropogenic disturbance (Latham et al. 2011; Environment Canada 2011, 2012; Wittmer et al. 2013; Hervieux et al. 2013, 2014; McLoughlin et al. 2016).

Less is known about the demographic responses of caribou to disturbance by wildfire. We should expect a higher, more natural fire return interval in areas with low human footprint like the SK1 range, as fire suppression is generally directed at areas holding infrastructure and linear features provide fire breaks (e.g., strong, negative relationships exist for % area burned vs. buffered by industry for ranges of Environment Canada's [2011] assessment of woodland caribou habitat in both Alberta [$R^2 = 0.70$; $P < 0.002$] and Saskatchewan [$R^2 = 0.59$; $P < 0.025$]). Fire is thought to influence the distribution of caribou (Environment Canada 2011, 2012), but effects of fire on caribou habitat and how it may render areas unsuitable (e.g., by loss of mature conifer stands, lichens, and other forage, and increasing barriers to movement) has received much less attention compared to effects of anthropogenic disturbance. COSEWIC (2014) identifies fire as a 'low risk' to boreal caribou in terms of a limiting factor, and acknowledges that caribou co-evolved with forest fires; further, the effect of fires on caribou range occupancy is complex and subject to conflicting reports in the literature. Indeed, how disturbance plays a role in modifying the relationship between demography of caribou and habitat use is poorly understood, particularly

with respect to habitat responses of fire in areas of non-commercial forests like those of the Saskatchewan Boreal Shield. The assumption that fire will directly affect forage availability and habitat quality for woodland caribou is one that is frequently cited (Coxson and Marsh 2001; Dunford et al. 2006; Rupp et al. 2006; Dalerum et al. 2007; Collins et al. 2011), but demographic responses of loss of forage availability are not well known. Further, the assumption that fire might also indirectly affect caribou demographics through habitat-mediated apparent competition (Hervieux et al. 2014) has never been tested. We also do not know whether the mechanism of habitat-mediated apparent competition functions the same regardless of disturbance type (random polygons of fire *vs.* cutblocks *vs.* linear disturbances [roads, cutlines]).

As the Saskatchewan Boreal Shield is unique amongst most other caribou ranges in Canada, we had little information upon which to specifically base study predictions with respect to caribou status and population trend. Following what is known or expected from other caribou ranges in Canada, and what has been assumed for caribou in the SK1 range based on modelling, we drafted the following predictions with respect to status, trend, and population size for woodland caribou in our study area:

Prediction 1: Environment Canada (2011) reported that the national average for annual adult survival of boreal woodland caribou was 0.852 (i.e., 85.2% of tracked adult females [ages 1+], on average, survive from one year to the next). They also reported that the SK1 caribou unit was characterized as being 55% burned within the past 40 years, with 3% lying within 500 m of an anthropogenic disturbance, i.e., 58% of habitat was 'disturbed'. This is substantially higher than the $46.5\% \pm 23.9\%$ [3.3%] ($\bar{x} \pm 1$ SD [SE]) average disturbance footprint across all caribou ranges in Canada (Environment Canada 2012). Hence, we expected that the survival of adult female caribou in the Saskatchewan Boreal Shield would be ≤0.85, as compared to estimates obtained for other populations. This is because the mechanism purported to drive caribou population dynamics in areas of higher disturbance is directly related to expectations of higher predation rates by habitat-mediated apparent competition (Environment Canada 2011, 2012).

Prediction 2: Combinations of natural and anthropogenic disturbances do not seem to generally result in changes in pregnancy rates nor body condition of woodland caribou. Pregnancy is typically high in most caribou populations, even those in decline (Festa-Bianchet et al. 2011), excepting populations initially declining as a result of density-dependence (e.g., decline phase of George River caribou [Messier et al. 1986] or Newfoundland caribou [Morrison et al. 2012; Mahoney et al. 2016]) . Wittmer et al. (2005) noted high late-winter plasma progesterone levels indicating a 92.4% pregnancy rate across 8 sub-populations of caribou in British Columbia, with no relationship to population density and thus range condition. Pregnancy rates (90–100%) were relatively high in six ranges in northeast Alberta where populations were declining (McLoughlin et al. 2003). Despite the high amount of disturbance in the Saskatchewan Boreal Shield, we predicted pregnancy rates to be ≈90% based on results from other jurisdictions.

Prediction 3: Environment Canada (2011) showed a significant, negative linear relationship between winter calf:cow ratios as presented for 24 different study populations of boreal

woodland caribou and the non-overlapping, combined percentage of habitat within each unit that is either <40 years of age and/or within 500 m of an industrial disturbance (reproduced here as Fig. 3.1). The model predicting self-sustainability of populations does not distinguish between type of disturbance (i.e., total disturbance is used). Following Fig. 7 of Environment Canada (2011), we predicted that cow:calf ratios in the SK1 unit would fall near a ratio of 0.20, i.e., 20% of females in March would be accompanied by calves born the previous spring. Note, however, that the recruitment *vs.* disturbance model of Environment Canada (2011) is strongly driven by variation in anthropogenic disturbance, for which the SK1 unit has very little (only 3%). Environment Canada (2011) stated that: "...nearly 70% of the variation in caribou recruitment across twenty-four study areas spanning the full range of boreal caribou distribution and range condition in Canada was explained by a single composite measure of total disturbance (fire + buffered anthropogenic), most of which could be attributed to the negative effects of anthropogenic disturbance (p. vi)."
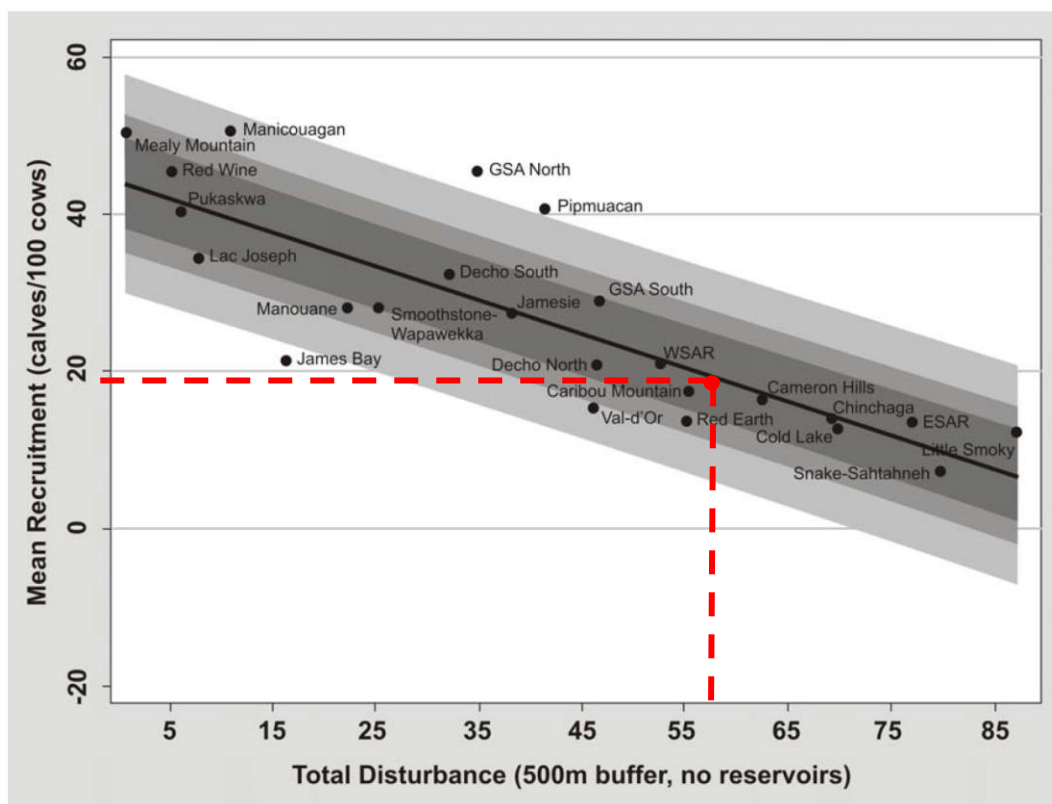
Fig. 3.1: Graph showing 50, 70 and 90% prediction bands (decreasing shading, respectively) for the best univariate regression model relating caribou recruitment (winter calf:cow ratios) and landscape disturbance (percentage combined footprints of areas burned within the past 40 years and non-overlapping, industrial features buffered at 500 m). Points are study areas (names of regions indicated). Data available in Environment Canada (2011) and figure reproduced from Environment Canada (2011). Expected recruitment at 58% total disturbance (i.e., conditions of the SK1 administrative unit), is indicated by the hatched red line and red circle, i.e., approximately 0.20.

Prediction 4: The finite rate of population growth (λ) is typically estimated for caribou populations by balancing the recruitment of female offspring into the breeding age category against the mortality of breeding females. The most commonly used equation is that of Hatter and Bergerud (1991), $\lambda = \frac{S}{1-R}$ (where S is survival and R is recruitment). This model assumes a 50:50 sex ratio in the structure of calves observed in March, when data on age and sex ratios (and adult female survival) are typically collected. Here, R is adjusted to reflect the total number of females of all age classes, including juveniles, counted at the end of a measurement year as opposed to simple calf:cow ratios (DeCesare et al. 2012). Given an average survival rate of 0.852 and calf:cow ratio of 0.200 (predictions P1 and P3, above), we were prepared for a declining population (geometric mean average) in the SK1 caribou range if Environment Canada's (2011) predictions and assumptions were true. Our naïve prediction was $\lambda = 0.942$ (estimated using Hatter and Bergerud [1991] but using recruitment [R] as the adjusted age-ratio [X] as recommended by DeCesare et al. [2012]). Note that values of $\lambda < 1.0$ indicate population decline, values of $\lambda > 1.0$ indicate population increase, and $\lambda = 1.0$ indicates stability. Hence, the population was predicted to not be self-sustaining and potentially declining at a rate of up to 5.8% annually. In terms of future population projections, which we conducted using an age- and sex-structured simulation model (*Section 3.2.5*), we expected that after 3 generations (20 years, assuming a 6–7 year generation length in caribou [Environment Canada 2012: Appendix 7.6; COSEWIC 2014), the proportion of time simulations resulted in population decrease would be substantially greater than population increase. We also expected that longer-term simulations would verify declines suggestive of a *Threatened* population, e.g., following Committee on the Status of Endangered Wildlife in Canada (COSEWIC) criteria for quantitative analyses of future trends (e.g., ≥10% chance of population extirpation after 100 years; COSEWIC 2010: see http://www.cosewic.gc.ca/pdf/assessment_process_e.pdf).

Prediction 5: We had little information on which base a prediction of population density or size for our study area, however we expected that caribou density estimates for the SK1 administrative unit would fall within the range observed for other provinces and territories. COSEWIC (2014: pp. 36–37) cites the following average densities of boreal woodland caribou across mainland Canada: Alberta (15.9 caribou/1000 km^2), British Columbia (4.3/1000 km^2), Labrador (18.7/1000 km^2), Manitoba (7.3/1000km^2), NWT (14.7/1000 km^2), Ontario (10.0/1000km^2), and Québec (10.4/1000 km^2).

3.1 Methods

3.1.1 ANIMALS AND TELEMETRY

In March, 2014, we engaged our field collaring program that saw to the deployment of 94 new GPS collars on caribou across the study area (Fig. 3.2). All caribou were captured and equipped
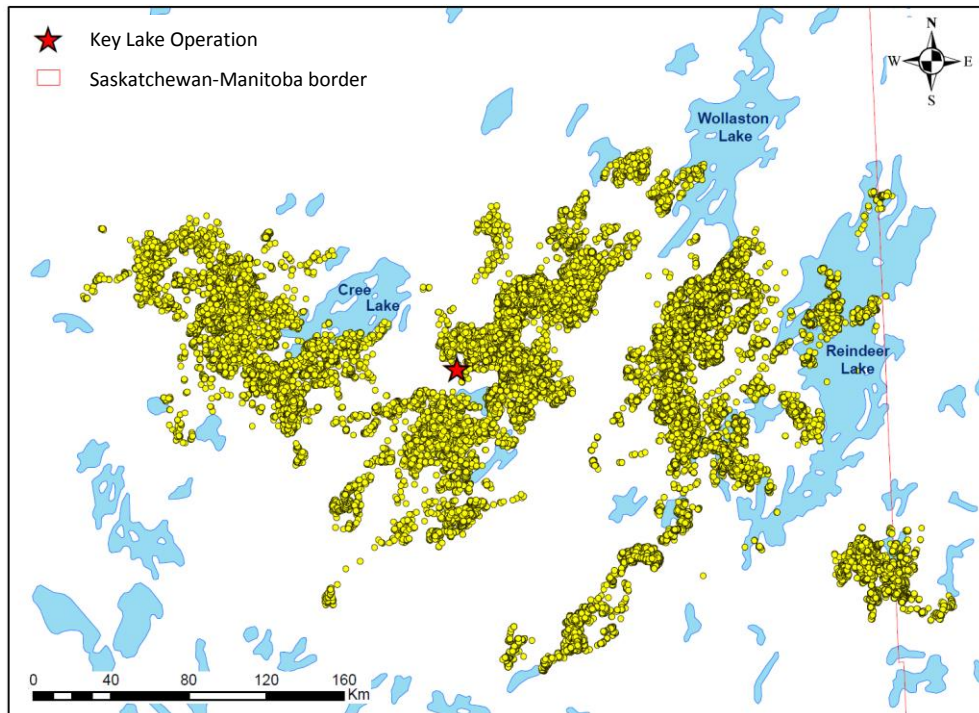
Fig. 3.2: Data generated from of 94 GPS-collared caribou in the study area (March 2014 to September 2016). The Key Lake mine is represented by the red star.
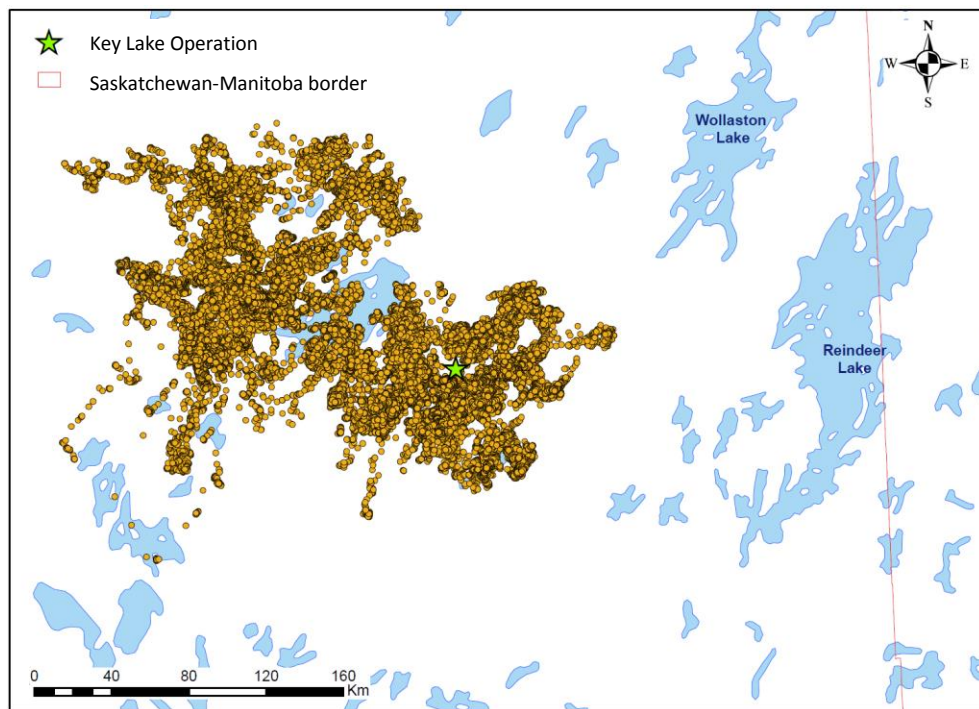
Fig. 3.3: Location data from GPS-collared caribou in the Key Lake and Cree Lake regions, being provided to the project as in-kind support by Cameco Corporation (data collection commencing March, 2013). The Key Lake mine is represented by the green star.

UNIVERSITY OF SASKATCHEWAN

with collars after physical immobilization (net gun) through the tendered services of Bighorn Helicopters Inc. (Cranbrook, British Columbia, Canada), following approved animal care protocol 20130127 of the University of Saskatchewan (guided by the Canada Council on Animal Care and the U of S Animal Research and Ethics Board) and permit 14FW037 of the Saskatchewan Ministry of Environment. These data add to collar data collected by industrial partners commencing in 2013 in the Cree Lake and Key Lake regions of the SK1 range (Fig. 3.3), which supplemented our GPS telemetry data (49 original [2013] + 7 redeployments [2014] plus 3 redeployments [2015] = 59 deployments to date) in these areas (collars and data being provided as documented in-kind support). Throughout this report, we report on results primarily from the perspective of the University of Saskatchewan telemetry data set, and rely on the data of our industrial partners as a 'truthing set', i.e., as an independent sample to gauge trends and directions determined using our data.

In all instances we only collared adult females (aged 1+), as female dynamics will determine λ as long as there are enough males to mate with available females (Caughley 1977). All caribou were physically immobilized by Bighorn helicopters Inc. (Cranbrook, British Colombia, Canada) using nets projected from a net gun and fired from a helicopter. Individuals collared by the University of Saskatchewan were equipped with Global Positioning System (GPS) collars including 25 Lotek Iridium® Track M 3D GPS collars (Lotek wireless Inc., Newmarket, Ontario, Canada) and 69 TGW 4680-3 GPS/Argos instrumentation units with CR-2A auto-release mechanism (Telonics Inc., Mesa, Arizona, USA). All caribou collared by our industrial partners were Lotek Iridium® collars. GPS data were programmed to transmit approximately every 4–5 hours and collars were provided with Very High Frequency (VHF) system to allow radio-telemetry tracking of caribou on the field. Upon capture (Fig. 3.4) we collected biological samples (blood, tissue, hair, scat [rectal collection]) for use in analyses of diet, parasitology, and pregnancy (progesterone, see *Section 3.1.2*). Fecal samples and whole blood spots on filter paper were submitted to the lab of Dr. Paul Wilson at Trent University for microsatellite and mitochondrial DNA analysis, as part of collaborative research with the University of Manitoba, Trent University, and the province of Saskatchewan on woodland caribou genetics. Remaining samples are currently stored in the freezers of the Department of Biology, University of Saskatchewan (including those of animals captured by the University of Saskatchewan and those of our industrial partners). Hair samples, red blood cells, remaining serum sub-samples, and fecal pellets are retained at the University of Saskatchewan for future potential analyses involving stable isotopes and contaminant analysis.

We conducted relocations of collared caribou by helicopter annually during autumn to determine if collars were dropped by caribou, if collars were malfunctioning, or if animals were dead (services provided by Helicopter Transport Services Canada Inc., La Ronge, Saskatchewan, Canada). We also relocated collared caribou annually in March to determine the number of cows observed with calves for estimating annual recruitment rates (below) from calf:cow and sex and age ratios. In determining these ratios, we considered all individuals observed in groups in which

Fig. 3.4: Capture crew members obtaining a blood sample from an immobilized female caribou in the SK1 caribou administrative unit, March, 2014.

collared females (whether a female had a calf with her or not, as determined by movements of calf with a targeted collared female during observation). We determined the sex of observed caribou according to the presence (female) or absence (male) of a black vulvar patch. When we were not able to determine the sex of at least one individual in a group, we removed the entire group from our dataset to ensure that sex and age ratios were accurately recorded.

3.1.2 ESTIMATING PREGNANCY RATES

Upon capture we collected biological samples (blood, tissue, hair, scat [rectal collection]) for use in analyses of diet, parasitology, pregnancy (progesterone), and caribou genetics. For this project, with respect to status and trend, our primary interest was in testing serum progesterone levels to estimate pregnancy rates (late gestational) in our sample population. On collection and prior to freezing at –20°C, whole blood samples were spun to separate serum from red blood cells. We submitted serum samples to Prairie Diagonistic Services Inc. at the University of Saskatchewan to determine progesterone levels in ng/ml. We assigned pregnancy as positive where progesterone levels were >1.3 ng/ml (min. 1.34 ng/ml). Rehbinder et al. (1981) reported annual maximum serum progesterone levels in non-pregnant captive reindeer of about 0.4 ng/ml and minimum levels in pregnant animals (between 20 and 200 days post conception) of about 1.3

ng/ml. Pregnancy rates are reported as percentages for March 2013 (industrial partner samples) and March 2014 (University of Saskatchewan samples).

3.1.3 POPULATION STRUCTURE AND SIZE

We were interested in determining the standing (i.e., current) age and sex structure of the population and population density to help interpret trends observed from analysis of survival, recruitment, and population growth; and to help us populate an age- and sex-structured projection model (*Section 3.1.5*). Data on standing age- and sex-structure are typically obtained from survey data. We could not use our capture data or data specific to surveying collared caribou, however, as target animals were biased to adult females and groups of females and their calves. Rather, to determine standing age distribution, we sought out data independently collected in the study area from our industrial partners using aerial surveys. We determined that there were 15 systematic and comparable aerial surveys conducted to survey ungulates (woodland caribou and moose, no other ungulates being observed) in the SK1 caribou range applicable to where we collared caribou since 2008. There was also a large survey conducted in January 1987 (Brewster 1988). Here, we report on surveys conducted since 2008 and use Brewster's (1988) survey as a comparator.

Surveys conducted since 2008 were located throughout the region where we had collared caribou. Surveys were focused on areas of specific mining interests as opposed to regions biased to where caribou or moose were already known to occur. Surveys varied in aerial extent (range = 320–2,285 km^2; $\bar{x}$ = 825 km^2), coverage (percentage of study area flown within where animals could be observed within 200 m [40–100%]), and intensity (km^2 covered per minute of on-grid flying time [range = 1.4–2.0 mins/km^2; $\bar{x}$ = 1.7 mins/km^2]). Most were conducted in late winter, i.e., March (n = 10) or February (n = 4); two were conducted in December. All used helicopters and in all cases 'minimum counts' of animals were obtained, from which bulls/100 cows and calves/100 cows and density estimates (animals/km^2) could be determined (n = 15 for caribou, n = 12 for moose).

In March, 2015, the University of Saskatchewan also conducted a survey. We elected to use the most common design of previous surveys (380 km^2 survey area, 100% coverage); however, we also conducted our survey in an area where within the previous 24 hours we had determined the location of collared caribou and their groupings. We used this data to estimate 'sightability' of caribou during a survey, i.e., the extent to which caribou that were known to be on the survey grid were missed.

Our survey area was located in the northeast SK1 range, near Courteney Lake. The study area was systematically surveyed on 17–18th March, 2015, by helicopter (Bell 206B Jet Ranger). The same pilot, navigator, and two rear observers were used for the entire survey. We flew west-east parallel and immediately adjacent transects while maintaining an observation width of 200 m on either side of the helicopter. The helicopter was flown 50 to 150 m above ground level with air speeds ranging from 70 to 100 km/h. Speeds were reduced and heights were increased in areas

with particularly dense conifer canopy. A combination of the route navigation tool in the helicopter GPS and maps were used for navigation and for mapping animal locations. Complete turns were made when animals were observed. This provided additional time for age and sex classification and an accurate count of the number of animals observed. Sex and age of moose and/or caribou were determined by sight and using combination of the presence or absence of antlers, antler scars, vulval patch, and nose colour. All animal observations were recorded using hand-held GPS units and on maps. Survey conditions were considered to be excellent (e.g., close to100% of stumps and downed logs covered with snow). Winds were low, ranging from 0 to 10 km/h, and temperatures ranged from –15°C to –30°C.

From these surveys, we were able to determine our initial estimate of abundance of caribou and moose in the region corresponding with our tracked caribou as the average (minimum) density for each species obtained across all 16 surveys conducted since 2008, and average age- and sex-structures (bull:cow; calf:cow; with calves = age 0 and all other categories aged 1+).

3.1.4 SURVIVAL, RECRUITMENT, AND POPULATION GROWTH

From our collared caribou datasets, we estimated adult female survival rates (S_{adf}) using the staggered-entry modification (Pollock et al., 1989) of Kaplan and Meier's (1958) survivorship model:

$$S(t) = \prod_{t_{(i)} \leq t} \frac{n_{(i^-)} - d_{(i)}}{n_{(i^-)}}$$

In this equation, $n_{(t^-)}$ is the number of individuals at risk (collared and alive) just before time t and $d_{(t)}$ the number of deaths recorded at time t. Individuals at risk were computed based on days at risk, survival from day of mortality, and censoring according to days on which collars malfunctioned or were dropped and hence caribou were no longer followed. Our measurement year was from March 16 to March 15, which roughly corresponded with the timing of our recruitment surveys (March 4–6 and 15–18, 2015; March 9–12, 2016).

We calculated recruitment (R) as the adjusted age-ratio (X) following DeCesare et al. (2012), assuming a 50:50 sex-ratio in observed 10-month-old calves (which is less than the observed calf:cow ratio; also reported):

$$R = \frac{X/2}{1 + X/2}.$$

We estimated the deterministic (snap-shot) population growth (λ) for each year from the equation $\lambda = \frac{S}{1-R}$ (Hatter and Bergerud, 1991). We determined λ over the 2 years of study as the geometric mean of annual estimates.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

We also estimated productivity of the population, and age 0 survival rates (although these measures did not factor into the deterministic measure of λ, as estimated above, they did factor into our age-and sex-structured population projection [population viability analysis] below). The survival of age 0 caribou was based on our data on productivity of adult females and the survival of their calves to the next census. This follows the computation used to determine calf survival by other jurisdictions, like the Newfoundland Department of Environment and Conservation (Morrison et al. 2012). Using productivity data (here, late gestational pregnancy rates) is noted as a being a preferred measure of reproduction compared to simple ratios of calves per 100 cows, which tends to underestimate productivity due to calf loss which may occur prior to visual classification and late calving which may not occur until after visual classification. Productivity is the proportion of adult females of a sample that show signs of being likely to have produced a newborn, i.e., having been successfully bred. Survival rate of those calves is then determined as the proportion of newborns (or fetuses, depending on timing of surveys) that survive to the set census date. In our case, for our population projections and other estimations we used the census date of March 15; all of our data used this point in the calendar year for estimating survival. Survival of age 0 caribou was thus the ratio of the average number of calves alive at March 15 relative to the number that were present at the same time the previous year. Note that survival rate of the age 0 category thus included late gestational losses from March to parturition, if any occurred (e.g., if there were 500 fetuses at March of year t, and 200 were both born and survived to March of year t+1, age zero survival would be 0.40 with adult survival rates for calves [now classed as age 1] commencing at March 16 of year t+1). Several researchers have also indicated that when calves reach between 9 and 12 months of age they face the same mortality risk as adults and have thus been effectively recruited into the population (Fuller and Keith 1981; McLoughlin et al. 2003; Wittmer et al. 2005).

Lacking specific survival data from collared males meant that we needed to estimate adult male (age 1+) survival rates based on the relative reduction in survival necessary (compared to adult female survival) in order to reach a bull:cow ratio as observed in our population surveys (i.e., 0.571 or 57.1 bulls:100 cows; Table 3.1).

In all cases, excepting adult male estimated survival, we were able to bootstrap our data (10,000 replicates) to obtain 95% confidence intervals (95% CI) for average survival, reproduction, and population growth estimates. We estimated all demographic parameters using our data and those collected by our industrial partners independently, and as pooled datasets for comparison purposes. All estimations were performed using the R software (Version 3.2.4).

3.1.5 POPULATION VIABILITY ANALYSIS

Deterministic estimates of population growth (λ) are useful for gauging current population trends; however, to identify or categorize status ideally we would like to also project populations over some period of time into the future, based on current survival and reproduction data, to determine likelihoods of further population declines (or increases). Such models generally incorporate uncertainty in data (standard errors or confidence intervals about parameter estimates) as part of these projections, which are termed population viability analyses (PVAs). Adding stochasticity (unpredictability due to one or more random variables) into these simulations increases realism of model projections, and in general uncertainty will work to lower expected population growth rates (Caughley and Gunn 1996). The rationale here is that all populations experience environmental stochasticity and other forms or random events; therefore, all populations can potentially go extinct (Pulliam and Dunning 1994) and hence extinction is best described as a probabilistic phenomenon. PVAs are frequently used in conservation biology to determine the probability that a population will go extinct within a given number of years (Caughley and Gunn 1996).

Here, we used an age- and sex-structured, individual-based stochastic population model coded in Microsoft Virtual Basic (RISKMAN v. 1.9.003; see Taylor et al. 2001, 2002; McLoughlin et al. 2003, 2006) to examine likelihoods of quasi-extinction in the SK1 caribou unit based on available data. We parameterized the model using survival and reproduction data as recorded by the University of Saskatchewan, assuming static conditions of habitat.

The model we developed incorporated minimum and maximum ages of reproduction (R_F, R_L), and maximum age of life, *w*. For boreal caribou, we used age 2 years as R_F (i.e., first age of adults), with caribou producing offspring up to a maximum age of 20 years (based on estimates of *w* and R_L reported for boreal caribou in COSEWIC 2014). For input data on rates of survival and reproduction, we principally relied on the University of Saskatchewan data set, 2014–2016, averaged across years of study (using geometric means). We used this data set to the extent possible as we felt it best presented the information as it applies to the whole of the SK1 unit.

In our projection model, we used the survival of adult females collared throughout the study area by the University of Saskatchewan as the geometric average 2014–2015 and 2015–2016 (*Table X*), as this was the least geographically biased estimate of survival available and thus best represented the sample with inference to across the SK1 caribou range. We used the adult male estimated survival as determined from adult female rates and the observed standing age distribution (*Section 3.2.4*). We were limited in our data to estimating an average calf (age 0) survival rate to the intervals in which we had obtained both pregnancy data and calf recruitment data, i.e., for the years 2013–2014 and 2014–2015 (our captures focused on March 2013 and March 2014). For the first year, we used the productivity data collected by our industrial partners when they collared caribou and the calf:cow ratio that they observed during the relocation of their collared individuals in March 2014 (Tables 3.2, 3.3). For the second year, we used the productivity data that we collected during our captures in 2014 and the calf:cow ratio we

observed during relocations in March 2015, where we could assign the true productivity fates of caribou sampled for pregnancy (Table 3.3). For population projection modelling, we used the 2-year geometric mean of our age 0 survival rates as input (Table 3.3). Although this measure of productivity would have some geographic bias to the Key Lake-Cree Lake area, we wanted a minimum of two years of productivity data in generating and average for age 0 survival rates (there was a trade-off between using multiple years for sampling vs. some geographic bias in year 1 to the Key Lake-Cree Lake area).

To initiate our population age and sex distribution, we could not use sex and age ratios observed during cow:calf surveys because of bias associated with relocating collared females (all-male groups would likely have been missed). Hence, we relied on sex and age ratios observed during aerial surveys independently conducted by the University of Saskatchewan and our industrial partners across the SK1 unit, from 2009 to 2014 (Table 3.1). Calves were assumed to have a 50:50 sex ratio. The age structure was parameterized and model initiated according to a pre-birth pulse survey. (Note: Ours was a 'pre-birth pulse census'. The alternative, a 'post-birth' pulse census, e.g., centered in late June or July [i.e., after calves are born], is problematic for collecting data on caribou because the actual number of calves born during May and June is not easy to determine using our [aerial] survey methods.)

Our model was stochastic, and was capable of incorporating three types of stochasticity: sampling, environmental, and demographic (review in White 2000); however, as we had too little data (time series) to partition variance about our vital rates (survival and reproduction) and convert it back to the respective standard errors associated with parameter and environmental uncertainty, we elected to pool both sampling uncertainty and environmental uncertainty. Recent research has suggested this may lead to unduly pessimistic likelihoods of persistence (White 2000) and hence our simulations should be regarded as conservative.

Inputted data used means and 1 SE about means (SE and 95% confidence intervals are related as each confidence limit = SE × 1.96 if data are assumed to follow a normal distribution [Zar 1984]). For normally-distributed parameters (e.g., starting population size, N), random normal deviates were obtained using the polar method of Law and Kelton (1991). For binomial parameters (e.g., survival or death, success or failure to produce a litter), random deviates are based on sample size, n, and Bernoulli trials. We chose to use Bernoulli trials for binomial parameters because the behaviour of random deviates from a transformed-scale (e.g., arcsin or logit), and truncated symmetrical distributions, tended to bias binomial random deviates. We used Monte Carlo simulations (Manly 1997) to generate a distribution of results, and then used this distribution to estimate the variance of summary parameters, such as population size at a future time, final age and sex structure, population growth rate, and proportion of runs that result in a population decline set at a predetermined level by the user. We adopted the latter to estimate persistence probability in this study.

COSEWIC uses two criteria when assessing risk status based on population projections, like that of a population viability model (quantitative assessment). *Endangered* status may be applied

when quantitative analysis like a PVA shows the probability of extinction in the wild is at least 20% within 20 years or 5 generations (30 years for boreal caribou, assuming 6-year generation length as in COSEWIC 2014), whichever is longer, up to a maximum of 100 years. *Threatened* status is assigned when projections suggest a 10% chance of extinction within 100 years. We determined if either of these criteria applied to the SK1 caribou population, adopting the definition of 'extinction' as a decline to 20 individuals (i.e., quasi-extinction, where population size is so low that immediate extirpation is imminent due to Allee effects or other stochastic events [Engen and Sæther 2000]). We felt that 20 individuals would represent roughly 10 breeding females, which was the quasi-extinction level used by Environment Canada (2012) in their simulation modelling for boreal caribou in Canada. We also modelled the population using less-stringent requirements, where a successful outcome was defined as a population decline of less than 10% over 20 years. A 10% decline over 3 generation lengths, where generation length is defined as the average age of parents of a newborn cohort (6-7 years for species modeled in this paper; Environment Canada [2012]), is a criterion used by the World Conservation Union (IUCN) to classify small (i.e., $N < 10,000$), discrete demographic units as *Vulnerable* to endangerment (IUCN 2001:22–23). For each simulation, we ran 10,000 stochastic population projections to report the proportion of outcomes falling below a set level of persistence. We also report the population finite rate of increase as at the end of 3 generation lengths (20 years) and its standard error.

We assumed a 50:50 sex ratio and initial population size (3380 caribou [95% C.I. 2436–4304]), which we based on our size estimate only for they study area in which we had collared individuals, *Section 3.2.3*; Fig. 3.5) and a 50:50 sex ratio at birth. Although there are provisions within the model to include density-dependent effects on survival and reproduction, we modeled growth rates exponentially. We wished to err on the size of caution and avoid bias associated with unknown curves describing density-dependence. Although we suspected (see *Section 3.3*) that the vital rates and densities that we observed already reflected high-density conditions, we did not increase calf recruitment and/or modified survival as population size decreased in our population. Hence, our population projections should be regarded as conservative in terms of likelihood of population persistence.

3.2 Results

3.2.1 GPS COLLARING AND COLLAR PERFORMANCE

As at writing, all collars from industrial partners have now ceased in their transmissions. Of the original 94 caribou collars deployed by the University of Saskatchewan 61 remain transmitting and will be used to estimate survival and recruitment, and population trend of caribou in the SK1 unit into the future. The remainder of collars have either ceased to work due to malfunction, death of an animal, or premature dropping due to opening of the release mechanism.

Among the 25 Lotek Iridium collars deployed by the University of Saskatchewan in March, 2014, 13 remain transmitting as at the time of writing (53% of initial deployments). Ten collars malfunctioned by prematurely falling offline while two ceased to work due to the death of the caribou. Forty percent of the Lotek collars were offline 2.5 years after initial deployment on caribou.

At the beginning of the study, we also deployed 69 Telonics collars. At time of writing 48 functional collars remain on caribou (70% of initial deployments). Seven animals are dead, six collars were dropped, one collar turned offline and seven collars are currently transmitting stationary. Stationary-collar investigations are scheduled to occur in late September, 2016, and results of these visits will be included in the next version of this report. Although only 1/69 Telonics collars went offline on a live caribou compared to 10/25 Lotek Iridium collars, none of the Lotek Iridium collars were prematurely dropped by early release of the mechanical drop-off mechanism which was a problem for our Telonics collars. Collar pick-ups of outstanding stationary collars are scheduled to occur in late September, 2016, and results of these pick-ups will be included in the next version of this report.

3.2.2 PREGNANCY RATES

From 47 caribou captured by our industrial partners in March, 2013, we assessed the pregnancy rate as 0.862 (95% C:I 0.745–0.958). For one individual, we were unable to determine if the female was pregnant or not as the concentration of progesterone was a 'borderline result' (>1.3 ng progesterone/ml but <1.34 ng/ml); hence, when we estimated our rate we assumed randomly that this individual had 50% chance of being pregnant. From 93 caribou captured by the University of Saskatchewan in March, 2015, the pregnancy rate was 0.933 (0.878–0.978). The annual geometric mean of the pregnancy rate assessed from these two years, pooling both samples, was 0.897 (0.834–0.951).

3.2.3 POPULATION SIZE AND STRUCTURE

Ungulate aerial survey results are presented in Table 3.1. Of surveys conducted since 2008, 11/16 detected woodland caribou in their respective study areas. Over all 16 surveys conducted since 2008 (including surveys where no caribou were observed), the average density was 36.9 caribou/1000 km^2 (95% CI: 26.7–47.2 caribou/1000 km^2). Thirteen surveys recorded instances of moose when observed (3 surveys did not include counting moose as an objective of their survey). Of the applicable surveys, the average density was 45.7 moose/1000 km^2 (37.8–53.6 moose/1000 km^2).

The caribou-survey sightability test conducted by the University of Saskatchewan in March 17–18, 2015, indicated that identification of woodland caribou ($n = 49$) from the air was likely biased low: only 7 of 11 collared caribou known to be in the survey area within the past 24 hours were observed. There were four caribou near the edges of our survey gridlines, however, that had

Status of Woodland Caribou in the Saskatchewan Boreal Shield

Table 3.1. Ungulate aerial surveys conducted in the SK1 woodland caribou administrative unit in proximity to where the project has collared caribou, since 2008. Data provided by industrial partners.

Study	Survey Timing	Survey Area (km^2)	Coverage (%)	Search Intensity (mins. flown per km^2)	Species/km^2		Woodland Caribou Population Structure		
					Moose	Caribou	Bulls:Cow	Calf:Cow	Calves as a % of Total Population
Millennium TRSA 2014	Mar 2014	2,285	40	1.7	0.040	0.005	1.600	0.000	0
Millennium LSA 2014	Mar 2014	397	100	1.7	0.050	0.000	-	-	-
Key Lake 2014 (Unpublished)	Mar 3-12 2014	1616	40	1.7	0.030	0.030	-	-	-
Key Lake 2013 (Unpublished)	Mar 13-16 2013	1616	40	1.7	0.030	0.060	0.750	0.250	18
Key Lake 2012 (Unpublished)	Mar 15-17 2012	1616	40	1.5	0.050	0.090	0.310	0.130	9
Key Lake 2011 (Unpublished)	Dec 13-17, 2011	1616	40	2	0.040	0.060	0.714	0.330	12
914	Mar 2011	554	-	-	-	0.000	-	-	-
McArthur River 2011 (HAB-TECH 2012)	Feb 7-9 2011	400	100	1.8	0.050	0.040	0.270	0.270	18
914	Feb 2011	554	-	-	-	0.004	-	-	-
914	Dec 2010	410	-	-	-	0.027	-	-	-
Cigar Lake 2011 (HAB-TECH 2011)	March 7-9 2010	320	100	1.4	0.010	0.000	-	-	-
Four Bear 2010 (HAB-TECH 2010a)	March 5-6 2010	350	100	1.5	0.080	0.000	-	-	-
Key Lake 2010 (HAB-TECH 2010b)	Feb 23-24 2009	384	100	1.7	0.020	0.050	0.250	0.000	0
Virgin River 2009 (HAB-TECH 2009b)	March 21-24 2009	376	100	1.8	0.050	0.130	0.320	0.400	20
Courtenay Lake, U of S 2015	Mar 17-18 2015	380	100	1.7	0.024	0.0950	0.357	0.180	11.1
Tamarack 2009 (HAB-TECH 2009a)	Feb 27-29 2008	324	100	1.9	0.120	0.000	-	-	-
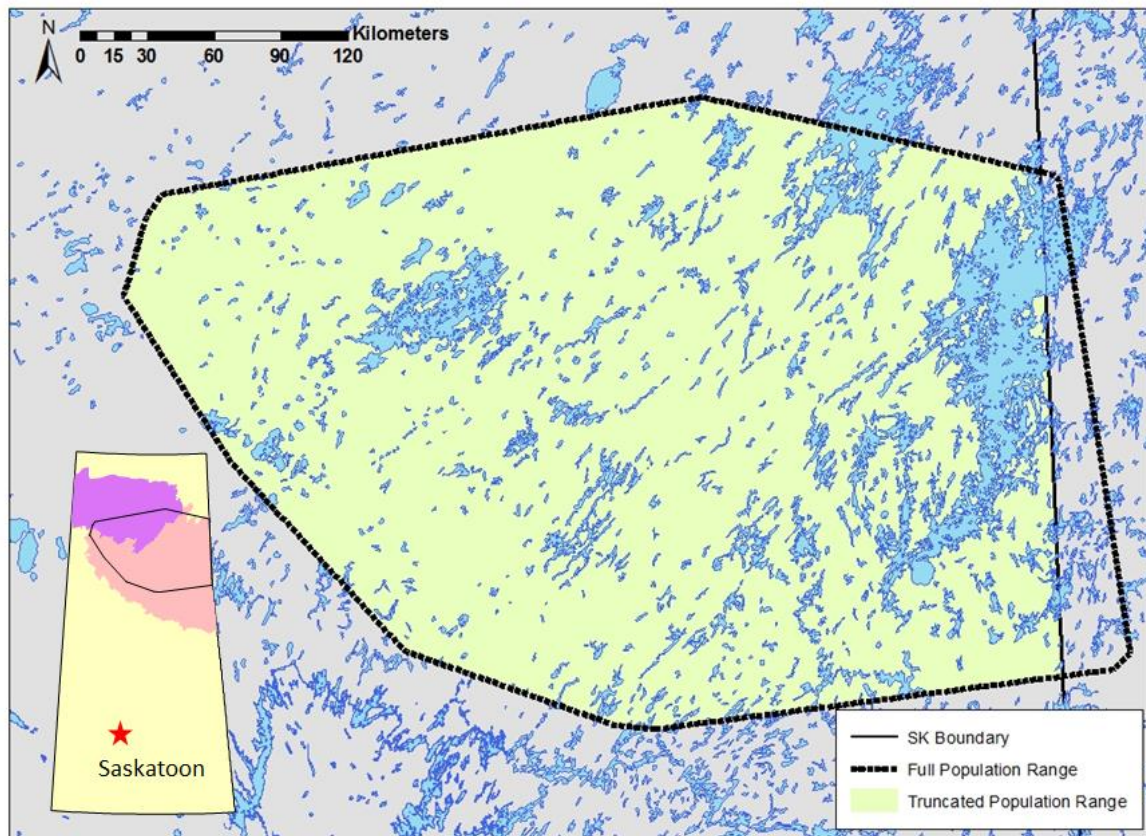
Fig. 3.5: Extent of occurrence (green, truncated at the Saskatchewan-Manitoba border) for GPS-collared caribou within the SK1 administrative unit (inset). The range was calculated over two years (March 2014 to March 2016) for 94 female caribou. Range was delineated as the 100% Minimum Convex Polygon (MCP, Mohr 1974) for locations of tracked caribou, buffered by 1 km which was the average daily step length. The truncated range covered an area of 91,238 km2. The coloured polygons in the inset denote the two ecoregions encompassed by the range: the Athabasca Plains Ecoregion (purple) and the Churchill River Upland Ecoregion (pink); together these ecoregions define the bounds of the SK1 caribou administrative unit.

potential to have moved off in the hours between relocations and surveys. Assuming that half of those had as much likelihood as moving onto vs. off the survey grid, then we computed that the survey we conducted was biased conservatively (in terms of true density) as 22%; i.e., we suspect that our estimate was approximately 22% below the true estimate. Nonetheless, we did not adjust any survey result to reflect bias due to detection probability. We only caution that estimates are minimum estimates and population density is likely higher than as reported, assuming that detection probability is approximately constant across all surveys.

Eight caribou surveys reported the ratios of bulls per cow and calves per cow in their sample. The average bull:cow ratio was 0.571 (95% CI: 0.444–0.699) and calf:cow was 0.195 (0.158–0.232).

Extrapolating to the region in which we have collared caribou (91,238 km^2; see *Section 3.3* and Fig. 3.5) including lakes and rivers, we estimated that the area supported 3380 caribou (95% CI: 2436–4304 caribou). This estimate would be a minimum if we were to assume that surveys used to estimate caribou densities (Table 3.1) were all biased low by the same extent as was our survey. Extrapolating to the entire SK1 caribou administrative unit (187,000 km^2) is more difficult due to habitat differences in northwestern Saskatchewan compared to our current study area (in the Athabasca Plains). However, we can expect a minimum of approximately 5000 caribou to be resident in the region pending additional analysis (e.g., matching population density estimates to resource selection function modelling [Boyce and McDonald 1999], as we propose for our final report in December, 2018).

3.2.4 SURVIVAL, RECRUITMENT, AND POPULATION GROWTH

Annual adult female survival rates estimated from University of Saskatchewan collars varied between 0.908 (0.843–0.965, 95% confidence intervals, or CI) for the first year of the study (2014–2015) and 0.945 (0.886–0.987) for the second year (2015–2016). Calf:cow ratios were 0.207 (0.147–0.271) and 0.216 (0.161–0.273) for the first and second years, respectively. Associated adjusted recruitment rates (*R*) assuming a 50:50 sex-ratio among 10-month old calves, which we used to assess population growth, were 0.094 (0.068–0.119) and 0.097 (0.075; 0.120), also presented in Table 3.2A. Mortalities were highest in the snow-free season (Fig. 3.6).
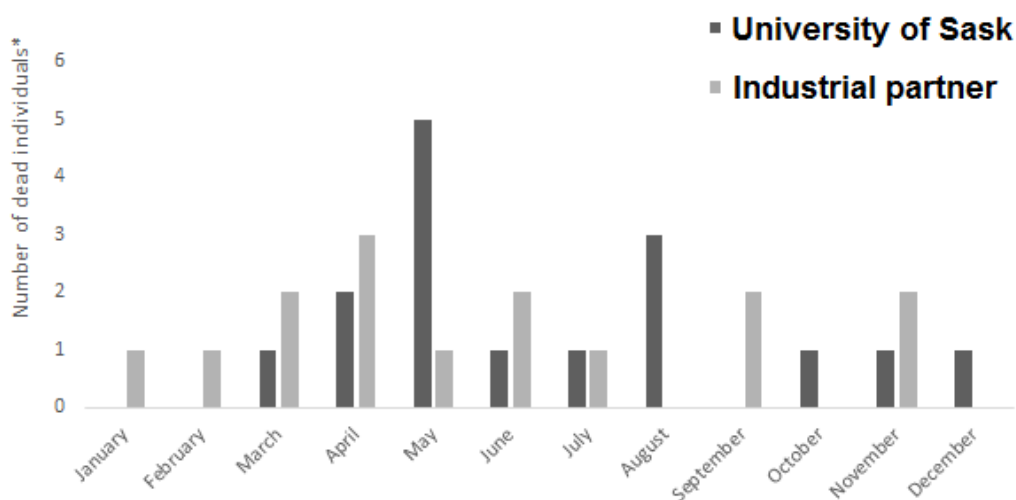
Fig. 3.6. Frequency of mortalities of GPS-collared boreal caribou in the Saskatchewan Boreal Shield by month and by data set (University of Saskatchewan collars and those of our industrial partners; see text).

According to the survival data collected by our industrial partners, annual adult female survival rates among three years of the study were, respectively, 0.895 (0.800–0.979) for 2013–14, 0.827 (0.711–0.933) for 2015–16 and 0.941 (0.848–1.000) for 2015–2016. In mid-March, at the end of each interval, they observed calf-cow ratios of 0.185 (0.118–0.254), 0.083 (0.041–0.129), and 0.274 (0.195–0.358), respectively. Corresponding adjusted values of *R* were 0.084 (0.056–0.113), 0.040 (0.020–0.061), and 0.120 (0.088–0.152); see Table 3.2C.

From our data, which sampled the whole of the study area, we estimated annual population growth rates of 1.002 (0.926–1.069) and 1.047 (0.977–1.107) for the first and second years of the study. The geometric mean, unweighted population growth rate among these two years averaged 1.024 (0.973–1.071). From the data collected by our industrial partners, which focused on the Key Lake and Cree Lake areas, annual population growth rates were more variable, and were estimated at 0.978 (0.871–1.070), 0.861 (0.742–0.972) and 1.070 (0.961–1.156) for the first, second and third year of the study. Among these three years, the population growth rate averaged 0.966 (0.900–1.025).

When we combined both data sets (possible for 2014–2015 and 2015–2016 only; Table 3.2C), adult females showed a survival rate of 0.880 (0.821–0.932) for the first common year of study and of 0.943 (0.896– 0.981) for the second. Calf:cow ratios were 0.150 (0.111–0.190) and 0.235 (0.189–0.280), respectively, and adjusted recruitment rates were 0.070 (0.053–0.087) and 0.105 (0.086– 0.123). We assessed the pooled population growth rate at 0.946 (0.881–1.004) for the first year and 1.054 (0.997–1.104) for the second. Among these two years, the geometric mean of growth rate was 0.999 (0.955–1.038).

3.2.5 POPULATION VIABILITY

Our simulations of population viability indicated that there was no chance of extinction in the wild within 5 generations (30 years), i.e., no simulated projections resulted in quasi-extinction (a decline to 20 individuals from current population size). After 100 years, 5/1000 of simulations (0.06%) showed that this level of population reduction was possible. Over shorter terms (3 generations or 20 years), the projected population finite rate of increase stabilizes at $\lambda = 1.006 \pm 0.016$ (SE), and annually averaged $\lambda = 1.017 \pm 0.016$ (SE). The latter value was less than the non-stochastic, 2-year estimate of the population's finite rate of increase using University of Saskatchewan input data, which was $\lambda = 1.024$ (Table 3.2). Despite showing overall stability in the population over the period of data collection, the distribution of simulation outcomes indicated that the chances of population decline and population increase were not equal. For example, if we considered the chance that the population might decline to 90% of its current population size over the next 20 years, we observed that 24.2% of simulations resulted in this outcome (75.8% did not). Alternatively, when we projected the likelihood of at least a 10% population increase from current size (3380 caribou in the area delineated by Fig. 3.5), 56.6% of simulations presented this result.

Table 3.2: Adult female (age 1+) annual survival rates (S_{adf}), calf-cow ratios (X), adjusted recruitment (R), and annual finite rate of population growth (λ) including 95% confidence intervals (95% CI) for the SK1 administrative unit of woodland caribou from 2013–2016. Estimates were obtained from data collected by the University of Saskatchewan (Table A), our industrial partners (Table B, with the additional year from 2013–2014), and with both data sets, pooled (Table C). n_{col} is the number of collared animals, D the number of dead animals, C the number of censored animals (i.e., those that dropped collars or had collars malfunction), n_{obs} is the number of observed cows during annual aerial survey and n_{calf} is the number of observed calves during these same surveys.

A.

Year	Survival				Recruitment				λ [95%CI]
	S_{adf} [95%CI]	n_{col}	D	C	X [95%CI]	R [95%CI]	n_{obs}	n_{calf}	
2014-2015	0.908 [0.843–0.965]	94	8	7	0.207 [0.147–0.271]	0.094 [0.068–0.119]	169	35	1.002 [0.926–1.069]
2015-2016	0.945 [0.886–0.987]	79	4	7	0.216 [0.161–0.273]	0.097 [0.075–0.120]	213	46	1.047 [0.977–1.107]
Geo mean	0.926 [0.883–0.964]				0.211 [0.170–0.254]	0.094 [0.078–0.112]			1.024 [0.973–1.071]

B.

Year	Survival				Recruitment				λ [95%CI]
	S_{adf} [95%CI]	n_{col}	D	C	X [95%CI]	R [95%CI]	n_{obs}	n_{calf}	
2013-2014	0.895 [0.800–0.979]	49	5	1	0.185 [0.119–0.254]	0.084 [0.056–0.113]	119	22	0.978 [0.871–1.070]
2014-2015	0.827 [0.711–0.933]	50	8	4	0.083 [0.041–0.129]	0.040 [0.020–0.061]	145	12	0.861 [0.743–0.972]
2015-2016	0.941 [0.848–1.000]	41	2	7	0.274 [0.195–0.358]	0.120 [0.089–0.152]	124	34	1.070 [0.960–1.156]
Geo mean	0.886 [0.827–0.939]				0.160 [0.120-0.198]	0.074 [0.056-0.089]			0.966 [0.900–1.025]

C.

Year	Survival				Recruitment				λ [95%CI]
	S_{adf} [95%CI]	n_{col}	D	C	X [95%CI]	R [95%CI]	n_{obs}	n_{calf}	
2014-2015	0.880 [0.821–0.932]	144	16	11	0.120 [0.111–0.190]	0.069 [0.053–0.087]	314	47	0.946 [0.881–1.004]
2015-2016	0.943 [0.896–0.981]	120	6	14	0.235 [0.189–0.280]	0.105 [0.086–0.123]	337	80	1.054 [0.997–1.104]
Geometric mean	0.911 [0.874–0.945]				0.188 [0.156–0.218]	0.086 [0.072–0.098]			0.999 [0.955–1.038]

UNIVERSITY OF SASKATCHEWAN

Table 3.3: Pregnancy rate (P), calf-cow ratios (X) and annual age 0 survival rate including 95% confidence intervals (95% CI) for the SK1 administrative unit of woodland caribou from 2013–2015. Estimates were obtained from data collected by our industrial partner for the first year and by the University of Saskatchewan for the second year. n_{preg} is the number of pregnant females that we captured, $n_{non-preg}$ the number of non-pregnant female, $n_{borderline}$ the number of female for which it was not possible to certify that they were pregnant (i.e. concentration of progesterone found was a "borderline result"), $n_{preg-unknown}$ the number of female for which we were not able to assess the pregnancy due to field hazards (e.g., sample dried in tube), N_{obs} is the number of observed cows during annual relocation, n_{calf} is the number of observed calves during these same surveys and $n_{calf-unknown}$ is the number of calves for which we didn't know if they belong to a collared females or another individual of the observed group.

Year	Productivity					Calf:cow ratio				S_{calf} [95%CI]
	P [95%CI]	n_{preg}	$n_{non-preg}$	$n_{borderline}$	$n_{preg-unknown}$	X [95%CI]	n_{obs}	n_{calf}	$n_{calf-unknown}$	
2013-2014 (Industrial partner data)	0.862 [0.745-0.957]	40	6	1	0	0.184 [0.118–0.256]	119	22	0	0.214 [0.136–0.303]
2014-2015 (University of Saskatchewan data: collared caribou only)	0.932 [0.875–0.978]	82	6	0	5	0.238 [0.141–0.343]	72	16	5	0.255 [0.151–0.370]
Geometric mean										0.233 [0.165–0.303]

3.3 Discussion

Our principal finding is that the current status of boreal caribou in the SK1 unit is one of a large and stable population, characterized by relatively high annual adult survival and low-moderate calf recruitment. Unexpectedly, adult female survival consistently ranked as being much higher than predicted, averaging well above the national mean of 0.852 for boreal caribou (Environment Canada 2011) in most years and across most samples. Using University of Saskatchewan data, which is the largest dataset covering the largest spatial area, we estimated annual adult female survival to be 0.926 from 2014 through 2016 (geometric mean over both years of research). Data on survival from our industrial partners, which was confined to the Key Lake-Cree Lake region, were more variable. This variation was expected due to smaller sample sizes; however, rates also averaged higher than the national average.

Both data sets were consistent in predicting an increasing trend in survival during the period of study. Although it might be tempting to pool datasets for further interpretation of SK1 caribou population dynamics (including projections for PVA) because of the tighter confidence intervals about estimates due to larger sample sizes (Table 3.2C), we believe that this would focus inference to trends with local geographic bias to the Cree Lake-Key Lake area where both partners deployed collars (Figs. 3.2 and 3.3). Because our intent here has been to estimate status and trends for the whole of the SK1 caribou administrative unit, we believe that the University of Saskatchewan dataset best represents the sample that applies to the SK1 unit and draw our principal conclusions from these data.

Pregnancy rates and calf:cow ratios and hence recruitment rates were more in line with what we were expecting from results obtained across Canada. The balancing of recruitment and survival suggests one of population stability or slight population increase across the SK1 caribou unit on a deterministic basis, over the period of study. Taken by itself, the University of Saskatchewan sample suggests population growth from 2014–2016 across the SK1 administrative unit; however, this is balanced by what would appear to be local population stability or slight decline in 2013–2014, decline in 2014–2015, and rapid population growth in 2015–2016 in the Cree Lake-Key Lake area (using data collected by our industrial partners). Again, this variability might be expected from smaller sample sizes, but encouragingly on a relative basis both samples showed lower population growth early in the study, followed by significant population growth from 2015–2016, with $\lambda = 1.05$ and 1.07 in the University of Saskatchewan and industrial partner datasets, respectively. Notwithstanding the potential for local and temporally variable declines and increases in the Key Lake-Cree Lake region of the SK1 unit, we conclude here that the caribou population in the SK1 region is secure in the sense that overall the population is showing clear signs of stability. On balance, we conclude stability with slight positive bias in the very recent population trajectory for SK1 caribou.

In terms of future population trajectory, a slight positive trend in population growth was also evident in our age- and sex-structured, stochastic population projections. This was not a foregone conclusion, as population projections depended not only on relative survival and reproduction data, but also the standing age distribution as obtained from available survey data. Basing assessment solely on criterion used by COSEWIC to characterize status of populations based on quantitative population projections (Category E of the COSEWIC Assessment Process and Criteria: http://www.cosewic.gc.ca/pdf/assessment_process_e.pdf), our PVA suggests that there is essentially no chance that caribou in the SK1 unit are categorically *Endangered* (would go functionally extinct within the next 30 years). Indeed, we also observed a very small (<1%) chance that they should be characterized as *Threatened* (the current classification for the Boreal population of caribou across Canada), if one were to assign status based on this quantitative analysis. Likelihood of population increase (e.g., 10%) was also greater than that of an equivalent decline over the next 3 generations, given current rates and trajectory. Based on these results, we suggest that the COSEWIC classification of *Special Concern*, as opposed to *Threatened*, might better apply to the population of caribou in the SK1.

What might account for the high adult survival, low-moderate calf recruitment, and current stability or slight increase in population growth? These characteristics are typical of a large mammal population that is experiencing density-related constraints on further population growth. It is now well established that density-dependent responses of large, wild herbivores follow a predictable pattern (Eberhardt 1977) involving a sequential response from juvenile survival to adult survival, and large herbivores (like caribou) have high adult survival rates that are resilient to environmental stresses (see Gaillard and Yoccoz [2003] for a review). Under conditions of intensifying competition or other density-related ecological interactions, brought about by increasing population size or changes in the environment, wild ungulates are expected to trade reproduction to better their own survival especially during the prime-age stage ('selfish mothers' hypothesis, *sensu* Festa-Bianchet and Jorgenson 1998). Bonenfant et al. (2002) outlined that because small animals are less competitive than large ones during periods of, e.g., food shortage (Begon 1984), juveniles, who are also subject to growth constraints (Stearns 1992) should be influenced first by density. Then in turn, after further increase of population density, the performance of adults should decrease. This is a widely observed phenomenon for large herbivores, with examples from red deer (Bonenfant et al. 2002), bighorn sheep (Festa-Bianchet and Jorgenson 1998), and woodland caribou (Mahoney et al. 2016). The review of Gaillard and Yoccoz (2003) presents several additional examples.

What constitutes stressful conditions for a population nearing carrying capacity, however, is relative. Clutton-Brock (1991) reported that costs of reproduction in terms of prime-aged female survival occurred only when August–September rainfall was >500 mm, but costs of reproduction in terms of fecundity (offspring born) occurred whatever the rainfall. Intensifying competition for resources may slow population growth, resulting in high adult survival but low recruitment (as we observe here), but stressful environmental conditions due to weather may result in similar same trade-off. In the case of boreal caribou in the SK1 range, the high amount of fire (forests

aged <40 years) is suggestive of a habitat-related link to the current characteristics of the population. However, our density estimates (Table 3.1) also are relatively high. Across 16 aerial surveys in the SK1 range conducted since 2009, we computed a mean density of 36.9 caribou per 1000 km^2. Note that these surveys were not solely focused on caribou habitat, and were located throughout the Saskatchewan Boreal Shield for various reasons. In fact, no caribou were observed in grid samples for 5/16 surveys. Hence, we believe that the mean of these surveys presents an accurate picture of the density of caribou through much of the SK1 range. Our observed caribou density was 2–3 times as high as the average for most other jurisdictions in Canada (data presented in COSEWIC [2014: pp. 36–37]): Alberta (15.9 caribou/1000 km^2), British Columbia (4.3/1000 km^2), Labrador (18.7/1000 km^2), Manitoba (7.3/1000km^2), NWT (14.7/1000 km^2), Ontario (10.0/1000km^2), and Québec (10.4/1000 km^2). Indeed, our data suggest that the SK1 caribou unit ranks among the highest densities (10th/40) and recorded population sizes (3rd/40) of woodland caribou for the species in Canada (COSEWIC 2004: pp. 37–39).

Relatively high densities in the SK1 range present a plausible explanation for why we may be observing high survival, but low recruitment, if the population is experiencing density-related constraints on population growth. Pregnancy rates remains high, however, which indicates that any negative effects of density on adult females may have yet to manifest fully. Densities of woodland caribou can far exceed that observed in the SK1 range, as is known for places like the island of Newfoundland or where herds are semi-migratory (forest-tundra type). For example, at the peak of the George-River herd expansion from 1954–1984, densities reached 1110 animals/1000 km^2 (472,200 caribou distributed over 442,000 km^2; Messier et al. 1988). The Newfoundland-wide population of woodland caribou reached a density of 2100 animals/1000 km^2 (94,000 caribou in 1996 [Morrison et al. 2012; Mahoney et al. 2016] distributed over an area of occupancy of 44,781 km^2 [est. in COSEWIC 2014]). Both populations showed trade-offs in adult survival relative to recruitment at very high density, but also with clear declines in pregnancy rates (something we have yet to observe). Of Newfoundland populations, characteristics of the Northern Peninsula herd appears to show the greatest similarity with what we observed in terms of adult female survival vs. recruitment (adult female survival of 0.919 *vs.* calf survival of 0.181 [Morrison et al. 2012]). Our obtained rates are not implausible with respect to rates observed for other populations of woodland caribou.

A closer examination of what defines critical habitat may help to illustrate why we suspect that the SK1 caribou unit can maintain high densities and population growth relative to other caribou ranges in Canada, despite relatively high amounts of natural disturbance. We identify the amount and type of critical habitat available to the population of caribou in the SK1 unit in *Section 4.6*, based on a detailed analysis of seasonal caribou movements and their selected use of habitat features as it determines probability of occurrence. In summary, four key habitat metrics: amount of mature (older than 40 yrs) jack pine and black spruce forests, black spruce bog, and open muskeg, stand out as influencing caribou probability of occurrence. Other habitats are used, but the presence of these habitat states are best at predicting occurrence, and they remain in high abundance (*Section 4.6*). Within our smaller study area (collar data range confined within the

SK1 boundaries; Fig. 3.5, which was 91,238 km^2 including lakes and rivers [72,858 km^2 in land mass], supporting an estimated 3380 caribou), we mapped 14,944 km^2 and 5,246 km^2 of old growth pine and black spruce forest, and 8530 km^2 and 7102 km^2 of black spruce bog and open muskeg, respectively (*Section 4.6.1*). Covering more than 49.2% of the terrestrial area, these preferred vegetation associations by collared caribou combined to provide 35,823 km^2 of high-quality habitat, or 1060 ha per caribou. Our preliminary estimates of the amount of forage lichen (*Cladina mitis*, *C. rangiferina*, *C. stellaris*, and *Cladonia uncialis*) available in our study area in these habitats was high (*Section 4.6.1*), providing a preliminary estimate of >6,000,000 kg per caribou of lichen forage species in old growth forests being available within the collar study area. Winter forage does not appear to be limiting to further population growth at this time.

But it is not just that critical habitat components like old growth pine and black spruce forests remain available to caribou in the SK1 range, despite its history of fire. Critically, we also have very low anthropogenic disturbance and extremely low hunting pressure (only 1 of 156 caribou with tracking collars [all data sets combined] was observed to be harvested during the period of study, from 2013–2016). Of equal importance, we believe the SK1 unit to be characterized by very low wolf and alternate prey (moose) abundance.

Predation by wolves is important to caribou in our system, but our low-moderate recruitment rates cannot be linked to abnormally high levels of wolf predation as might be found elsewhere in boreal caribou range subject to high anthropogenic disturbance (review in McLoughlin et al. 2016). Although recruitment rates for the Saskatchewan Boreal Shield fall in line with what we might expect from a region with 58% total disturbance *sensu* Environment Canada (Fig. 3.1), we believe that this is coincidental and not a direct result of the hypothesized link between disturbance and habitat-mediated apparent competition (Hervieux et al. 2014, Environment Canada 2011, 2012).

Risk of predation is believed to be a direct result of predator densities, with a numerical link between wolf and/or bear densities and disturbance being fundamental to the hypothesis of habitat-mediated apparent competition (McLoughlin et al. 2016). Predator densities can be determined directly or by proxy, including by estimating measures like wolf or bear territory or home range sizes, or wolf pack sizes, given inverse relationships between density and these measures (see Messier 1994; McLoughlin and Ferguson 2000). In *Section 5.1* we document established wolf territory sizes in the Saskatchewan Boreal Shield, which averaged 3531 ± 598 km^2 ($\bar{x} \pm$ SE, $n = 12$ packs; 100% minimum convex polygon [MCP] for unduplicated wolves in packs with at least one full year of data and excluding $n = 4$ wolves and packs that appeared to have large migratory movements). These territories are on average 3.5× larger than other recorded territory sizes for wolves in boreal caribou range (and across most of North America), including northeast Alberta where Latham (2009) recently documented average territory size (100% MCP) to be $\bar{x} = 1087 \pm 452$ (95% CL, $n = 8$ packs). In west-central Alberta, territory sizes (also 100% MCP) were 937 km^2 in the study of Kuzyk (2002). Latham (2009) observed winter pack sizes of 2–22 wolves ($\bar{x} = 7.8 \pm 3.37$, 95% CL, $n = 11$ packs). Kuzyk (2002)

observed late winter wolf pack size ranging from 4–18 members per pack with a mean pack size of 8.2 wolves/pack. Our pack sizes were much smaller, ranging from 2–9 wolves ($\bar{x}$ = 4.6 ± 0.6 [SE], n = 19 packs, lone wolves = 4). The Saskatchewan Boreal Shield does not support wolf packs comparable, or territory sizes as small, as would be expected if our recruitment rates were regulated in the same manner as in Alberta.

Further, the only other alternate ungulate prey available year-round to predators in our study area, moose, also exist at low density: among 13 surveys where moose were observed in the study area (Table 3.1), densities averaged 45.7 moose/1000 km^2. This is the second-lowest density of moose observed by Messier (1994) in his North American-wide survey of 33 studies (where both moose and wolves were sympatric). Importantly, our estimated abundance of moose is not likely to be able to support high numbers of wolves (or other predators), as ungulate biomass is strongly correlated with wolf density (review in Messier 1994). Following equations presented in Messier (1994), we computed that wolves in our study area would be encountering and killing moose at a very low rate, 0.3 moose killed per 100 days per wolf, which is capable of supporting a density of <2.0 wolves/1000 km^2. This compares to other caribou ranges in Alberta, e.g., where moose densities can be as high as 120 to 250 moose per 1000 km^2 (e.g., Little Smoky [pre-wolf removal, unpubl. data cited in Kuzyk et al. 2006]) overlapping with a diversity of other ungulates including elk, mule deer, and/or white-tailed deer, supporting densities as high as 25 wolves/1000 km^2 (e.g., Hervieux et al. 2014; wolf densities were 11.0 wolves/1000 km^2 in the study of Kuzyk [2002]). In comparison to northeast Alberta, Latham et al. (2011) estimated an average of 11.5 wolves/1000 km^2 for the West Side-Athabasca River caribou range concomitant with deer densities of 700–1700 deer/1000 km^2 and moose densities averaging 170 moose/1000 km^2, noting a recent shift in diet of wolves toward invading deer compared to moose. In an earlier study for east-central Alberta, Fuller and Keith (1980) estimated 11.1 wolves per 1,000 km^2 on a prey base of 230 moose/1000 km^2. Despite comparability of snap-shot estimates of calf recruitment (Fig. 3.1) between northeast Alberta and the Saskatchewan Boreal shield, abundances of both wolves and alternate prey are at least an order of magnitude higher in the former. Given the limited availability of high quality habitat for moose in the study area (e.g., deciduous and mixed wood forests, estimated as <8%; *Section 4.6.1*), and seasonal presence of wintering barren-ground caribou in the north and west parts of the study area, we are presently considering whether the Saskatchewan Boreal Shield might be better characterized as more of a 'wolf-caribou' system as opposed to 'wolf-moose' system. If moose are not the predominate ungulate biomass available to wolves in the study area, it is possible that wolf densities may not be accurately predicted by equations presented in Messier (1994). Further, hypotheses about how disturbance and habitat-mediated apparent competition might relate to caribou population dynamics (Hervieux et al. 2014) also may not equally apply.

Although we are still working on launching our black bear study (*Section 5.2*), we also do not believe that black bears are occurring at densities that are capable of regulating caribou (our future research will test this). Although we have only very preliminary information on black bears at this point based on a pilot study (*Section 5.2*), our first data also suggests very large

UNIVERSITY OF
SASKATCHEWAN

home range sizes. For example, the adult female (with cub) we captured and tracked throughout 2016 presented an annual home range size that surprised us in terms of it size: 90.1 km^2 (90% utilization distribution), which was 3× the average size of home ranges of adult female black bears with cubs in east-central Alberta and outside the range of variation observed (Cold Lake, females with cubs only, 90% kernel range: mean 27.5 km^2, range 15–63 km^2, n = 8 home ranges; Czetwertynski et al. 2007). In Québec, Brodeur et al. (2006) observed the multiannual home range size of 12 mature females (100% MCP) as 65.1 ± 20.0 km^2 ($\bar{x}$ ± SE); by comparison the 100% MCP annual range of the female we captured was 117.3 km^2. However, home range sizes of female black bears can be larger than this, especially without cubs and where hunted, e.g., Riding Mountain National Park (Pacas and Paquet 1994).

At this point we have no evidence that low recruitment in the Saskatchewan Boreal Shield is the result of habitat-mediated apparent competition. In short, despite having high levels of habitat disturbance (through fire), the SK1 administrative unit lacks the wolves (and likely bears), lacks the alternate prey, and lacks the demographic characteristics of a population being limited by abnormally high predation rates.

Our data suggests that we might do well to reconsider pre-conceived notions about how boreal caribou populations may function where disturbance is almost exclusively driven by natural disturbance through forest fire, and predator-caribou relationships are not influenced by the presence of high predator and alternate prey densities. Unfortunately, almost all research on caribou dynamics comes from regions with substantial industrial activity, especially those related to petroleum extraction and forestry. Indeed, despite supporting a combined 8.5% of the forest-dwelling woodland caribou population in Canada, Alberta and Québec have generated 58.5% of the published research on caribou in recent years (McLoughlin et al. 2016). Caribou living in these landscapes exist in much closer approximation to human disturbance and less natural disturbance than is found in the Saskatchewan Boreal Shield (Alberta: 26.4% <40 yrs age, 57.2% within 500 m of industry; Québec: 9.4% <40 yrs age; 42.5% within 500 m of industry [data in Appendix F of Environment Canada 2012). At the same time, wolf densities are much higher than as observed in the Saskatchewan Boreal Shield, moose densities lower, and more developed landscapes may be affected by increasing densities of alternate prey species like white-tailed deer (e.g., Latham et al. 2011c). We believe that one of the great values of our research may be in describing the dynamics of a woodland caribou population in a region that has little-changed from historic conditions, i.e., the conditions in which the species originally evolved. As such, our data on woodland caribou of the Saskatchewan Boreal Shield may now serve as a 'benchmark' for the study and conservation of other caribou populations.

3.4 Conclusion

In consideration of all data available at the time of writing, we have come to the following preliminary conclusions with respect to SK1 caribou population status and trend: (1) the population occupies some of the most pristine habitat available to non-migratory, forest-dwelling

caribou in Canada, with very low levels of anthropogenic disturbance; (2) although being subject to large fires in the past 40 years, the SK1 unit retains large tracts of high-quality habitat available for woodland caribou; (3) selected habitat supports some of the highest densities known for non-migratory, boreal caribou in mainland Canada; (4) at the same time, wolf densities in the region are thought to be low and densities of the only other alternate ungulate prey in the system, moose, are recorded as being among the lowest in all of North America; and (5) hunting pressure on woodland caribou in the region is extremely low. We believe that, collectively, these conditions resulted in our finding that: (6) the population is presently characterized by high adult female survival rates and moderate-low recruitment, but yet high pregnancy rates; (7) these traits are suggestive of a large herbivore population that may be experiencing density-related constraints on further population growth, but not so much as to result in phasic population decline; and (8) the standing age- and sex-structure, combined with known survival rates and reproductive data, indicates a stable to slightly increasing population over the recent past and as a future projection. Finally, (9) we believe that the best available evidence suggests that the status of woodland caribou in the SK1 unit is one of a large and self-sustaining population, perhaps one of the most secure of all boreal caribou populations in Canada. As we continue to collect data, our picture on the dynamics of caribou in the Saskatchewan Boreal Shield will become clearer (our final report on the status and trend of caribou in the region is scheduled for December, 2018).

4.0 CRITICAL HABITAT

In addition to identifying status and trend information for woodland caribou of the Saskatchewan Boreal Shield, a principal goal of our project was to inform on all three required components (location, amount, type) of 'critical habitat' for the SK1 unit. We need to know what constitutes critical habitat for caribou in the region not only to help complete the Canada-wide *Recovery Strategy*, but also to develop a better understanding of how boreal caribou might persist under the high-fire, low anthropogenic disturbance regime that was historically the case for many boreal caribou populations in Canada (especially in boreal shield regions). We believe that this may serve as a benchmark for all jurisdictions managing caribou.

The current *Recovery Strategy* identifies action being required where: "a minimum of 65% undisturbed habitat in a range as the disturbance management threshold, which provides a measurable probability (60%) for a local population to be self-sustaining. This threshold is considered a minimum threshold because at 65% undisturbed habitat there remains a significant risk (40%) that local populations will not be self-sustaining (Environment Canada 2012: p. 34)". Here, disturbance is the combination of buffered (500 m) anthropogenic footprints and forest <40 years old. This is a guideline to meet the strategy's overarching objective that: "habitat disturbance within a range needs to be managed by the responsible jurisdiction at a level that will allow for a local population to be self-sustaining (p. 34)".

At first glance, it might appear that the Saskatchewan Boreal Shield presents an unsustainable situation for caribou given the natural, short fire-return interval that averages 99–104 years (fires are predominately caused by lightning strikes, with only 6.1% of fires being human-caused; data in Parisien et al. 2004). The extent of fires driving this interval requires a large footprint of forests to be aged <40 years at any point in time (e.g., 55% burned in the past 40 years for the SK1 unit [data in Environment Canada 2012]; but see Kansas et al. 2016 [estimate should be revised downwards to approx. 37.4% to account for unburned residuals and exclusion of water]). Human disturbance on the landscape is very small in comparison (3%).

The initial conclusion that the caribou population in the SK1 unit should not be self-sustaining, based on the ECCC disturbance threshold (Environment Canada 2012), is at odds with what we know about the population (*Section 3.0*) which exists at high relative density and is stable to slightly growing in size.

ECCC recognizes that: "[…] there is variation in habitat and population conditions between boreal caribou local populations across their distribution, for some ranges it may be necessary to manage the range above the 65% undisturbed habitat threshold, while for others it may be possible to manage the range below the 65% undisturbed habitat threshold (p. 34)." For the SK1 range, to avoid management based on a random event (fire ignitions and spread) and, essentially, recovery of a single environmental condition (i.e., gross spatial extent of burned habitat), information on how caribou respond to existing habitat and disturbance is needed.

The term 'critical habitat', which is a legal definition with respect to SARA, is often vaguely interpreted: in practice the term has been quantified from habitat use by species or degree of habitat selection (90,91) and by meta-analyses of population growth or viability and habitat occupancy (92,93). Despite its Canadian definition as "habitat that is necessary for the survival or recovery of a listed wildlife species", the link between survival and recovery (i.e., reproduction) of species to habitat features is rarely measured. Here we are speaking about the fitness consequences of habitat selection: why a species might use habitat is a distinctly different question from how (i.e., patterns of habitat selection). Our ideal approach to understanding why caribou use habitat is based on identifying the link between fitness (survival and reproduction) and the process of habitat selection, and how it is modified by ecological processes including competition, predation, and habitat change (McLoughlin et al. 2010). We are currently developing methods for computing individual-based models of resource selection, to link to individual caribou fates of survival and reproduction, and this deliverable will be presented (as planned) as part of the final report for our project (December 31, 2018).

Here, we present on the biophysical attributes of habitat that best predict probability of woodland caribou occurrence based on our sample of tracked caribou (GPS-collared adult females; *Section 3.1*), the amount (in terms of area) of these habitat features located in the region where our population data is being collected, and where these critical aspects of habitat occur. We first describe our process of defining our study area and base map of habitat as it is available to caribou; how we delineated a parsimonious set of habitat classes that were ecologically meaningful to female boreal caribou in Saskatchewan's Boreal Shield; divided the calendar year into an ecologically meaningful set of seasons to interpret habitat selection patterns; and then used movement and habitat data to estimate the probability that any given point or pixel in space could predict the likelihood of caribou occupancy. We present our analysis at two scales: a broad scale where caribou are assumed to be able to use habitat throughout the area where collared caribou occurred; and on a finer scale where caribou were restricted to using habitat only as it occurred within their home ranges. For the purpose of defining location, amount, and type of critical habitat in our study area, we principally rely on broad-scale habitat selection patterns.

4.1 Mapping

4.1.1 FIELD SAMPLING AND MAP PRODUCTION

Habitat selection results presented in this interim report relied on mapping products that we were able to produce based on a combination of existing data and new field sampling. Existing data were derived from the Saskatchewan Forest Ecosite (FEC) field records, consisting of 718 samples in the Saskatchewan boreal shield ecoregion (McLaughlan et al. 2010). We augmented the existing FEC data with new samples to increase the age range of sampled sites and number of sites sampled away from roads, and collect new data related to successional transitions after fire

and availability of key forage lichens. We collected new data at 206 sites in the SK1 range from October 1, 2014 to August 15th, 2015. Our surveys covering a range of 24 different ecosites and stand ages from 1 or 2 years post-fire to mature stands >150 years old. For each site, we collected data on tree composition, density, and age; topographic position and soil properties; understory vegetation composition and abundance of forage lichens. New sites were classed within the FEC framework and the combined FEC and new field sites were used as input for developing a new map of vegetation types within the SK1 range.
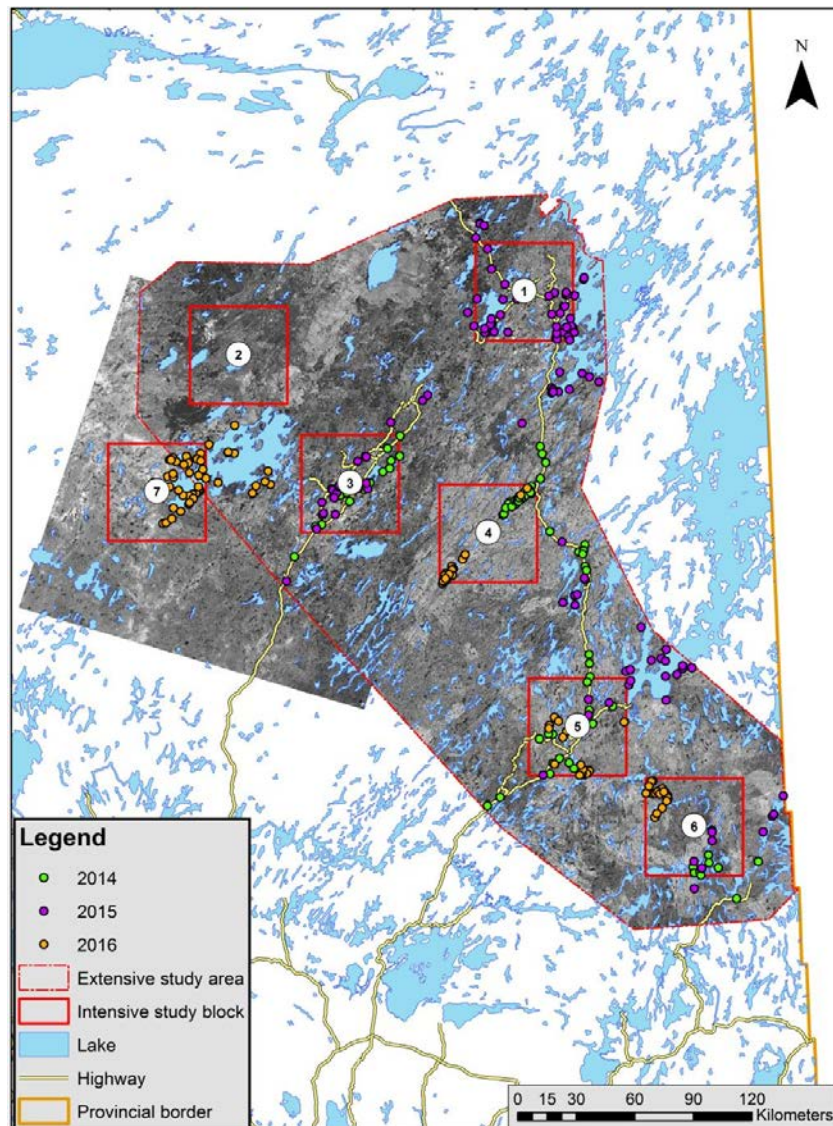
Figure 4.1: Location of vegetation sampling sites in the Saskatchewan Boreal Shield. Each of 7 blocks were used to help focus sampling at each site to cover the full range of habitat conditions available in the SK1 caribou range. The grey region on the map (shaded to represent visual reflectance from Landsat data) represents the broad area of vegetation sampling.
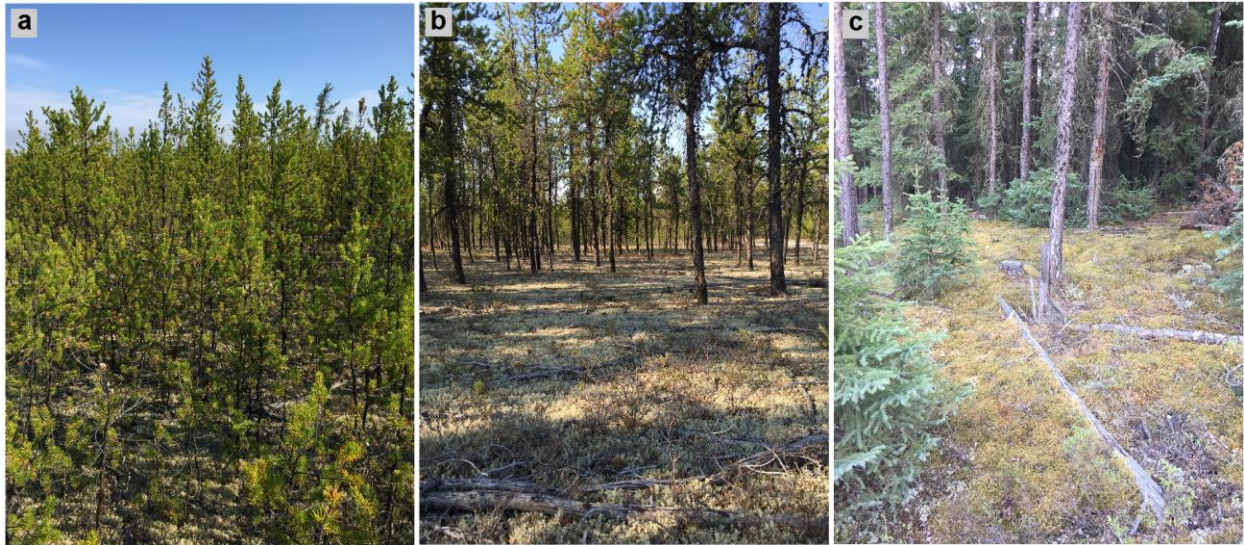
Figure 4.2: Examples of dominant forest stand types in Saskatchewan's Boreal Shield. (a) immature and (b) mature stands of ecosite BS3 (jack pine/blueberry/lichen) with a the canopy dominated by jack pine (*Pinus banksiana*), and the understory of reindeer lichens (*Cladina mitis*) that develops in older stands, and (c) ecosite BS9 (black spruce - jackpine/feathermoss), showing ground cover dominated by feathermoss (*Pleurozium schreberi*).
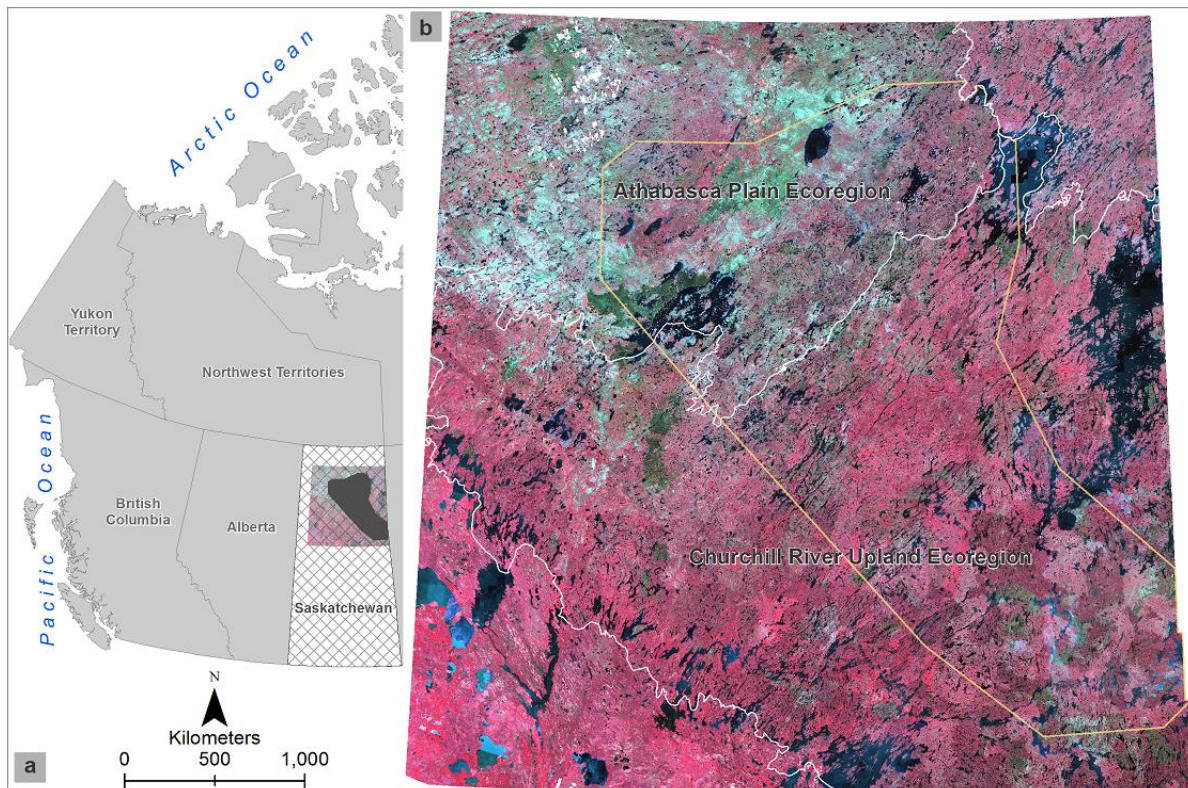
Figure 4.3: (a) Location of vegetation sampling, and (b) the extent of Landsat 8 composite images with an overlay of ecoregions and study area available for map processing used to estimate habitat classes available to woodland caribou.

The vegetation map was built from a composite image of multispectral Landsat 8 tiles collected in 2013 and 2014 and covering the entire study area (30 × 30 m pixel resolution). The sensors of Landsat 8 (operational land imager—OLI and thermal infrared sensor—TIRS) operate in the visible, near infrared, short infrared, panchromatic, and thermal infrared portions of electromagnetic spectrum. We used 7 out of 11 available bands: three from the visible (blue, 0.45–0.51 μm; green, 0.53–0.59 μm; red, 0.64–0.67 μm) and two each from the near infrared (nir, 0.85–0.88 μm; cirrus, 1.36-1.38 μm) and short infrared (sir1, 1.57–1.65 μm; sir2, 2.11-2.29 μm; Fig. 4.3). We used the composite to create vegetation indices (NDVI, EVI, and NDWI), band ratios, and the tasseled cap transformation (Fig. 4.4). We acquired tiles of a matching resolution digital elevation model (DEM) from the US Geological Survey data portal for creating nine indices representing topographic characteristics of the SK1 range, including solar radiation index, topographic compound index, and topographic roughness surface, or TRI (Fig. 4.4). We then used a backward stepwise analysis to reduce the dimensionality and collinearity of our input data for the map building.

Using a custom script package that we developed in the statistical program R (v.3.3.1, R Core Team 2016), we compared different approaches of machine learning algorithms for building the vegetation map classification. We applied the gradient boosting (GB), nearest neighbor (NN), and random forest (RF) algorithms to classify the input data into FEC classes across the SK1 study area. Gradient boosting models produced the highest overall and class-level accuracies, outperforming both the NN and RF models. GB analysis produced a total mapping accuracy of 78%, approximately 48%, and 45% higher than NN and RF. We used the GB model to provide a vegetation map of the full 27 FEC types for the SK boreal shield (Figure 4.5). FEC types were then grouped together as needed for resource selection modelling (*Section 4.2*).

Variables derived using Landsat & DEM

Band 6,5,4   MASAVI   NDVI   Aspect   Hill shade   Slope   TRI
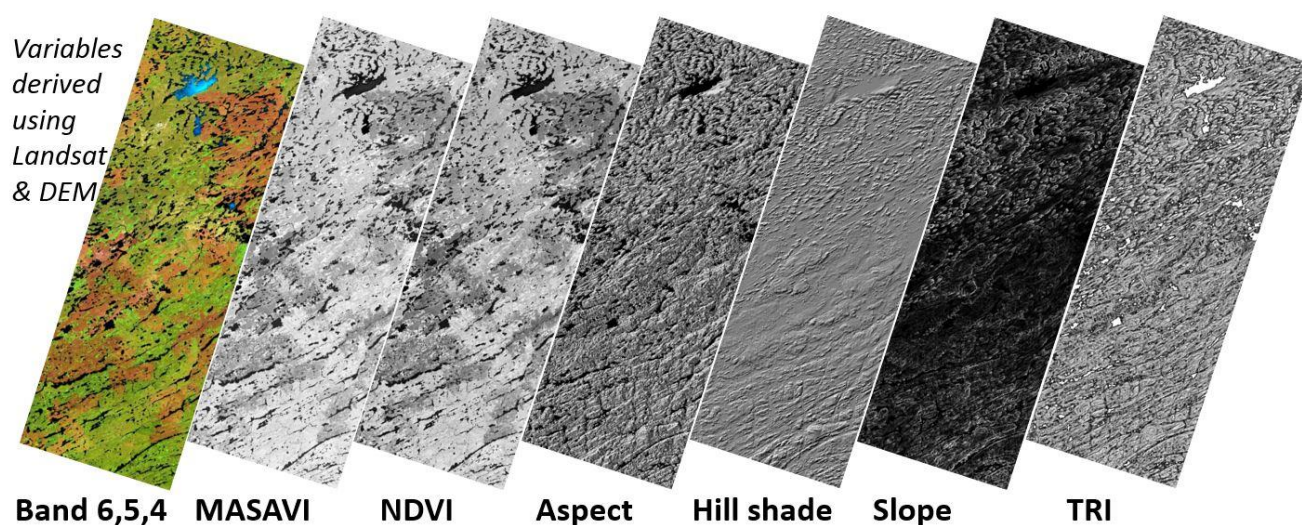
Fig. 4.4: Important predictor variables derived from Landsat 8 imagery and digital elevation model for estimating ecosites of the Saskatchewan Boreal Shield.
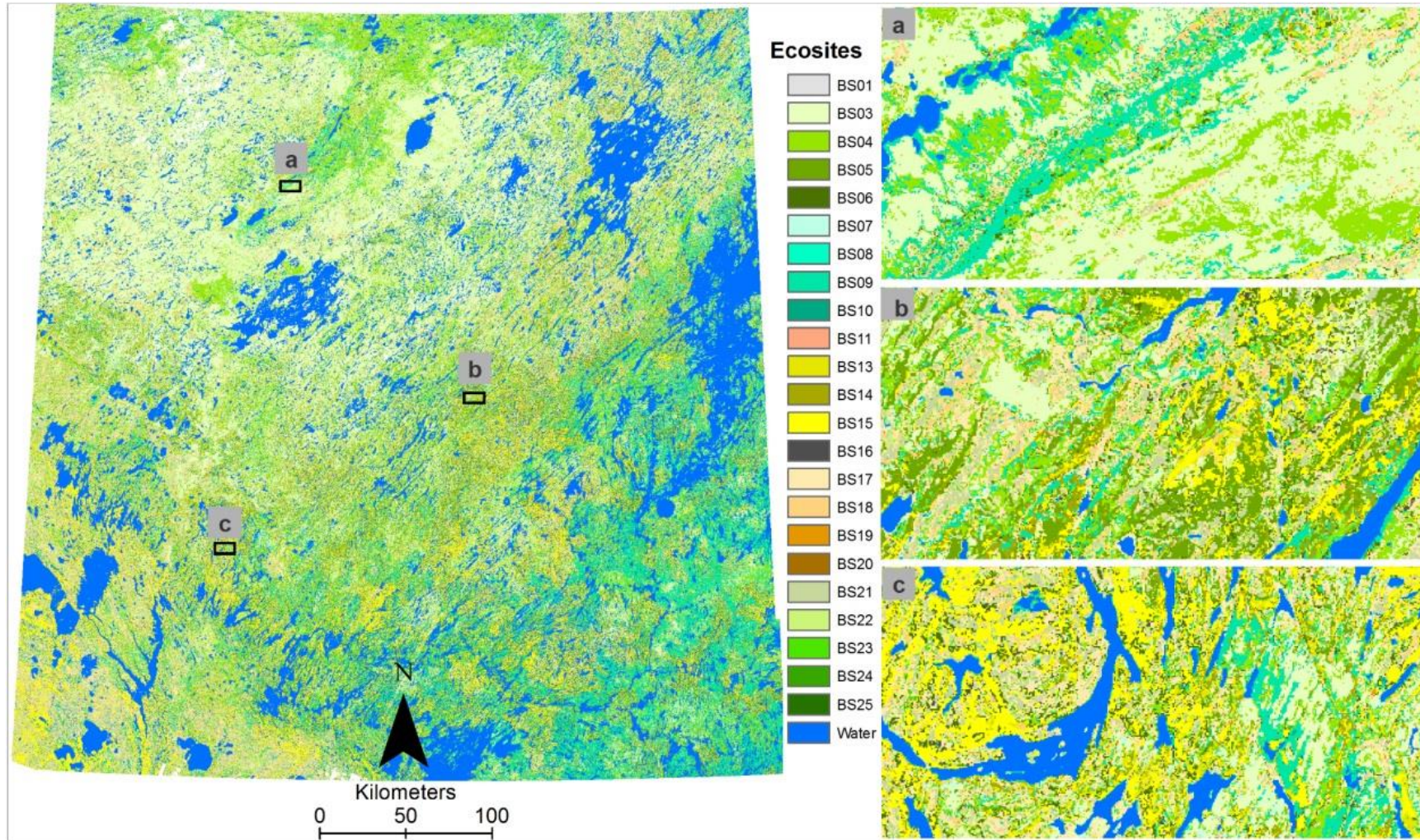
Figure 4.5: Complete and detail views (a, b, and c) of boreal forest ecosites derived from the gradient boosting algorithm using the Forest Ecosystem Classification scheme. Detail views highlights distinction among ecosite types and their distribution across the boreal shield ecozone of Saskatchewan. Common cover types in the detail views include BS03 (jack pine/blueberry/lichen), BS05 (jack pine-birch/feathermoss), BS09 (black spruce-jack pine/feathermoss), and BS15 (trembling aspen-white birch/green alder).

UNIVERSITY OF
SASKATCHEWAN

4.2 Defining Habitat Classes for Caribou

4.2.1 BACKGROUND AND OBJECTIVES

Resource units, which are often delineated on maps as points or pixels in space (Manly et al. 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, forest age, elevation, proximity to roads, etc.). Depending on the species of interest, different factors may be more important than others in determining whether or not an individual selects a resource unit. In addition, the importance of some factors 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 landscape features, 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]; reviews in Boyce et al. 2002 and McLoughlin et al. 2010). Ideally, researchers should delineate habitats according to intrinsic and extrinsic factors governing the study animal's behaviour over the scale(s) of their study.

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 our study area where we had data on collared caribou (Fig. 3.5), seven of these FECs were either extremely rare (<5 km^2 total area, $n = 4$) or absent ($n = 3$) and hence not very useful for characterizing resource units. We partitioned the remaining FECs into habitat classes that we believed were ecologically meaningful to female boreal caribou. That is, we defined a set of habitat classes that can be distinguished according to factors that govern caribou resource selection at the spatiotemporal scales of our resource selection analyses. We 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 female boreal caribou occurrence in the SK1 unit (*Section 4.4*).

4.2.2 FEC METRICS AND CARIBOU

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 as it relates to diet may be more important at finer scales (Johnson et al. 2001). As we were investigating resource selection at both coarse and fine spatial scales, we chose to group FECs according to 13 metrics related to either

predation risk (i.e., factors that may mitigate or enhance risk) or forage availability. All metrics 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 (xi) –(xiii) percent cover of three shrub categories: 'risky shrubs' such as willow (*Salix spp.*) and trembling aspen (*Populus tremuloides*) that may attract alternate prey species (moose); 'berry-bearing shrubs' such as lingonberry (*Vaccinium vitis-idaea*) and blueberry (*Vaccinium myrtilloides*) that may attract black bears during the summer, but whose leaves may provide winter forage for caribou (Boertje 1984; Thomas et al. 1994); and 'Labrador tea (*Ledum groenlandicum*) shrubs', which are a potential forage item common to 16 of the 20 FECs. FEC values for each metric are presented in Table 4.1.

McLaughlan et al. (2010) describe percent coverage 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 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, we 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 FEC BS3, we multiplied the 10% percent cover value for black spruce by 0.5 (i.e., percent constancy = 50%) to get a weighted percent cover value of 5% (i.e., a value representing the percent cover across all of the sample plots). In doing so, we hoped to (a) better capture the importance of each tree, shrub or lichen species to the overall description of each FEC, and (b) make percent cover values somewhat comparable between FECs.

It is important to note that the number of releves 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 metrics derived from them) may not accurately represent the true range of conditions possible for each FEC. We 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 we could derive the 13 FEC metrics described above.

Table 4.1: Summary of the metrics used to cluster 20 forestry ecosite classes (FECs) within Saskatchewan's Boreal Shield. (%C) refers to the *percent cover*, which is defined by McLaughlan et al. (2010) as the percent area of ground within a sample plot that is covered or shaded by a species or material. Here, the percent cover value is weighted by the *percent constancy,* which is the percentage of sample plots within which the species was recorded. 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	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)	Risky Shrubs (%C)	Berry Shrubs (%C)	Lab. Tea (%C)	Canopy Closure (%)
BS3	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	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	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	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	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	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	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	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	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	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	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	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	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	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	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	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	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	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	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	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

UNIVERSITY OF SASKATCHEWAN

4.2.3 METHODS: STATISTICAL ANALYSIS

We initially grouped FECs using a hierarchical, agglomerative clustering method called the Unweighted Pair-Group Method using Arithmetic Averages (UPGMA, see Rohlf 1963; Sneath and Sokal 1973). 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 compromise between single-linkage agglomerative clustering (nearest neighbor sorting) and complete linkage agglomerative clustering (farthest-neighbor sorting). Its use was justified after a comparison of cophenetic correlations (c.c.), showed 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), and 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.

We validated the final UPGMA solution 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). We chose a random start for the NMDS, but ran the wrapper `alt.bestnmds` (no. random starts = 50, maximum no. iterations = 100) to also estimate the final stress values. Code for this wrapper, which is compatible with the function `metaMDS` from the R package `vegan` (Oksanen et al. 2016), is available online from Montana State University (http://ecology.msu.montana.edu/labdsv/R/labs/lab9/lab9.html). We 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 well positions objects in the ordination space should produce a Shepard diagram with a fairly smooth regression line (i.e., with fewer steps) and minimal scatter about that line. We conducted all statistical analyses using open-source R statistical software (v.3.3.1, R Core Team 2016).

4.2.4 UPGMA CLUSTER ANALYSIS

Comparison of Mantel's correlation (Mantel 1967) for $k = 1$ to $k = 20$ clusters indicated that the 20 FECs were 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, we 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. 4.6). Interestingly, moisture regime and the relative percent cover of the seven characteristic tree species appeared to be the primary distinguishing metrics between classes. Two FECs, BS14 (blue box, Fig. 4.6) and BS16 (red box, Fig. 4.6), remained independent, likely due to their unique canopy compositions. Specifically, BS16 was dominated by white spruce and balsam poplar while BS14 was dominated by white birch. Most other forested FECs were dominated by either jack pine ($n = 4$, pink box, Fig.4.6) or black spruce ($n = 4$, green box, Fig. 4.6), although BS13 and BS15 (purple box, Fig.4.6) were characterized by mixed deciduous or mixed deciduous-conifer canopies. The largest cluster (orange box, Fig. 4.6) encompassed eight FECs that can all be described as open ($\leq 55\%$ 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. 4.7) for all FECs were positive, which suggests that none of the sites were misclassified (note: the silhouette widths for BS14 and BS16 were
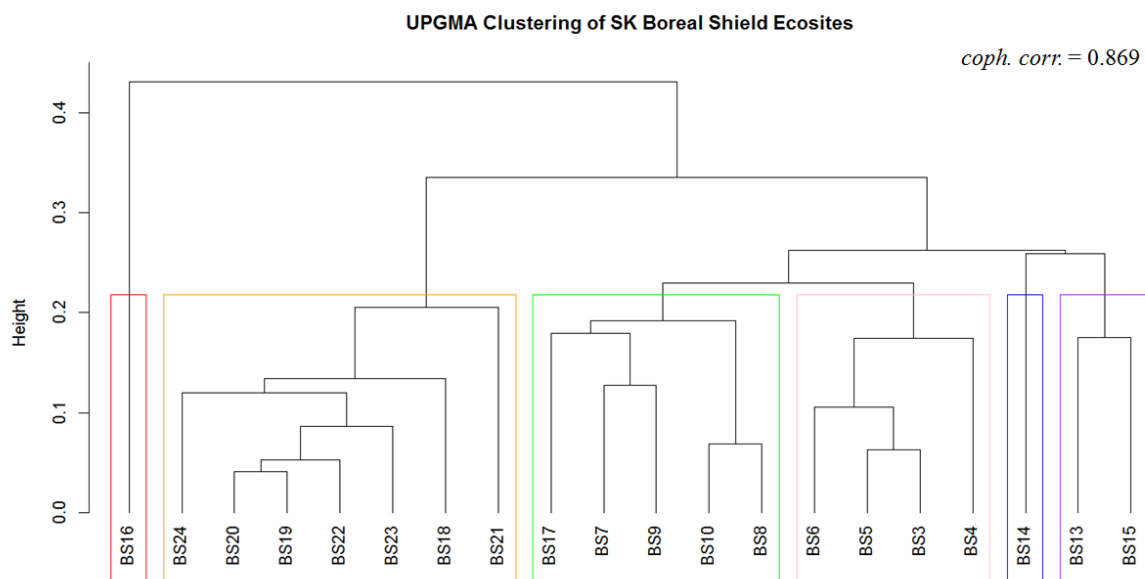
Figure 4.6: Final dendogram for the clustering of 20 forestry ecosite classes (FECs) in Saskatchewan's Boreal Shield using the Unweighted Pair-Group Method Arithmetic Averages (UPGMA) clustering method. The coloured boxes represent the optimal number of clusters ($k = 6$) according to Mantel's Correlation (Mantel 1967) . The *cophenetic correlation,* which is a measure of the goodness of fit of the clustering, is presented at the top of the graph.

$n = 20$

6 clusters C_j

$j : n_j \,|\, \text{ave}_{i \in C_j} \; s_i$

1 : 4 | 0.33

2 : 4 | 0.28

3 : 2 | 0.23

4 : 1 | 0.00

5 : 1 | 0.00

6 : 8 | 0.54

Silhouette width s_i

Average silhouette width : 0.36
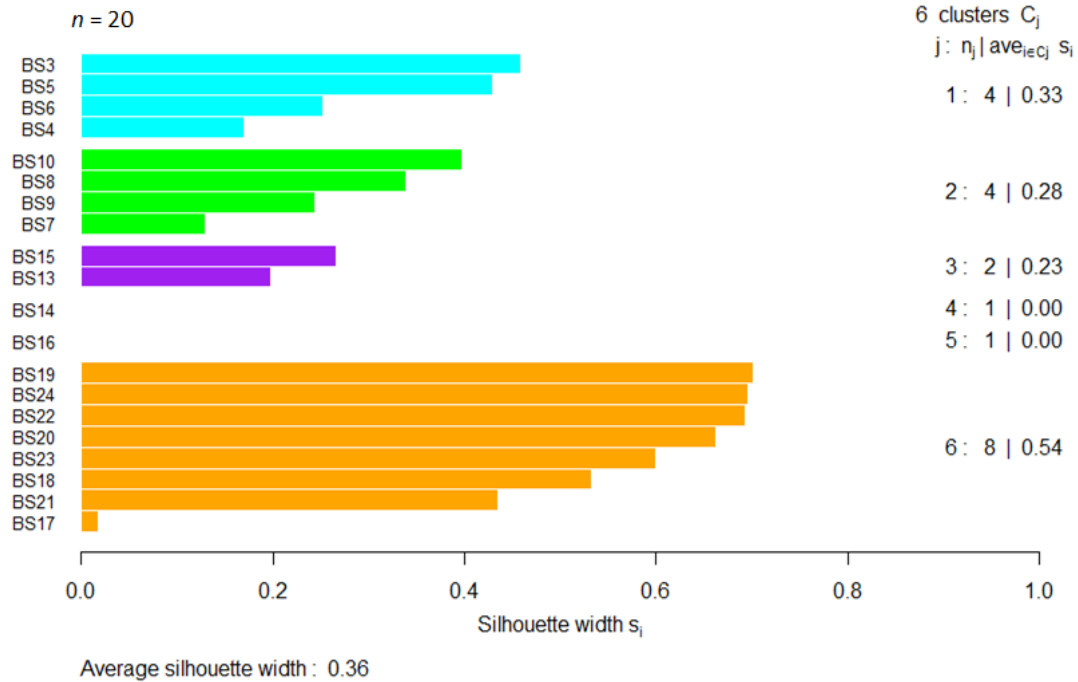
Fig. 4.7: Diagnostic silhouette plot showing the silhouette widths (a measure of the degree of membership of an object to its cluster) for the 20 ecosites. Different colours indicate different clusters. A positive silhouette width indicates an object has been correctly classified. BS14 and BS16 have silhouette widths equal to zero because they are independent classes.

(a) $k = 3$ dimensions

Non-metric fit, $R^2 = 0.993$
Linear fit, $R^2 = 0.959$

Ordination Distance

Observed Dissimilarity

(b) $k = 4$ dimensions

Non-metric fit, $R^2 = 0.999$
Linear fit, $R^2 = 0.99$

Ordination Distance

Observed Dissimilarity
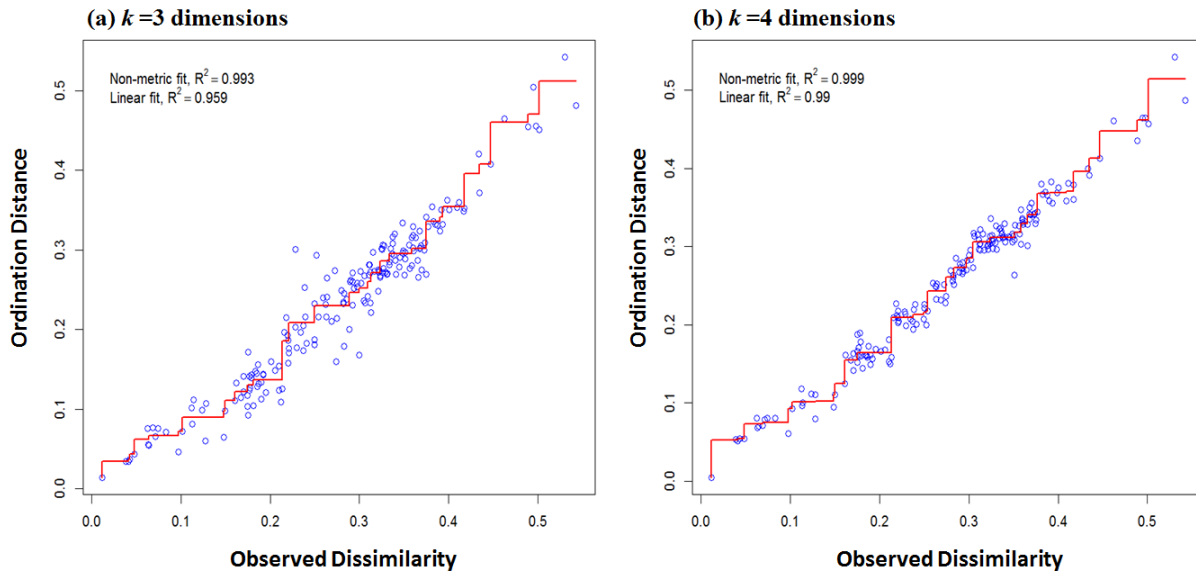
Fig. 4.8: Shepard diagrams comparing the original distances in the dissimilarity matrix to the distances among the 20 FECs in (a) 3-dimensional (3D) space and (b) 4-dimensional (4D) space. Ideally, the regression line (red line) should be fairly smooth with little scatter about it. The R^2 values in 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.

UNIVERSITY OF SASKATCHEWAN

zero because they were independent; hence, the average distance between them and other members of their respective clusters was zero). However, the small silhouette width for BS17 indicates it had a low degree of membership to the wetland habitat class; hence it may be better classed as a separate group.

4.2.5 VALIDATION OF CLUSTER SOLUTION

To validate the UPGMA cluster solution, we 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, we 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 adequately fits the data). Despite this favourable stress value, the Shepard's diagram for the 3-dimensional (3D) NMDS model (Fig. 4.8) was characterized by a stepped 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 ($R^2 = 0.993$) suggested that the distances between FECs were sufficiently represented in 3 dimensions. We ran an NMDS with $k = 4$ dimensions in order to compare the diagnostics. The stress value for this model was 0.036, which suggests 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. 4.8) had a somewhat smoother regression line with tighter points. That said, NMDS solutions in four dimensions are rather 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, we chose to continue the analysis with the 3D model.

We used an interactive plot (shown from three alternate perspectives in Fig. 4.9 a-c) to examine the relative position of the twenty FECs in 3-dimensional space. The solution was rotated using a Principle Components Analysis (PCA; Hotelling 1933) so that the greatest amount of variance was captured along the first axis (i.e., axis NMDS1). The diameters of the black circles indicate how far distant 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 well with the UPGMA cluster solution (Fig. 4.6). The incongruity between the relative positions of BS14, BS17, and BS21 in the NMDS solution (Fig. 4.9 a-c) and their relative positions in the UPGMA solution (Fig. 4.6) suggests one or more of these FECs may be misclassified.

Fig. 4.9: 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).

4.2.6 STAND AGE

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 avoid early successional forests; Metsaranta and Mallory 2007; Hins et al. 2009; Courbin et al. 2009). Hence, as part of our classification system, we partitioned each conifer-dominated habitat class into two broad age categories: mature forests (>40 years post-fire) and young/mid-successional forests (≤40 years post-fire). These ages were consistent with current age categories used by ECCC to determine what is disturbed *vs.* undisturbed habitat in caribou range (rationale presented in Environment Canada 2011, 2012).

4.2.7 ECOLOGICAL INTERPRETATION AND FINAL CLUSTERING

An important step in any ecological cluster analysis is to assess whether the final cluster solution makes biological sense. Examining the UPGMA cluster solution (Fig. 4.6), there were six broad habitat classes (irrespective of age): jack pine-dominated forests (*n* = 4 FECs, pink box, Fig 4.6); black spruce-dominated forests (*n* = 4 FECs, green box, Fig. 4.6); mixed-canopy forests (*n* = 2 FECs, purple box, Fig. 4.6); white birch-dominated forests (*n* = 1 FEC, blue box, Fig. 4.6); mixed-canopy swamps (*n* =1 FEC, red box, Fig. 4.6); and open bogs/fens (*n* = 8 FECs, orange box, Fig. 4.6). A qualitative comparison of the raw FEC metrics (see Table 4.1) indicated that most FECs were logically partitioned into one of these groups; however, there were two FECs—

BS17 and BS21—that appeared to be misclassified from an ecological perspective. The difference in the relative positions of these FECs in the NMDS solution (Fig. 4.9 a-c) *vs.* the UPGMA solution (Fig. 4.6) offered further support for this conclusion. Therefore, before dividing the conifer-dominated classes by age, we critically evaluated the properties of each of these FECs to decide on their final placement in the cluster solution. We did the same for FEC BS14 due to a similar disparity in its relative positions in the NMDS *vs.* UPGMA solutions.

According to the final UPGMA solution (Fig. 4.6), BS17 belonged in a cluster with seven other open, wetland-habitat types (BS18–BS24, inclusive); however, its small silhouette width (Fig. 4.7) indicated that BS17 was only marginally similar to the other members of its group. In the NMDS solution (Fig. 4.9 a-c), BS17 occurred 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 4.1) suggested that boreal caribou may perceive BS17 differently than either class. McLaughlan et al. (2010) describes 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 for summary of FEC characteristics); hence, with respect to seasonal foraging opportunities, we believed that a caribou may not perceive BS17 in the same manner as it may perceive BS7–BS10. While similar seasonal foraging opportunities might be available in the seven wetland habitats, BS17 may still present a more attractive option because 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, we decided to allocate BS17 to its own habitat class, which we called 'black spruce bog'.

Like BS17, 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. We asked whether the addition of tamarack trees to a wetland might qualify it as increasing its value to boreal caribou? Trees can provide shelter and may offer cover from predators. In the case of mature conifer forests, they can also support terricolous lichens. However, as a component of FEC 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. Thus, despite its isolated position in the NMDS solution (Fig. 4.9 a-c), we felt justified leaving it in the cluster of wetland habitats.

Finally, although the UPGMA solution (Fig. 4.6) partitioned FEC BS14 as its own class, its position in the 3-dimensional space of the NMDS solution suggested it should be grouped with BS13 and BS15. A comparison of FEC metrics (see Table 4.1) favours the latter grouping. All three of these FECs were characterized by fairly dense, deciduous-dominated canopies and had similar percent cover values for shrubs and lichen. BS14 was unique in that it was the only FEC with a white birch-dominated canopy; however, the actual species of deciduous tree forest likely has less ecological significance to boreal caribou than the fact that the canopy is dominated by one or more deciduous tree species. This is because, regardless of their canopy composition, deciduous-dominated forests in Saskatchewan's Boreal Shield have similar understories (as evidenced by their similar percent cover values for shrub categories and lichen), which suggests that they likely offer similar levels of risk, shelter, and foraging opportunities to caribou. Hence, we clustered BS14 with BS13 and BS15. We 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.

After reclassifying 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 muskeg' (*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), we 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). We did not partition the black spruce bog cluster into age classes because 93.9% of black spruce bogs in the study area were classified as mature (the category appeared to be relatively resistant to fire). The final eight habitat classes are summarized in Table 4.2 and a map illustrating the distribution of each class across the study area is presented in Fig. 4.10. Table 4.2 (% area column) illustrates how these categories occur in the entire mapped region available for the SK1 caribou unit. 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%), we still included it for analysis because it comprised a larger proportion for a subset of caribou home ranges in the southeastern section of the study area.

Table 4.2: 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 classes (FECs) that were grouped together based on 13 metrics 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.

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; generally open overstory (<55% canopy cover); relatively high percent cover of berry-bearing shrubs (>10%).
Young/Mid-Succesional Jack Pine Forest	BS3, BS4, BS5, BS6	39.2	Jack pine-dominated forests ≤40 years post-fire; generally open overstory (<55% canopy cover); relatively high percent cover of berry-bearing shrubs (>10%).
Mature Black Spruce Forest	BS7, BS8, BS9, BS10	7.1	Black spruce-dominated forests >40 years post-fire; jack pine and white birch may also be present; relatvely high percent cover of terrestrial lichens and generally denser overstory (total canopy cover >40%).
Young/Mid-Succesional Black Spruce Forest	BS7, BS8, BS9, BS10	5.0	Black spruce-dominated forests ≤40 years post-fire; jack pine and white birch may also be present; relatvely high percent cover of terrestrial lichens and generally denser overstory (total canopy cover >40%).
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.).

Our results suggested that moisture regime, canopy composition, and canopy cover were the primary distinguishing features between the six vegetation associations we classed. In Saskatchewan's Mid-Boreal Upland ecoregion, Rettie et al. (1997) found a strong relationship between canopy characteristics and understory vegetation, which led them to suggest that over story characteristics were sufficient to distinguish between vegetation community types. If this were true, it would make on-the-ground assessment of resource units much easier. Although we did not quantitatively assess the relationship between over story species and understory species in each FEC, we did re-run the UPGMA analysis using only canopy composition (i.e., percent cover of seven characteristic tree species, see Table 4.1) and percent canopy cover. According to Mantel's correlation (Mantel 1967), the resulting cluster solution (Fig. 4.11a) was optimally divided into two habitat classes: one consisting of a single FEC (BS16) and the second consisting of the remaining 19. This was not a very useful arrangement. When we cut the tree at the next most optimal number of clusters ($n = 8$), the resulting solution (Table 4.11b) more closely resembled that obtained using the 13 FEC metrics. Given that the Mantel correlations for these two models differed by less than 0.03, one could make an argument (as we did with our own analysis) that the second solution is as equally valid as the first solution. Although a more rigorous analysis is needed, this exercise provides some support for Rettie et al.'s (1997) suggestion that canopy characteristics alone can be used to derive vegetation community types.

The above exercise emphasizes a key feature of cluster analyses: they are inherently subjective because objects are partitioned according to descriptors that are deemed relevant by the researcher. It is therefore critical 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. We clustered FECs using 13 metrics related to boreal caribou predation risk and forage availability because these two factors have been shown to govern caribou resource selection across the spatial scales of our resource selection analyses. For the most part, the cluster solution (Fig. 4.6) made ecological sense; however, there were some discrepancies between the UPGMA cluster solution and the NMDS solution (Fig. 4.9 a-c) that forced us to re-evaluate the relative positions of the FECs BS14, BS17, and BS21. This last point highlights the importance of critically evaluating the final solution of a cluster analysis to ensure that it makes sense with respect to the research goal(s) and study system.
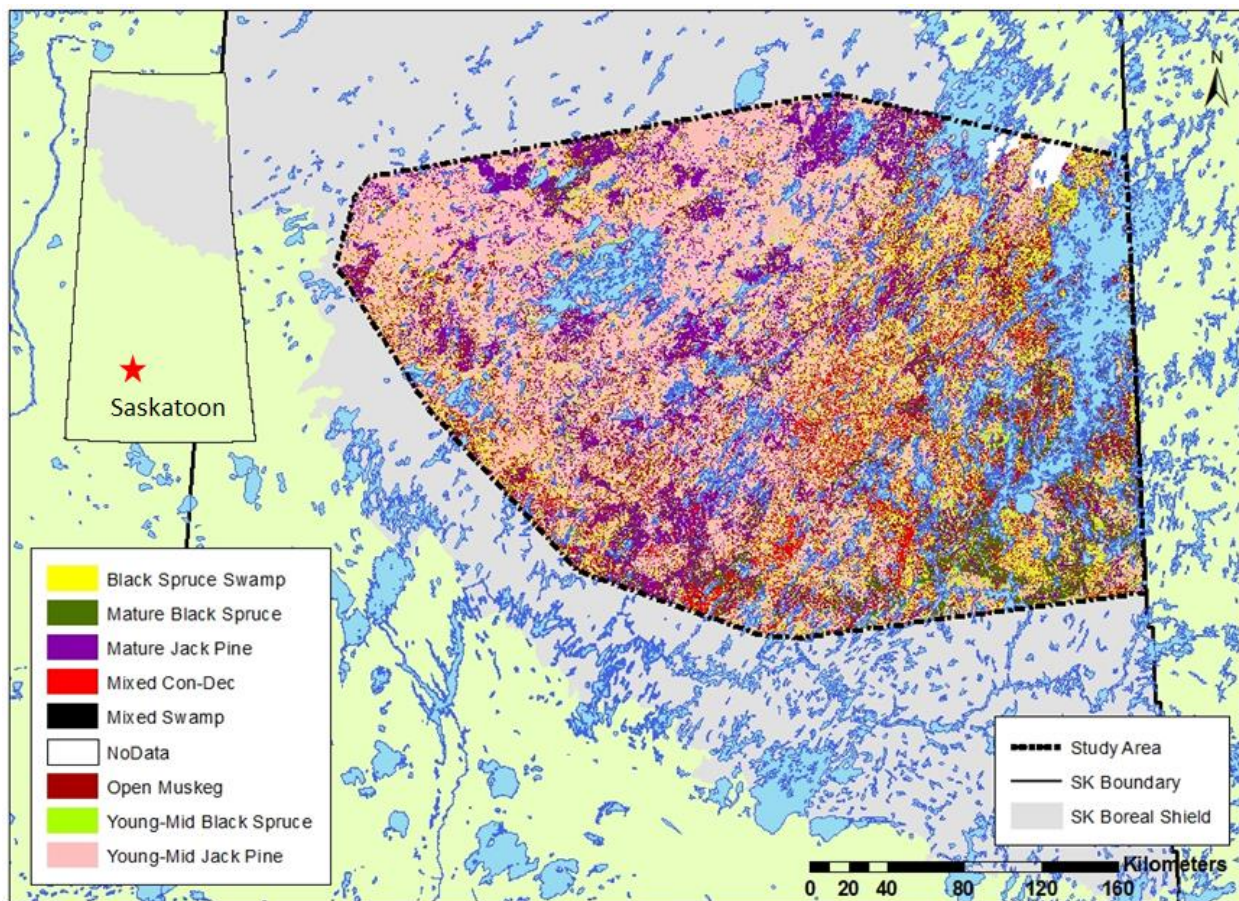
Fig. 4.10: Distribution of the final eight habitat classes used to characterize 30m x 30m resource units within the study area (black dashed line). Habitat classes were delineated by using a combination of multivariate clustering techniques and ecological interpretation to group 20 forestry ecosite classes (FECs) according to 13 metrics 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).
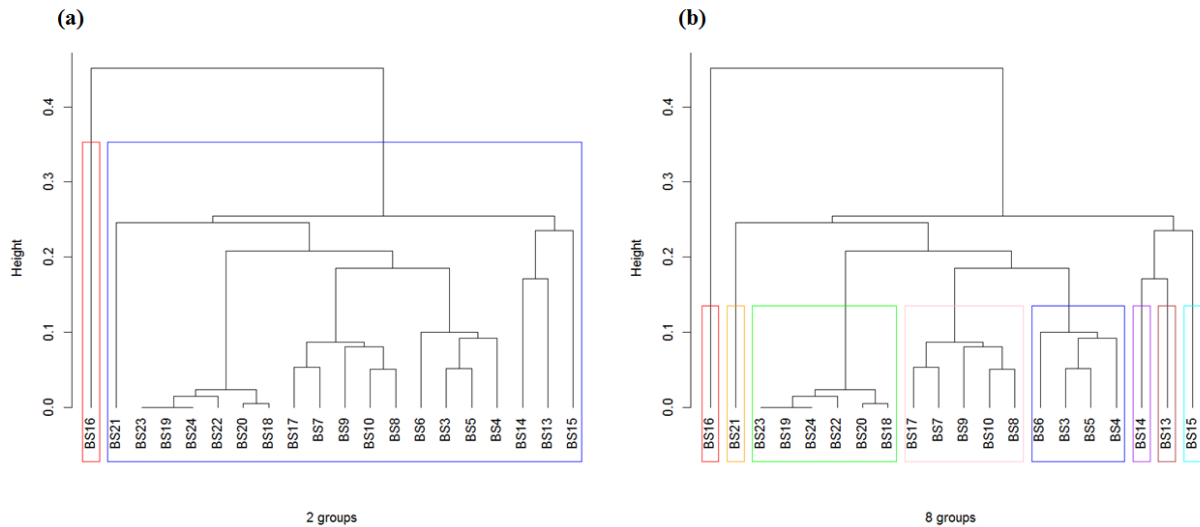
Fig. 4.11: Final dendogram for the UPGMA clustering of 20 forestry ecosite classes (FECs) in Saskatchewan's Boreal Shield according to canopy characteristics alone. A comparison of Mantel's correlation statistics for $k = 1$ to $k = 20$ clusters indicated the dendogram was optimally cut at two clusters (a), with eight clusters (b) representing the second-most optimal solution. This analysis was meant to investigate whether FECs in Saskatchewan's Boreal Shield can be delineated into ecologically meaningful classes based solely on canopy characteristics. A more rigorous analysis is required to test this hypothesis, but these results do show the dependence of the cluster solution on the clustering criteria.

It is also important to select a clustering method that fits with the structure of the data and the aims of the aims of the analysis (Borcard et al. 2011). Since FECs within Saskatchewan's Boreal Shield were hierarchically nested within ecosections, which were in turn nested within ecoregions, then ecoprovinces, and finally ecozones (see Table 1, McLaughlan et al. 2010), we chose a hierarchical, agglomerative clustering method (i.e., UPGMA). Here, objects (e.g., FECs) start off as independent clusters. The two most similar objects are grouped together first, and then objects are successively grouped into larger and larger clusters until all objects belong to a single cluster. How objects are grouped depends on how the dissimilarities (distances) are qualified between clusters. The UPGMA method defines distances between two clusters as the average distance between all pairs of objects in the two clusters. It is a fairly robust algorithm, but there are a number of other algorithms we could have used (e.g., nearest neighbor (single linkage), furthest neighbor (complete linkage), centroid or Ward's method) to arrive at a final cluster solution. When a number of clustering methods are possible, Legendre and Legendre (1998) recommended applying all of them and then comparing the results. We ran cluster models using single-linkage, complete-linkage, UPGMA, Weighted Arithmetic Average Clustering (WPGMA), and Ward's Minimum Variance clustering. According to a comparison of cophenetic correlation coefficients, the UPGMA model fit the data the best. Thus, we felt that the UPGMA cluster analysis was the appropriate method by which to cluster the 20 forestry ecosite classes in our study area.

4.3 Defining Ecological Seasons for Caribou

4.3.1 OBJECTIVES

Woodland caribou live in seasonal environments generally characterized by long winters and shorter spring and summer periods (Environment Canada 2012). Accordingly, they experience cyclical changes in weather conditions, forage availability, predation risk (e.g., from wolves and 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 winter (Johnson et al. 2001), while insect harassment may drive caribou to seek refuge in remnant snow patches during spring or early 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 (often 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 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 important to define temporal units of analyses that capture ecologically relevant changes in 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 tend to capture a significant amount of the temporal variation in 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 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 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 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. 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 is imperative that researchers think critically about whether the methods they employ will delineate seasons that are ecologically meaningful to their study population.

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 proxy for animal behaviour rather than having to make assumptions about how variables such as plant phenology and snow depth affect resource selection. Our objective here was to use movement rates to inform the delineation of an ecologically relevant set of seasons for female woodland caribou in Saskatchewan's Boreal Shield. Ultimately, these seasons were used as the temporal unit of analysis for our study of caribou resource selection (*Section 4.4*).

4.3.2 STATISTICAL 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. 4.17). Using movement rates to delineate seasons for such a population can be challenging because: (1) individual movement patterns are often highly variable (e.g., Mueller et al. 2011; Rudolph and Drapeau 2012); and (2) 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 canadensis manitobensis*) in southern Manitoba. Therefore, we, employed GAMMs to identify annual, population-level changes in the movement rates of female woodland caribou in the Saskatchewan Boreal Shield.

We calculated movement rates using spatial data remotely collected from 68 adult female caribou between March 18th, 2014 and March 17th, 2016. These 68 individuals represent the subset of the original collared population (*n* = 94) 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 (although it should be noted that we ran the model with the full data set and received almost identical partition dates). After screening the data for erroneous GPS locations and, in the case of our Lotek Iridium® collars, any 2D fixes 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), we further excluded all points less than 4.95 hours or greater than 5.05 hours apart to ensure a uniform step length. This left us with *n* = 44,155 GPS locations for analysis.

Rather than use movement rates (meters per hour [m/hr]) calculated over individual step lengths (i.e., 5 hour intervals), we chose to use daily movement rates (meters per hour per day [m/hr/day]) as the response variable for our 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), which we 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), we 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: (1) allow individual splines to connect and form a continuous curve; and (2) 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]). We identified seasonal boundaries as the inflection points (i.e., 2nd derivatives) of the model smoother.

4.3.3 RESIDENCE TIME ANALYSIS AND CALVING SEASONS

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, we conducted Residence Time (RT) analyses (Barraquand and Benhamou 2008) to ensure that the boundaries of the calving/post-calving season encompassed (1) the sample population's range of calving dates, and (2) 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 RT method). A visual interpretation of this method is provided in Fig. 4.12.
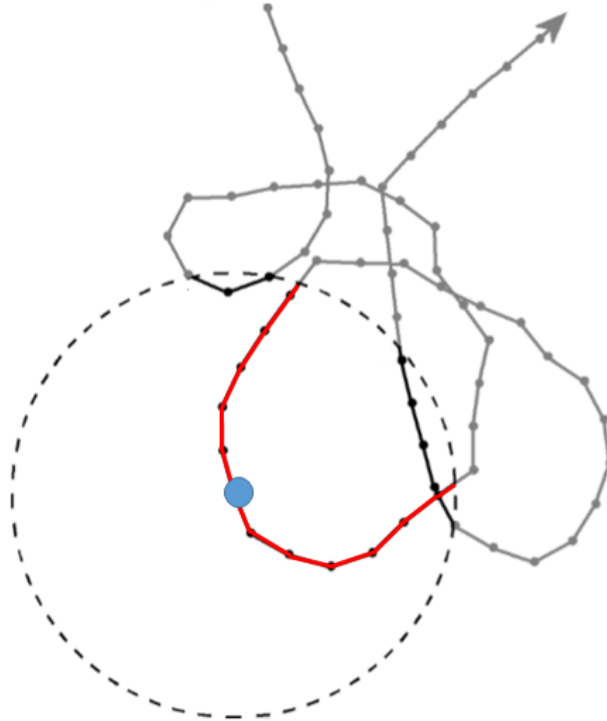
Fig. 4.12: Illustration of Barraquand's and Benhamou's (2008) Residence Time (RT) method (adapted from Barraquand and Benhamou [2008]) . A circle with a pre-defined radius (dashed line) is drawn around a focal GPS location (blue dot). This circle describes the boundary of the patch for which the RT value 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, we 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). We only retained locations that were >4.95 hours apart, thus setting a minimum step length of 4.95 hours. Consistent with Coleman et al. (2015), we set the patch radius at 200 meters and 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). We 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), we set the calving date as the start date of the first RT peak.
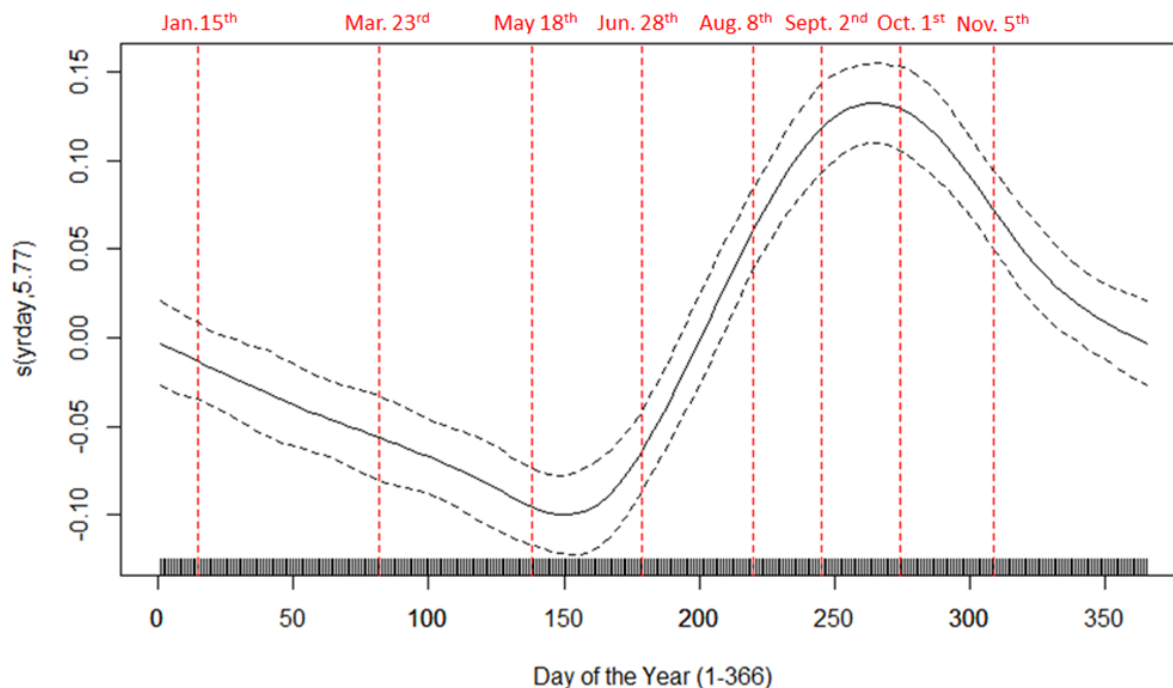
Fig. 4.13: Plot of the smoother from a generalized additive mixed model (GAMM) that fit the natural log of daily movement rates (m/hr/day) for 68 adult female caribou as a function of the day of the year (1-366 days due to a leap year during the two year study period). The solid line is the predicted 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.

4.3.5 RESULTS: GAMM

Caribou movement rates varied non-linearly with time (see Fig. 4.13) and so we were 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, we 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. 4.14 a-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, we accepted that, based on movement rates alone, there are eight potential
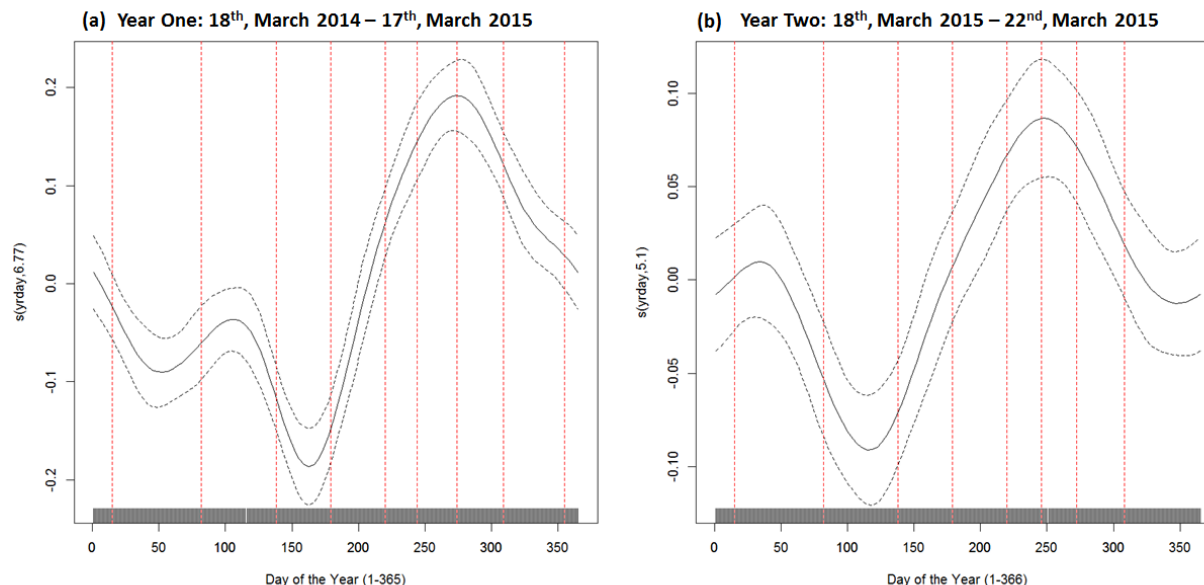
Fig. 4.14: Plot of the predicted value for daily movement rate (m/hr/day) as a function of the day of the year (1-365 or 1-366 if a leap year) for (a) Year One (18th March, 2014 – 17th March , 2015) and (b) Year Two (18th March, 2015 – 17th March 2016). The units of the response have been scaled to liner 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.

seasons for woodland caribou in the Saskatchewan Boreal Shield (summarized in Table 4.8): *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).

Table 4.3: Summary of the 8 annual seasons delineated for woodland caribou in Saskatchewan's Boreal Shield. Seasons were delineated using daily movement rates 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
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

Mean daily movement rates for each of these seasons are summarized in Table 4.4. 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 bottoming during the late winter spring season ($\bar{x}$ = 151.5 ± 1.8 m/hr/day), it gradually increased throughout the post-calving and first two summer seasons before dipping marginally again during the third summer season. Interestingly, the maximum daily movement rate over the two year study period—3547.4 m/hr/day— was recorded during the post-calving period rather than the autumn/rut 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.

Table 4.4: 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
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

4.3.6 RESULTS: RESIDENCE TIME ANALYSIS AND CALVING DATES

From the Residence Time analyses (see sample plots, Fig. 4.15), we identified 146 calving events over the two year study period (2014: 80 events; 2015: 66 events). 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 and 25th May. For caribou with calving events during the first 3 days of May (n = 3), we 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
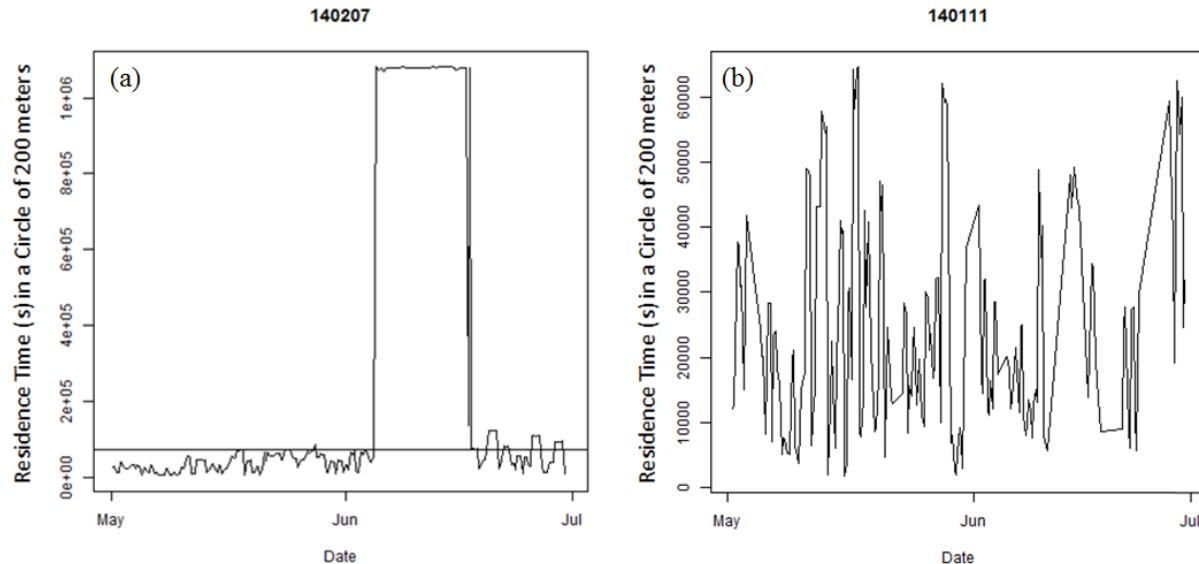
Fig. 4.15: Sample plots of the Residence Times (RT, in seconds) of two adult female caribou within a 200 meter radius patch from May 1st, 2014 – July 1st, 2014. The solid horizontal line in plot (a) demarks 20 hours; if a caribou spent more than 20 hours within a 200m radius *and* that RT peak above 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.

calving period for woodland caribou in the Saskatchewan Boreal Shield should extend from 1st May to 17th June. Looking at the seasonal boundaries delineated by movement rates (Fig. 4.13), the segment extending from 18th May–28th June comes closest to capturing this period.

4.3.7 INTERPRETATION AND SEASON DATES

According to population-level changes in the movement rates of adult females, 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 indicates 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 the Saskatchewan 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. 4.13). 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. 4.13). 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. These small scale migrations may account for the inflection point observed on 18th May. However, the RT analyses indicates 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 indicated that 35% of calving events occurred on or after 18th May, which means that the post-calving period delineated by changes in movement rates may actually represent a calving period for over a quarter of the collared animals. Hence, we decided to adjust the boundaries of the post-calving period to encompass all potential calving events (i.e., the period spanning 1st May–17th June). We then added a two-week buffer to the date of the last calving event (i.e., June 17th) to allow for a full two-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.

The inflection points on 8th August and 2nd September created three short summer seasons collectively spanning 28th June–30th September (see Fig. 4.13). 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. 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. 4.14 a-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) may 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). Using plant phenology, snow cover, and calving dates as criteria, Rettie and Messier (2000) defined the summer season for boreal woodland caribou in the Saskatchewan Boreal Plains ecoregion as a period extending from 1st July–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 that are ecologically meaningful but also practical for land managers, we decided to condense the three summer periods into a single summer season.

The final season to consider is the autumn/rut season, a 35 day period extending from 1st October to 4th November. The mean daily movement rate was highest during this season, which is consistent with Environment Canada's (2011, 2012) assessment that caribou are most active during the rutting period. Compared to the length of autumn/rut season delineated for other caribou populations (e.g., 76 days for boreal caribou in central Saskatchewan [Rettie and Messier 2000] or 66 days for caribou in the James Bay region, Quebec [Rudolph et al. 2012]), the autumn/rut period delineated here is considerably shorter and may be more representative of a rutting period.

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 (Mueller et al. 2011). The sample population used for this analysis ($n = 68$ caribou) was distributed across a 95,632 km^2 area (Fig. 4.16) and, according to trajectory analyses conducted by L. Debeffe and P.D. 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 the Saskatchewan 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). With respect to this analysis, the study area may have been too large to effectively apply a movement analysis to delineate caribou seasons. Indeed, both the disparity in calving dates estimated by the RT analyses and Debeffe and McLoughlin's (2016) analyses of caribou trajectories indicate that individual movement patterns are highly variable within the study area. That said, the eight seasons delineated using daily movement rates were mostly ecologically sensible given the climate of Saskatchewan's Boreal Shield and general woodland caribou biology. We therefore adjusted the boundary of the late winter/spring and post-calving period to better reflect the calving and post-calving period of the sample population and condensed the three summer periods into a single season that aligns more closely with the summer season delineated by Rettie and Messier (2000) for boreal caribou

Table 4.5: Summary of the final six ecologically meaningful 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

in central Saskatchewan. The result was a final set of six annual seasons that we believe are ecologically meaningful when considering a typical female caribou in Saskatchewan's Boreal Shield. They are as follows: **Early Winter** (*EW*, 5th November – 14th January); **Mid-Winter** (*MW*, 15th January – 22nd March); **Late 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 4). These seasons (summarized in Table 4.5) were used to define the temporal units of our resource selection analyses (see *Section 4.4*).

4.4 Quantifying Caribou Habitat Selection

4.4.1 BACKGROUND AND OBJECTIVES

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). They have also been used to 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 RSFs are offer a spatially-explicit, reproducible method for quantifying resource selection (Boyce et al. 2002, Johnson et al. 2004a), they 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; McLoughlin et al. 2010). They are defined by the following fixed-effects, exponential equation:

$$w(x) = \exp\left(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots\ldots \beta_k x_k\right) \qquad [4.1]$$

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 an animal will use a resource unit. Note that for logistic models without random effects (i.e., random intercepts and/or slopes [Gillies et al. 2006]), the model intercept, β_0, is often dropped from the corresponding RSF equation (Manly et al. 2002). 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 (point locations from radio-collared animals) is often used to derive the coefficients for RSFs. When dealing with these spatial data, researchers need to be cognizant of several things. First, the data is 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

of single individuals may be spatially and temporally auto-correlated depending on the time between fixes (Fieberg et al. 2010) which also violates the assumption of independence underlying the simplest 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. 2006:889). 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); $\ln[\pi(x)/1-\pi(x)]$ 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, 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 (Gilles et al. 2006). The 'beta coefficients' (β_0, β_1,…, β_n) derived from a GLMM become the model coefficients for the RSF (e.g., β_0, 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). By understanding the role ecological trade-offs play 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' (Hebblewhite and Merrill 2009) 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.

Rettie and Messier (2000) offered support for this hypothesis when they suggested that the selection of resources by boreal caribou was limited by predation risk at a coarser spatial scale, but depended more on forage availability at a finer spatial scale. However, ungulates have also been shown to make risk-forage trade-offs within the same scale (e.g., moose in Québec [Dussault et al. 2005] and non-migratory elk in Banff National Park [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 focus on predator avoidance at broader spatial and temporal scales (e.g., Rettie and Messier 2000). As discussed in *Section 4.2*, forage availability and accessibility may exert greater influence on boreal caribou behaviour at finer spatiotemporal scales.

Our objective here was to quantify resource selection by female boreal caribou in the Saskatchewan Boreal shield at two spatial scales and across six seasons (delineated in *Section 4.3*) in order to test hypotheses related to the importance of predation risk vs. foraging at multiple spatiotemporal scales. Ultimately, our goals were to: (1) test whether risk-forage trade-offs occurred between or within spatial scales; and (2) 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 (see *Section 4.4.9*).

4.4.2 HYPOTHESES AND PREDICTIONS

Traditional hypothesis testing in biostatistics involves establishing a null and alternate hypothesis and then using a statistical test or tests to determine the probability that the given alternate hypothesis is true. However, in the context of resource selection modelling, this approach is not very useful. As Cherry (1998) explains, resource selection function models, or RSFs (which we use here to predict caribou proportional probability of occurrence), 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) *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 this project, we were interested in quantifying female boreal caribou resource selection in the SK1 unit 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 (Rettie and Messier 2000), while forage availability and accessibility is more important at finer spatial scales (Johnson et al. 2001). Therefore, we 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 4.4.6*, for a description of the available habitat attributes). However, because we generated our models using a modelling technique that lacks a robust means by which to compare alternate models, we did not build a set of candidate models for each season and scale. Rather, we employed rigorous step-wise selection on a global model (i.e., a model containing all predictor variables relevant to a season) 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 probability of occurrence in Saskatchewan's Boreal Shield.

In terms of ecological hypothesis and predictions, we were interesting in testing the following:

Hypothesis 1: Predation risk has been shown to be a limiting factor at coarser spatial scales of selection (Rettie and Messier 2000). Therefore, caribou should select for resource units that are

expected to 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, assuming predator abundances are associated with alternate prey especially moose, which favour early seral stage forests or disturbances that result in reducing forest age (Environment Canada 2011, 2012). They will consistently avoid young/mid-successional forest, deciduous-dominated forests, and linear features across all seasons.

Hypothesis 2: At finer spatial scales, caribou resource selection patterns may be better explained by forage availability (Bergerud et al. 1990; Rettie and Messier 2000;, Johnson et al. 2001). Therefore, relative to resource selection at the coarse spatial scale, female caribou should show stronger selection for resource units associated with seasonal forage.

Prediction 2a: During the calving/post-calving, summer and autumn/rut seasons, female woodland caribou will show stronger selection (relative to the coarse scale) for open muskegs and black spruce bogs because these habitats support seasonal abundances of deciduous 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 4.1), which are a staple winter food source for woodland caribou (Thomas et al. 1994; Rominger et al. 1996; Thompson et al. 2015). In addition, these habitat classes tend to have denser canopies, which may impede snow accumulation, thus making it easier for caribou to access terrestrial lichens and move around.

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 (1) females are migrating to calving sites; and (2) females are allocating a greater proportion of resources to their unborn offspring (Adamczewski et al. 1993). Therefore, we predict that female caribou will show stronger selection 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 more important later in the season because bogs may provide both new spring forage and suitable calving habitat.
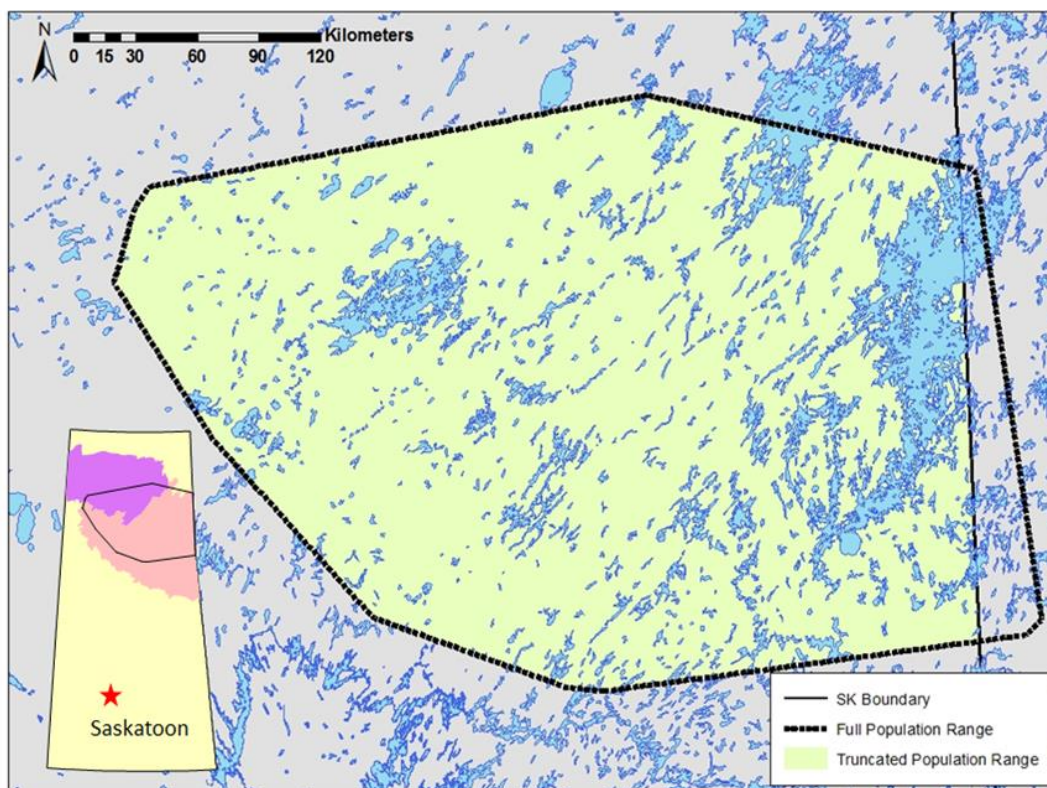
Fig. 4.16: The complete population range (dashed line) and truncated population range (green polygon) calculated over two years (23rd March, 2014 – 22nd, March 2016) for 94 female woodland caribou in Saskatchewan's Boreal Shield. Range were delineated using 100% Minimum Convex Polygons (MCPs, Mohr 1974) 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 area) and the Churchill River Upland Ecoregion (pink area).

4.4.3 METHODS: STUDY AREA OF INFERENCE

The study area (Fig. 4.16) was defined as the area of the Saskatchewan Boreal Shield (SK1 caribou administrative unit) encompassed by the population range of a sample of 94 adult, female caribou (see *Sections 4.4.4 and 4.4.5,* 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. 4.16). 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.

4.4.4 METHODS: TELEMETRY DATA

In March, 2014, the University of Saskatchewan fit 94 adult female caribou in Saskatchewan's Boreal Shield with Global Positioning System (GPS)-equipped radio-collars in (see Fig. 1.4). 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 (id nos.140158 and 140209) died within a month of being collared and were therefore censored from the data set. We 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). Before beginning our analyses, we discarded all obviously erroneous fixes (e.g., GPS locations in Hawaii or South America, $n = 102$ points); fixes that occurred in 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) less than 10 (as per Poole, http://www.radioelectronics.com/info/satellite/-gps/accuracy-errors-precision.php; $n = 242$ points). We 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, we removed all GPS points that fell outside the 95% contours of individual home ranges ($n = 10,778$ points), while at the fine scale, we removed all points that fell outside the 95% contours of individual annual seasonal ranges ($n = 11,131$ points; see *Section 4.4.5*, for a more details regarding range delineation). For each season, we then excluded all individuals with fewer fixes than the total number of days encompassed by that season. As an example, we removed caribou 140105 from the fine-scale summer models because she only had 54 points remaining for this season after we 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, we were left with $n = 194,713$ GPS locations for the coarse-scale analyses and $n = 194,312$ GPS locations for the fine-scale analyses.

UNIVERSITY OF SASKATCHEWAN

4.4.5 METHODS: 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). Since resource selection patterns may change with the spatial scale(s) at which used and available points are sampled, it is useful to define multiple scales over which to examine resource selection in order to better understand the factors limiting to a species (Rettie and Messier 2000; Mayor et al. 2009). We 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-km buffers around individual GPS locations. This meant that for each season at the coarse scale, we were modelling which factors influenced the placement of seasonal ranges within the population range. At the fine scale, we were modelling which factors influenced the selection of resource patches (e.g., for foraging, resting, travelling, etc.) over a five-hour interval.

For the coarse-scale analyses, used points were sampled from within individual home ranges (Fig. 4.17), which we 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 1.0 km and then truncated at the eastern border of Saskatchewan (green polygon, Fig. 4.16). 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 1-km 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 ($h_{plug-in}$), which greatly improved the accuracy 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). We 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, we aimed to remove these aberrant points and thereby avoid overestimating the size of each home or seasonal range. We 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).

4.4.6 METHODS: 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). Therefore, it is important to characterize resource units using habitat attributes that are relevant to the scales of a resource selection study, as well as to the questions being posed (Leblond et al. 2011). We selected eight habitat attributes to characterize 30 m × 30 m resource units in Saskatchewan' Boreal Shield: elevation (m), slope (degrees), heat load index, mean daily temperature (^{o}C), mean daily snow depth (cm), habitat class ($n = 8$, see Table 4.2), proximity (m) to the nearest linear feature (e.g., major road, trail, geophysical survey line, fire break, etc.), and reproductive status (i.e., females estimated to have given birth to a calf or not, as determined in *Section 4.3.3*). All of these variables have the potential to influence caribou behaviour and thus risk-forage trade-offs, at the two spatial scales of our analyses. We used a combination of ArcGIS v. 10.2.1 software and R statistical software (R Core Team 2016) to extract values for each habitat attribute to each used and available point.

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 30 m × 30 m resource unit) based on its slope, aspect and latitude, was calculated using the second heat load equation from 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, we decided to include both slope (in degrees) and heat load index as covariates in our 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. For example, 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]).

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/). For each point, we assigned mean daily temperature and snow depth values from the nearest weather station. 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.

We derived habitat classes from an updated forestry ecosite class (FEC) layer (*Section 4.2*). We initially derived six major habitat classes (see *Section 4.2.4*) and then partitioned the black spruce-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, we first built three fire layers corresponding to three fire seasons (1st July, 2013–30th June, 2014; 1st July, 2014–30th June, 2015; and 1st July, 2015–30th June, 2016). The value for a given 30 m × 30 m pixel in a fire layer represented the number of years that had elapsed since the most recent fire. We then combined each seasonal fire layer with the FEC layer to create three distinct habitat class layers: one with conifer age classes defined by the first fire season (1st July, 2013–30th June, 2014), one with conifer age classes defined by the second fire season (1st July, 2014–30th June, 2015), and one with conifer age classes defined by the third fire season (1st July, 2015–30th June, 2016). We assigned used and available points habitat class values from the habitat class layer that encompassed the period in which they were recorded. For example, if a point was recorded on 22nd June, 2015 it would have been assigned a habitat class from the habitat-class layer with age values corresponding to the second fire season. Fire-age data was provided by G. Pittoello from the Fish and Wildlife Branch of the Saskatchewan Ministry of Environment and M. Charlebois and H. Skatter from Omnia Ecological Services (Omnia Ecological Services, Calgary, Alberta, Canada).

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 us to remove insignificant habitat classes from the model. We 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).

Each location's 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 S. Francis Consulting Inc. (Drumheller, Alberta, Canada) and B. Bitter, J. O'Neil and A. 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 60 m (30 m buffer on either side of the road's center line representing the maximum road allowance, including ditches). The proximity to linear features variable in our models describes the Euclidean distance between a point location and the unbuffered edge (based on average width) of the linear feature.

We assigned a reproductive status ('calf-yes' or 'calf-no') to each caribou based on combination of Residence Time analyses (Barraquand and Benhamou 2008; see *Section 4.3.3* 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 March surveys were used to assign reproductive status in other seasons. Calf mortality is generally high during the first six weeks post-partum (Gustine et al. 2006b; Pinard et al. 2012) so to partition our dataset we 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 we 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, a calf's influence on their mother's behaviour is likely to be minimal.

All model covariates were screened for multicollinearity using methods outlined in Zurr (2010). As recommended by Gelman et al. (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).

4.4.7 METHODS: STATISTICAL ANALYSIS

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). We 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, we 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 have our random-slope models to converge in the time needed to produce this report was beyond the capability of both our lab computer and the research computers available to us 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.). Although 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 we were experiencing convergence issues running mixed-effects models in other packages, we 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 three 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 our 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 $I*1e^{10}$ (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 (as we do here) 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 mired 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 our models, we 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)))
```

We then modified the prior to test for model sensitivity to prior specification. Specifically, we 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, we split the data into a training set and a validation set. The training set consisted of all caribou fit with the 'Telonics' radio-collars (Telonics Inc., Mesa, Arizona, USA) radio-collars (up to $n = 68$ caribou); it was used to train the models for each season and scale.

UNIVERSITY OF
SASKATCHEWAN

Our validation sets consisted of all caribou fit with Lotek radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada; divided according to U of S deployments ['Lotek', up to $n = 24$ deployments]; and industry-partner deployments ['Industry', up to $n = 54$ deployments]). If the coefficients from the validation models fell within the 95% credible intervals of the corresponding coefficients from the training model (Telonics collars), 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 4.4.9*, for an in-depth description of how model and individual covariate comparisons were scored).

For each season and scale, we 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: (1) trace plots, which show coefficient estimates after each iteration (should resemble white noise with few major spikes); (2) density plots, which show the posterior distribution of each model parameter (should resemble a normal distribution); (3) autocorrelation between iterations (<0.05 is considered good, Hadfield 2015); and (4) the Highest Probability Density (HPD) intervals for each coefficient. Coefficients with HPD intervals (hereafter 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, we 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). We 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 burn-in value at least equal to 10% of the total number of model iterations. For example, if we ran a model for 1,100,000 iterations, we would sample (at most) every 1000 iterations and discard the initial 100,000 iterations as the burn-in period. The burn-in 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 burn-in value, although 10% is usually considered sufficient (Dr. J. Lane, Department of Biology, University of Saskatchewan, *pers. comm.*).

4.4.8 RESULTS: RANGE DELINEATION

The range of our 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. 4.16) had a total area of 95,632 km^2 while the truncated range (i.e., truncated at the Saskatchewan – Manitoba border, green polygon, Fig. 4.16) 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.
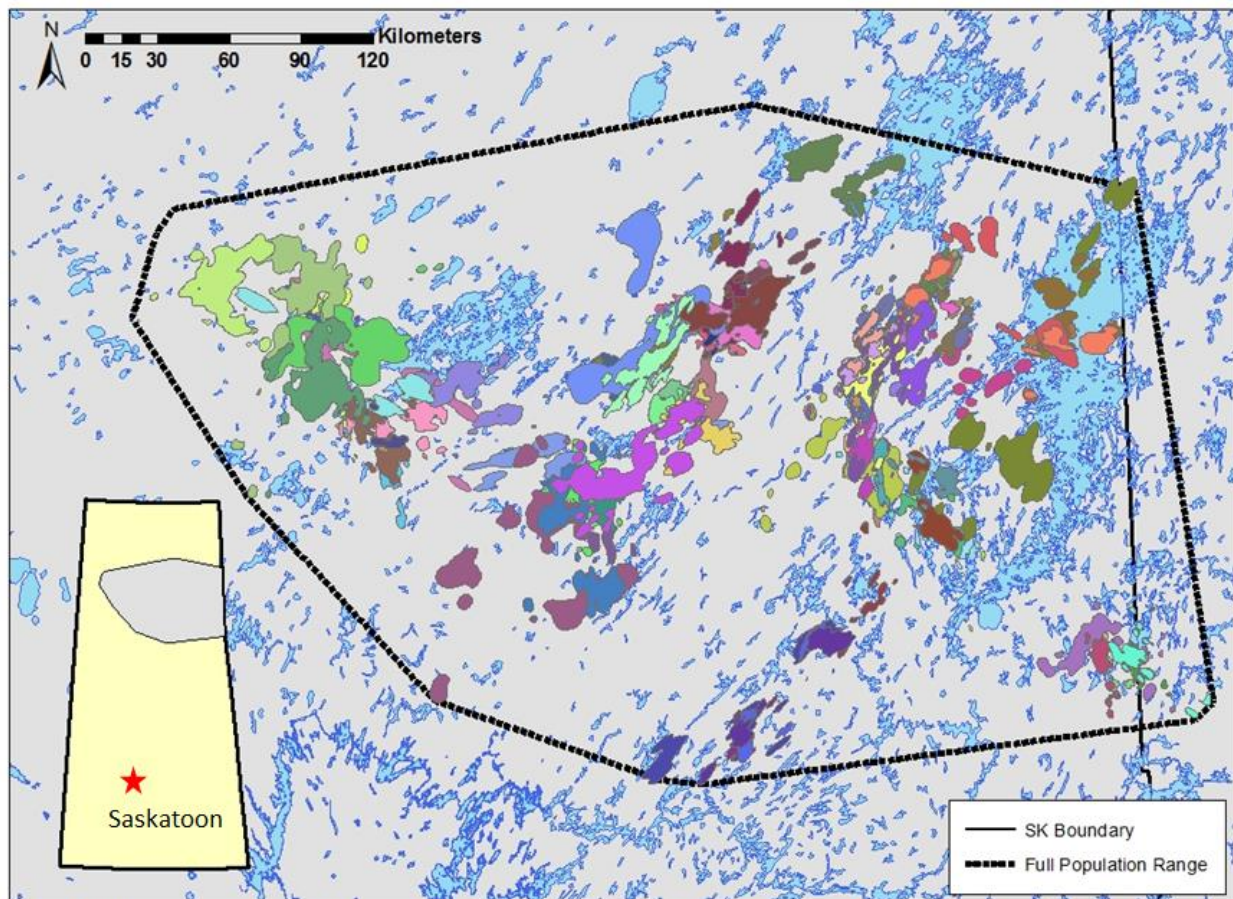
Fig. 4.17: Home ranges for 92 female woodland caribou in Saskatchewan's Boreal Shield. Ranges were delineated as 95% utilization distributions (UDs, van Winkle 1975) using up to two years of GPS point locations recorded from individual caribou. Excluding ranges belonging to caribou that did not survive for the full two years ($n = 24$), mean range size was 435.2 +/- 34.3 km^2.

Individual home ranges (Fig. 4.17), 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 (± 1 SE [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 our 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 km^2; for the subset that survived the full two years ($n = 68$ animals), the mean core size was 57.7 ± 4.5 km^2.

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 ± SE, n = sample size): early winter (267.9 ± 16.3 km^2, $n = 149$); mid-winter (106.5 ± 7.0 km^2, $n = 147$ ranges); late 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 4.6: 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

After 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 between seasons over the two year study period (see summary of range sizes in Table 4.11). 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 4.7), 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. 4.18). There were also significant differences between (1) the mean range sizes of the two early winter seasons and all other seasons, except for the second late winter/spring season; (2) the mean range size for the second late winter/spring season and all other seasons except for the two mid-winter seasons; and (3) 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.
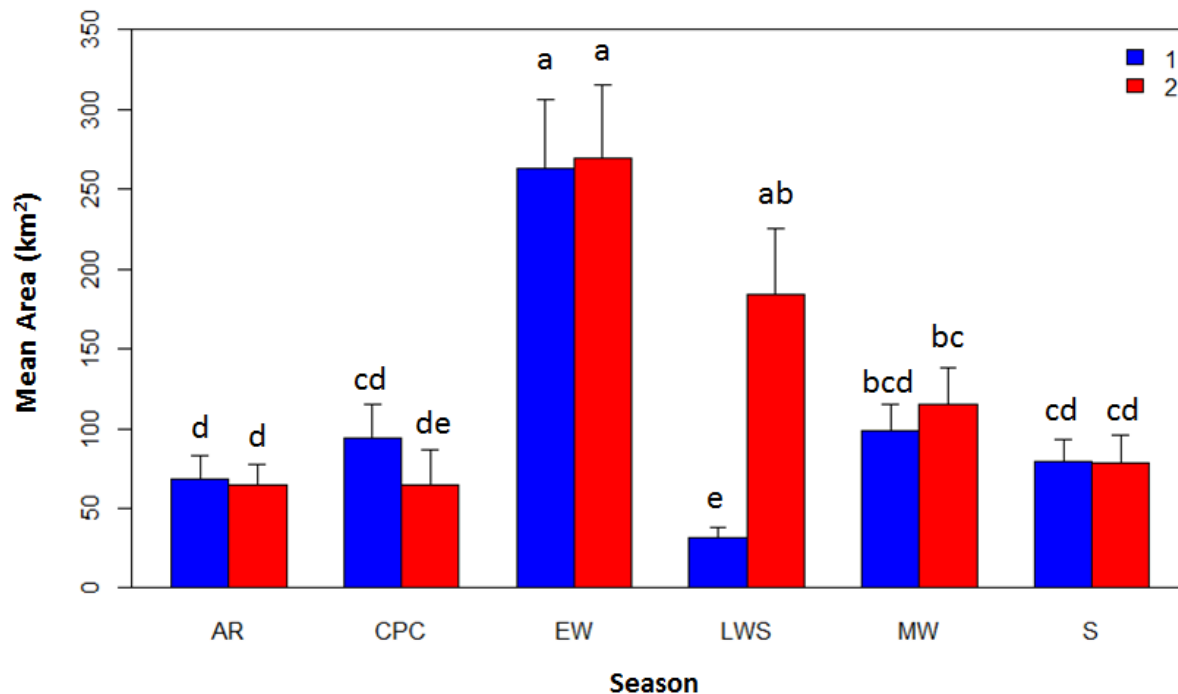
Fig. 4.18: Mean annual range sizes (with standard error bars) for each of six seasons by study year (Year 1 [blue] or Year 2 [red]). A Kruskal-Wallis Test (i.e., a non-parametric one-way ANOVA; Kruskal and Wallis 1954) was used to compare mean range sizes between seasons and years (*Kruskal-Wallis* χ^2 = *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 78 caribou who survived for two full LWS seasons recorded a decrease in range size from year one

to year two. The remaining seventy-one 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 4.7: 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	-1.717									
	1.000	1.000									
CPC_2	1.267	1.213	3.026								
	1.000	1.000	0.163								
EW_1	-8.340	-8.053	-6.766	-9.416							
	0.000	0.000	0.000	0.000							
EW_2	-8.059	-7.805	-6.544	-9.102	-0.094						
	0.000	0.000	0.000	0.000	1.000						
LWS_1	3.806	3.651	5.718	2.419	12.331	11.845					
	0.009	0.017	0.000	1.000	0.000	0.000					
LWS_2	-5.359	-5.182	-3.733	-6.492	2.883	2.851	-9.235				
	0.000	0.000	0.012	0.000	0.260	0.288	0.000				
MW_1	-3.314	-3.208	-1.637	-4.494	4.944	4.819	-7.153	2.031			
	0.061	0.088	1.000	0.000	0.000	0.000	0.000	1.000			
MW_2	-3.724	-3.612	-2.121	-4.854	4.217	4.134	-7.412	1.423	-0.533		
	0.013	0.020	1.000	0.000	0.002	0.002	0.000	1.000	1.000		
S_1	-1.619	-1.570	0.128	-2.857	6.780	6.566	-5.490	3.797	1.735	2.208	
	1.000	1.000	1.000	0.283	0.000	0.000	0.000	0.010	1.000	1.000	
S_2	-1.275	-1.242	0.411	-2.476	6.804	6.607	-4.981	3.934	1.949	2.400	0.283
	1.000	1.000	1.000	0.877	0.000	0.000	0.000	0.006	1.000	1.000	1.000

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

4.4.9 RESULTS: RESOURCE SELECTION FUNCTIONS

Top models for each season and scale are presented in Table 4.8. 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-odds of a successful response (i.e., a point being used) changes with a one unit increase in these variables. For example, if the coefficient for the variable 'elevation' was –1.3, this would mean that for every one meter increase in elevation, a caribou would be 1.3 times less likely to occur in a resource unit (i.e., a 30 m × 30 m pixel on the landscape). Similarly, if the coefficient for the variable 'proximity to linear features' was –0.9, this would mean that for every one meter increase in the distance to linear feature, a caribou would be 0.9 times less likely

to select that resource unit (note: a negative coefficient for this variable indicates that the caribou would be more likely to occur near linear features).

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 4.8). 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-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 5/8 habitat classes were retained in the top, coarse-scale model for the autumn/rut season (see Table 4.8). 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 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, we interpreted this to mean that having a calf caused a significance difference in how female woodland caribou selected resources in the Saskatchewan 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.

Table 4.8: 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

4.4.8.1 Late Winter/Spring Season

At the coarse-scale level of selection (i.e., the population range), we used 17,439 GPS locations recorded from 68 adult female caribou over two late winter/spring seasons to generate our models. After backwards selection on a global model containing 14 fixed covariates, we arrived at a top model consisting of ten covariates (see Table 4.8). Coefficients from this model (Fig. 4.19) indicated 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) and 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, we did not suppress it because in doing so we would have made the assumption that the response is zero if all of the predictors are zero, which is not likely true for this system.

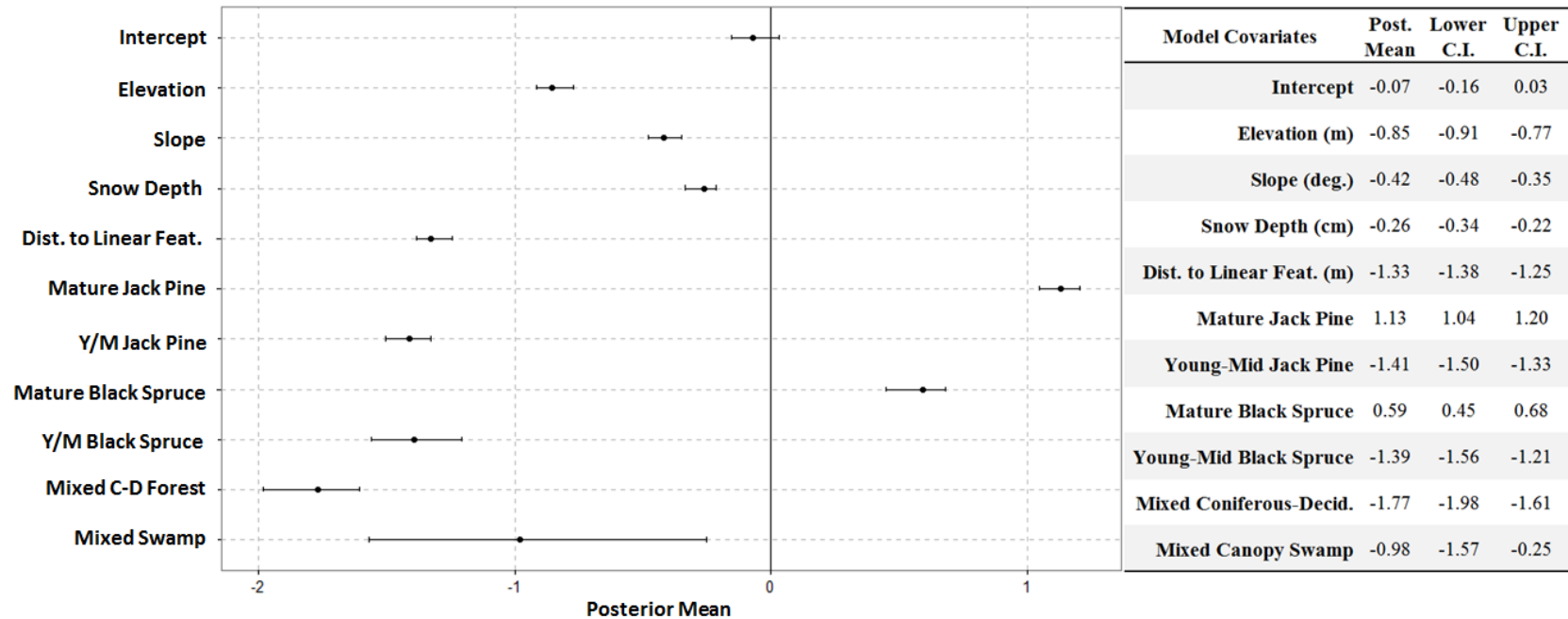| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.07	-0.16	0.03
Elevation (m)	-0.85	-0.91	-0.77
Slope (deg.)	-0.42	-0.48	-0.35
Snow Depth (cm)	-0.26	-0.34	-0.22
Dist. to Linear Feat. (m)	-1.33	-1.38	-1.25
Mature Jack Pine	1.13	1.04	1.20
Young-Mid Jack Pine	-1.41	-1.50	-1.33
Mature Black 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. 4.19: 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

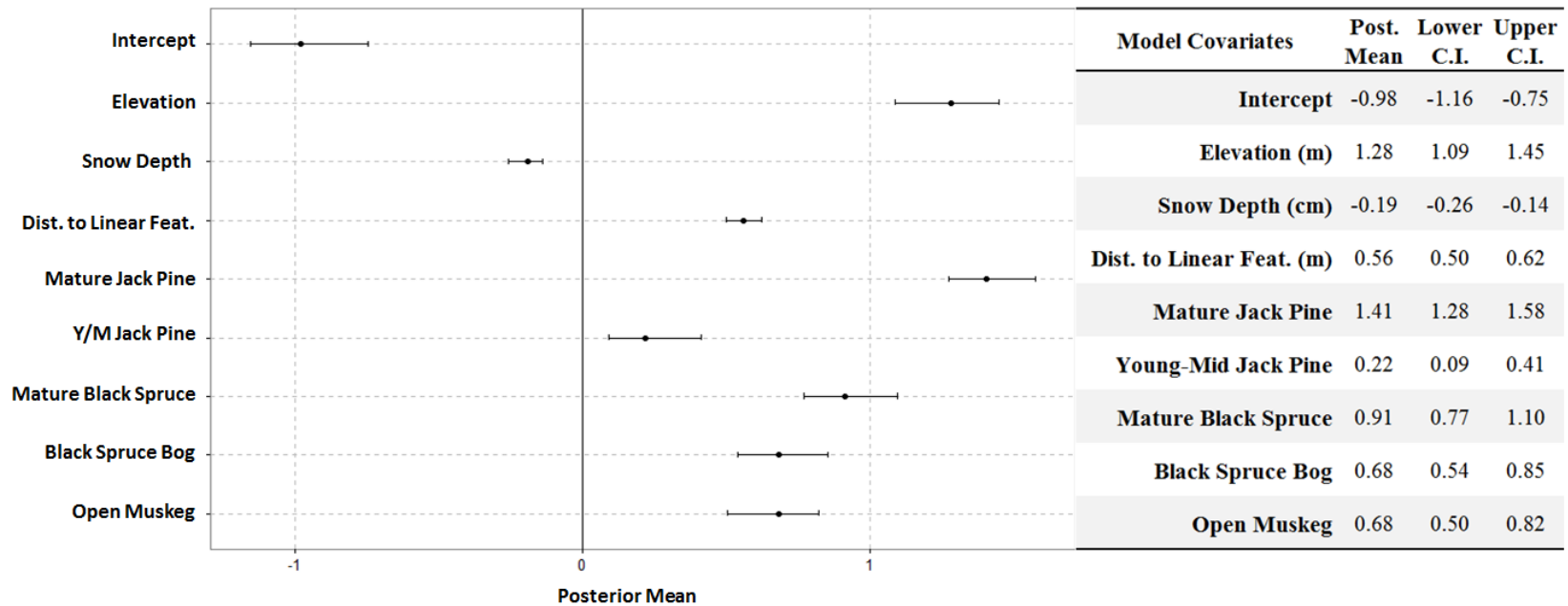| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.98	-1.16	-0.75
Elevation (m)	1.28	1.09	1.45
Snow Depth (cm)	-0.19	-0.26	-0.14
Dist. to Linear Feat. (m)	0.56	0.50	0.62
Mature Jack Pine	1.41	1.28	1.58
Young-Mid Jack Pine	0.22	0.09	0.41
Mature Black Spruce	0.91	0.77	1.10
Black Spruce Bog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

Fig. 4.20: 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.

UNIVERSITY OF SASKATCHEWAN

At the fine-scale level of selection (i.e., 1-km 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. 4.20. Although caribou continued to select for resource units with shallower snow depths, they were more likely to be found at higher elevations and somewhat 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.

4.4.8.2 Calving/Post-Calving Season

To model coarse-scale resource selection during the Calving/Post-Calving (CPC) season, we 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 4.8). Model coefficients (Fig. 4.21) 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 25,267 GPS points distributed across 167 individual caribou seasons ($n = 67$ caribou). According to the top model (see Table 4.8 and Fig. 4.22), 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 slightly 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.

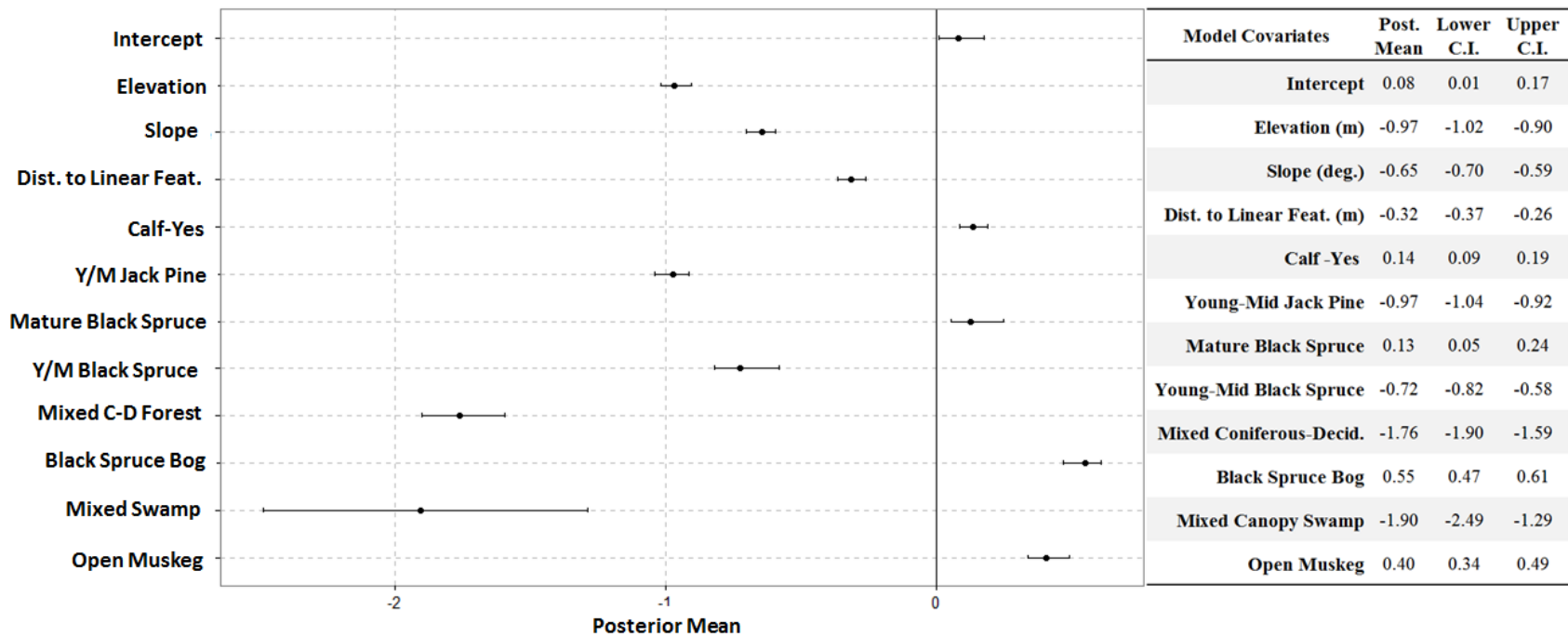| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.08	0.01	0.17
Elevation (m)	-0.97	-1.02	-0.90
Slope (deg.)	-0.65	-0.70	-0.59
Dist. to Linear Feat. (m)	-0.32	-0.37	-0.26
Calf -Yes	0.14	0.09	0.19
Young-Mid Jack Pine	-0.97	-1.04	-0.92
Mature Black Spruce	0.13	0.05	0.24
Young-Mid Black Spruce	-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. 4.21: 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

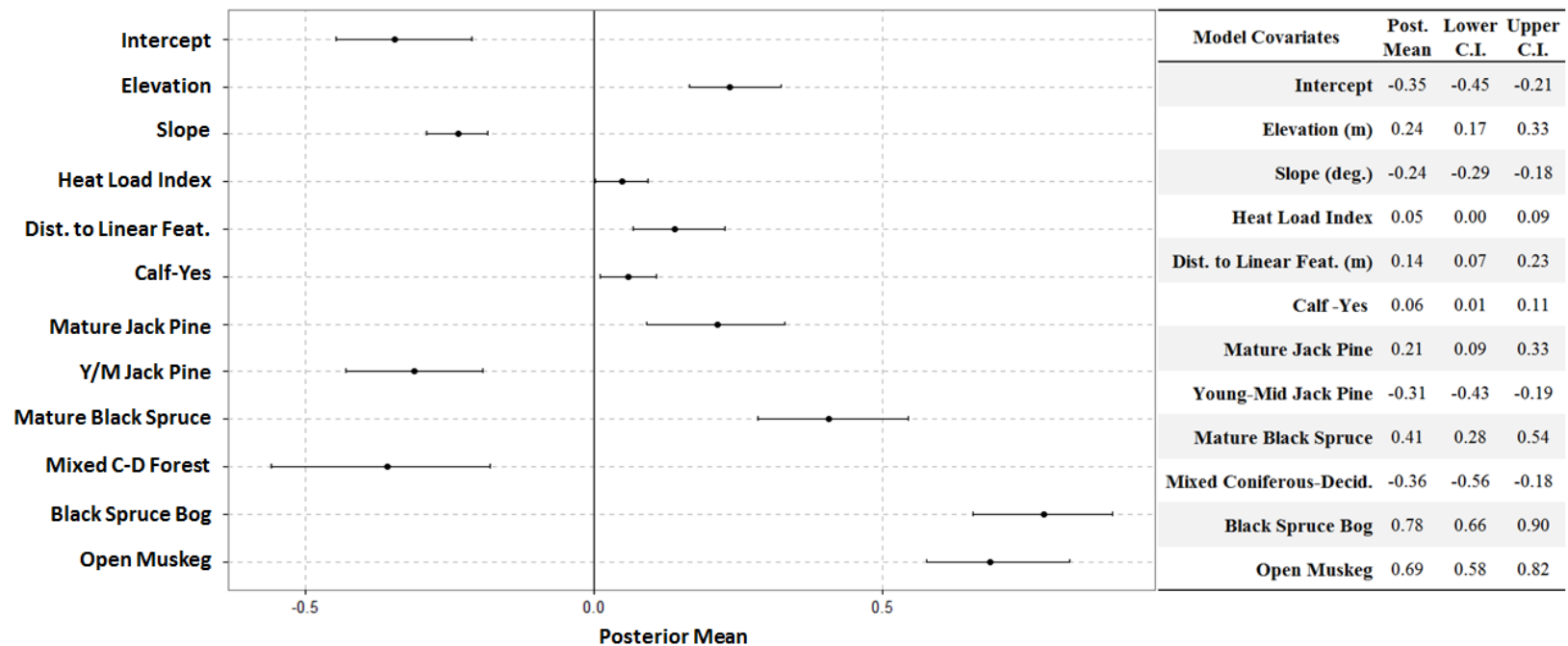| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.35	-0.45	-0.21
Elevation (m)	0.24	0.17	0.33
Slope (deg.)	-0.24	-0.29	-0.18
Heat Load Index	0.05	0.00	0.09
Dist. to Linear Feat. (m)	0.14	0.07	0.23
Calf -Yes	0.06	0.01	0.11
Mature Jack Pine	0.21	0.09	0.33
Young-Mid Jack Pine	-0.31	-0.43	-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. 4.22: 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.

UNIVERSITY OF SASKATCHEWAN

4.4.8.3 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, we arrived at a top model containing nine covariates (see Table 4.8 and Fig. 4.23). 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. 4.24) 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 was not as strong compared to the coarse spatial scale for the last two classes. They also continued to select for mature black spruce forests.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

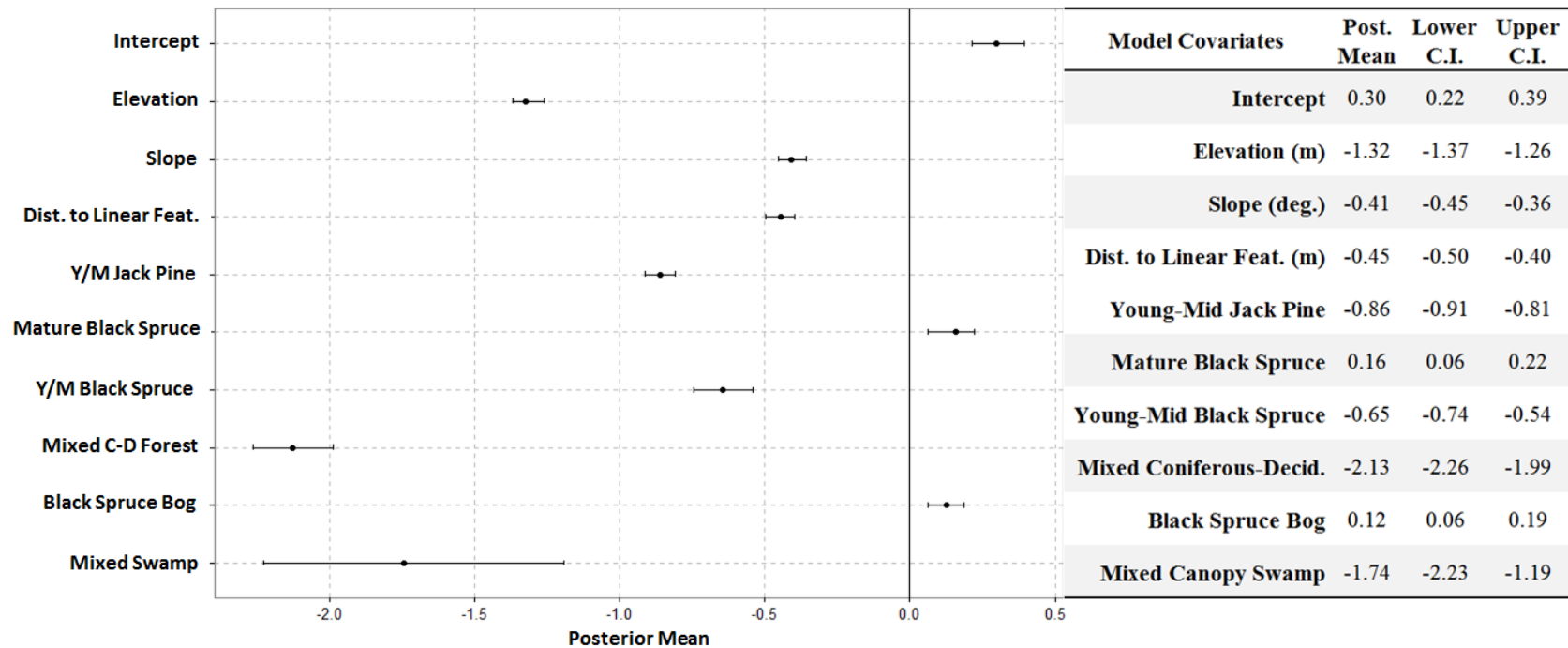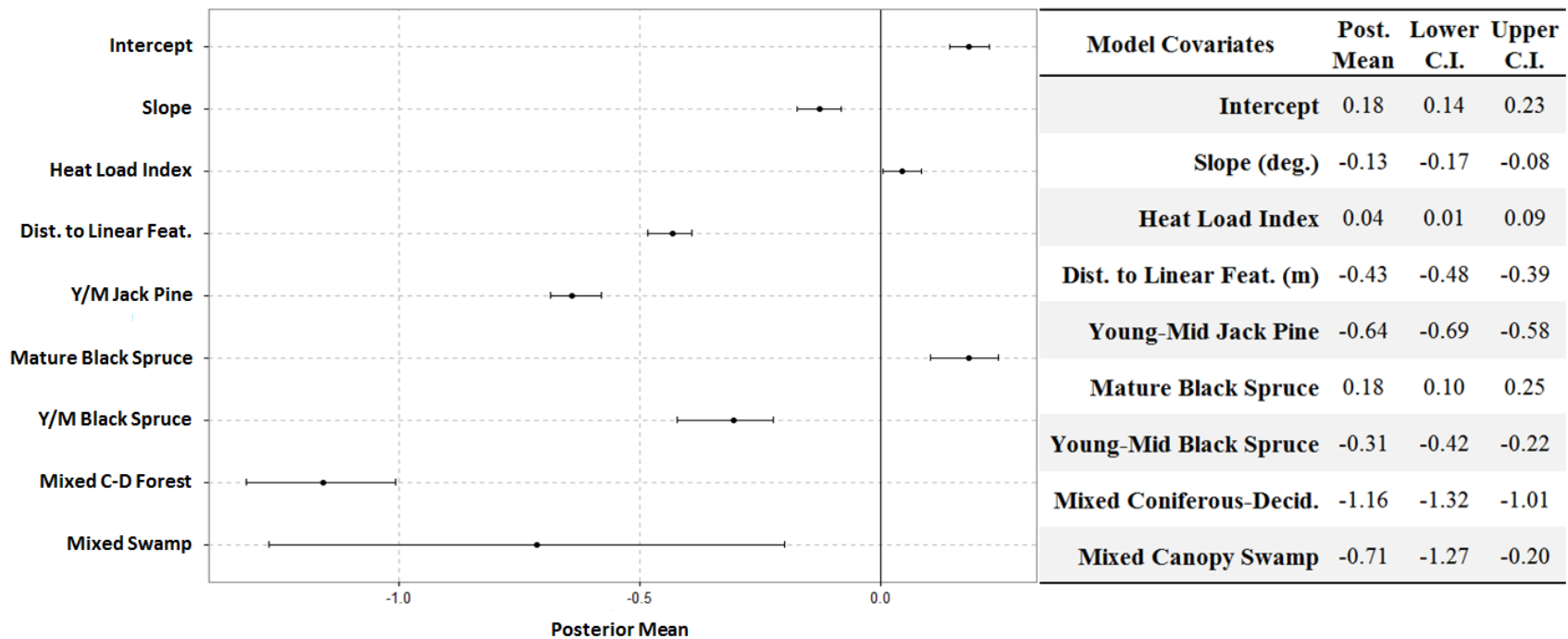| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.30	0.22	0.39
Elevation (m)	-1.32	-1.37	-1.26
Slope (deg.)	-0.41	-0.45	-0.36
Dist. to Linear Feat. (m)	-0.45	-0.50	-0.40
Young-Mid Jack Pine	-0.86	-0.91	-0.81
Mature Black Spruce	0.16	0.06	0.22
Young-Mid Black Spruce	-0.65	-0.74	-0.54
Mixed 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. 4.23: 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

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. 4.24: 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.

UNIVERSITY OF SASKATCHEWAN

4.4.8.4 Autumn/Rut Season

We 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. 4.25. Consistent with the three previous seasons, caribou were more likely to be found at lower elevations, on shallower slopes, and closer to linear features. 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, we used 12,203 GPS points distributed over 110 individual caribou seasons (*n* = 60 caribou) to generate our models. The top model retained 8 of the original 14 covariates included in the global model (see Table 4.8 and Fig. 4.26). According to this model, female caribou continued to occur on shallower slopes (although 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 verify 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 (we ran the model for up to 8,800,000 iterations), nor did it extinguish the issues with convergence. However, because: (1) the mixing of chains between independent models was excellent; (2) the autocorrelation between samples was well below the threshold of 0.05; and (3) the model was not sensitive to prior specification, we accepted the top model presented in Table 4.8 and Fig. 4.26, while acknowledging that results from this model need to be interpreted with caution.

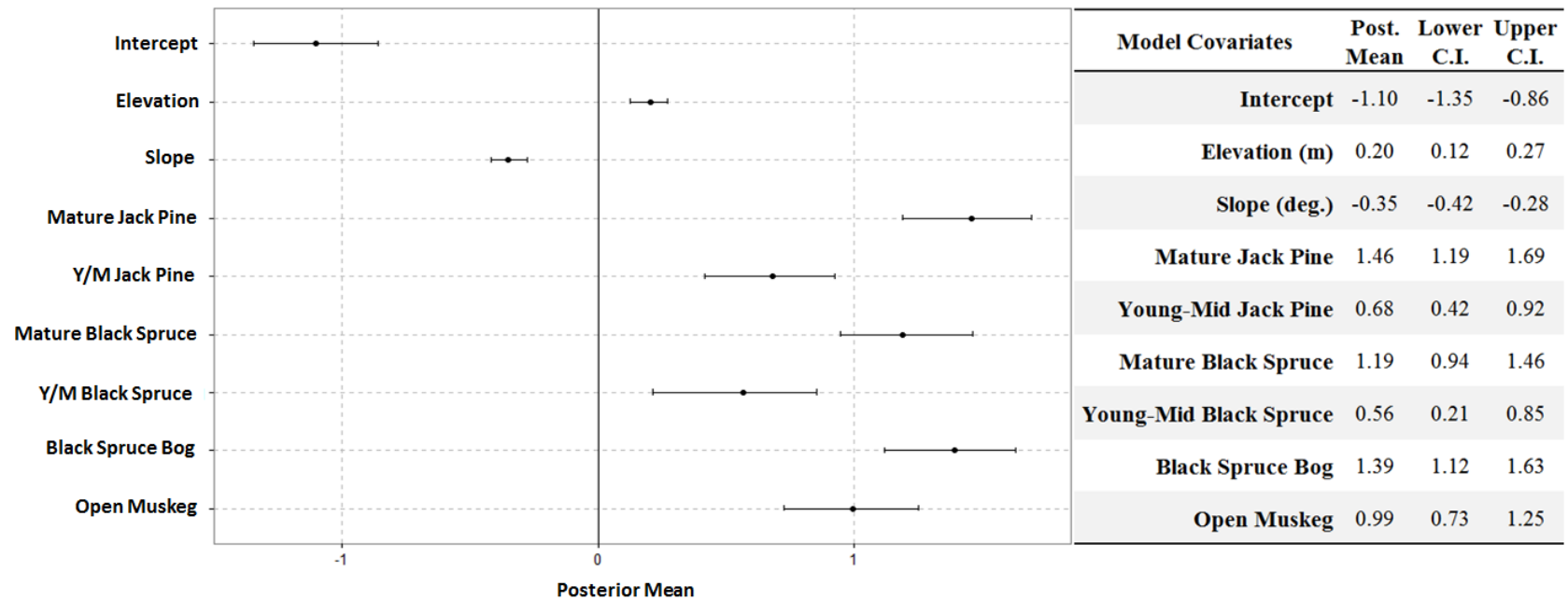| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	0.29	0.19	0.37
Elevation (m)	-1.37	-1.45	-1.28
Slope (deg.)	-1.05	-1.13	-0.97
Temperature (^{o}C)	-0.21	-0.28	-0.15
Dist. to Linear Feat. (m)	-0.90	-1.00	-0.84
Young-Mid Jack Pine	-0.86	-0.93	-0.76
Young-Mid Black Spruce	-1.68	-1.91	-1.51
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
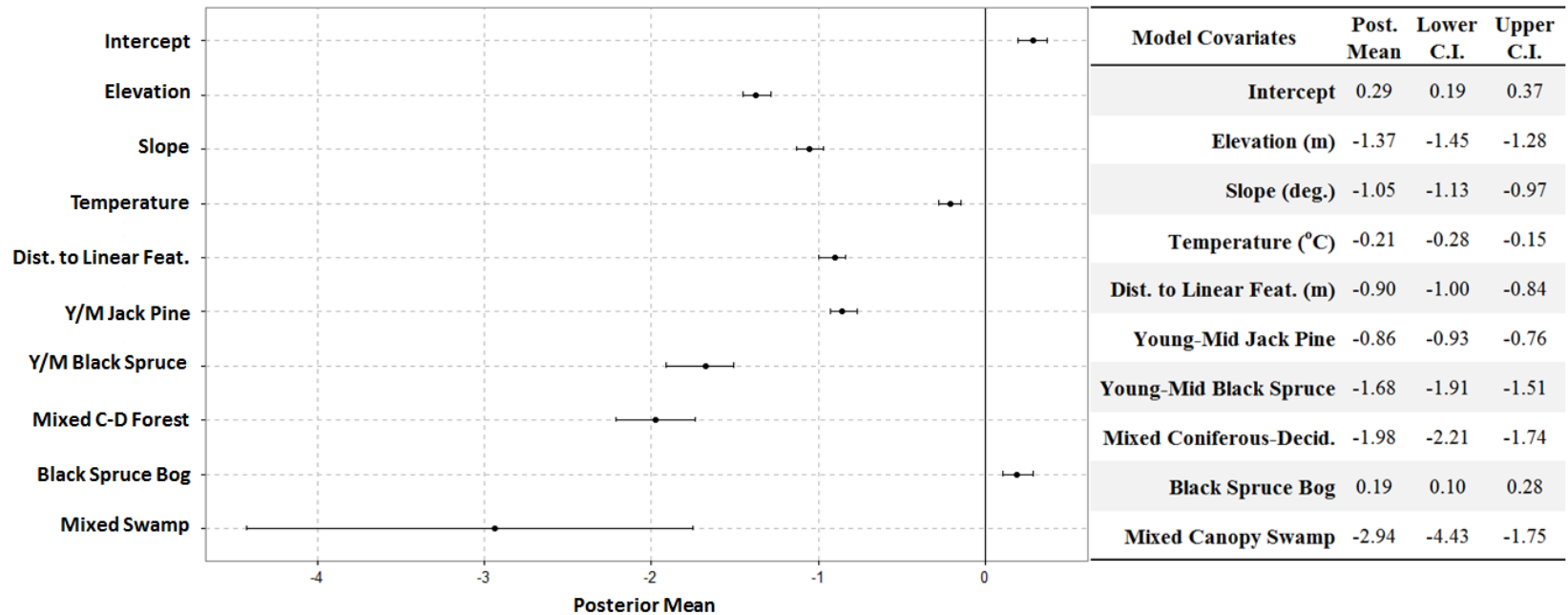
Fig. 4.25: Plot of the posterior means and 95% credible intervals for the 9 fixed covariates retained in the top resource selection model for the autumn/rut season (1st October–4th November) at the coarse spatial scale. The model was fit in the R$^©$ Package *MCMCglmm* (Hadfield 2015) using a training 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

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. 4.26: 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.

4.4.8.5 Early Winter Season

To generate models at the coarse spatial scale for the early winter season, we 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, we arrived at a top model containing 11 of these covariates (see Table 4.8 and Fig. 4.27). 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, we 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.

We 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 4.8 and Fig. 4.28) 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 farther 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.

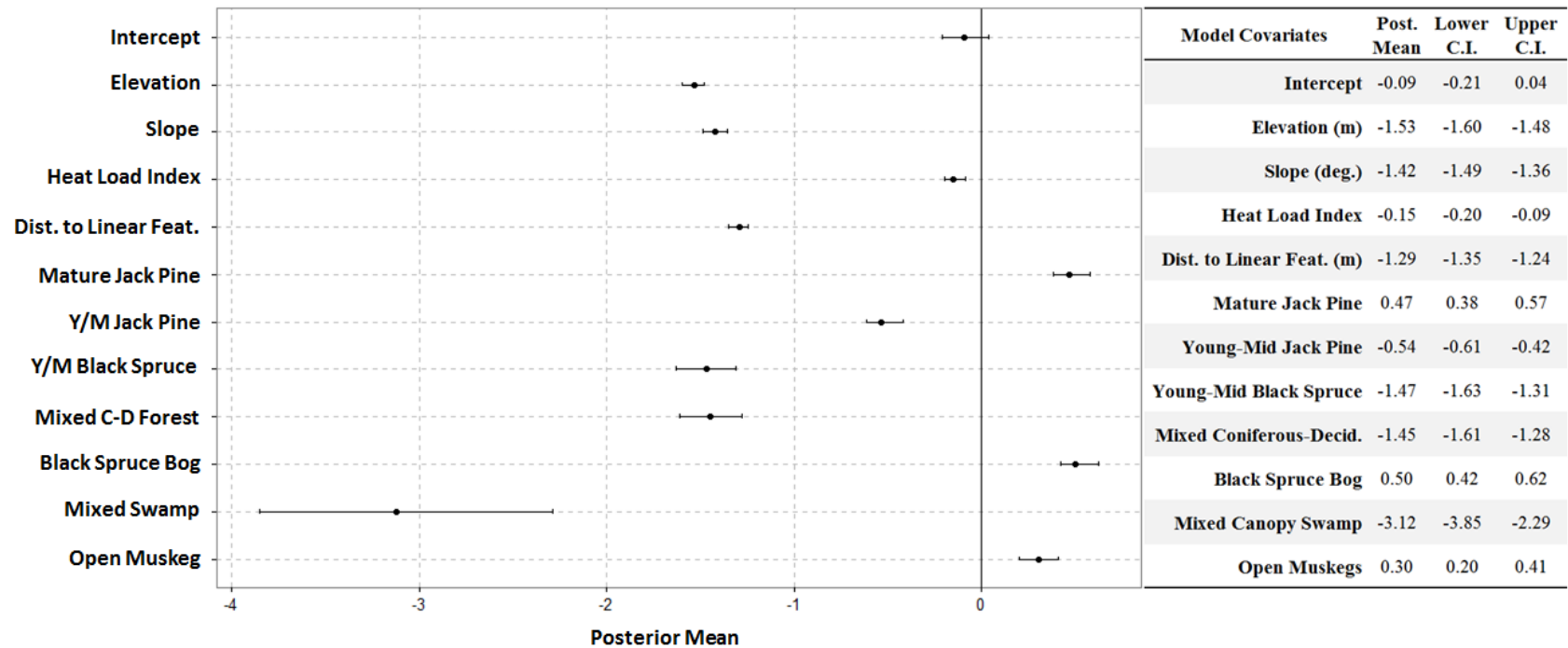# Status of Woodland Caribou in the Saskatchewan Boreal Shield

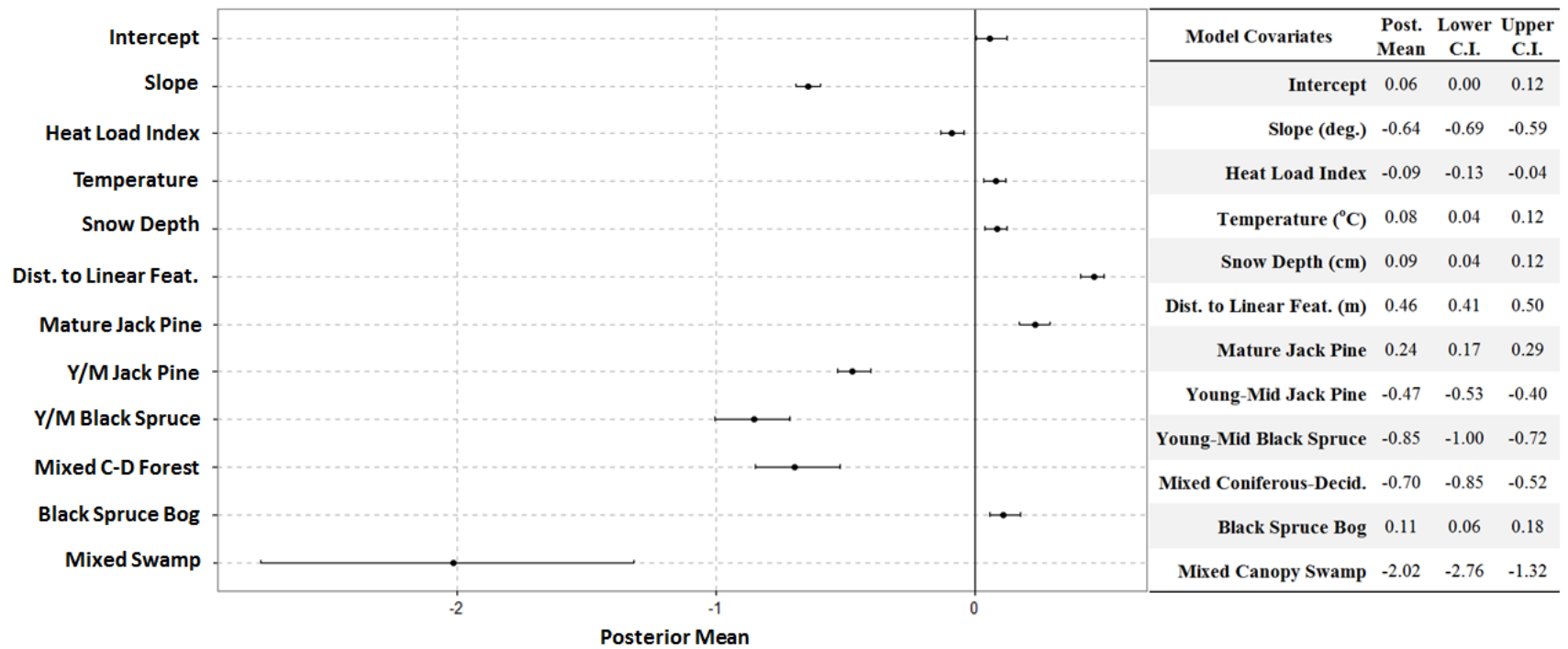| Model Covariates	Post. Mean	Lower C.I.	Upper C.I.
Intercept	-0.09	-0.21	0.04
Elevation (m)	-1.53	-1.60	-1.48
Slope (deg.)	-1.42	-1.49	-1.36
Heat Load Index	-0.15	-0.20	-0.09
Dist. to Linear Feat. (m)	-1.29	-1.35	-1.24
Mature Jack Pine	0.47	0.38	0.57
Young-Mid Jack Pine	-0.54	-0.61	-0.42
Young-Mid Black 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. 4.27: 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

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 ($^\circ$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. 4.28: 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.

UNIVERSITY OF SASKATCHEWAN

4.4.8.6 Mid-Winter Season

At the coarse scale level of selection, we used 24,279 GPS locations recorded from 57 adult female caribou over two mid-winter seasons to generate our models. After backwards selection on a global model containing 15 fixed covariates, we arrived at a top model consisting of 12 covariates (see Table 4.8). Model coefficients from this model (Fig. 4.29) 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. 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. 4.30). 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 farther from linear features. Like during 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.

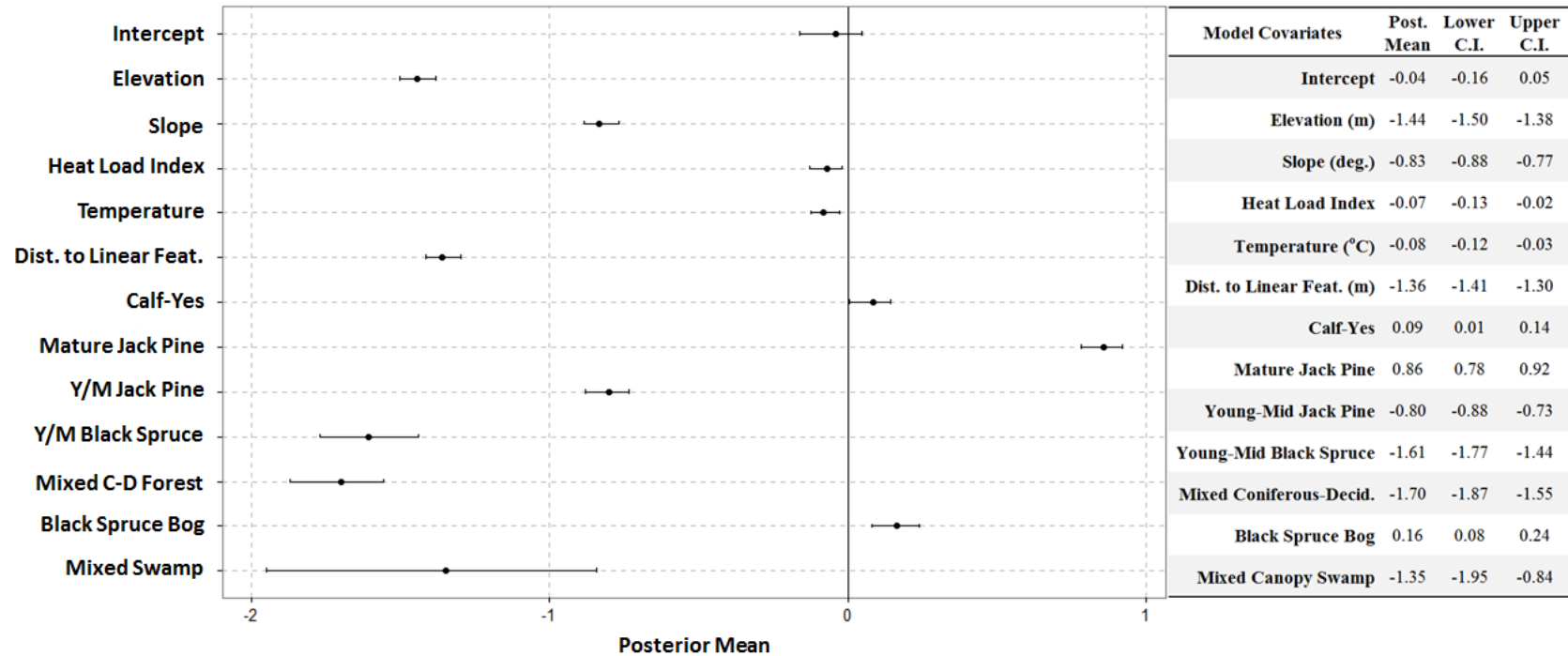# Status of Woodland Caribou in the Saskatchewan Boreal Shield

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. 4.29: 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

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
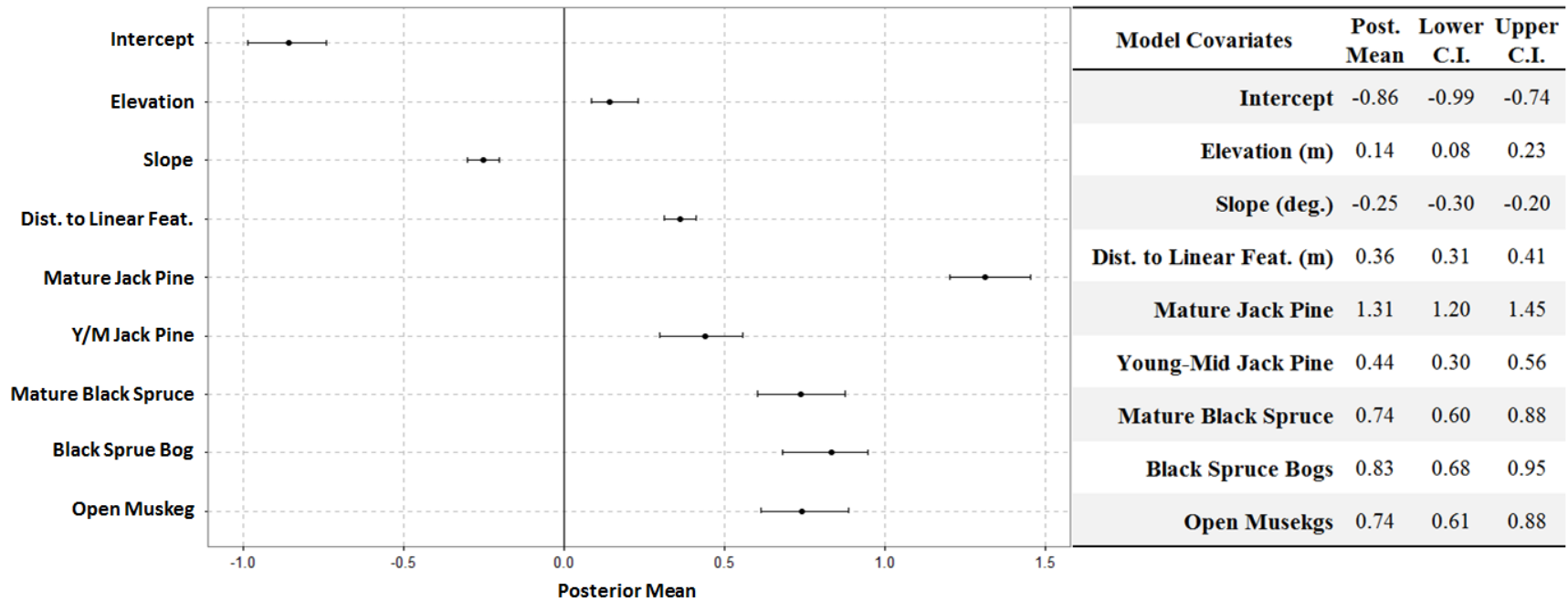
Fig. 4.30: Plot of the posterior means and 95% credible intervals for the 8 fixed covariates retained in the top resource selection model for the mid-winter season (15th January– 22nd March) at the fine spatial scale. The model was fit in the R® Package *MCMCglmm* (Hadfield 2015) using a training set 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.

4.4.9 MODEL VALIDATION

To validate the top model for each season and scale (n = 12 total), we re-ran each model using subsets of female caribou (see Table 4.9) fit with Lotek Iridium® radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) by the U of S ('Lotek', n = 24) and by our industry partners working in the Key Lake and Cree Lake regions ('Industry', n = 54). Because the U of S samples spanned the entire SK1 range, we only formally compared patterns observed in the top models (i.e., those trained using the sample of caribou fit with 'Telonics' radio-collars (Telonics Inc., Mesa, Arizona, USA; n = 68) to the patterns observed in the validation models (however, for visual comparison we show the performance of the Industry collars alongside the U of S samples in Figs. 4.31 to 4.42). 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 across the Saskatchewan 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 than the posterior mean for the corresponding trained covariate (e.g., see the comparison for the covariate 'Slope' in Fig. 4.31), this was more suggestive of a general trend in the response to that covariate. Finally, 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').

It is 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. 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 strong *vs*. weak trends in the data, rather than make rigorous comparisons between the values for each covariate.

Table 4.9: 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

We scored comparisons made between models and individual covariates according to their percent congruency. 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 either: (1) 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. 4.31); or (2) the posterior mean for that covariate had the same sign as the posterior mean for that covariate in the training model (e.g., see the comparison for the covariate mature jack pine forest in Fig. 4.31). The term "percent congruency" describes the percentage of total covariate comparisons that were congruent (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, we found that 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 ($n = 1$) and general trends ($n = 2$) divided by the total number of comparisons ($n = 10$), then multiplied by 100%. Thus, the percent congruency for the covariate elevation was (3/10)*100% = 30%. Detailed summaries of covariate comparisons by season and scale and by individual covariates and by are presented in Tables 4.10 and 4.11 respectively.

Table 4.10: 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 congrunecy for a covariate represents the sum of the consitent predictor and same general trends columns divided by the total number of comparisons for that covariate and then multiplied by 100%.

Season	Spatial Scale	Consistent Predictor	Same General Trend	Opposing Trend	Not Relevant	Percent Congruency
Late Winter/Spring	Coarse	4	3	0	3	70.0
Late Winter/Spring	Fine	3	1	0	4	50.0
Calving/Post-Calving	Coarse	5	4	2	0	81.8
Calving/Post-Calving	Fine	6	0	0	5	54.5
Summer	Coarse	3	4	1	1	77.8
Summer	Fine	4	2	0	2	75.0
Autumn/Rut	Coarse	4	4	1	0	88.9
Autumn/Rut	Fine	7	1	0	0	100.0
Early Winter	Coarse	1	7	1	2	72.7
Early Winter	Fine	4	4	1	2	72.7
Mid-Winter	Coarse	3	7	0	2	83.3
Mid-Winter	Fine	2	4	1	1	75.0
	TOTAL	46	41	7	22	

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 patterns of resource selection (see Fig. 4.31– 4.42 and Table 4.11). For example, three of the nine covariates in the validation model for summer coarse-scale selection had posterior means that overlapped with the 95% credible intervals of the corresponding covariates in the training model (see Fig. 4.35), while four of the nine covariates had posterior means with the same sign (i.e., positive or negative) as the corresponding covariates in the training model. Overall, covariates between the training and validation model for this season and scale were ~77.8% congruent. The

highest percent (p.c.) congruency occurred during the autumn/rut season at the fine spatial scale (p.c. = 100%), while the lowest percent congruency occurred during the calving/post-calving and early winter seasons at the fine spatial scale (p.c. for both = 54.5%). The mean percent congruency (+/- standard error) was 74.7 ± 3.9%, which suggests that the training models (i.e., top models for each season and scale presented in Figs. 4.19-4.30) are fairly representative of general resource selection patterns of female woodland in Saskatchewan's Boreal Shield. Partitioning the models by scale, the mean percent congruency for comparisons made at the coarse scale was 79.1 ± 2.9% while the mean percent congruency for comparisons made at the fine scale was 20.3 ± 7.7%. These values suggest that resource selection patterns at the coarse spatial scale are generally more consistent across populations of woodland caribou in the Saskatchewan Boreal Shield.

Table 4.11: 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 represents the sum of the consitent predictor and same general trends columns divided by the total number of comparisons for that covariate and then multiplied by 100%.

Model Covariate	Consistent Predictor	Same General Trend	Opposing Trend	Not Relevant	Percent Congruency
Elevation	1	2	4	3	30.0
Slope	6	5	0	0	100.0
Heat Load Index	2	0	0	3	40.0
Temperature	1	2	0	0	100.0
Snow Depth	1	1	1	0	66.7
Dist. to Lin. Feat.	2	7	0	2	81.8
Calf-Yes	1	0	0	2	33.3
Mature Jack Pine	5	3	0	0	100.0
Y/M Jack Pine	5	5	1	1	83.3
Mature Black Spruce	3	1	1	3	50.0
Y/M Black Spruce	3	4	0	2	77.8
Mixed C-D Forest	6	2	0	1	88.9
Black Spruce Bog	4	6	0	0	100.0
Mixed Swamp	4	0	0	4	50.0
Open Muskeg	2	3	0	1	83.3
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 4.11). Of these, 44 covariates came out as consistent predictors; 42 covariates came out as showing a general trend in resource selection, had the same sign as the corresponding training covariates); 9 covariates came out as having an opposing trend (i.e., posterior means had the opposite sign); and 21 covariates were not comparable (i.e., the 95% credible intervals of the validation covariates overlapped zero). Interestingly, of the nine covariate comparisons that showed opposing trends, four of them were for the covariate elevation. At the coarse spatial scale for the autumn/rut (Fig. 4.37), calving/post-calving (Fig. 4.33), and summer (Fig. 4.35) 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. 4.42), 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. 4.38) 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 much stronger response to an increase in elevation than the Lotek caribou during both the early winter and mid-winter seasons at the coarse spatial scale (see Figs. 4.39 and 4.41). 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 4.11 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 Figs. 4.19-4.30) seem to do a reasonable job of describing patterns of selection and avoidance for different habitat classes in the SK1 caribou administrative unit.

In general, this validation exercise showed that our top models were fairly representative of how female woodland caribou select resource units in the Saskatchewan 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, and mixed canopy swamps influences caribou resource selection outside the sample of Telonics caribou.
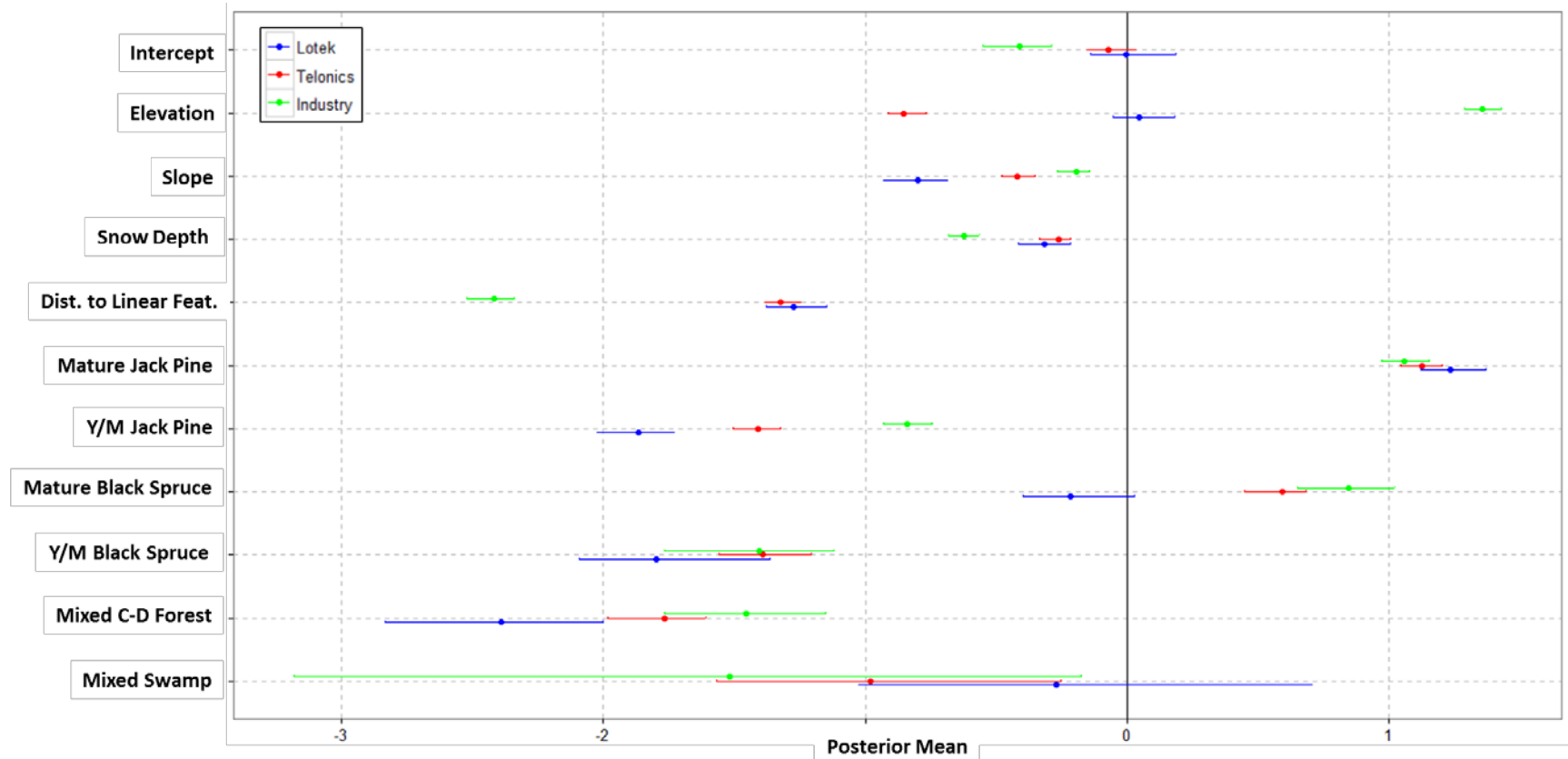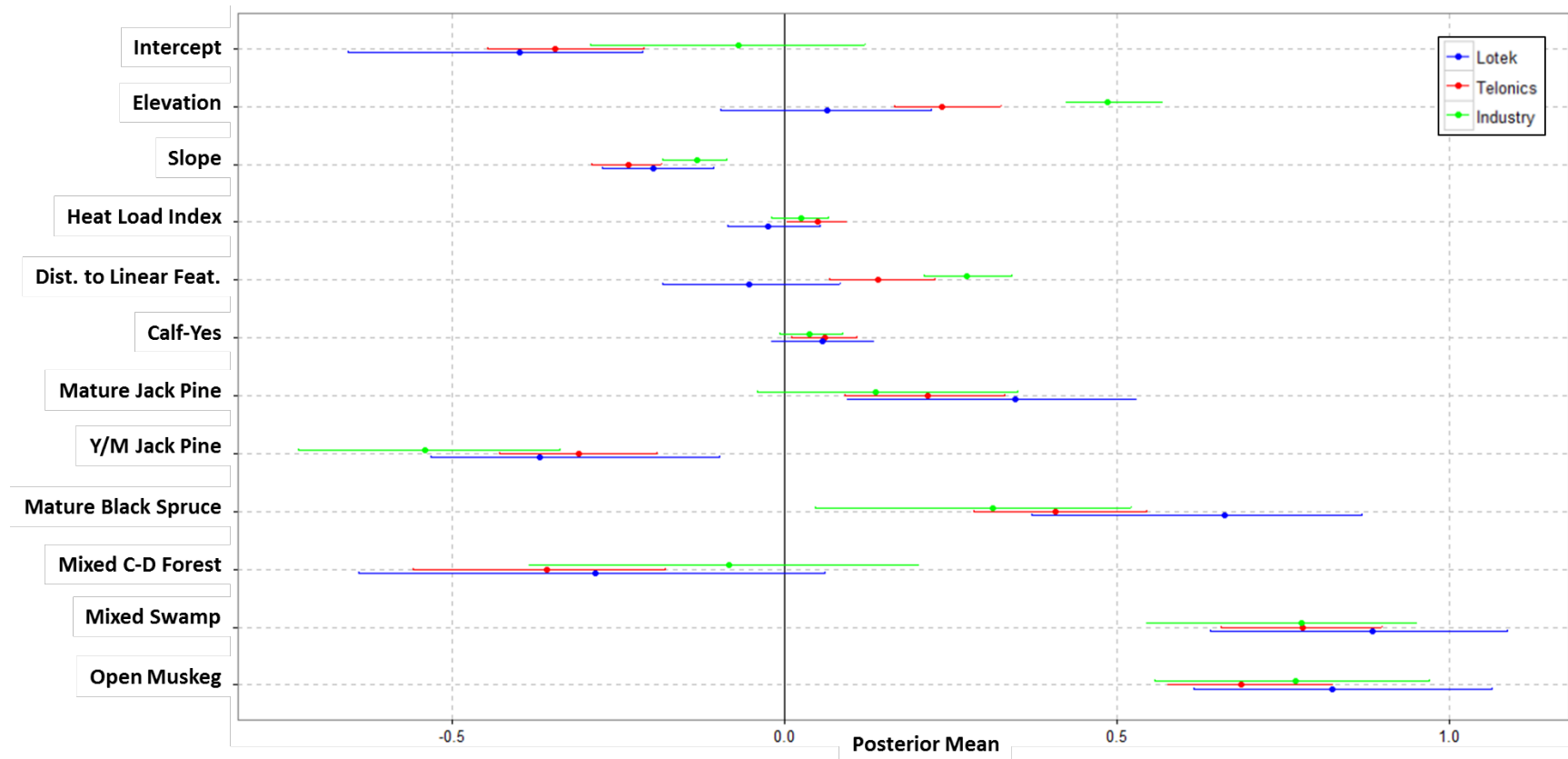
Fig. 4.31: Comparison between the top model (red) and validation models (blue and green) for the late winter/spring (LWS) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (*n* = 17,439 GPS locations recorded from 68 individuals over two LWS seasons) and validated using (a) a sample of female woodland caribou fit with *Lotek®* GPS collars (*n* = 6,495 GPS locations recorded from 24 individuals over two LWS seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (*n* = 18,592 GPS locations recorded from 58 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).
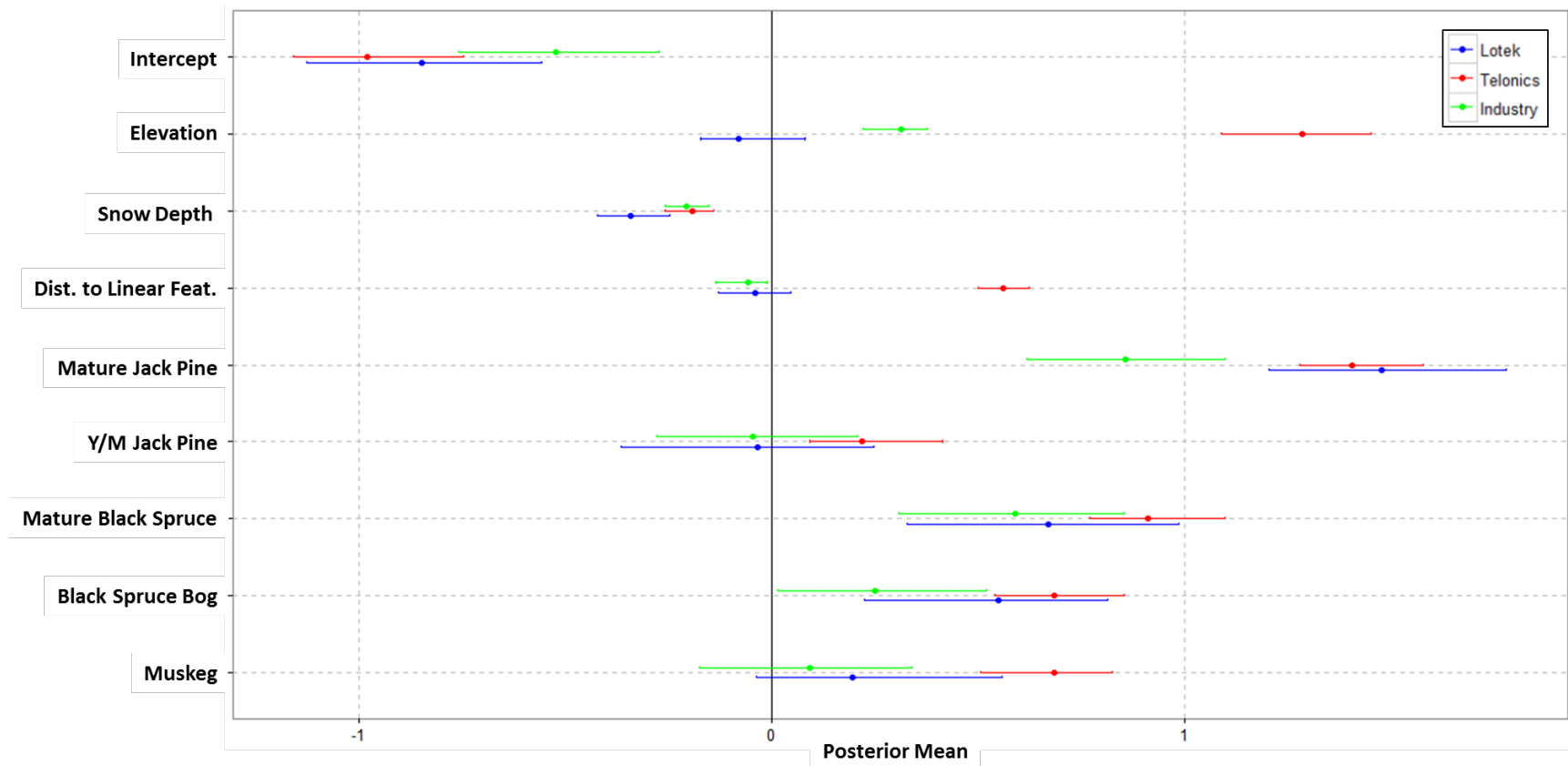
Fig. 4.32: Comparison between the top model (red) and validation model (blue and green) for the late winter/spring (LWS) season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 17,490 GPS locations recorded from 68 individuals over two LWS seasons) and validated using (a) a sample of female woodland caribou fit with *Lotek* ® GPS collars (n = 6,594 GPS locations recorded from 24 individuals over two LWS seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (n = 18,732 GPS locations recorded from 58 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).
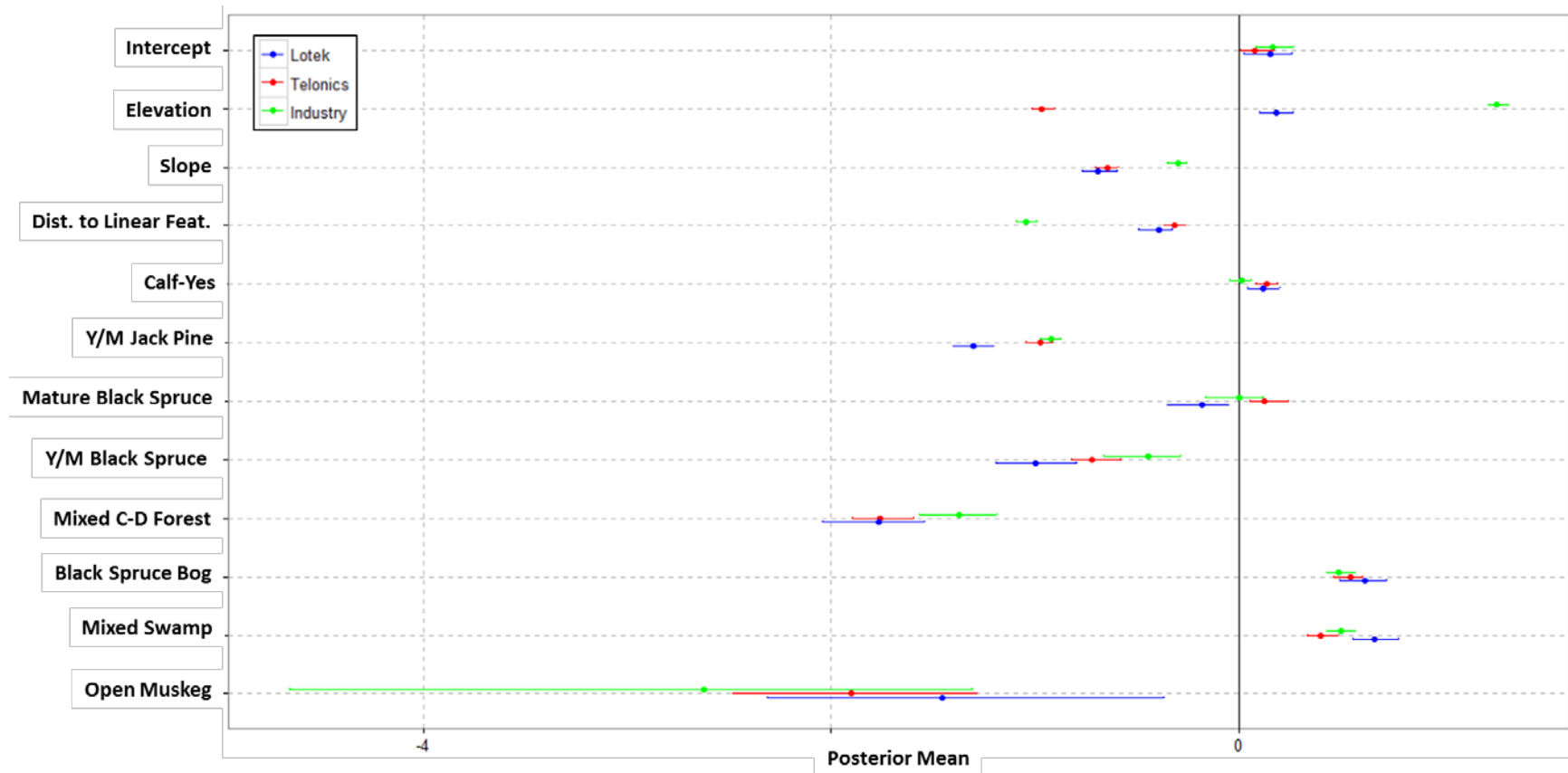
Fig. 4.33: Comparison between the top model (red) and validation model (blue and green) for the calving/post-calving (CPC) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 25,747 GPS locations recorded from 67 individuals over two CPC seasons) and validated using (a) a sample of female woodland caribou fit with *Lotek* ® GPS collars (n = 10,678 GPS locations recorded from 24 individuals over two CPC seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (n = 29,040 GPS locations recorded from 54 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

Fig. 4.34: Comparison between the top model (red) and validation model (blue and green) 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) a sample of female woodland caribou fit with *Lotek* ® GPS collars (*n* = 10,411 GPS locations recorded from 24 individuals over two CPC seasons)); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (*n* = 28,661 GPS locations recorded from 54 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).

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Status of Woodland Caribou in the Saskatchewan Boreal Shield
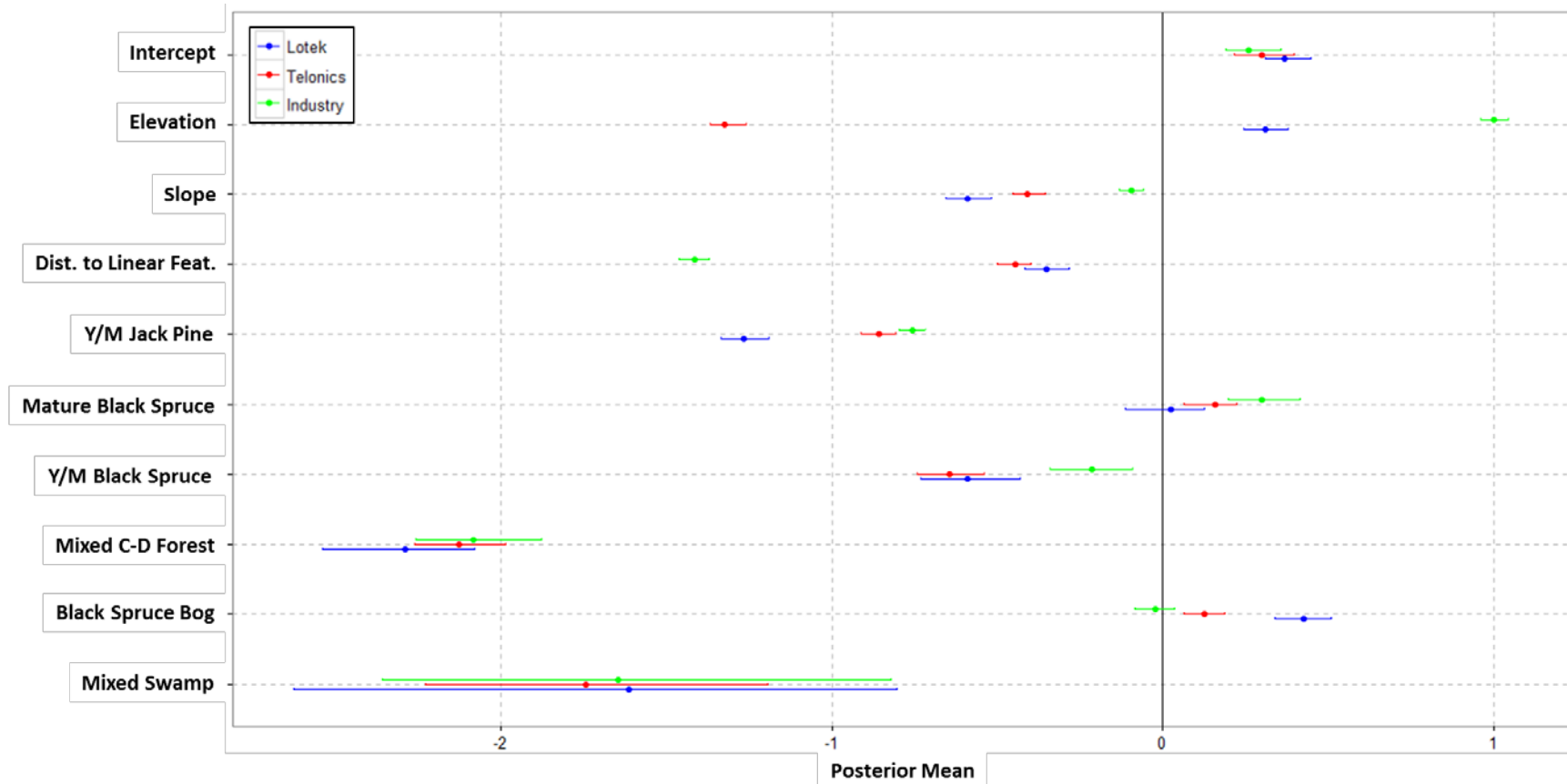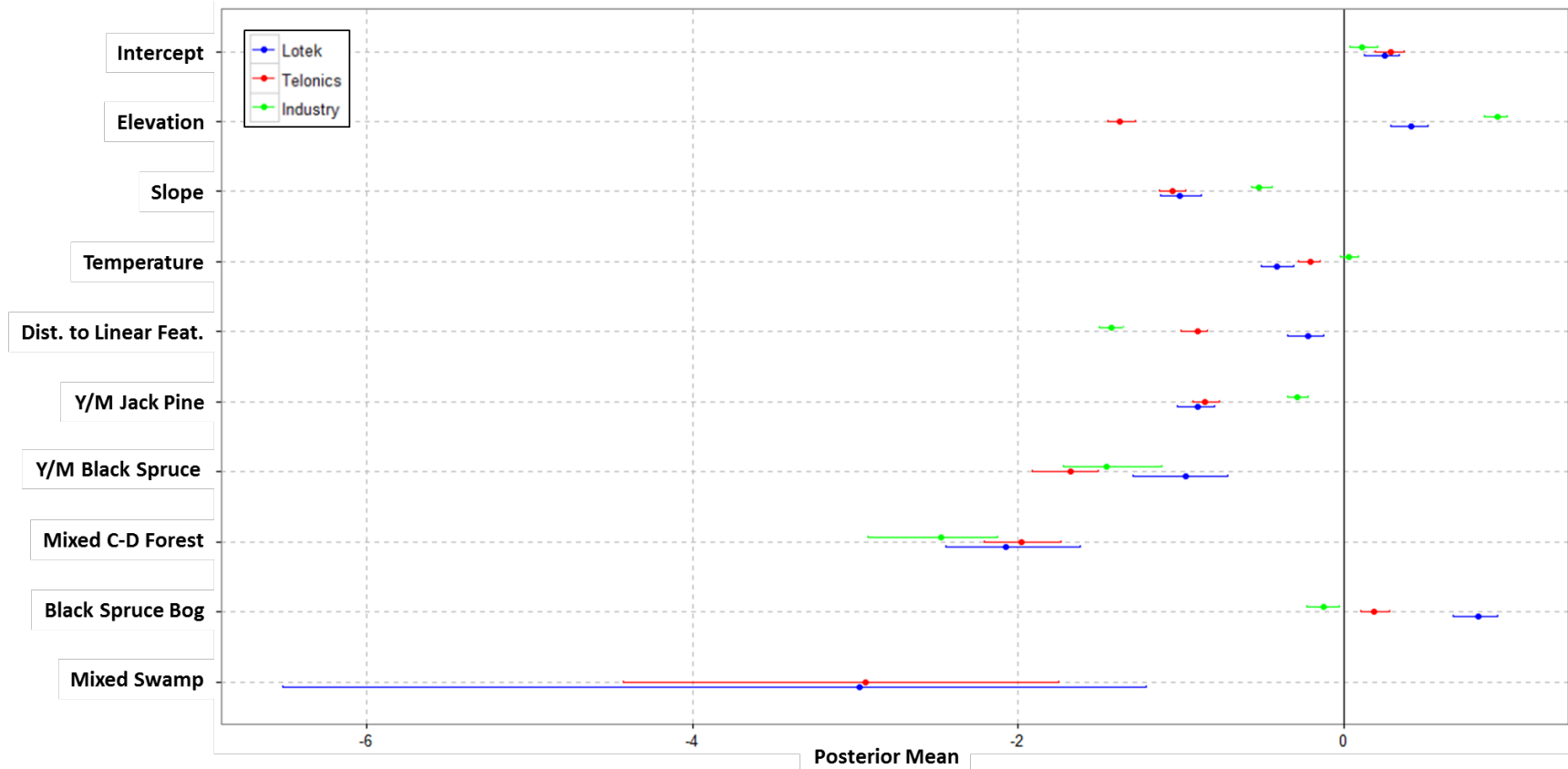

Fig. 4.35: Comparison between the top model (red) and validation model (blue and green) for the summer season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 30,616 GPS locations recorded from 64 individuals over two summer seasons) and validated using (a) a sample of female woodland caribou fit with *Lotek* ® GPS collars (n = 15,229 GPS locations recorded from 23 individuals over two summer seasons)); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (n = 42,135 GPS locations recorded from 54 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).

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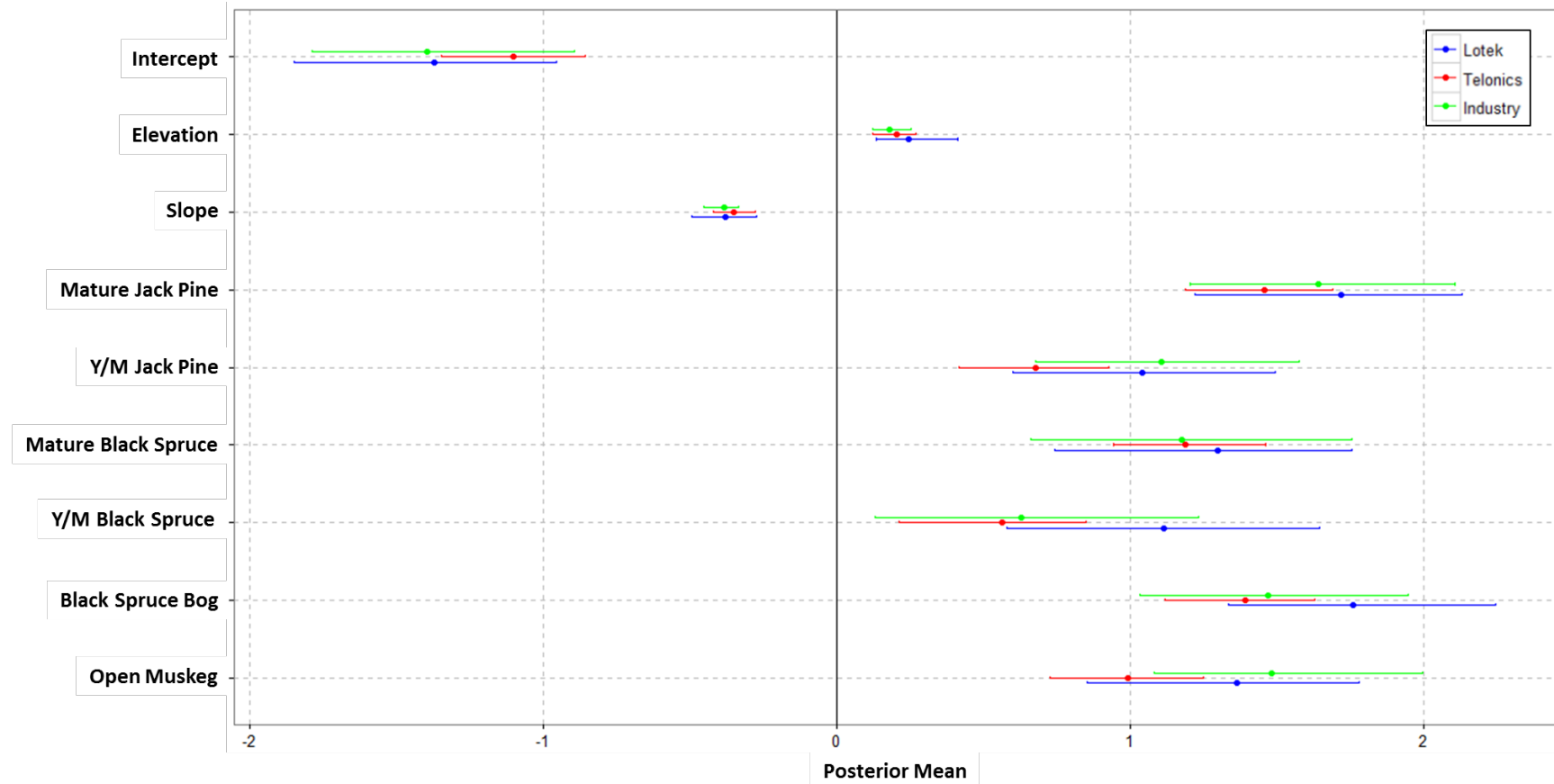
Status of Woodland Caribou in the Saskatchewan Boreal Shield
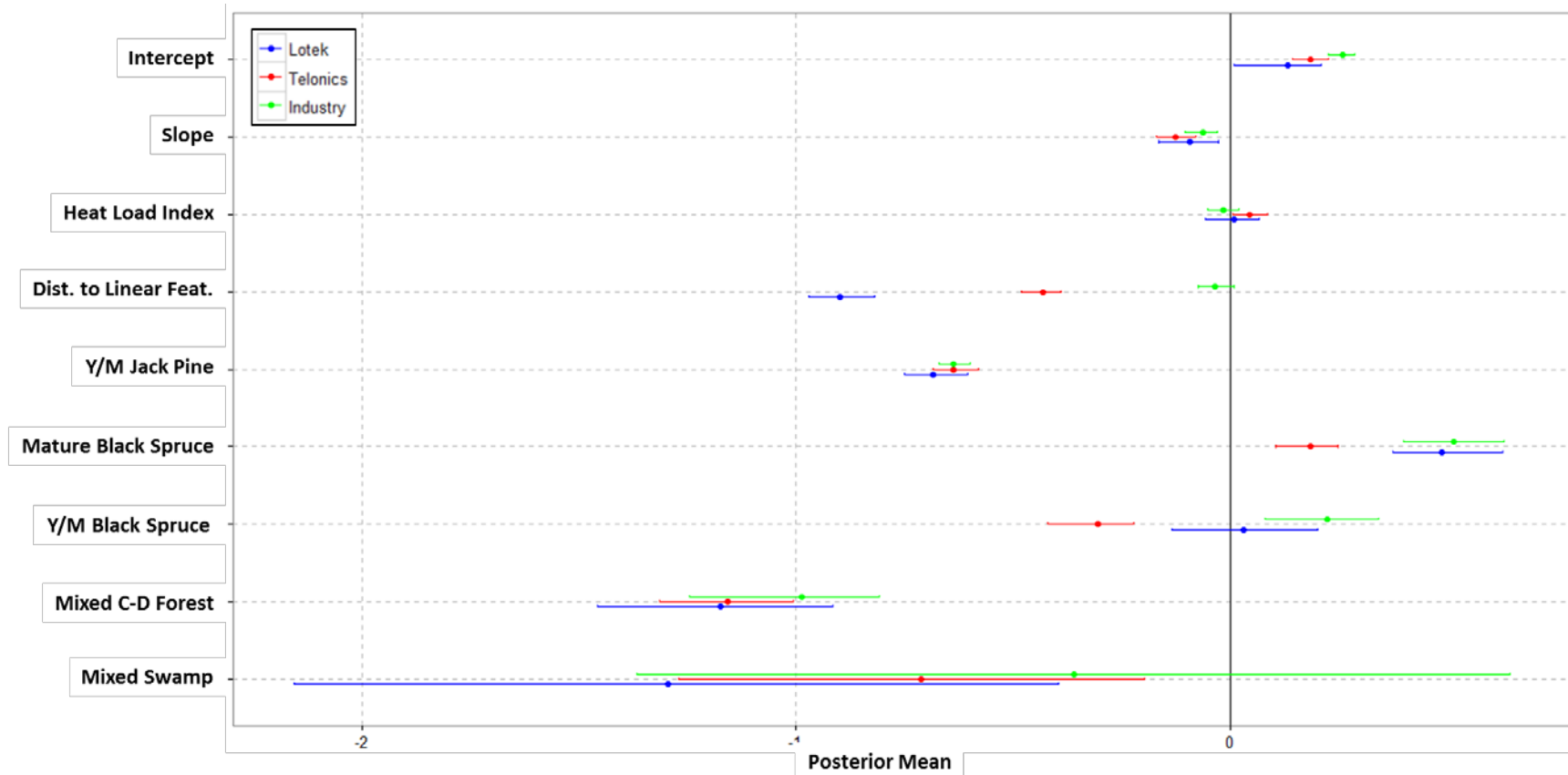
Fig. 4.36: Comparison between the top model (red) and the validation model (blue and green) for the summer season at the fine spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars ($n = 29,741$ GPS locations recorded from 64 individuals over two summer seasons) and validated using (a) a sample of female woodland caribou fit with *Lotek®* GPS collars ($n = 14,794$ GPS locations recorded from 23 individuals over two summer seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan ($n = 40,848$ GPS locations recorded from 54 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).
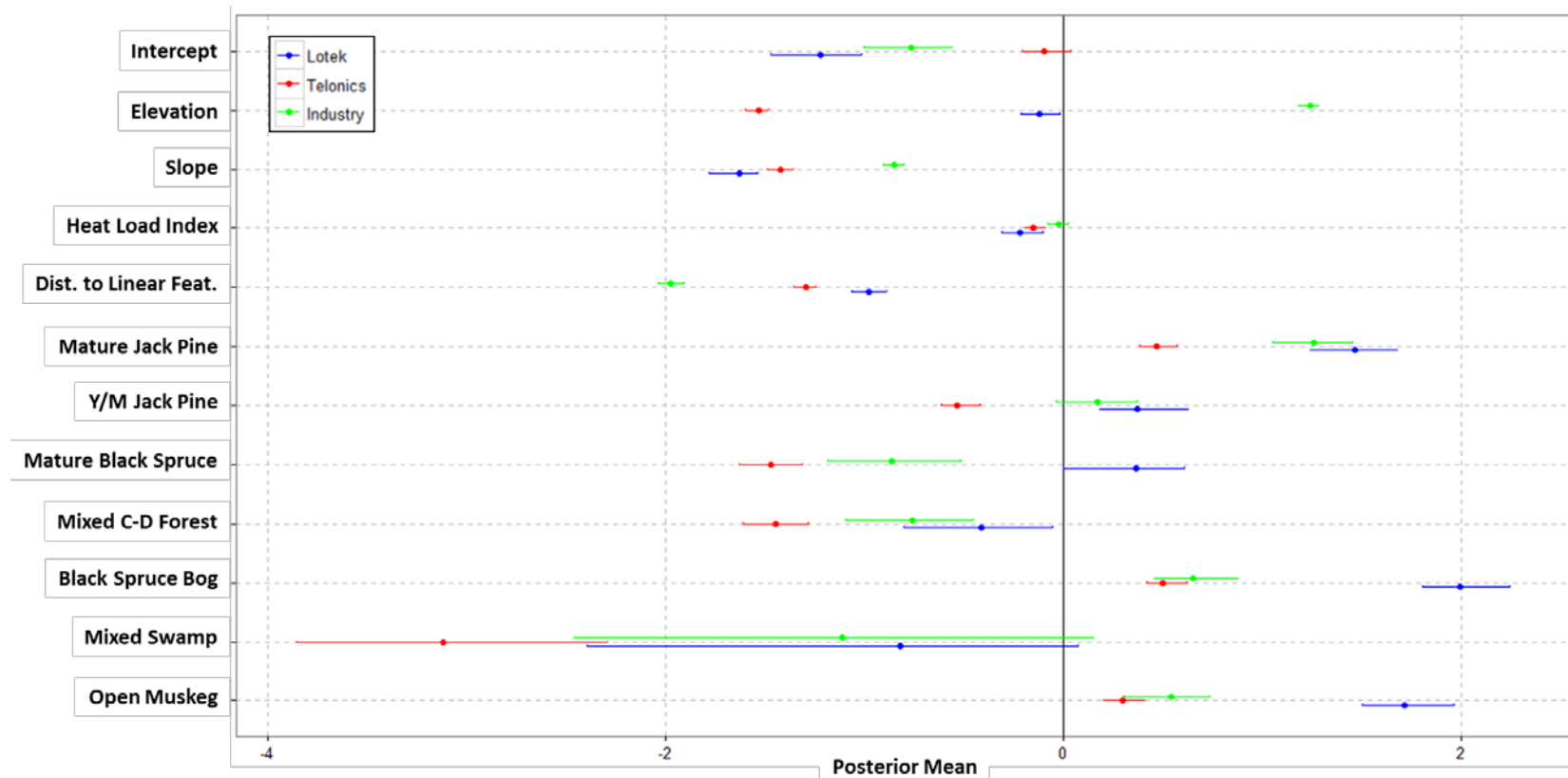
Fig. 4.37: Comparison between the top model (red) and the validation model (blue and green) for the autumn/rut (AR) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (*n* = 12,483 GPS locations recorded from 60 individuals over two AR seasons) and validated using (a) a sample of female woodland caribou fit with *Lotek*® GPS collars (*n* = 5,405 GPS locations recorded from 23 individuals over two AR seasons)); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (*n* = 15,362 GPS locations recorded from 52 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). **The posterior mean and credible intervals for the habitat class mixed swamp are not shown because the posterior mean was estimated to be -71.06; hence, it could not be reasonably plotted on the scale of the other coefficient estimates.**

Fig. 4.38: Comparison between the top model (red) and the validation model (blue and green) 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) a sample of female woodland caribou fit with *Lotek* ® GPS collars (*n* = 5,342 GPS locations recorded from 23 individuals over two AR seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (*n* = 15,308 GPS locations recorded from 52 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).

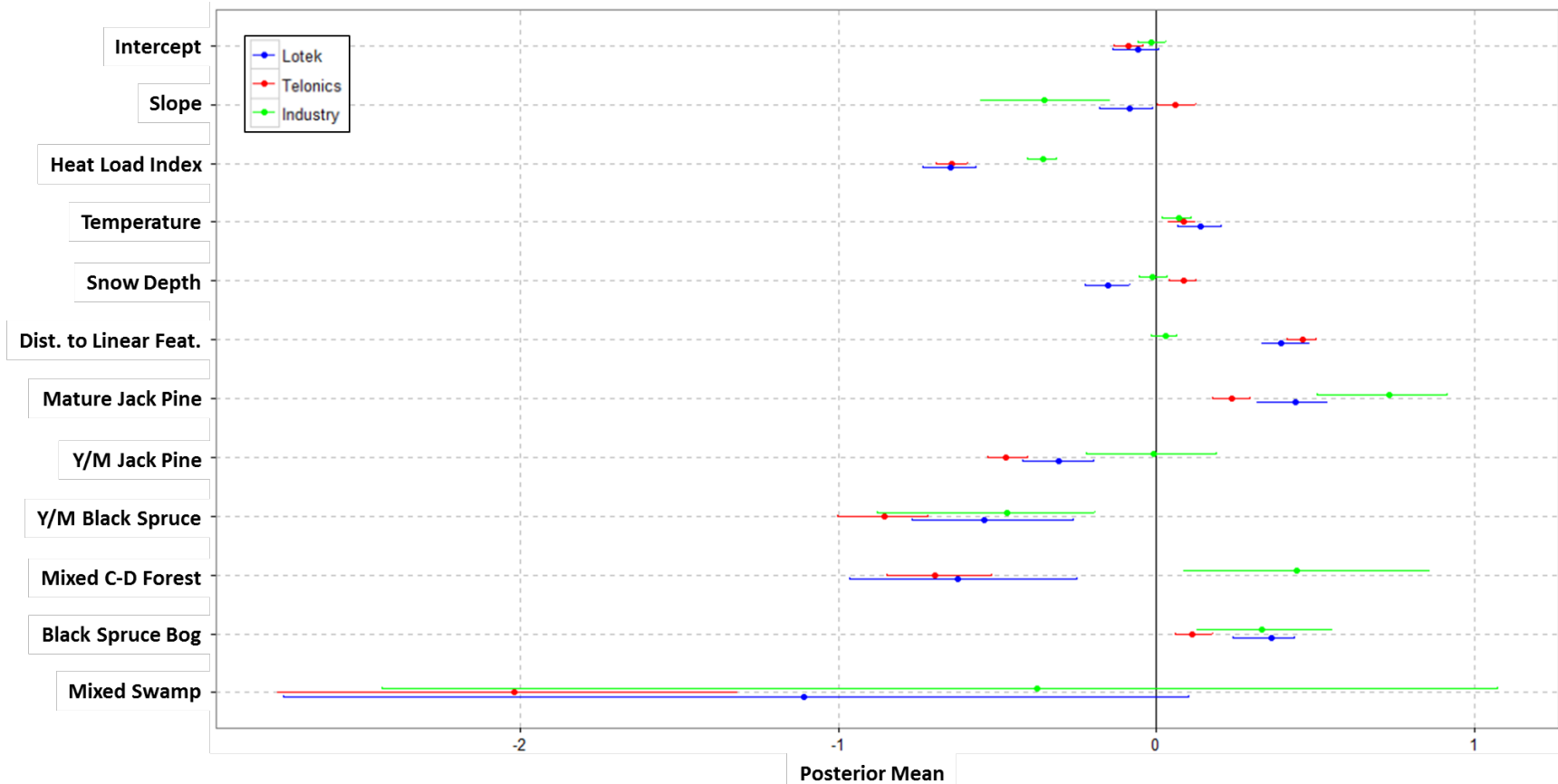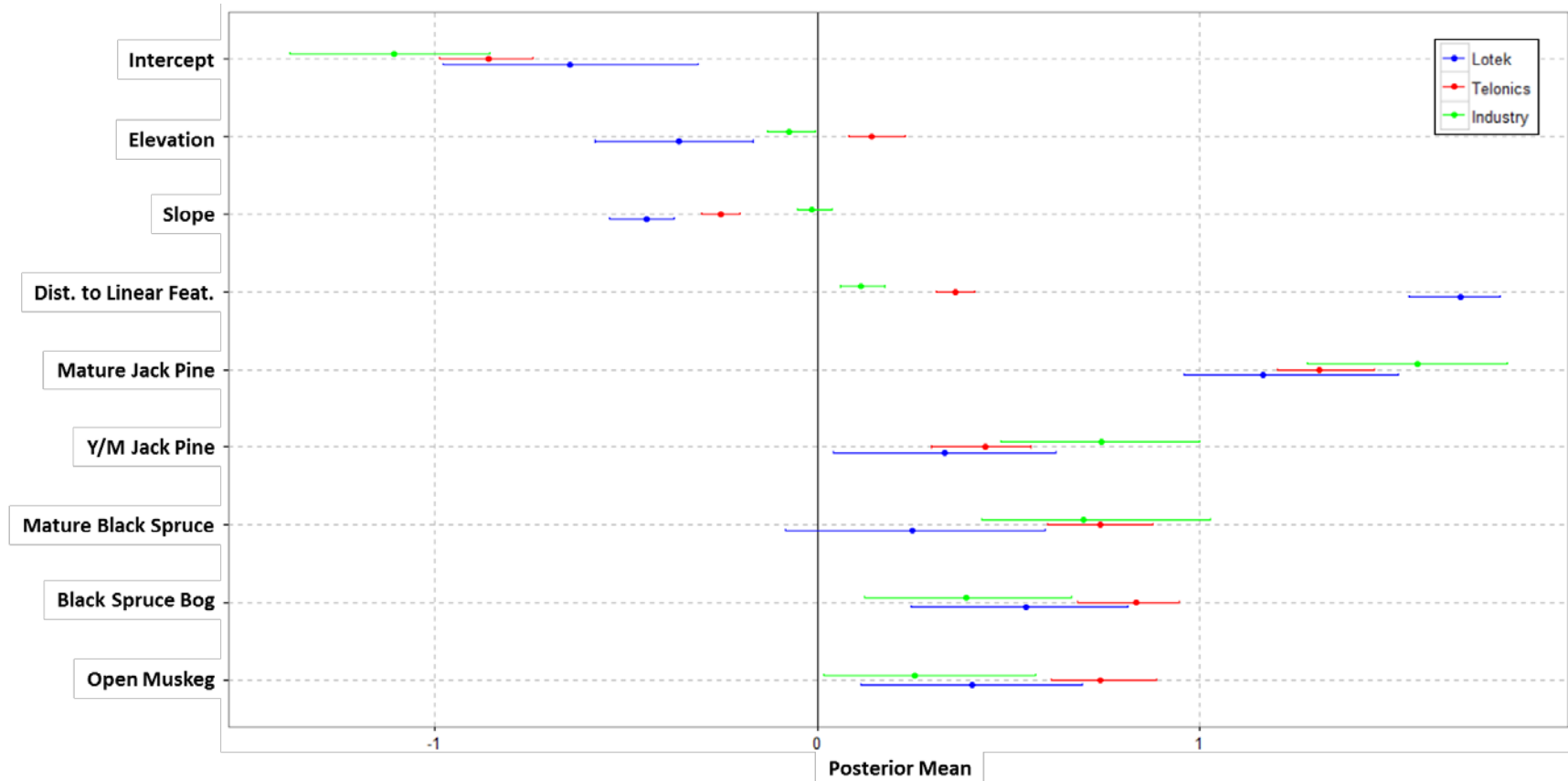# Status of Woodland Caribou in the Saskatchewan Boreal Shield

Fig. 4.39: Comparison between the top model (red) and the validation model (blue and green) 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) a sample of female woodland caribou fit with *Lotek* ® GPS collars (n = 9,388 GPS locations recorded from 22 individuals over two EW seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan (n = 27,771 GPS locations recorded from 50 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.

Status of Woodland Caribou in the Saskatchewan Boreal Shield

Fig. 4.40: Comparison between the top model (red) and the validation model (blue and green) 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) a sample of female woodland caribou fit with *Lotek*® GPS collars ($n = 10{,}005$ GPS locations recorded from 22 individuals over two EW seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan ($n = 29{,}277$ GPS locations recorded from 50 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).
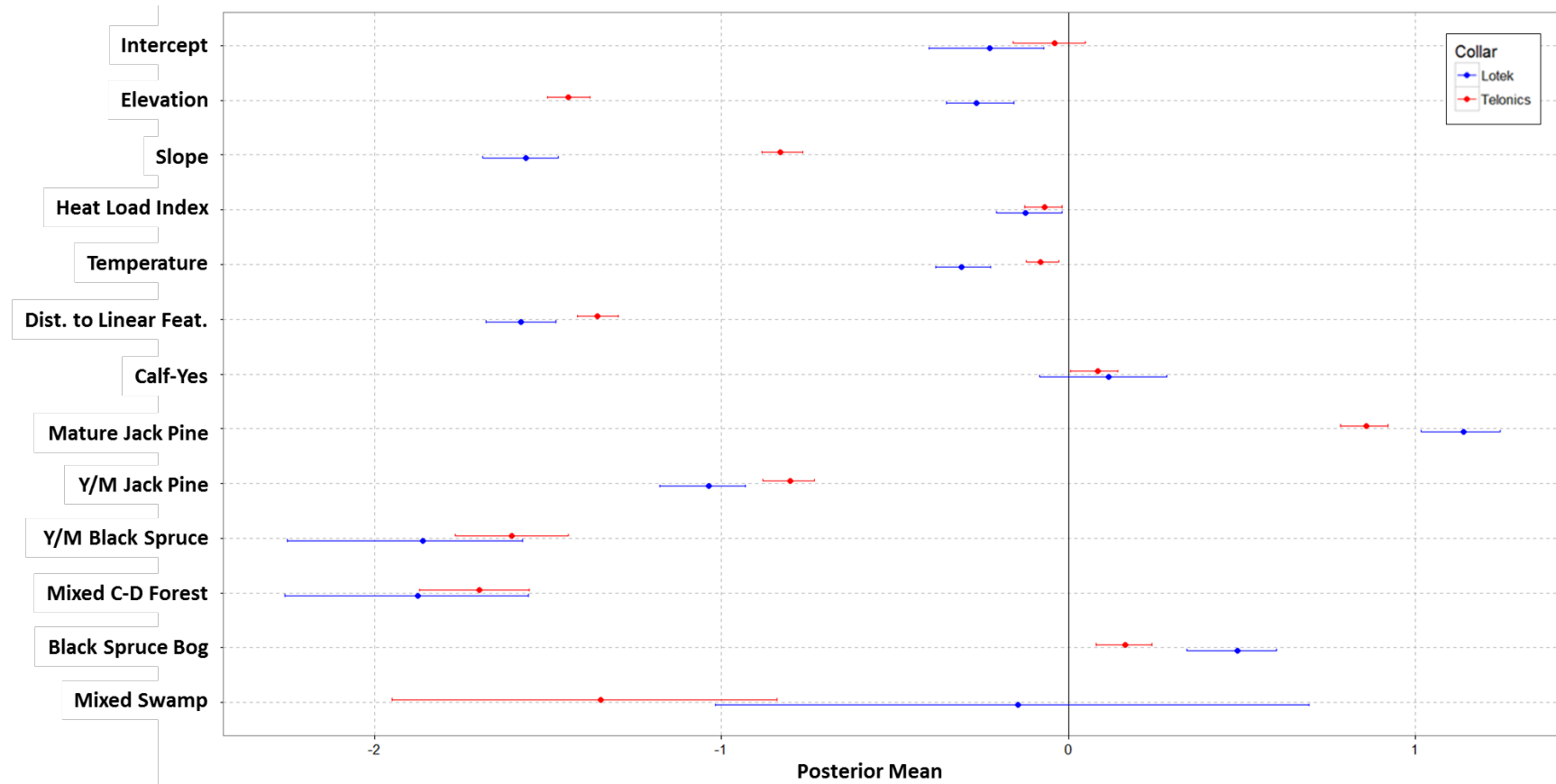
Fig. 4.41: Comparison between the top model (red) and the validation model (blue) for the mid-winter (MW) season at the coarse spatial scale. The top model was trained using a sample of female woodland caribou fit with *Telonics* GPS collars (n = 24,279 GPS locations recorded from 57 individuals over 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. 4.42: Comparison between the top model (red) and the validation model (blue and green) 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) a sample of female woodland caribou fit with *Lotek®* GPS collars ($n = 9,447$ GPS locations recorded from 22 individuals over two MW seasons); and (b) a sample of female woodland caribou remotely monitored by industry partners around Key Lake and Cree Lake, Saskatchewan ($n = 26,471$ GPS locations recorded from 49 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).

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4.5 Interpreting Caribou Habitat Selection

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 our study, we 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 our 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 our 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.

We explored whether linear features constrained local migration 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: (1) the overall density of linear features in Saskatchewan's Boreal Shield is very low (0.1 km/km^2), and (2) 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. 4.17) so we 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. Although 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. Some potential mechanisms for this relationship are that seasonal resources become more patchily distributed moving east to west across the study area (which may promote migration ; Dingle and Drake 2007) or that caribou densities 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 the Saskatchewan Boreal Shield, we used a combination of movement analyses, calving dates and climate data to partition the year into six seasons (see *Section 4.3*). We calculated ranges on an annual basis so that caribou who survived the full two years had a total of 12 seasonal ranges (i.e., two 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 4.7 for summary of adjusted *P*-values). When we compared mean range sizes using less conservative, unadjusted *P*-values, we 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. We 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*, 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 Québec have been estimated to be near 100% [Courtois et al. 2007]), and the pregnancy rate for our collared caribou in 2014 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 (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 ANALYSIS

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 198; 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. We 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), we 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 our 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 our fine scale analyses suggest that predation risk continues to govern caribou behaviour at the fine spatial scale. Unlike Rettie and Messier (2000), we 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 within spatiotemporal scales. An in-depth review of the resource selection patterns as they relate to predation risk and forage availability is presented below.

4.5.3.1 Topographical Variables

Topographical features such as elevation and slope vary in how they influence woodland caribou select resources 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 our study show that, at the coarse spatial scale, female boreal caribou are much 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, we included heat load index as a topographical variable in our resource selection models. Heat load is derived from transformations of slope, aspect and latitude (see McCune and Keon 2002). 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), we were curious to see whether heat load index captured the response of caribou to the topographical effects of slope aspect. More specifically, we were asking whether caribou were more likely to be found on warmer, drier south-facing slopes or on cooler, wetter north-facing slopes. At the coarse spatial scale, caribou were marginally more likely to occur on north-facing slopes during the early and mid-winter seasons. At the fine spatial scale, caribou were slightly more likely to occur on north-facing slopes during the early winter season and slightly more likely to occur on south-facing slopes during the summer and calving-post-calving seasons.

During the winter seasons, selection for north-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 north-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. We used it as a proxy for slope aspect; however, it may have been more prudent to just use aspect because: (1) this would have guarded against any confounding effects the non-linear relationship between slope and heat load index had on resource selection; and (2) made the models more comparable to other studies of caribou resource selection (e.g., Poole et al. 2000; Gustine et al. 2006a; Jones et al. 2006 all included aspect in their resource selection studies).

4.5.3.2 Climate

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), we 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) and rates of change in activity in 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, we 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, we 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.

4.5.3.3 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, we predicted that female boreal caribou would avoid linear features at both spatial scales 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, roads may be disproportionately constructed through preferred caribou habitat (e.g., black spruce bogs and mature conifer-dominated forests). At the coarse spatial scale, female caribou were more likely to be found at lower elevations and on shallower slopes across all seasons. These habitat attributes, which are associated with black spruce bogs and some mature conifer-dominated forests (DeLong et al. 1991: 237–250), may be more conducive to road and trail construction. Hence, linear features may be constructed more frequently through important caribou habitat. We 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 water features (total area of intersection = 27%). Since black spruce bogs have high spatial correlation with water features, roads, trails and other linear features are commonly constructed adjacent to this habitat class; hence, caribou that select for black spruce bogs may also be selecting for linear features by proxy. 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 12 established territories, we recently documented wolf home range sizes in the Saskatchewan's Boreal Shield to average >3,500 km² (*Section 5.1*). These territories are 3.5× larger than territories recorded for wolves in other boreal caribou ranges, including northeast Alberta (as discussed in *Section 3.3*). Wolf densities are estimated to be much lower than in other parts of boreal caribou range where linear features more prominently factor into caribou population dynamics (*Section 3.3*). Hence, wolves may not use linear features as expected. Further, since 96.9% of linear features in the study area are geophysical survey lines and trails with minimal vehicle traffic, human-caused mortality associated with linear features is likely very low.

The response of caribou to linear features was more variable at the fine spatial scale. During the calving/post-calving and three winter seasons, Telonics-collared caribou were more likely to be found farther from linear features, whereas Lotek and Industry collared-caribou were generally found to be closer, or less or not associated with lines (see differences for early winter, mid-winter, and late winter/spring). During the summer and autumn/rut seasons, all caribou data sets continued to show caribou selecting for resource units that were in closer proximity to these features or not associated with linear features. Because caribou mortality risk across the boreal forest is highest during summer (McLoughlin et al. 2016; also see Fig. 3.6), given the latter result we do not believe that fine-scale responses to linear features reflect higher predation risk being associated with linear features. Rather, seasonal shifts reflecting changes in diet (including increasing diet breadth), coupled with non-random distribution of linear features among habitats, may better explain fine-scale responses to these features.

4.5.3.4 Reproductive Status

Female caribou with calves (hereafter CWC) may behave differently than female caribou without calves (hereafter CNC) because: (1) they incur greater energetic costs associated with lactation (Chan-McLeod et al. 1994), and (2) 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 approximately160 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,

we 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-adverse behaviour in order to focus on building up sufficient protein and fat stores for the long winter ahead. 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, young-medium aged 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 mosaics of 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 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: (1) they support high cover values of *Ledum* spp. (Labrador Tea), which may be minor, but important winter food item (Thomas et al. 1994); and (2) 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 during which males chase down and corral female caribou into small harems for the purpose of mating (Environment Canada 2012). It is 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 Table 4.4). 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.

4.5.3.6 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. We used two samples of 24 and 54 caribou fit by the U of S and our industry partners, respectively, with Lotek Wireless Inc. Iridium® Track M 3D radio-collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) to validate our top models for each season and scale. The U of S Lotek ('Lotek') sample was not spatially or temporally independent from the sample used to train our models (n = 68 caribou fit with Telonics TGW 4680-3 GPS/Argos radio-collars [Telonics Inc., Mesa, Arizona, USA]); however, the collars fit by our industry partners ('Industry') were concentrated in the Key Lake and Cree Lake region (with collaring beginning in 2013). For interpretation, the two U of S populations ('Telonics' and 'Lotek') are used for primary validation (as both samples spanned the entire SK1 administrative unit);

however, we also include the 'Industry' collar data set for visual comparison in our graphs (Figs. 4.31 to 4.42.

Models were evaluated by comparing the posterior means of covariates in corresponding training and validation models. Generally, if the posterior mean of a covariate from one model (Lotek or Telonics) 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 unit across the SK1 unit. Most 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 the magnitudes were considerably different). We scored training models according to their percent congruency, which was the percentage of covariate comparisons between training and validation models that were either consistent or showed the same general trends (see *Section 4.4.9* for details). The coarse- and fine-scale models for the autumn/rut season recorded the highest percent congruencies while the fine-scale models for the late winter/spring and calving/post-calving seasons had the lowest percent congruencies. With respect to individual covariates, comparisons between the posterior means for slope, temperature, mature jack pine forest and black spruce bogs were 100% congruous. Thus, we can be fairly confident that inferences made about the effects of these variables on caribou resource selection are generalizable across the study area. In contrast, comparisons made between reproductive status, heat load index, mixed canopy swamps and elevation were ≤50% congruous. Accordingly, inferences made regarding the influence of these variables on caribou resource selection may be limited to the sample population used to train the top models (i.e., the sample of Telonics caribou). Other variables were ranked between 50 and 100% congruent. Overall, top models were fairly representative of general trends in caribou resource selection. Trends in resource selection shown by the Lotek and Telonics collars were also by and large echoed by trends shown by the Industry collars, with some minor exceptions. For example, for the fine-scale analysis of early winter and late winter/spring, whereas the Lotek and Telonics collars showed some effect of distance to linear features on selection, the Industry collars did not.

The poor predictive power of some covariates (e.g., elevation) may be due to the fact that habitat attributes are heterogeneously distributed across a vast area (truncated population range = 91,238 km^2). 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 et al. 2002). In other words, all resource units should be equally available to all organisms. This assumption is violated in this study, particularly at the coarse scale of analysis. First, habitat classes are distributed along latitudinal and longitudinal gradients throughout the study area (see habitat class map, Fig. 4.10). The western half of the study area is characterized by a mosaic of mature and young to mid-successional jack pine forests with scattered pockets of young to mid-successional black spruce forests and black spruce bogs, while the eastern half is characterized by a medley of mixed coniferous-deciduous forests, mature and young to mid-successional conifer-dominated forests, with higher concentrations of black spruce bogs and open muskegs. Mature black spruce forests are primarily concentrated in the southeast quadrant

of the population range while mixed canopy swamps are exiguously scattered throughout the eastern two-thirds. In hindsight, we should have excluded mixed canopy swamps from the coarse scale models because the resolution of those models was too coarse to accurately capture the response of caribou to this class.

Elevation also follows a longitudinal gradient, with higher elevation sites observed in the western and central portions of the study area and lower elevation sites observed in the eastern third. This variable had the lowest percent congruency of all covariate comparisons (percent congruency = 30%; see Table 4.11), which suggests that either the response of female caribou to elevation is intrinsically, highly variable, or that female caribou in the training and validation samples were exposed to different ranges of elevation values. We performed a Wilcoxon-Mann-Whitney U test to compare the mean elevation associated with a sample of GPS locations drawn from each population (Telonics caribou: $n = 148,910$; Lotek caribou: $n = 60,948$) and found a statistically significant difference between the two ($W = 5603100000$, $P < 0.001$). An evaluation of range of elevation values available to each population revealed that although the overall range was similar, values for the Lotek caribou followed a bimodal distribution with local means centered at ~415 m and ~515 m while values for the Telonics caribou followed an approximately normal distribution with a mean of ~444 m. This disparity may be due to the uneven sampling of the two populations across the study area. In any case, this exercise provides evidence that the two populations, and indeed individual caribou, were exposed to varying ranges of elevation values. A more even sampling design would have corrected for this.

4.6 Defining Critical Habitat

4.6.1 AMOUNT, LOCATION, AND TYPE OF CRITICAL HABITAT

In interpreting critical habitat for boreal caribou, we focused on our observations of broad-scale habitat selection choices, which are likely most relevant to landscape management. Some general trends at the coarse scale that inform us as to what best predicts caribou probability of occurrence in the Saskatchewan Boreal Shield, includes:

- caribou are consistently more likely to be found at lower elevations, on shallower slopes and closer to linear features (we have no data to suggest caribou preferentially avoid industrial features at the density in which they currently exist);
- caribou generally avoided mixed canopy swamps, mixed coniferous-deciduous forests and young to mid - successional jack pine and black spruce forests (<40 years);
- they generally selected for mature conifer forests (jack pine and/or black spruce), black spruce bogs and open muskegs (>40 years);
- mature jack pine (>40 years) was especially important during the mid-winter and late winter/spring, but was not included in the top models for the summer, autumn/rut and calving/post-calving season;
- black spruce bogs (almost all bogs were aged >40 years) were the most important habitat class during the calving/post-calving season;
- reproductive status (i.e., having a calf) came out in the top models for the calving/post-calving season and mid-winter (presence of a calf affected how collared caribou selected habitat).

The location of the four primary habitat-class predictors of caribou habitat selection (mature jack pine and mature black spruce forests, black spruce bogs, and open muskeg) are mapped in Figs. 4.43 and 4.44. The shape files for all habitat classes and linear feature database are available upon request. Tables 4.12 and 4.13 present amounts (km^2) of each of the habitat classes evaluated in our analysis, at the scale of our collared caribou and across the mapped portion of the entire SK1 caribou administrative unit.

In defining the current proportion of habitat to boreal caribou in our study area, we have come to the following summary conclusions. First, we do not observe linear features as detrimental to probability of occurrence at the broad scale (it is a positive predictor of occurrence), and their influence is equivocal at the fine scale. Understanding why we found this will require further research; however, we suspect that it is because at the current density at which linear features occur there may be no functional relationship between lines and predation or hunting risk to caribou, as suggested from other jurisdictions (see McLoughlin et al. 2016 for review). In fact, not all caribou had linear features within their home range and their densities across the region were very low, averaging 0.1 km/km^2 for the area in which caribou were tracked.
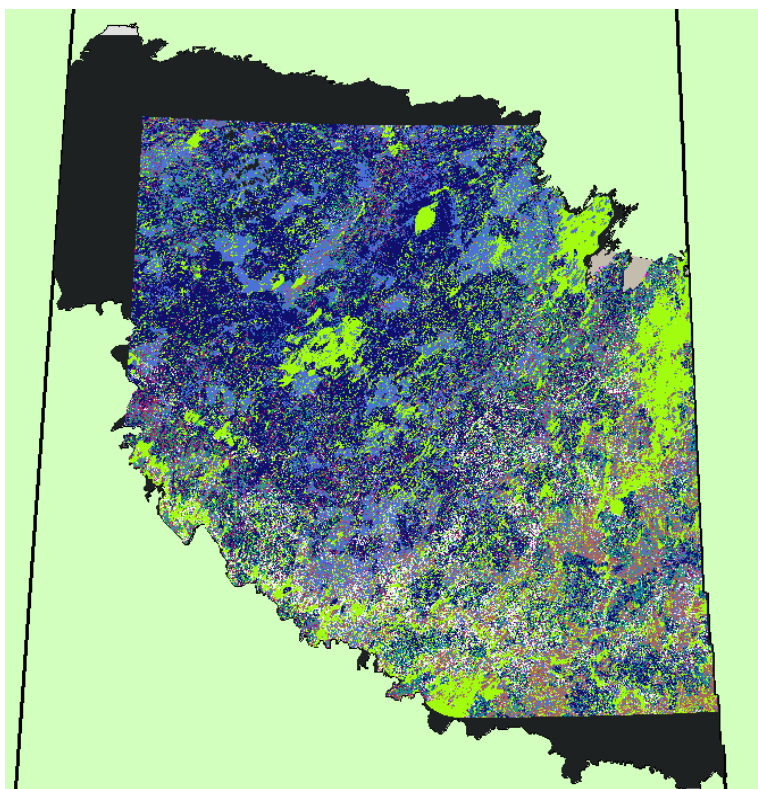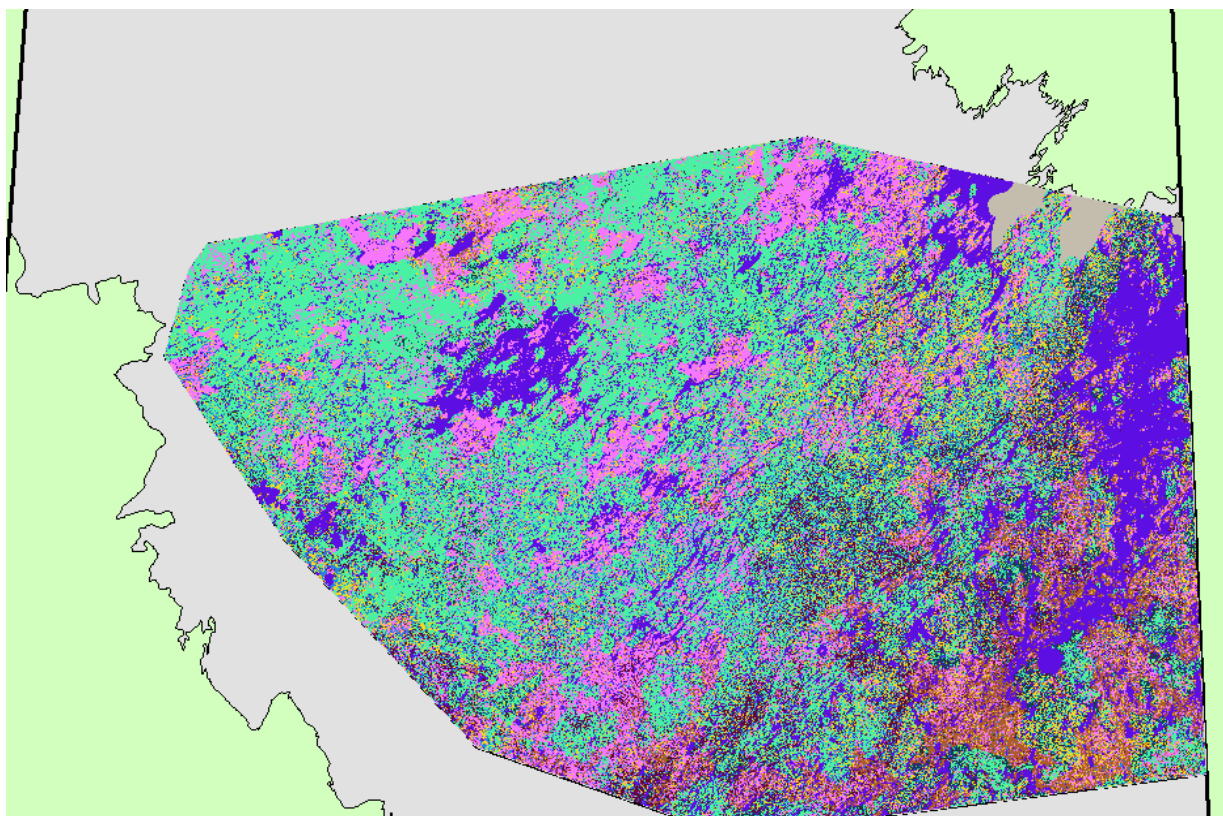
Fig. 4.43. Classified map at 30 m × 30 m resolution of various available vegetation associations (classes) used to evaluate habitat selection of female boreal caribou in the Saskatchewan Boreal Shield (SK1 caribou administrative unit). See Table 4.12 for amounts (water is indicated in green, no data in black). Note that water is light green in this map.

Table 4.12. Number of map pixels (30 m × 30 m), area (km^2), and percentage coverage of vegetation classes used to analyze caribou habitat selection for the SK1 caribou administrative unit, as it relates to the mapped region of Fig. 4.43. Habitat classes interpreted as best predicting caribou probability of occurrence at the broad scale (*Section 4.5.3*) are indicated in green shading.

Vegetation Class	No. Pixels	Area (km^2)	% Total Area	% Land Area
Mature Jack Pine	29884212	26895.8	14.4	21.0
Young-Mid Jack Pine	51945120	46750.6	25.0	36.6
Mature Black Spruce	11911748	10720.6	5.7	8.4
Young-Mid Black Spruce	7930118	7137.1	3.8	5.6
Mixed Coniferous-Deciduous	10402314	9362.1	5.0	7.3
White Spruce	3666	3.3	0.0	0.0
Mixed Canopy Swamp	527753	475.0	0.3	0.4
Black Spruce Bog	16182026	14563.8	7.8	11.4
Open Muskeg	13217377	11895.6	6.4	9.3
No Data (black)	32752284	29477.1	15.8	n/a
Water	33017291	29715.6	15.9	n/a
Sand Dune	1436	1.3	0.0	0.0
Total Area		186997.8		
Total Land		127805.2	(Water and No Data excluded)	

Fig. 4.44. Classified map at 30 m × 30 m resolution of available vegetation associations (classes) used to evaluate habitat selection of female boreal caribou in the Saskatchewan Boreal Shield for the area in which caribou were radio-collared and relocated for analysis (i.e., bounds of caribou ranges; see Fig. 4.16). See Table 4.13 for amounts.

Table 4.13. Number of map pixels (30 m × 30 m), area (km^2), and percentage coverage of vegetation classes used to analyze caribou habitat selection for the area in which caribou were radio-collared and relocated for analysis, as it relates to the mapped region of Fig. 4.44 (i.e., bounds of caribou ranges; see Fig. 4.16). Habitat classes interpreted as best predicting caribou probability of occurrence at the broad scale (*Section 4.5.3*) are indicated in green shading.

Vegetation Class	No. Pixels	Area (km^2)	% Total Area	% Land Area
Mature Jack Pine	16604864	14944.4	16.4	20.5
Young-Mid Jack Pine	32059529	28853.6	31.6	39.6
Mature Black Spruce	5829154	5246.2	5.8	7.2
Young-Mid Black Spruce	4069666	3662.7	4.0	5.0
Mixed Coniferous-Deciduous	4850585	4365.5	4.8	6.0
White Spruce	2182	2.0	0.0	0.0
Mixed Canopy Swamp	167693	150.9	0.2	0.2
Black Spruce Bog	9478322	8530.5	9.3	11.7
Open Muskeg	7890692	7101.6	7.8	9.7
NoData	812876	731.6	0.8	n/a
Water	19609399	17648.5	19.3	n/a
Sand Dune	972	0.9	0.0	0.0
Total Area		91238.3		
Total Land		72858.3	(Water and No Data excluded)	

Our observed density of 0.1 km lines/km^2 is an order of magnitude lower than as documented in regions where linear features have been associated with caribou avoidance of lines. For example, Dyer et al. (2002), in their study of caribou avoidance of linear features in northeast Alberta, documented geophysical seismic cutlines alone averaging 1.0–1.3 km/km^2 in home ranges of caribou. Linear features across six woodland caribou populations in eastern Alberta spanned 0.7 to 3.5 km/km^2 (McCutchen 2007). Current levels of anthropogenic disturbance in the SK1 range show no detrimental effect on caribou movements and habitat selection, and do not indicate functional habitat loss associated with the estimated 3% of area that is located within 500 m of an industrial feature. Rather, critical habitat for caribou appears to be driven (as expected) from natural disturbance and natural biophysical habitat attributes.

In summing the proportions of the most important, positive predictors of caribou in the SK1 unit, we observed that in the region where we tracked collared caribou (Fig. 4.44; 91,238 km^2 [72,858 km^2 of land mass]), mature jack pine and black spruce forests, black spruce bogs, and open muskeg accounted for 49.2% of the land mass, or 35,823 km^2. For the available mapped portion of the SK1 unit at fullest extent (127,805 km^2 in land mass; Fig. 4.43), these critical habitats comprised 50.1% of the land mass, or 64,076 km^2.

Within our collared-caribou study area (Fig. 4.44), preferred vegetation associations by collared caribou combined to provide 1060 ha of prime habitat per caribou, as we estimated a local population size in the smaller study area of 3380 caribou (*Section 3.2.3*). Our preliminary estimates of the amount of forage lichen (*Cladina mitis*, *C. rangiferina*, *C. stellaris*, and *Cladonia uncialis*) available in our study area in these habitats was very high. In our next report, we will be able to present a final quantification of lichen biomass; however, given our preliminary results on lichen biomass we believe that winter forage does not appear to be limiting in terms of gross abundance to caribou on a per capita basis.

As yet we do not know what other features of habitat may be critical to limiting population growth of caribou in SK1 unit, but it does not appear to be availability of lichen forage or presence of linear features. Our future analyses will aim to directly link caribou survival and reproduction to biophysical habitat features, predator (wolf and black bear) likelihood of occurrence, linear or other anthropogenic features, and weather-related variables to provide a more definitive answer to what may govern survival and reproduction of woodland caribou in the Saskatchewan Boreal Shield.

4.7 Conclusion

As a general conclusion, approximately half of the available habitat in the SK1 caribou unit is comprised of vegetation associations that positively predicted caribou probability of occurrence on a seasonal basis (50.1% of land mass). Selected habitat classes included mature stands of jack pine, black spruce, black spruce bog, and open muskeg. Other habitat types, including young and mid-successional jack pine and black-spruce forest, mixed-wood forests of various ages, white spruce forests of various ages, and mixed-wood canopy swamps may have been used by caribou, but were not good predictors of occurrence. Caribou did not show avoidance of anthropogenic (linear) features on the landscape, and in fact caribou were shown to select for linear features in all seasons at the broad scale. Lichen forage availability within the amounts and types of vegetation associations selected by woodland caribou did not appear to be limiting.

Our finding that approximately half of the available vegetation associations were mature forests selected by caribou was expected and reflects the natural fire-cycle in the region (roughly 100 years; Parisien et al. 2004). Our data show that this amount of disturbance is associated with supporting a secure population of boreal caribou at a relatively high density exhibiting stable to slightly increasing population growth (*Section 3.4*). Woodland caribou of the Saskatchewan Boreal shield are self-sustaining and persist in close to the same conditions as they have historically. The initial conclusion that the caribou population in the SK1 unit should not be self-sustaining, based on the ECCC disturbance threshold (Environment Canada 2012), is incorrect with what we know about the population and how it responds to available habitat.

So how do we manage for caribou in the Saskatchewan Boreal Shield? ECCC recognizes that: "[…] there is variation in habitat and population conditions between boreal caribou local populations across their distribution, for some ranges it may be necessary to manage the range above the 65% undisturbed habitat threshold, while for others it may be possible to manage the range below the 65% undisturbed habitat threshold (p. 34)." We contend that the Saskatchewan Boreal Shield presents a clear case where managing for habitat above the advised disturbance threshold makes sense. To do otherwise would be to target increasing the length of the region's natural fire-return interval, to the benefit of a caribou population that by all accounts is secure and self-sustaining, and, as we argue in *Section 3.4*, perhaps the most secure of all boreal caribou populations in Canada.

5.0 PREDATORS

Integral to understanding the population dynamics of caribou is understanding the species' relationship with its year-round predator, the wolf (Rettie and Messier 1998, 2000; Wittmer et al. 2005; Latham 2009; Whittington et al. 2011; Johnson et al. 2012; Robinson et al. 2012). Wolves are thought to limit distribution and abundance of boreal caribou (Rettie and Messier 2000); however, we do not know how wolf distribution might influence caribou spatial and temporal dynamics in the Saskatchewan Boreal Shield where linear features are not prominent on the landscape (averaging 0.1 km/km^2, an order of magnitude lower than in northeast Alberta (*Section 4.6.1*). Linear features are thought to play a role in enhancing predator access into caribou habitat, or make landscapes more amenable to alternate prey that benefit from clearings (Environment Canada 2012). In the coming years, as we aim to refine our analysis of caribou habitat selection and critical habitat (*Section 4.0*), we will estimate the relative exposure of caribou in the study area to resident wolves, which will require knowledge of year-round probability of occurrence in the study area.

In addition to understanding how wolf numbers and distribution might affect the caribou population—and the influence of disturbance on this relationship—we cannot ignore the potential role of black bears in regulating caribou numbers or affecting caribou distribution. Predation risk for calves and adults is highest in summer when bears are active. McLoughlin et al. (2003) showed that for boreal caribou in northeast Alberta, 78.8% of adult mortalities occurred within the snow-free period; and in northern Manitoba, almost all calf mortality occurs before September (Joro Consultants Inc. 2012). The potential for black bears in boreal shield habitat to affect caribou recruitment may be greater than for wolves (e.g., accounting for almost 60% of calf mortality in a Québec caribou population [Pinard et al. 2012]): although caribou may avoid habitat used by wolves during the calving season, this may not be true for bears (Pinard et al. 2012). How bears and caribou overlap in range in the Saskatchewan Boreal Shield is unknown.

Here we can present preliminary results for what we currently know about wolf movements and home range size based on our tracking of GPS-collared wolves in the study area since 2014, and a pilot study on black bear tracking initiated in May, 2016 (with full launch of our bear study planned for May, 2017).

5.1 Wolves

5.1.1 METHODS

In March, 2014, we deployed 26 GPS collars on wolves across the study area. In March, 2015, we deployed an additional 12 GPS collars on wolves to improve sample size following collar malfunction and wolf mortality after the first year of tracking. In total, 38 wolves (16 males, 19
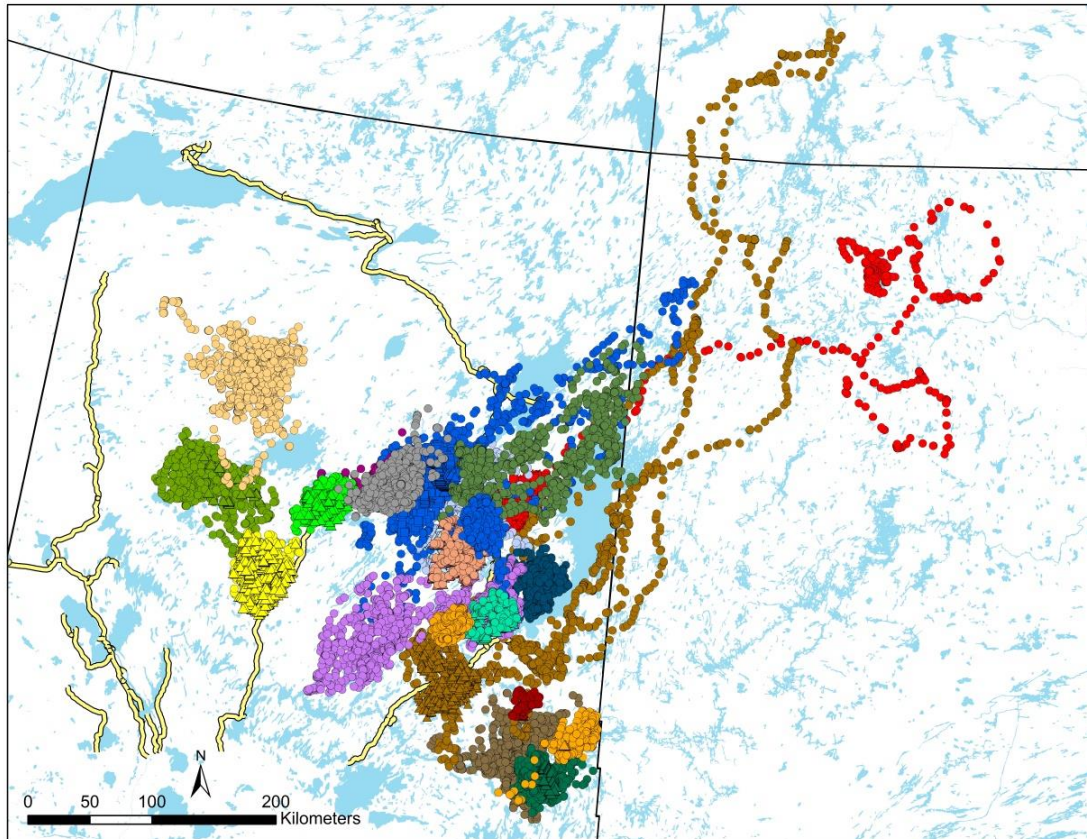
Fig. 5.1. GPS location data obtained from 38 wolves occupying 18 suspected packs within Canada's Western Boreal Shield collected between March 2014–2016. Circles, squares and triangles represent GPS locations of individual wolves while symbol colour indicates pack membership. Yellow lines are roads in the study area.

females, 3 unrecorded sex) occupying 18 suspected packs were fitted with GPS collars in the study area (Fig. 5.1). All wolves were captured and equipped with collars after physical immobilization (net gun) through the tendered services of Bighorn Helicopters Inc. (Cranbrook, British Columbia, Canada), following approved animal care protocol 20130127 of the University of Saskatchewan (guided by the Canada Council on Animal Care and the U of S Animal Research and Ethics Board) and permit 14FW037 of the Saskatchewan Ministry of the Environment. Individuals were equipped with Lotek Iridium® Track M 2D GPS collars (Lotek wireless Inc., Newmarket, Ontario, Canada). GPS data were programmed to transmit approximately every 3 hours and collars were provided with Very High Frequency (VHF) system to allow radio-telemetry tracking of wolves in the field. Upon capture (Fig. 5.1) we collected biological samples (blood, hair) for use in analyses of diet, and genetic analysis. Whole blood spots on filter paper will be submitted for microsatellite and mitochondrial DNA analysis in 2017 for genetic analysis. Remaining samples are currently stored in the freezers of the Department of Biology, University of Saskatchewan. Hair samples, red blood cells, and remaining serum sub-samples are retained at the University of Saskatchewan for future analyses involving stable isotopes.

5.1.2 PRELIMINARY RESULTS

At time of writing, all collars have now ceased in their transmissions. Over the course of two years 28 of the wolf collars went offline (76%), six wolves were confirmed dead (16%), the status of two collars are unknown (dead or dropped), and one collar prematurely released. Forty-six percent of wolf collars lasted at least one year on the animal, while two collars lasted at least two years.

Territory sizes averaged 3531 ± 598 km^2 ($\bar{x} \pm$ SE, $n = 12$ packs; 100% minimum convex polygon [MCP] for unduplicated wolves in packs with at least one full year of data and excluding $n = 4$ wolves and packs that appeared to have large migratory movements, Fig. 5.1). These territories are considerably larger than elsewhere in woodland caribou range, including northeast Alberta where Latham (2009) recently documented average territory size (100% MCP) to be $\bar{x} = 1087 \pm 452$ (95% CL, $n = 8$ packs). In west-central Alberta, territory sizes (also 100% MCP) were 937 km^2 in the study of Kuzyk (2002). Latham (2009) observed winter pack sizes of 2–22 wolves ($\bar{x} = 7.8 \pm 3.37$, 95% CL, $n = 11$ packs). Kuzyk (2002) observed late winter wolf pack size ranging from 4–18 members per pack with a mean pack size of 8.2 wolves/pack. Our pack sizes were much smaller, ranging from only 2–9 wolves.

5.1.3 FUTURE ANALYSIS

Wolf spatial dynamics can influence the distribution and abundance of prey species, including woodland caribou (Latham et al. 2011b,c). Recent studies of wolf resource selection have demonstrated wolf selection for anthropogenic linear features, sometimes resulting in improved hunting efficiency and subsequent caribou population decline (Lesmerises et al. 2012; DeCesare et al. 2014). Given the low amount of linear disturbances in the study area, it is uncertain the degree to which wolves select linear features on the landscape. Further, it is unknown to which the degree fire disturbance influences wolf selection patterns across the highly burned landscape. Using GPS collared individuals ($n = 37$), we will quantify seasonal wolf resource selection at the home range and landscape scales (corresponding to 2nd and 3rd orders of selection) to predict wolf occurrence across our study area. Ultimately, we would like to predict the spatial risk imposed by wolves across the landscape to improve our predictions surrounding woodland caribou habitat selection and effects on population dynamics.

Wolves are opportunistic generalists that eat a wide variety of prey items, but are also thought to be major predators of woodland caribou in some boreal systems (e.g., McLoughlin et al. 2005). To help understand the role of wolf predation on woodland caribou in Saskatchewan's Boreal Shield, we plan to reconstruct the proportional diet of wolves using stable isotope analysis (using carbon [^{13}C] and nitrogen [^{15}N] isotopes) and a hierarchical multivariate Bayesian stable isotope mixing model. Wolf blood and hair samples collected during the capture period will be used to obtain wolf isotopic signatures; prey item sample collection is ongoing through 2017. A description of wolf diet will serve as a valuable baseline for Saskatchewan's Boreal Shield, as well as contribute to our understanding of wolf predation on woodland caribou in the system.

Distinct genetic partition between grey wolf populations occupying boreal coniferous forest and tundra/taiga habitats have been previously described in the North West Territories, Canada (Musiani et al. 2007). Individual wolves within our study have demonstrated distinct movement patterns (i.e., long distance movements), and unique phenotypic characteristics (i.e., white coat colour) that may be indicative of genetic distinctness. To understand if unique sub-populations of wolves exist in Northern Saskatchewan, we plan to analyze autosomal microsatellites and mitochondrial DNA from blood samples collected at the time of capture.

5.2 Black Bears

In May, 2016, we launched a project on black bear habitat selection the Saskatchewan Boreal Shield. The project is aimed to be complimentary to our research aimed at understanding caribou movements and population dynamics, and how they relate to wolves (the main predator of caribou in winter). However, in addition to understanding how wolf numbers and distribution might affect boreal caribou in our study area—and the influence of disturbances like wildfire and human activities on this relationship—we cannot ignore the potential role of black bears in limiting caribou numbers or affecting caribou distribution (Latham et al. 2011a; McLoughlin et al. 2016). Predation risk for caribou calves and adults is highest in summer when bears are active. McLoughlin et al. (2003) showed that for boreal caribou in northeast Alberta, 78.8% of adult mortalities occurred within the snow-free period; and in northern Manitoba, almost all calf mortality occurs before September. For adult caribou of the Saskatchewan Boreal Shield, mortalities of collared individuals were also primarily focused on the snow-free period (*Section 3.0*, Fig. 3.6). The potential for black bears to affect caribou recruitment may also be greater than for wolves. For example, in the Charlevoix region of Québec, confirmed predation events on adult caribou were caused by wolves, while 95% of confirmed predation events on calves were by black bears (Pinard et al. 2012; Leblond et al. 2013). Further, although caribou may avoid habitat used by wolves during the calving season, this may not be true for bears. Estimated black bear densities and how bears and caribou overlap in range and habits of selection is unknown for the Saskatchewan Boreal Shield.

5.2.1 METHODS

In May 2016, following University of Saskatchewan Animal Use Protocol 2016011 and permit 16FW051 from the Saskatchewan Ministry of Environment, we collared three black bears in the boreal shield of Saskatchewan as part of a pilot study to determine feasibility of launching a full-scale project on black bear habitat selection as it relates to woodland caribou. The bears were captured by baiting to a removable culvert trap provided by our industrial and government partners. Once in the trap, bears were chemically immobilized using mix of medetomidine and Telazol® projected from a low-velocity dart following our Animal Use Protocol. After collecting biological data, samples of hair and blood, we fitted a Telonics Argos GPS telemetry collar, administered a reversal agent, and released the bear.
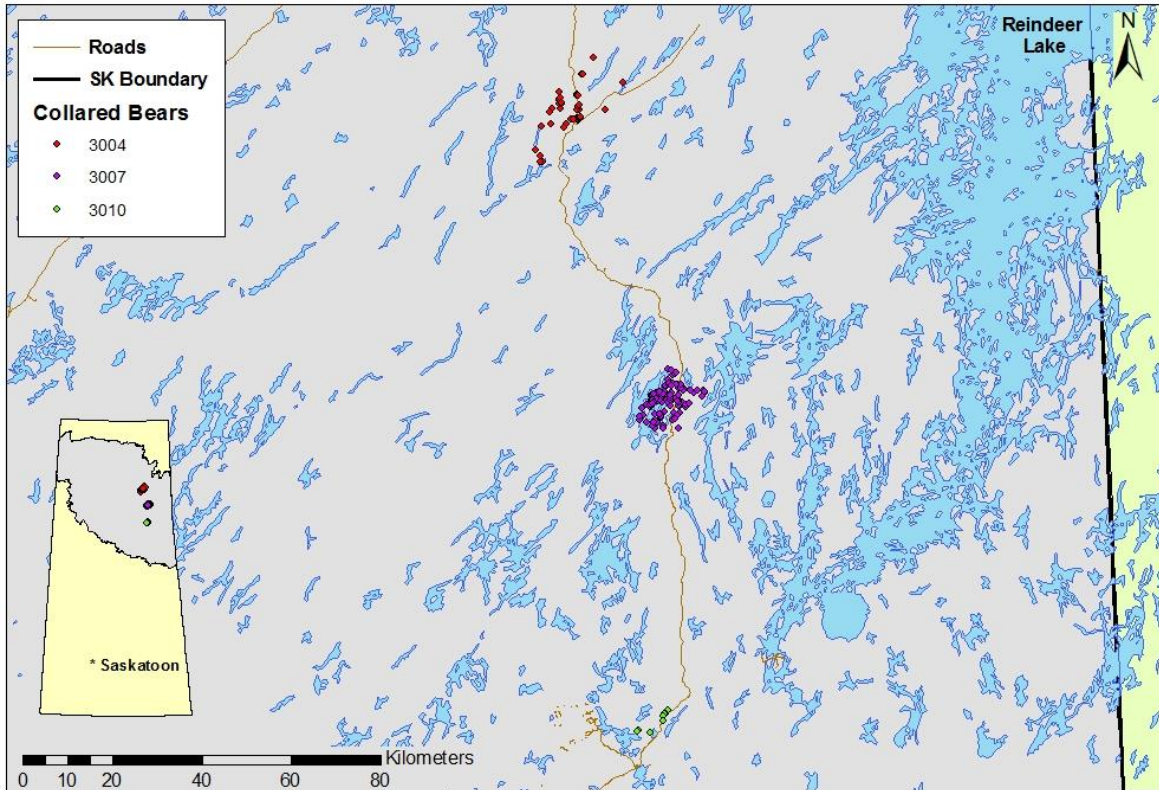
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Fig. 5.12. Locations of three GPS-collared black bears in the Saskatchewan Boreal Shield, 2016. Bears were captured and tracked as part of a pilot study of black bear habitat selection as it may relate to woodland caribou. Areas in blue are water.

5.2.2 PRELIMINARY RESULTS

Bear 3004 (adult male) was captured May 6, 2016 near kilometer 147 of highway 905. Bear 3010 (adult male) was captured May 9, 2016 just off highway 102, near Boettcher Lake. Bear 3007 (adult female, one cub left in tree) was captured May 11, 2016 near Davin Lake campground. Bear 3004 likely released its GPS collar prematurely in late May 2016 (currently unconfirmed in the field). The GPS collar of bear 3010 went offline mid-May 2016. The remaining bear, 3007, was remained transmitting around Davin Lake up to September 29, 2016 (Fig. 5.2), and we suspect she has now entered a den. With this small dataset from bear 3007, we estimated 50, 90, 95 and 99% utilization distributions for $n = 128$ GPS locations. These represent her range between 11-May-2016 and 16-Sept-2016.

- 50% UD: 27.96 km^2
- 90% UD: 90.11 km^2
- 95% UD: 99.91 km^2
- 99% UD: 122.51 km^2

In terms, of the 100% MCP estimator the female's annual range was 117.3 km^2.

5.2.3 FUTURE ANALYSIS

The initiation of the bear study in 2016 was a pilot study. In 2017, we will alter some of our methods to aim to capture more bears in a wider range across the study area, and will now focus almost exclusively on adult females. Captures of bears in 2017 will involve collaboration with outfitters within the study area to access bait sites farther off the main highway. These sites are not accessible by vehicle and therefore we will use a rubber padded snare trap (the RL04, following Lemieux and Czetwertynski 2006).

With the GPS data, we will determine resource selection functions (RSF) for black bears. These RSFs will provide insight to bear habitat use in potential woodland caribou calving grounds. Along with RSFs, we are collecting tissue, blood, and hair samples from bears and their prey for isotope work. We can analyze stable isotopes of carbon and nitrogen found in bears and their prey to determine what black bears are feeding on in our study area following methods as identified for wolves (*Section 5.1.3*).

6.0 LITERATURE CITED

Acton, D. F., G. A. Padbury, and C. T. Stushnoff. 1998. *The Ecoregions of Saskatchewan*. Hignell Printing Ltd., Winnipeg, Manitoba, Canada.

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-Dependent Habitat Selection by Mountain Caribou, Columbia Mountains, British Columbia. The Journal of Wildlife Management 65: 65-77.

Adamczewski, J. Z., C. C. Gates, B. M. Soutar, and R. J. Hudson. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology 66: 1986-1996.

Adamczewski, J. Z., R. J. Hudson, and C. C. Gates. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. Canadian Journal of Zoology 71: 1221-1229.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null Hypothesis Testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64: 912-923.

Barraquand, F., and S. Benhamou. 2008. Animal movement in heterogeneous landscapes: Identifying profitable places and homogeneous movement bouts. Ecology 89: 3336–3348.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat Use by female caribou: trade-offs associated with parturition. Journal of Wildlife Management 65:77-92.

Basille, M., D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2013. Ecologically based definition of seasons clarifies predator-prey interactions. Ecography 36: 220-229.

Begon, M. 1984. *Density and individual fitness: asymmetric competition.* In Evolutionary ecology, Blackwell, pp. 175–194.

Bergerud, A. T. and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as anti-predator tactics. Canadian Journal of Zoology 65: 1597-1606.

Bergerud, A. T., R. Ferguson, and H. E. Butler. 1990. Spring migration and dispersion of Woodland caribou at calving. Animal Behavior 39: 360-368.

Bergerud, A. T., S. N. Luttich, and L. Camps. 2007. *The Return of Caribou to Ungava*. McGill Queen's University Press, Montreal, Quebec, Canada.

Bertram, B. C. R. 1978. Living in groups: predators and prey. In *Behavioural ecology* (ed. J. R. Krebs and N. B. Davies), pp. 59-114. Plenum Publishing Corporation, New York, USA.

Boertje, R. D. 1984. Seasonal diets of the Denali caribou herd, Alaska. Arctic 37: 161-165.

Bonenfant, C., J.-M. Gaillard, F. Klein, and A. Loison. 2002. Sex- and age-dependant effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. Ecography 25: 446-458.

Bonferroni, C. E. 1935. *Il calcolo delle assicurazioni su gruppi di teste*. In Studi in Onore del Professore Salvatore Ortu Carboni. Rome: Italy, pp. 13-60.

Borcard, D., F. Gillet, and P. Legendre. 2011. *Numerical Ecology with R*. Springer New York, New York, USA.

Borger, L., N. Franconi, F. Ferretti, F. Meschi, G. D. Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist 168: 471-485

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14: 268-272.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157: 281-300.boyce

Boyce, M. S. 2006. Scales for resource selection functions. Diversity and Distributions 12: 269-276.

Brodeur, V., Ouellet, J.P., Courtois, R., and Fortin, D. 2008. Habitat selection by black bears in an intensively logged boreal forest. Canadian Journal of Zoology 86: 1307–1316

Brown, G. S., F. F. Mallory, and W. J. Rettie. 2003. Range size and seasonal movement for female woodland caribou in a boreal forest of northeastern Ontario. Rangifer 23: 227-223.

Brown J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7: 999-1014.

Buttigieg, P. L. and A. Ramette. 2014. A guide to statistical analysis in microbial ecology: a community – focused, living review of multivariate data analyses. FEMS Microbiology Ecology 90: 543–550.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516-519.

Calenge, C. 2015. Analysis of Animal Movements in R: the adehabitatLT Package. Available at: https://cran.r-project.org/web/packages/adehabitatLT/vignettes/adehabitatLT.pdf.

Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R.G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 73: 480-486.

Caughley, G. 1997. Sampling in aerial survey. The Journal of Wildlife Management 41: 605-615.

Caughley, G., and A. Gunn. 1996. *Conservation biology in theory and practice* (No. 333.9516 C3). Blackwell Science Publisher, Cambridge, Massachusetts, USA.

Chamberlain, T. C. 1890. The method of multiple working hypotheses. Science 15: 92-96.

Chan-McLeod, A. C. A., R. G. White, and D. F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. *Canadian Journal of Zoology* 72: 938-947.

Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1999. Comparative body composition strategies of breeding and nonbreeding female caribou. Canadian Journal of Zoology 77: 1901-1907.

Cherry, S. 1998. Statistical tests in publications of The Wildlife Society. Wildlife Society Bulletin 26: 947-953.

Ciarniello, L. M., M. S. Boyce, D. C. Heard, and D. R. Seip. 2007. Components of grizzly bear habitat selection: density, habitats, roads, and mortality risk. Journal of Wildlife Management 71: 1446-1457.

Coleman, J. E., D. Tsegaye, K. Flydal, I. M. Rivurd, E. Reimers, and S. Eftestol. 2015. High-voltage power lines near wild reindeer calving areas. European Journal of Wildlife Research 61: 881-893.

Collins, W. B., B. W. Dale, L. G. Adams, D. E. Mcelwain, and K. Joly. 2011. Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska's taiga. Journal of Wildlife Management 75: 269–377.

COSEWIC. 2014. COSEWIC assessment and status report on the Caribou *Rangifer tarandus*, Northern Mountain population, Central Mountain population and Southern Mountain population in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxii + 113 pp.

Coxson, D., and J. Marsh. 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. Canadian Journal of Botany 79: 1449–1464.

Courbin, N., D. Fortin, C. Dussault, and R. Courtois. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. Landscape Ecology 24: 1375-1388.

Courtois, R., C. Dussault, F. Potvin, and G. Daigle. 2002. Habitat Selection by Moose (*Alces alces*) in clear-cut landscapes. Alces 38: 177-192.

Courtois, R., J.P. Ouellet, L. Breton, A. Gingras, and C. Dissault. 2007. Effects of forest disturbance on density, space use and mortality of woodland caribou. Ecoscience 14: 491-498.

Culling, D.E., and D. Cichowski. 2010. Scientific update for the boreal caribou (*Rangifer tarandus caribou*) in British Columbia, 2010. British Columbia Ministry of Environment, Victoria, B.C. 60p.

Curatolo, J. A., and S. M. Murphy. 2002. The effects of pipelines, roads and traffic on the movement of caribou, *Rangifer tarandus*. Canadian Field Naturalist 100: 218-224.

Czetwertynski, S. M., M. S. Boyce, and F. K. Schmiegelow. 2007. Effects of hunting on demographic parameters of American black bears. Ursus 18:1–18.

Dalerum, F., S. Boutin, and J. S. Dunford. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Canadian Journal of Zoology 85: 26–32.

Davies, T. D., M. Tranter, and H. G. Jones (Eds.). 1991. *Seasonal Snowpacks: Processes of Compositional Change*. NATO ASI Series G: Ecological Sciences. Vol.28. 471pp. Springer Verlag, New York, USA.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L.E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22: 1068-1083.

Delong, C., R. M. Annas, and A. C. Stewart. 1991. Chapter 16: Boreal White and Black Spruce Zone in Special Report Series 6, Ecosystems of British Columbia. *Ed*. D. Meidinger and J. Pojar. Published by the Research Branch, Ministry of Forests, Victoria, B.C., Canada.

Dickie, M., R. Serrouya, S. McNay, and S. A. Boutin. 2016. Faster and farther: Wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology doi:10.1111/1365-2664.12732.

Dingle, H., and V. A. Drake. 2007. What is Migration? BioScience 57: 113-121.

Downes, C. M., J. B. Theberge, S. M. Smith. 1986. The influence of insects on the distribution, microhabitat choice, and behavior of the Burwash caribou herd. Canadian Journal of Zoology 64: 622-629.

Dunford, J. S., P. D. McLoughlin, F. Dalerum, and S. Boutin. 2006. Lichen abundance in the peatlands of northern Alberta: implications for boreal caribou. Ecoscience 13: 469–474.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6: 241–252.

Dussault, C., J.-P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11: 321-328.

Dussault, C., J.-P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolioeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28: 1-10.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology 80: 839-845.

Eberhardt, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4: 205-212.

Engen, S., and B.-E. Sæther. 2000. Predicting the time to quasi-extinction for populations far below their carrying capacity. Journal of Theoretical Biology 205: 649-658.

Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Environment Canada, Ottawa.

Environment Canada. 2012. Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal population, in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. xi + 138pp.

Fauchald, P., and T. Tverra. 2003. Using the first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84: 282-288.

Ferguson, S. H., A. T. Bergerud, and R. Ferguson. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia 76: 236-245.

Ferguson, S. H. and P. C. Elkie. (2004), Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). Journal of Zoology 262: 125–134.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75: 580-586.

Festa-Bianchet, M., and J. T. Jorgenson. 1997. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9: 144-150.

Festa-Bianchet, M. J. C. Ray, S. Boutin, S. Cote, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Canadian Journal of Zoology 89:419–434.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity. Philosophical Transactions of the Royal Society B 365: 2233-2244.

Fraser, D. F., and Huntingford, F. A. 1986. Feeding and avoiding predation hazard: the behavioural response of the prey. Ethology 73: 56-68.

Fretwell, S. D. and H. R. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta Biotheoretica 19: 16-36.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131: 781-798.

Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in Northeastern Alberta. The Journal of Wildlife Management 44: 583-602.

Fuller, T. K., and L. B. Keith. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management 45: 197–211.

Gadgil, M., and W. H. Bossert. 1970. Life Historical Consequences of Natural Selection. The American Naturalist 104: 1-24.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamic of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58-63.

Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84: 3294-3306.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B 365: 2255-2265.

Garland Jr., T. 2014. Trade-offs. Current Biology 24: R60-R61.

Gelman, A. and D. B. Rubin. 1992. Inferences from iterative simulation using multiple sequences. Statistical Science 7: 457 -511.

Gelman, A. 2002. *Prior distribution*. In Encyclopedia of Environmetrics 3: 1634-1637. Ed. A.H. El-Shaarawi and W.W. Piegrosch. John Wiley and Sons, Ltd. Chichester, England.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis 1(3): 515-534. doi:10.1214/06-BA117A.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27: 2865-2873.

Gelman, A. and Y-S. Su. 2015. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R Package Version 1.8-6. https://CRAN.R-project.org/package=arm.

Gervasi, V., H. Sand, B. Zimmermann, J. Mattisson, P. Wabakken, and J. D. C. Linnell. 2013. Decomposing risk: landscape structure and wolf behaviour generate different predation patterns in two sympatric ungulates. Ecological Applications 23: 1722 – 1734.

Geweke, J. 1992. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In *Bayesian Statistics 4*. Ed. Bernado, J. M., J. O. Berger, A. P. David, A.F.M. Smith, Clarendon Press, Oxford, UK.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75: 887-898.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006a. Interpreting resource selection at different Scales for woodland caribou in Winter. Journal of Wildlife Management 70: 1601-1614.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006b. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165: 1-32.

Gustine, D. D., and K. L. Parker. 2008. Variation in the seasonal selection of resources by woodland caribou in northern British Columbia. Canadian Journal of Zoology 86: 812-825.

Hadfield, J. D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33: 1-22. URL:http://www.jstatsoft.org/v33/i02/.

Hadfield, J. D. 2015. *MCMCglmm Course Notes*. URL: https://cran.rproject.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf

Hatter, I. W., and W. A. Bergerud. 1991. Moose recruitment, adult mortality, and rate of change. Alces 27:65–73.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90: 3445-3454.

Heidelberger, P. and P. D. Welch. 1983. Simulation run length control in the presence of an initial transient. Operations Research 31: 1109-1144.

Henshaw, J. 1968. The Activities of the Wintering Caribou in Northwestern Alaska in Relation to Weather and Snow Conditions. International Journal of Biometeorology 12: 21-27.

Hernandez, L. and J. W. Laundre. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk (*Cervus elaphus*) and bison (*Bison bison*). Wildlife Biology 11: 215-220.

Hervieux, D., M. Hebblewhite, N. J. DeCesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. Canadian Journal of Zoology 91: 872-882.

Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. Canadian Journal of Zoology 92: 1029–1037.

Hins, C., J. P. Ouellet, C. Dussault, and M. H. St-Laurent. 2009. Habitat Selection by forest dwelling caribou in a managed boreal forest of eastern Canada: Evidence of a landscape configuration effect. Forest Ecology and Management 257: 636-643.

Hornseth, M. L., and R. S. Rempel. 2015. Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across a gradient of anthropogenic disturbance. Canadian Journal of Zoology 94: 79-93.

Hotelling, H. 1933. Analysis of a complex of statistical variables into principal components. Journal of Educational Psychology 24: 417-441 and 498-520.

Houston, A. E., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society of London B 341: 375-397.

Jacqmain, H., C. Dussault, R. Courtois, and L. Belanger. 2008. Moose-habitat relationships: integrating Cree native knowledge and scientific findings in northern Quebec. Canadian Journal of Forest Research 38: 3120-3132.

James, A. R. C. and A. K. Stuart-Smith. 2000. Distribution of Caribou and Wolves in Relation to Linear Corridors. The Journal of Wildlife Management 64: 154-159.

James, A. R. C., S. Boutin, D. M. Herbert, and B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

Johnson, H.E., M. Hebblewhite, T.R. Stephenson, D.W. German, and B.M. Pierce. 2012. Apparent competition limits the recovery of an endangered ungulate: quantifying the direct and indirect effects of predation. Oecologia 171: 295–307.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia 127: 590-602.

Johnson, C. J., Alexander, N. D., Wheate, R. D., and Parker, K. L. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. *Forest Ecology and Management*: 180: 241-248.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004a. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41: 238-251.

Johnson, C. J., K. L. Parker, D. C. Heard, and D. R Seip. 2004b. Movements, foraging habits, and habitat use strategies of northern woodland caribou during the winter: Implications for forest practices in British Columbia. BC Journal of Ecosystems and Management 5: 22-35.

Jones, E. S., M. P. Gillingham, D. R. Seip, and D. C. Heard. 2006. Comparison of seasonal habitat selection between woodland caribou ecotypes in central British Columbia. Rangifer 17: 111-128.

Joro Consultants Inc. 2012. Bipole III transmission line caribou technical report with supplemental update. Unpublished reports (2011 and 2012) to Manitoba Hydro, Winnipeg, MB. 222 + 153 pp.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist 142: 59-81.

Kansas, J., J. Vargas, H. G. Skatter, B. Balicki, and K. McCullum. 2016. Using landsat imagery to backcast fire and post-fire residuals in the Boreal Shield of Saskatchewan: implications for woodland caribou management. International Journal of Wildland Fire 25: 597-607.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American statistical association 53: 457-481.

Kinley, T. A., J. Bergenske, J.-A. Davies, and D. Quinn. 2003. Characteristics of Early-Winter Caribou, *Rangifer tarandus caribou*, Feeding Sites in the Southern Purell Mountains, British Columbia. Canadian Field-Naturalist 117: 352-359.

Kruskal, W. H., and A. Wallis. 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47: 583–621.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrik 29: 115-129.

Kuzyk, G. W. 2002. *Wolf Distribution and Movements on Caribou Ranges in West-Central Alberta*. Thesis, University of Alberta, Edmonton, Alberta, Canada.

Kuzyk, G. W., J. Kneteman, and F. K. A. Schmiegelow. 2006. Pack size of wolves, *Canis lupus*, on caribou, *Rangifer tarandus*, winter ranges in west central Alberta. Canadian Field-Naturalist 120: 313–318.

Latham, A. D. M. 2009. *Wolf Ecology and Caribou-Primary Prey–Wolf Spatial Relationships in Low Productivity Peatland Complexes in Northeastern Alberta.* Thesis, University of Alberta, Edmonton, Alberta, Canada.

Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011a. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. Canadian Journal of Zoology 89: 267-277.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011b. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications 21: 2854–2865.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011c. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. Journal of Wildlife Management 75: 204–212.

Lavielle, M. 1999. Detection of multiple changes in a sequence of dependent variables. Stochastic Processes and their Applications 83: 79–102.

Lavielle, M. 2005. *Using penalized contrasts for the change-point problem.* Report number 5339, Institut national de recherche en informatique et en automatique.

Lavigueur, L. and C. Barrette. 1992. Suckling, weaning, and growth in captive woodland caribou. Canadian Journal of Zoology 70: 1753-1766.

Law, A. M., and W. D. Kelton. 1991. Simulation Modeling and Analysis. Third Edition, McGraw-Hill, New York.

Leblond, M., J. Frair, D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landscape Ecology 26: 1433-1446.

Leblond, M., C. Dussault, J.-P. Ouellet, M.-H. St-Laurent. 2016. Caribou avoiding wolves face increased predation by bears – Caught between Scylla and Charybodis. Journal of Applied Ecology 53: 1078-1087.

Legendre, P. and L. Legendre. 1998. *Numerical Ecology, Developments in Environmental Modelling, 2nd English Ed*. Elsevier Science B.V., Amsterdam.

Lemieux, R., and S. Czetwertynski. 2006. Tube traps and rubber padded snares for capturing American black bears. Ursus 17: 81-91.

Lendrum, P. E., C. R. Anderson Jr., R. A. Long, J. G. Kie, and R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere 3: 1-19.

Lesmerises, F., C. Dussault, and M.H. St-Laurent. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. Forest Ecology and Management 276: 125-131.

Li, B., H. F. Lingsma, E. W. Steyerberg, and E. Lesaffre. 2011. Logistic random effects regression models: a comparison of statistical packages for binary and ordinal outcomes. BMC Medical Research Methodology 11: 77. doi: 10.1186/1471-2288-11-77.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131-135.

Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. Journal of Theoretical Biology 125: 351-360.

Mahoney, S. P., K. P. Lewis, J. N. Weir, S. F. Morrison, J. G. Luther, J. A. Schaefer, D. Pouliot, and R. Latifovic. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. Population Ecology 58: 91–103.

Manly, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Second Edition, Chapman & Hall, London.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

Maren, I. E., S. Karki, C. Prajapati, R. K. Yadav, and B. B. Shrestha. 2015. Facing north or south: does slope aspect impact forest stand characterisitics and soil properties in a semiarid trans Himalayan valley? Journal of Arid Environments 121: 112-113.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat Selection at Multiple Scales. Ecoscience 16: 238-247.

Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic 41: 279-287.

Metsaranta, J. M., and F. F. Mallory. 2007. Ecology and habitat Selection of a woodland caribou population in West-Central Manitoba, Canada. Northeastern Naturalist 14: 571-588.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13: 603-606.

McLaughlan, M. S., R. A. Wright, and R. D. Jiricka. 2010. Field Guide to the ecosites of

Saskatchewan's provincial forests. Saskatchewan Ministry of Environment, Forest Service, Prince Albert, Saskatchewan. 343pp.

McLoughlin, P. D., and Ferguson, S.H. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7: 123-130.

McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management 67: 755-761.

Mcloughlin, P.D., J.S. Dunford, and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74: 701-707.

McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society of London Series B 237: 1449-1454.

McLoughlin, P. D., L. Debeffe, and A. Arsenault. 2016. A review of our direct and indirect effects on woodland caribou: implications and recommendations for conservation. Wildlife Monographs (*in review*).

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.

Mohr, C. O. 1974. Table of equivalent populations of North American small mammals. The American Midland Naturalist 37: 223-249.

Morschel, F. M., and D. R. Klein. 1997. Effects of weather and parasitic insects on behaviour and group dynamics of caribou of the Delta Herd, Alaska. Canadian Journal of Zoology 75: 1659-1670.

Mueller, T., K. A. Olson, G. Dressler, P. Leimgruber, T. K. Fuller, C. Nicolson, A. J. Novaro, M. J. Bolgeri, D. Wattles, S. DeStefano, J. M. Calabrese, and W. F. Fagan. 2011. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography 20: 683 - 694.

Musiani, M., J.A. Leonard, H. Cluff, C.C. Gates, S. Mariani, P.C. Paquet, C. Vilà, and R.K. Wayne. 2007. Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. Molecular Ecology 16: 4149-4170.

Oberg, P. R. 2001. *Response of Mountain Caribou to Linear Features In a West-central Alberta Landscape*. Thesis, University of Alberta, Edmonton, Canada.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, and H. Wagner. 2016. Vegan: Community Ecology Package. R package version 2.4.0. https://CRAN.R project/package=vegan.

Pacas, C. J., and P. C. Paquet. 1994. Analysis of black bear home range using a Geographic Information System. Int. Conf. Bear Res. Manage. 9: 419–425.

Panzacchi, M., B. Van Moorter, and O. Strand. 2013. A road in the middle of one of the last wild reindeer migration routes in Norway: crossing behaviour and threats to conservation. Rangifer 33:15–26.

Parisien, M.-A., K. G. Hirsch, S. G. Lavoie, J. B. Todd, and V. G. Kafka. 2004. Saskatchewan fire regime analysis. Inf. Rep. NOR-X-394, Natural Resources Canada, Canada Forest Service, Northern Forestry Centre, Edmonton, AB.

Parker, K. L., and B. Milakovic. 2007. *Defining the predator landscape in the Besa-Prophet*. Part 3 of Project "An Ecosystem Approach to Habitat Capability Modelling and Cumulative Effects Management". Report prepared for the Muskwa-Kechika Advisory Board.

Parker, K. L., P. S. Barboza, P. S., and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57-69.

Pinard, V., C. Dussault, J. P. Ouellet, D. Fortin, and R. Courtois. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. The Journal of Wildlife Management 76: 189-199.

Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News*, 6: 7-11.

Polfus, J. L., M. Hebblewhite, and K. Heinemeyer. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain caribou. Biological Conservation 144: 2637-2646.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. The Journal of Wildlife Management 53: 7-15.

Poole, K. G., D. C. Heard, and G. Mowat. 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. Canadian Journal of Zoology 78: 1552-1561.

Powell, R. A., and M. S. Mitchell. 2012. What is a home range? Journal of Mammology 93: 948-958.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reimers, E. 1983. Growth Rate and Body Size Differences in Rangifer, a Study of Causes and Effects. Rangifer 3: 3-15.

Rettie, W. J., J. W. Sheard, and F. Messier. 1997. Identification and description of forested vegetation communities available to woodland caribou: relating wildlife habitat to forest cover data. Forest Ecology and Management 93: 245-260.

Rettie, W. J, and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology 76: 251-259.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466-478.

Rettie, W. J., and F. Messier. 2001. Range use and movement rates of woodland caribou in Saskatchewan. Canadian Journal of Zoology 79: 1933-1940.

Robinson, H.S., M. Hebblewhite, N.J. DeCesare, J. Whittington, L. Neufeld, L., M. Bradley, and M. Musiani. 2012. The effect of fire on spatial separation between wolves and caribou. Rangifer: 20: 277–294.

Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York, USA.

Roff, D. A. 2001. *Age and Size at Maturity*. In Evolutionary Ecology: Concepts and Case Studies. Ed. C. W. Fox, D. A. Roff, and D. J. Fairbairn. Oxford University Press, New York, USA.

Rohlf, F. J. 1963. Classification of *Aedes* by numerical taxonomic methods (Diptera: Culicidae). Annals of the Entomological Society of America 56: 798-804.

Rominger, E. M., and J. L. Oldemeyer. 1990. Early-winter diet of woodland caribou in relation to snow accumulation, Selkirk Mountains, British Columbia, Canada. Canadian Journal of Zoology 68: 2691-2694.

Rominger, E. M., C. T. Robbins, and M. Evans. 1996. Winter foraging ecology of woodland caribou in northeastern Washington. Journal of Wildlife Management 60: 719-728.

Rudolph, T. D., P. Drapeau, M.-H. St-Laurent, and L. Imbeau. 2012. *Status of Woodland Caribou (Rangifer tarandus caribou) in the James Bay Region of Quebec*. Scientific report presented to the Ministère des Resources naturelles et de la Faune du Québec and the Grand Council of the Crees (Eeyou Istchee). Montreal, QC. 72pp.

Rudolph, T. D., and P. Drapeau. 2012. Using movement behaviour to define biological seasons for woodland caribou. Rangifer 32: 295 – 307.

Rupp, T. S., M. Olson, L. G. Adams, B. W. Dale, K. Joly, J. Henkelman, W. B. Collins, and A. M. Starfield. 2006. Simulating the influences of various fire regimes on caribou winter habitat. Ecological Applications 16: 1730–1743.

Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993. range ecology of the porcupine caribou herd in Canada. Rangifer Special Issue No. 8. 170pp.

Saher, D. J., and F. K. A. Schmiegelow. 2005. Movement pathways and habitat selection by woodland caribou during spring migration. Rangifer, Special Issue No. 16: 143-154.

Secoy, D. 2006. *Ecozones and Ecoregions*. In The Encyclopedia of Saskatchewan, Canadian Plains Research Center, University of Regina. URL: http://esask.uregina.ca/entry/ecozones_and_ecoregions.html

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494-1503.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using predator-prey theory to predict outcomes of broadscale experiments to reduce apparent competition. American Naturalist 185:665–679.

Shepard, R. N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. Psychometrika, 27: 125-139.

Shipley, L. A. 2010. Fifty Years of Food and Foraging in Moose: Lessons in Ecology from a Model Herbivore. Alces 46: 1-13.

Sneath, P. H. A., and R.R. Sokal. 1973. *Numerical taxonomy – The principles and practice of numerical classification.* W. H. Freeman, San Francisco, USA.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3: 259–268.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, London, England. xii+ 249 pp.

Stoen, O.-G., W. Neumann, G. Ericsson, J. E. Swenson, H. Dettki, J. Kindberg, and C. Nellemann. 2010. Behavioural response of moose *Alces alces* and brown bears *Ursus arctos* to direct helicopter approach by researchers. Wildlife Biology 16: 292-300.

Taylor, M. K., S. Akeeagok, D. Andriashek, W. Barbour, E. W. Born, W. Calvert, H. D. Cluff, S. Ferguson, J. Laake, A. Rosing-Asvid, I. Stirling, and F. Messier. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis movements. Canadian Journal of Zoology 79: 690-709.

Taylor, M. K., J. Laake, H. D. Cluff, M. Ramsay, and F. Messier. 2002. Managing the risk from hunting for the viscount Melville sound poplar bear population. Ursus 13: 185-202.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptations of some large North American mammals for survival in snow. Ecology 65: 1828-1834.

Thomas, D. C., J. E. Edmonds, and W. K. Brown. 1994. The diet of woodland caribou populations in west-central Alberta. Rangifer, Special Issue No. 9: 337-342.

Thomas, D. C., and D. R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada, in COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-98 pp.

Thompson, I. D., P. A. Wiebe, E. Mallon, A. R. Rodgers, J. M. Fryxell, J. A. Baker, and D. Reid. 2015. Factors influencing the seasonal diet selection by woodland caribou in (*Rangifer tarandus tarandus*) in boreal forests in Ontario. Canadian Journal of Zoology 93: 87-98.

Timmerman, H. R., and J. G. McNicol. 1988. Moose Habitat Needs. The Forestry Chronicle 64: 2238-245.

Van Beest, F. M., E. Vander Wal, A.V. Stronen, and R. K. Brook. 2013. Factors driving the variation in movement rate and seasonality of sympatric ungulates. Journal of Mammalogy 94: 691-701.

Van Beest, F. M., P. D. McLoughlin, E. Vander Wal, and R. K. Brook. 2014. Density-dependent habitat selection and partitioning between two sympatric ungulates. Oecologia 175: 1155-1165.

Vander Wal, E., and A. R. Rodgers. 2009. Designating Seasonality Using Rate of Movement. Journal of Wildlife Management 73: 1189-1196.

Waugh, D. 2002. *Geography: An Integrated Approach, 3rd Edition*. Nelson Thornes publishing, Cheltenham, United Kingdom.

Weir, J. N., S. F. Morrison, J. G. Luther. And S. P. Mahoney. 2014. *Caribou Data Synthesis. Progress Report #2. Status of the Newfoundland population of woodland caribou*. Technical Bulletin No. 008, Sustainable Development and Strategic Science, Government of Newfoundland and Labrador, St. John's, Canada.

White, G. C. 2000. *Population viability analysis: data requirements and essential analyses.* In Research Techniques in Animal Ecology, Columbia University Press, New York, USA.

Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144: 257-267.

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Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation strategies for species affected by apparent competition. Conservation Biology 27: 254-260.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J.W., and Musiani, M. 2011. Caribou encounters with wolves increases near roads and trails: a time-to-event approach. Journal of Applied Ecology 8, 48: 1535–1542.

Wood, S. and Scheipl, F. 2014. gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-3. https://CRAN.R-project.org/package=gamm4

Zuk, M., and A. M. Stoehr. 2002. Immune defense and host life history. The American Naturalist 160: S9-S22.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. *Analyzing Ecological Data*. Springer Science + Business Media LLC, 223 Spring Street, New York, NY, 10013, USA.

Zurr, A. F., E. N. Leno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3-14.

7.0 ACKNOWLEDGEMENTS

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