Mortality sources and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia

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EXECUTIVE SUMMARY

The coexistence of moose and caribou is a recent event in central and southern British Columbia after a significant natural range expansion of moose in the 1900's. The recent decline of caribou populations are linked to the expansion of moose and the subsequent increase of wolves throughout their range. To reduce the threat of predation, woodland caribou attempt to isolate themselves from predators and other more abundant prey species. This study examined the mortality sources and spatial relationships between mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia between 2003 and 2006. Using Latent Selection Functions (LSD), we quantitatively compared the habitat selection of caribou, moose, and wolves using habitat, terrain, and human-use variables. These types of detailed spatial and temporal analysis can be used as effective tools to better focus mountain caribou recovery efforts, forest harvest planning and wildlife management decisions in the Columbia basin. Our specific objectives were to: (1) to identify mortality factors affecting adult caribou, (2) determine if spatial separation was occurring between moose, caribou, and wolves, (3) explore how this relationship changed between seasons, and (4) identify what terrain, habitat, and human-use factors were important in separating these species.

The study area (~9,000 km^2) was located in the Northern Columbia Mountain ecoregion in southeastern British Columbia (51°N 118°W). Rugged, mountainous terrain (550 m to 3,050 m) and high precipitation levels (946 mm/yr, 425 cm falling as snow) characterize the area.

Predation accounted for 40% and 68% of all adult collared-caribou deaths before and after 2000, respectively. The main predator of adult mountain caribou, before and after 2000, were bears (grizzly and black), with wolf predation increasing in importance after 2000.

Caribou, wolves and moose experienced different levels of spatial separation and this varied by season. The highest degree of spatial separation between caribou and wolves occurred in the late winter, with old forests (>140 yrs), low-use roads (0 – 100 m), and alpine being important factors contributing to their separation. The calving season had the lowest spatial separation between caribou and wolves, but caribou still used more rugged terrain and alpine areas while using areas between 0 - 100 m from low-use roads less than wolves. Moose and caribou varied in their usage of alpine areas, distances > 2000 m and 100 – 500 m of low-use roads resulting in high spatial separation in the spring. The lowest degree of spatial separation between caribou and moose occurred in the early winter where alpine, and distance to low-use road categories were weak factors contributing to their separation. Moose used areas between 0 – 500 m from a cutblock differently than wolves in the early winter, resulting in a high level of spatial separation. Moose had little spatial separation from wolves during the rest of the year especially summer. The distance to road variable may be a surrogate for elevation in some seasons when caribou are at higher elevations and not within proximity to interact with low-use roads and trails (late winter, summer). Overall, the selection of older forests (101 – 680 yrs), Engelmann spruce and subalpine fir forests, alpine areas, and

avoidance of areas 0 – 100 m from low-use roads by caribou relative to wolves were consistently important variables that separated these species across all seasons. The antipredator strategy of caribou to "space-away" from predators and alternate prey may be insufficient to reduce predation during spring and calving seasons.

With moose populations doubling in the past 10 years, and caribou subpopulations declining since 1997, it is possible that the reduction in spatial separation from predators and alternate prey, as well as degradation of spatial refuges are contributing to caribou population declines. Survival of mountain caribou in the north Columbia Mountains may be dependent on the integrity of spatial and temporal refuges and the connectivity between these refuges. Any management or recovery scenarios should focus on maintaining important variables contributing to spatial separation and in seasons when the probability of overlap between these three species is most likely to occur.

Keywords: *Alces alces, Canis lupus*, caribou, Columbia Mountains, Latent Selection Difference (LSD), moose, *Rangifer tarandus caribou*, spatial separation, wolves.

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INTRODUCTION

In North America, moose (*Alces alces*) and woodland caribou (*Rangifer tarandus caribou*) are sympatric over most of their current range (Boer 1998). The coexistence of moose and caribou is a relatively recent event in central and southern British Columbia (B.C.), although historical records cite scattered moose populations in the Southern Interior Mountains (Spalding 1989). Expansion and population increases of moose occurred subsequent to a significant natural range expansion in the 1900's, when human alteration of habitat, and climatic warming, created favorable conditions for expansion (Kelsall and Telfer 1974; Tefler 1984; Spalding 1989; Karns 1998). Common predators of woodland caribou and moose are wolves (*Canis lupus*), grizzly bears (*Ursus arctos),* black bears (*Ursus americanus*) and cougars (*Felis concolor*; e.g. Bergerud et al. 1984; Seip 1992; Flaa and McLellan 2000; Kinley and Apps 2001; James et al. 2004; Wittmer et al. 2005). Recent declines of woodland caribou populations (e.g. northern B.C., Bergerud and Elliot 1986) are linked to the expansion of moose and the subsequent increase of wolves and associated predation throughout their range. To reduce predation, woodland caribou isolate themselves from predators and other more abundant prey species (Bergerud 1983; Bergerud and Page 1987; Seip 1992; McLoughlin et al. 2005). Bergerud et al. (1984) suggest that the dispersion tactic adopted by woodland caribou is no longer sufficient to reduce predation because recent predator increases have increased the number of predators searching per unit area resulting in higher mortality rates of caribou. Researchers also suggest that loss of mature forests (Wittmer et al. 2005) and fragmentation of caribou winter range (Smith et al. 2000) may also be compromising the 'spacing away' antipredator strategy used by caribou.

Interactions of animals in time and space are common themes in ecological studies (Sih 2005). Animals can respond to each other randomly, with attraction, or with avoidance, and these responses can be spatial, temporal, or a mixture of the two (Minta 1992). Predator-prey interactions are an example of both avoidance and attraction. Prey avoid predators while maximizing their energy intake (Lima and Dill 1990; Lima 1998; Sih 1992) while predators are attracted to prey . Predator avoidance can lead to reduced energy intake and have long-term effects on an animal's fitness (Lima 1998). Both immediate and long-term effects of predation may be reflected in an animal's use of space (e.g., choice of habitats; Lima 1998).

The theory of optimal foraging predicts that individuals should maximize their net rate of energy intake subject to various constraints that result in the greatest fitness for the animal (Pyke et al. 1977; Krebs and Davies 1993; Caughley and Sinclair 1994). When both predators and prey are present, prey should avoid areas used by predators while ensuring adequate forage, and predators should concentrate their activity where prey are most dense (Lima 2002). Furthermore, if predators can select from more than one prey species, then the most profitable species should be selected based on the amount of energy gained, the time and effort used in the search and handling of that prey item, and any risk (Royama 1970; Krebs and Davies 1993).

Prey can adopt antipredator strategies to reduce predation risk (Sih 1987; Mech and Peterson 2003). Antipredator strategies may include physical traits, behaviour, and landscape use (Sih 1987; Mech and Peterson 2003). For example, if a predator is less successful in a specific habitat type, then prey may select this habitat to reduce risk (Sih 2005). The use of refuges can have a stabilizing effect on predator-prey interactions (Rosenzweig and MacAurthur 1963). Differential use of space can cause a negative correlation between the spatial distributions of predators and prey (Sih 1984; Sih 2005). Therefore, the absence of prey from certain habitat types may reflect the effect of predators on the broad-scale habitat use patterns of prey (Lima 1998). The degree of spatial separation between predator and prey may be reflected in the associated level of predation experienced by the prey species. Caribou-moose-wolf systems present an opportunity to examine such patterns.

In mountainous areas, mountain caribou show distinct seasonal elevation shifts to take advantage of food availability, and/or avoid predation (Bergerud et al. 1984; Seip 1992; Apps et al. 2001), creating seasonal variation in the pattern of spatial separation between moose, and wolves. For instance, mountain caribou (obligate arboreal lichen-feeding ecotype of woodland caribou) in the extremely high-snowfall regions of southeastern B.C, prefer old western red cedar (*Thuja plicata)*, and western hemlock (*Tsuga heterophylla*) forests at lower elevations in early winter (Apps et al. 2001). In late winter, when snow is deep and consolidated enough to access to arboreal hair lichen in the canopy of standing trees, they move to forests at higher elevations dominated by subalpine fir (*Abies lasiocarpa*; Simpson et al. 1987; Apps et al. 2001). In spring, they descend to low elevation cedar and hemlock forests and in summer shift to higher elevations of old Englemann spruce (*Picea Engelmannii*) and subalpine fir forests to access forbs and deciduous vegetation (Simpson et al. 1987; Rominger et al. 2000; Apps et al. 2001).

Seasonal habitat preferences of moose differ from those of mountain caribou. Moose living in mountainous areas in North America, select open, upland (stream valley shrub, alluvial) and aquatic habitats in the spring (Tefler 1984; Peek 1998). These habitats provide high quality abundant forage and protection against heat (Peek 1998). In summer and fall, moose migrate to higher elevations to subalpine forests, and shrublands above the timberline to take advantage of wet meadow complexes (Tefler 1984). In the early winter, moose move to open areas with high biomass of low shrubs (Peek 1998; Tefler 1984). In western interior montane forests of B.C., moose move downhill in the late winter to gentler slopes with higher solar insolation to take advantage of high forage habitats and lower snow depths (Poole and Stuart-Smith 2006). Moose avoid alpine areas in all seasons (Boer 1998).

Wolf resource use at the landscape scale may be best predicted by prey availability and road abundance (e.g. Minnesota, Mladenoff et al. 1995), but features like snow depth and elevation are also important predictors in mountainous regions (e.g. Minnesota, Fuller 1991).

This study examines adult caribou mortality sources and the spatial relationships between mountain caribou, moose, and wolves in the north Columbia Mountains, B.C., between 2003 and 2006. Wolves are major predators of adult mountain caribou in northern (Bergerud et al. 1984), and central B.C. (Seip 1992), shifting to cougar the southeast (Kinley and Apps 2001). Considering these geographical shifts in mortality, the role of wolf predation in the decline of mountain caribou in the north Columbia Mountains was of primary concern. Previous studies in various regions have described patterns of resource selection between moose, caribou, and wolves, but have not quantified the strength of these differences (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1992; Cumming et al. 1996; James et al. 2004; Neufeld 2006). We quantify habitat selection of caribou, moose, and wolves as well as identify caribou mortality factors in order to provide critical information for caribou recovery strategies and landscape management in caribou habitat. This information is also important to determine the role of wolves in structuring habitat use patterns of caribou, and the effectiveness of caribou antipredator tactics at reducing wolf predation. Our specific objectives were to: (1) to identify mortality factors affecting adult caribou, (2) determine if spatial separation was occurring between moose, caribou, and wolves, (3) explore how this relationship changes between seasons, and (4) identify what terrain, habitat, and human-use factors were important in separating these species.

STUDY AREA

The study area (~9,000 km^2) was located in the Northern Columbia Mountain ecoregion in southeastern B.C. (51°N 118°W; Figure 1; Demarchi 1996). Rugged, mountainous terrain (550 m to 3,050 m) and high precipitation levels (946 mm/yr, 425 cm falling as snow) characterize the area. The landscape was a mosaic of forests, regenerating clear-cuts, riparian area, shrublands, upper elevation basins, and avalanche chutes. Biogeoclimatic subzones range from Interior Cedar-Hemlock (ICH) in the valley bottoms and mid-elevations, to Engelmann Spruce-Subalpine Fir (ESSF) at approximately 1,280 m to 1,400 m (Braumandl and Curran 1992). The Alpine Tundra subzone occurs at elevations above the ESSF.

Western red cedar, and western hemlock dominate the ICH subzones whereas Douglas-fir (*Pseudotsuga menziesii*) is less common (Braumandl and Curran 1992). The ESSF zone comprises coniferous forests of primarily Englemann Spruce and subalpine fir (Braumandl and Curran 1992). Alpine meadows, shrublands, snowfields, glaciers and rock dominate the Alpine Tundra zone. Two hydroelectric developments in 1973 and 1984 flooded most of the low elevation riparian habitat and significantly altered the study area (BC Hydro 2007). Forest harvesting and silviculture, hunting, trapping, snowmobiling and heliskiing were the major human-use activities in the region during the research period.

Moose was the most abundant and widespread ungulate in the region, however low densities of mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) occurred in the southern portion of the study area (Poole and Serrouya 2003). Mountain goats (*Oreamnos americanus*) also inhabited the more mountainous portions of the study area. Mountain caribou existed at low densities and were delineated into four

subpopulations (Figure 1; Columbia North, Columbia South, Frisby/Queest and Central Rockies; Wittmer et al. 2005). Grizzly bears, black bears, wolverine (*Gulo gulo*), wolves, and cougars occurred throughout the area. Information on predator densities was not available at the time of this study.

In 2000, mountain caribou subpopulations within the study area were Red Listed in British Columbia (Conservation Data Centre; Mountain Caribou Technical Advisory Committee 2002) and nationally listed as Threatened in 2002 (Committee on the Status of Endangered Wildlife in Canada). Since 1997, these subpopulations experienced an annual decline of 10% after a relatively stable period between 1994 to 1997 (McLellan et al. 2006). Current caribou densities within the four subpopulations range from 0.035 – 0.05 caribou km^{-2} (Wittmer et al. 2005). In contrast, moose densities in the region doubled in the past decade from 0.7 moose km^{-2} to 1.54 moose km^{-2} (Poole and Serrouya 2003). This increase coincided with increases in the proportion of younger forests resulting from regeneration subsequent to forest harvesting. Large-scale forestry began in the 1960's, focused on harvesting of older age forests. Overlap between mountain caribou habitat, timber interests and extensive road networks occurred.

METHODS

Animal captures

Wolves, moose, and mountain caribou were captured from 2001 to 2006 by net-gunning from a helicopter (Bighorn Helicopters Inc., Cranbrook, B.C). We equipped animals with Global Positioning System (GPS) or Very High Frequency (VHF) radio-collars (Advanced Telemetry Systems, Insanti, Minnesota, USA; Lotek Inc.,Newmarket, Ontario, Canada; Telonics, Inc., Mesa, Arizona, USA; HABIT, Victoria, B.C., Canada; University of Alberta Protocol 2004-09D, 2005-19D and Parks Canada). Fourteen wolves from four packs (March 2004 and 2005) were captured and equipped with six GPS (Lotek GPS_3300s; HABIT) and eight VHF (Lotek LMRT_3) radio-collars. Twenty-six moose were captured in March 2004 and 2005 and affixed with 13 GPS and 13 VHF radio-collars. Thirty-seven mountain caribou were collared from March 2001 – March 2006 and affixed with 10 GPS and 27 VHF collars. Only data from 2003 – 2005 were used from these caribou. The GPS fix schedules were species specific (wolves every four hours, moose every five hours, mountain caribou every two - six hours).

Adult caribou mortality

All radio-collared animals were located bi-weekly from a fixed-wing aircraft and monitored for mortalities. Sensors in the radio-collars also registered mortalities by altering their beacon frequency when a collar was immobile for more than six hours. Field crews investigated an animal mortality by ground as soon as possible to determine the cause of death. The cause of death was identified as a predation event if there was blood, subcutaneous hemorrhaging at wound sites, or signs of a struggle (Kunkel et al. 1999). The species of predator was identified based on carcass use, scat, tracks and hair around the kill site.

To increase samples sizes, we used additional caribou mortality data from a long-term study (1992 – 2006) in the same study area. This data, prepared by the Revelstoke Mountain Caribou Research Project (Revelstoke, B.C.), was divided into pre 2000 and post 2000 to reflect changing predator-prey dynamics over the 14 year time period. The year 2000 was selected as the separating point between time periods, because moose populations were increasing at the greatest rate during this year, peaking in 2003 (Serrouya, pers. comm.). The data was corrected for sampling effort by dividing the raw number of deaths attributed to each mortality factor, by the number of "caribou years". A "caribou year" is the sum of the number of caribou monitored multiplied by the number of years each caribou was monitored (until the collar fell off, battery died, or animal died).

Modeling strategy

Variable selection
We selected terrain, habitat, and human-use variables to quantify the difference in habitat selection between moose, caribou, and wolves. Dummy coding was used for all categorical variables in the analysis (Stata Corp. 2006).

We extracted terrain variables such as elevation, slope, aspect, and terrain ruggedness index (TRI) from 1:50,000 digital elevation maps (DEM) and classified aspect as a binomial categorical variable (south or north). North aspect was coded as the reference category. We used equations modified from Nellemann and Cameron (1996) and the relative richness index of Turner (1989) to calculate a terrain ruggedness index. This calculation used slope and aspect data derived from a 30 m DEM according to the following formula:

equ 1

TRI = (aspect variation x average slope) / (aspect variation + average slope)
                                              100

where aspect variation measures the number of aspect classes in a 300 m moving circular window over the maximum number of aspect classes in the study area.

We derived habitat variables that included landcover (5 classes), forest age (4 classes), and crown closure from the British Columbia Ministry of Forests (MOF) inventory database at a 30 m x 30 m resolution (Table 1). Reference categories were designated as cedar/hemlock for landcover and 41-100 yrs for forest age. We used a courser resolution (300 m x 300 m) for habitat variables on private land because finer resolution information was not available.

We represented human-use variables as distance to cutblock and distance to low-use road (gravel, trail, powerline; e.g. Whittington et al. 2005). Distance to high-use paved roads was not included in the analysis because it was highly correlated to other variables. We split distance to cutblock into four distance categories (reference category = 501-2000 m; Table 1.). We acquired road and cutblock information from forest

licensees in the study area (Revelstoke Community Forest Corporation, Downie Street Sawmills Ltd.) and coverages from the National Topographic Data Base (Geomatics Canada). For areas without digital forest coverage (private land), We digitized cutblocks from ortho-photos and merged them to create a seamless map of cutblocks. We used four categories to evaluate the effect of roads on animal resource selection (reference category = 501-2000 m; Table 1; e.g. James and Stuart-Smith 2000; Oberg 2001; Dyer et al. 2002; Whittington et al. 2005). We used ARCMAP 9.1 (Environmental Systems Research Institute, Redlands, CA, USA) and Hawth's Analysis Tools Version 3.21. for all GIS analyses.

GPS bias model

We resampled the GIS layers at a 100 m x 100 m pixel size to account for average location error of GPS and VHF location data. We selected a 100 m pixel size because previous research in mountainous terrain estimates that 95% of location error is <113 m for GPS collars and < 200 m for VHF collars (Hebblewhite 2006). We corrected for fix-rate bias using methods developed by Frair et al. (2004) and D'Eon et al. (2002). We corrected for Type II errors and bias in LSD coefficients as per D'Eon et al. (2002) and used the inverse of the probability of fix to weight each animal location and adjust the frequency of occurrence (Frair et al. 2004).

Comparing resource selection

We used a Latent Selection Difference Function (LSD; Lele et al. Manuscript in Progress) to directly compare the resource selection of caribou and wolves, caribou and moose, and moose and wolves over five seasons. We assumed that resources were equally available to all species and applied this method to quantitatively compare groups at the landscape scale (Lele et al. Manuscript in Progress). We used logistic regression to estimate coefficients (Lele et al. Manuscript in Progress; Manly 1993); for example, coding caribou locations as (1) and wolf locations as (0), thereby eliminating the use of availability in the equation. The selection of what habitats are available to an animal can significantly affect the analysis in use-availability designs, and may result in misleading conclusions affected by sampling protocol (Keating and Cherry 2004) and the scale of investigation (Johnson 1980). This method allows for direct comparisons of habitat selection and results in meaningful measurements of strength of relationships. The relationship has the following log-linear form:

eqn 2

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_i x_i)$$

where w(x) represents the resource selection of one species compared to another and β_i are the coefficients estimated for environmental predictors x_i (Manly 1993).

Variable reduction was achieved by subjecting the full set of variables to a number of criteria to establish the final model set. Variables had to satisfy the following criteria: biologically relevant, ecologically plausible, uncorrelated, significant in univariate modeling (Graf et al. 2005), consistent algebraic sign in both univariate and multivariate models, satisfy the assumptions of logistic regression (Hosmer and Lemeshow 2000) and have the ability to be manipulated by management. If two

variables were correlated ($r > |0.7|$; Tabachnick and Fidell 1996), We retained the variable with the lowest log-likelihood value and the smallest p-value (Boyce et al. 2002). We omitted variables with low predictive power in univariate models (Walds Chi^2, $p > 0.25$), and used Box Tidwell regression models to detect nonlinearity in the logit. We removed elevation as a variable in the analysis because, although highly predictive, it was correlated with other variables that were more amenable to manipulation by resource managers. Because of nonlinearity, we categorized the variables forest age, distance to cutblock, and distance to low-use road. Due to the exploratory nature of this analysis, we used a stepwise regression algorithm to select variables, with cut-off values of 0.05 (P enter) and 0.10 (P remove; Montgomery and Peck 2001). We used the robust cluster option and the Huber/White/sandwich estimator of variance (Stata Corp 2003) in the logistic regression model to account for bias and temporal autocorrelation (Boyce et al. 2002; Thomas and Taylor 2006). We validated the models using *k*-fold cross-validation procedures (Fielding and Bell 1997). A Spearman's-rank correlation (rho) of > 0.64 is significant and indicates that the model has good predictive ability (Boyce et al. 2002).

Model interpretation

The model results represent the resource selection of the species coded as 1 compared to the resource selection of the species coded as 0 (Lele et al. Manuscript in Progress). For example, in the caribou and wolf comparison, the resource selection of caribou was always compared to wolf resource selection. The sign and magnitude of the β coefficients indicate the degree by which the two species differ in their resource selection (Lele et al. Manuscript in Progress). If there is no difference in resource selection between the two species, then the coefficients are close to zero or non-significant. Negative or positive signs indicate preference or avoidance of a resource by the species coded as 1 compared to the reference species coded as 0. The coefficient of a continuous variable is defined as the percent change in probability of use by one species, compared to the reference species, with every unit change of the variable while holding all other covariates constant. The coefficient of a categorical variable is the number of times the probability of one species use increases or decreases in that category, compared to the reference category, compared to the other species resource selection (Lele et al. Manuscript in Progress).

We overlaid model coefficients on GIS maps to visually separate areas where selection varied between species. There are no species interactions implied by these maps, but only where one species is more likely to occur than the other. For example, if we went into a green area in the caribou and wolf comparison, we would be more likely to see a caribou than a wolf, and in the red area we would be less likely to see a caribou than a wolf.

Distance between species

Spatial separation between species can be illustrated, not only by examining differences in resource selection, but proximity between species. Past studies used distance to nearest neighbour measurements of track densities (Cumming et al. 1996) and distance to travel routes of predators (Bergerud and Page 1987) to elucidate spatial

relationships between predators and prey. To gain a more throughout understanding of how moose, caribou, and wolves spatially separated themselves on the landscape, we measured the distance between each species telemetry locations. We made multiple circular buffer rings of 1000 m each, to a maximum distance of 5000 m, around each wolf and caribou telemetry point for each season. We randomly selected 1000 m for each buffer distance. We used multiple buffer rings (1000 m – 5000 m), instead of one distance, to represent the possible range that wolves may be able to detect moose or caribou. We calculated the proportion of caribou and moose telemetry points for each season within each wolf buffer to elucidate patterns of spatial separation. For the moose and caribou comparison, we calculated the proportion of moose locations within each caribou buffer for each season.

RESULTS

Animal capture and telemetry data

        Of the 14 wolf collars deployed, all six wolf GPS collars failed prematurely, however, two Lotek_3300s collars were located and retrieved. We used data from 22 collared-moose, (five GPS and 17 VHF) and 35 mountain caribou (10 GPS and 25 VHF). Animals with less than 15 locations, or that fell outside of the designated study area were not used in the analysis. We used both GPS and VHF (100 m) locations to increase sample sizes. The average fix-rates for GPS collars deployed on mountain caribou (50%), wolves (45%), and moose (67%) were below the 80% value deemed appropriate for RSF analyses (Friar et al. 2004), therefore we applied a GPS bias model. Steep, mountainous terrain, dense forest cover and collar malfunction may have attributed to these low GPS fix-rates. The average number of locations per season were 2027 ($SD = 884.7$), 1237 ($SD = 669.8$), and 699 ($SD = 359.8$) for caribou, moose and wolves respectively (Table 3). We pooled data for each species from Jan. 1, 2003 to March 31, 2006 and assumed that differences between years and wolf packs were negligible.

        We used Apps et al. (2001) definition of five caribou seasons using the average date of the greatest seasonal elevation shift made by collared caribou in the study area. These seasons were defined as: early winter (Oct. 23 – Jan. 15), late winter (Jan. 16 – Mar. 31), spring (Apr.1 – May 23), calving (May 24 – June 15), and summer (June 16 – Oct. 22).   We divided moose and caribou locations into these five seasons. We divided wolf locations into summer (April 1 – Oct. 22) and winter (Oct. 23 – Mar. 31) only, because of lower sample sizes. We compared "summer" wolf locations to spring, calving and summer caribou and moose locations. We compared wolf "winter" locations to caribou and moose early and late winter locations.

Adult caribou mortality

        There were 117 collars distributed between four caribou subpopulations in the study area during 1992 – 2006. Sampling effort in the post 2000 time period (110.5 caribou years) was approximately half that compared to pre 2000 (197.2 caribou years).

There were 51 adult radio-collared mountain caribou mortalities recorded, with predation being the number one source of adult caribou mortality in both time periods (Figure 5). The proportion of predation-related deaths increased by 28% after 2000 (Figure 5). This was due to increases in grizzly, cougar and wolf predation after 2000 (Figure 6). Grizzly and black bear predation was the major cause of adult caribou mortality before and after 2000 (Figure 6). Wolf predation increased from 0% to 21% after 2000 (Figure 6). Approximately 18.75% and 10.53% of mortalities were classified as unknown in < 2000 and >2000 respectively, but suspected to be predation-related.

Monitoring for adult radio-collared wolves and moose began in 2003, therefore sample sizes were small. Mortality sources for moose included wolf predation (3), hunting (3) and unknown causes (1). Adult radio-collared wolf mortalities were attributed to human (1), unknown (1) and accidental causes (1).

Variables used to partition space

Although a number of factors were important in discerning space selected by different species, we addressed the three variables with the highest Exp(β) to discuss in detail (Table 7), and referred to the marginal habitat use graphs (Figure 13 – Figure 16) to aid in interpretation. Maps of the seasonal distribution of telemetry points of the three species were also provided (Figure 2 – Figure 4).

Caribou and wolf comparison
Mountain caribou and wolves partitioned space by differential use of old forests, spruce/subalpine fir and alpine in the early winter (Table 4 & Table 7). For instance, mountain caribou used older forests 24.3 times more than wolves, and spruce/subalpine fir 6.3 times more than wolves and in the early winter (Table 4 & Table 7). Mountain caribou used alpine areas 85.6 times more than wolves in the early winter (Table 4 & Table 7). This level of interpretation can be applied to all of the variables in the analysis by referring to Table 7.

In the late winter, old forests, alpine, and areas within 100 m of roads were variables that mountain caribou and wolves used in different proportions (Table 4 & Table 7). The strength of these differences increased for these variables compared to early winter values (Table 7). Mountain caribou and wolves partitioned space in the spring by differentially selecting areas that were greater than 2000 m from a road, within 100 m of a road, and in the alpine (Table 4 & Table 7). Mountain caribou and wolves partitioned space in the calving season first by distances within 100 m of a road, then by alpine areas, followed by terrain ruggedness (Table 4 & Table 7). Mountain caribou and wolves used the following variables in different proportions on the landscape in the summer; distances from 0 – 500 m from a road, and alpine areas (Table 4 & Table 7). All caribou and wolf models were significant (Table 2) and had good predictive capability based on Spearman's-rank correlation from *k*-fold cross validation procedure (Table 4).

Caribou and moose comparison

   The spatial separation of mountain caribou and moose was indicated by their dissimilar use of areas between 100 – 500 m, and greater than 2 km from roads, as well as their use of alpine in the early winter (Table 5 & Table 7). In the late winter, mountain caribou and moose partitioned space first by their use of distances greater than 2000 m from roads, then by their use of alpine, followed by 100 – 500 m from roads (Table 5 & Table 7). Similar to the late winter season, mountain caribou and moose used areas greater than 2000 m and within 100 – 500 m from roads, and alpine areas differently in the spring (Table 5 & Table 7). Caribou selection of areas greater than 2000 m from a road was selected 1510 times more than moose. The three most influential variables separating mountain caribou and moose during calving were distances greater than 2000 m from roads, alpine, and old forests (Table 5 & Table 7). Mountain caribou and moose partitioned space based on distances greater than 2000 m and between 100 – 500 m from roads, and ruggedness of terrain in the summer (Table 5 & Table 7). All caribou and moose seasonal models were significant, (Table 2) and had good predictive ability based on *k*-fold cross validation results (Table 5).

Moose and wolf comparison

   Moose and wolves partitioned space by their differential use of 0 – 500 m from cutblocks (Table 6 & Table 7). Although distances >2000 m from a cutblock were significant in the model, moose and wolves used this category <5%, therefore it was not biologically significant (Figure 15). Moose and wolves selected 0 – 100 m and 100 – 500 m from roads, as well as forests of less common species (deciduous, pine, Douglas fir) in different proportions in the late winter (Table 6 & Table 7). The forest-other category composed <10% of the landscape, although moose and wolves selected this category close to available proportions (Figure 14). Moose and wolves differentially selected areas within 100 m and 500 m of cutblocks and old forests (141-680 yrs) in the spring (Table 6 & Table 7). Alpine habitat and areas greater than 2000 m from a cutblock were significant, but disregarded because moose and wolves used these variables less than <5% (Figure 14 & Figure 15). Moose used distances between 0 – 100 m from a cutblock, forests dominated by spruce/subalpine fir, and non-forested landcover types in different proportions than wolves during the calving season (Table 6 & Table 7). Similar selection for proximity to cutblocks was noted between moose and wolves in the summer, with exception of significant avoidance of distances between 100 – 500 m by moose compared to wolves (Table 6 & Table 7). All moose and wolf seasonal models were significant (Table 2), but the predictive capability varied seasonally based on *k*-fold cross validation results (Table 6). The predictive abilities of the models ranged from very good in the early winter, moderate in the spring, calving and summer, to poor in the late winter.

LSD map interpretation

   Differences in habitat selection between species resulted in patterns of small, isolated, high elevation patches where mountain caribou were more likely to be than wolves and moose in the early winter (Figure 8a & Figure 8b). Based on Figure 8c, moose were more likely to be in valley bottoms near cutblocks than wolves in the early winter.

The probability of encountering a mountain caribou was low across the study area compared to wolves in the late winter (Figure 9a). LSD models produced maps with few, small, isolated areas where mountain caribou were more likely to be than moose in the late winter (Figure 9b). Moose had a higher probability of being close to roads in the valley bottoms than wolves (Figure 9c).

Based on model results, Figure 10a & Figure 10b showed mountain caribou had a high probability of occurring in high, rugged, alpine areas compared to wolves or moose. Moose had limited areas where they were more likely to occur than wolves in the spring (Figure 10c).

Results produced patterns of small, isolated patches where the probability of encountering a mountain caribou was high compared to wolves during calving (Figure 11a). Similar to the spring pattern, mountain caribou were more likely to be in mid-high elevations, particularly on northern slopes compared to moose (Figure 11b). Moose were more likely to occur in a band between the extent of roads and cutblocks, and the alpine (Figure 11c).

Similar to the calving season, these models produced patterns on the landscape of small, isolated patches where mountain caribou were more likely to be than wolves and moose in the summer (Figure 12a & Figure 12b). Moose were more likely to be in areas situated away from cutblocks compared to wolves in the summer (Figure 12c).

Distance between species

The proportion of mountain caribou locations within wolf buffers differed by season, with spring and late winter representing the highest and lowest proportions respectively (Figure 7a). There proportion of caribou locations was small within 1000 m of wolves during all seasons (Figure 7a). Spring and summer represented seasons when moose had the highest proportion of locations in mountain caribou buffers until 3000 m when proportions declined in all seasons (Figure 7b). The proportion of moose locations within 1000 – 5000 m from wolves was high in all seasons except summer (Figure 7c). The proportion of moose declined by approximately 23% within 0 – 1000 m from wolf locations in all seasons (Figure 7c).

DISCUSSION

We quantitatively measured the differences in resource selection between three species to provide insights into the degree of spatial separation, factors that maintain spatial separation, and how spatial separation varies seasonally. We also examined caribou mortality factors to determine if current levels of spatial separation were sufficient to reduce wolf predation.

Adult caribou mortality

The main predator of adult mountain caribou were bears (grizzly and black), with wolf predation increasing in importance after 2000. A recent meta-analysis of caribou subpopulations in B.C., found that bear predation occurs at approximately equal rates across mountain caribou distribution in B.C. (Wittmer 2004). Grizzly and black bears are also found to be important predators of caribou neonates (e.g. Adams et al. 1995b; Rettie and Messier 1998), usually within the first 10 days after the onset of calving. Conversely, wolves are not a major cause of early calf mortality in areas directly west of the study area (Seip 1992), but factor prominently in summer calf mortality in northern British Columbia (Gustine et al. 2006). Our results and previous research suggest that the main predators of adult caribou seem to vary from wolves in Quesnel Lake (Seip 1992), bears (grizzly and black) in the northern Columbia Mountains and cougar in the Southern Purcell Mountains (Kinley and Apps 2001). However, the increase in wolf predation since 2000, suggested that wolves may be a concern for mountain caribou conservation, because wolves have the capacity to respond numerically to increases in moose densities (Messier 1994; Messier and Joly 2000). Thus, if current trends in moose densities continue, wolves may pose a future threat to mountain caribou persistence (i.e. apparent competition; Holt and Lawton 1994; Messier 1994; Messier et al. 2004). However, environmental (snow depth), behavioural (intraspecific competition), antipredator tactics (spatial refuge) and anthropogenic factors (hunting) may inhibit the ability of wolves to respond numerically to moose densities (Mech and Peterson 2003).

Spatial and temporal separation

Our analysis indicated that mountain caribou, wolves and moose experienced different levels of spatial separation and this varied by season. We designated the degree of spatial separation as high, medium or low (Table 8), depending on the proportion of the species within another species buffer (Figure 7a - Figure 7c), and the strength of the Exp(β) coefficients for the variables in the species comparison models (Table 7). Here, we discussed seasons with high and low spatial separation in more detail.

Caribou and wolf comparison
Mountain caribou and wolves experienced the highest level of spatial separation in the late winter, followed by moderate levels in the early winter and summer. The spring and calving seasons had the lowest level of spatial separation between caribou and wolves.

Past studies also report high levels of spatial separation between caribou and wolves in the winter, when preferences in elevation (Seip 1992; Allison 1998), habitat selection (Seip 1992; Cumming et al. 1996; James et al. 2004), and distances from wolf travel routes are examined (Seip 1992). Johnson et al. (2002) also found that wolves did not hunt in habitats strongly selected by caribou as foraging areas. Caribou may represent a less profitable prey choice for wolves with higher search times and lower energy return compared to moose (Bergerud et al. 1983; Adams et al. 1995; Hayes et al. 2000). This high level of spatial separation may also be attributed to the effect of snow and food availability on the distribution of caribou and wolves. In the late winter, mountain

caribou ascend to higher elevations as snows deepen and consolidate to gain access to arboreal lichen in old Englemann spruce and subalpine fir stands (Apps et al. 2001). Wolves have been shown to select valley bottoms with shallower snow depths and high concentrations of prey (Fuller 1991; Kunkel and Pletscher 2000; Callaghan 2001; Whittington et al. 2005; Hebblewhite 2006). Valley bottoms are especially important to wolves in the winter when shallower snow depths increase the efficiency of movement (Huggard 1993; Whittington et al. 2005). Strong selection of alpine by mountain caribou in this season, relative to wolves, may represent the predator avoidance strategy of 'spacing away' from wolves found in other studies (Bergerud and Page 1987; Johnson et al. 2002; Mech and Peterson 2003).

Our results suggested that mountain caribou and wolves had low spatial separation in the spring, similar to patterns of spatial overlap found by Neufeld (2006). In the spring, mountain caribou descend to lower elevations where they use old forests and young plantations where emergent vegetation is first available (Apps et al. 2001). Overlap between caribou and wolf resource selection was evident in their similar use of high biomass areas represented by young forests (0 – 40 yrs), non-forested areas (shrub, burns) and forests-other (deciduous, Douglas fir, lodgepole pine). Wolf resource selection studies in Alberta found that wolf use is associated with cutblocks (Neufeld 2006), shrubs (Kuzyk 2002) and younger forests (Neufeld 2006). Landscapes with these attributes may represent areas of high predation risk for caribou in the spring. In particular, Wittmer (2007) found that the amount of early-seral stands best explains the variation in caribou survival rates within 10 caribou distributions across B.C. Even during seasons that represented low spatial overlap, mountain caribou selected alpine and avoided areas closer to roads than wolves. The strength of avoidance of areas within 100 m of roads was higher than the winter, therefore there may be additional avoidance not strictly attributed to elevation. In other studies, caribou show avoidance of roads and linear features (Nellemann and Cameron 1998; Cameron et al. 1992; Nellemann and Cameron 1996; Dyer et al. 2001; Nellemann et al. 2001; Oberg 2001). Caribou may avoid roads to reduce predation because wolves use these features as travel routes to increase travel efficiency especially when snow depths off the trail may hamper movement (Musiani et al. 1998; Ciucci et al. 2003; Whittington et al. 2005).

Mountain caribou and wolves experienced the lowest level of spatial separation during the calving season. During the this season, mountain caribou ascend to high elevations to calve and access their summer range (Apps et al. 2001). These calving areas are most often located above treeline, favouring southern slopes, heterogeneous snow cover, and rugged, mountainous terrain (Bergerud et al. 1983; Bergerud and Page 1987). Our results were counter to what one would expect if caribou were spacing away from high wolf-risk areas during calving. Gustine et al. (2006) found that predation risk from gray wolves influenced where woodland caribou calve, resulting in caribou avoiding areas with high biomass likely associated with increased predation risk. Our results suggested that landcover and forest age variables, representing levels of high biomass (e.g. forest age 0 – 40 yrs; non-forested areas, forest-other), were used in similar proportions by caribou and wolves. However, caribou and wolves differed in their relative selection in of alpine, old forests and rugged terrain. There are three possible

explanations that might explain why there was low spatial separation between wolves and caribou during the calving season. Wolf predation-risk may not have a strong influence on the structure of caribou habitat selection, and that the influence of other predators should be considered. For instance, mountain caribou selected alpine habitats ten times as much as wolves, which is less than in other seasons, possibly due to the presence of grizzly bears in this habitat (McLellan pers. comm.; Simpson et al. 1987). Secondly, wolves were successful in accessing caribou calving areas. Data on survival of caribou neonates during this season is required to determine if low spatial separation resulted in higher predation rates. Thirdly, differences in terrain ruggedness, alpine and old forests were sufficient to maintain sufficient spatial separation between mountain caribou and wolves.

Caribou and moose comparison

Caribou and moose had the greatest spatial separation during spring and calving seasons. Early winter and summer are seasons when spatial separation was low, followed by moderate levels in the late winter.

Our results supported previous studies that demonstrate caribou and moose spatially separate themselves by using different habitats (Boonstra and Sinclair 1984; Bergerud and Page 1987; Seip 1992; Cumming et al. 1996; Boer 1998; James et al. 2004). We found that caribou and moose differed in their use of old forests (141 – 680 yrs), alpine areas, aspect and distances > 2000m from low-use roads in the spring and calving seasons. These differences in resource selection may be due to forage differences between the two species (Boer 1998; Hofmann 2000; Dussault et al. 2005) and/or the antipredator strategy of caribou to 'space away' from predators and alternate prey species (Seip 1992; Apps et al. 2001). Roads are commonly constrained along valley bottoms mountainous terrain, so the low-use road variable probably functioned as a surrogate for elevation during these seasons. During calving season, the relative selection of alpine, northerly slopes and high elevations are indicative of calving site selection by mountain caribou (Bergerud et al. 1983; Bergerud and Page 1987) compared to open, upland (stream valley shrub, alluvial) and aquatic habitats selected by moose (Tefler 1984); Peek 1998).

Mountain caribou and moose experienced the lowest degree of spatial separation in the early winter and summer relative to the other seasons, although the exp(β) values were still relatively high. In the early winter, overlap in resource selection between caribou and moose occurred in forests-other, spruce/subalpine fir forests and areas within 100 m of roads. Roads may be a surrogate for elevation in this season, because mountain caribou are at low elevations in the early winter (1200 m; Apps et al. 2001), but this also places them within the proximity to respond to roads. Caribou may avoid roads to reduce predation because both moose and wolves use these features as travel routes (Musiani et al. 1998; Ciucci et al. 2003; Whittington et al. 2005) and road sides may provide high-quality forage that attract moose (Peek 1998). Our results were inconclusive regarding the influence of roads on the spatial distribution of caribou and moose, because we could not separate possible avoidance of roads and elevation.

Spatial separation between mountain caribou and moose was low in the summer, possibly due to the overlapping forage preferences of the two species during this season (Boer 1998) as illustrated in their similar use of all landcovers and early age forests. Although there were similar use of alpine between the two species, mountain caribou selected steeper terrain and distance further from roads relative to moose.

Moose and wolf comparison

Moose and wolves had the highest degree of spatial separation in the early winter and low levels of spatial separation in all other seasons. Moose strong selection for areas within close proximity to cutblocks (0 – 100 m), relative to wolves, reflected their requirements for high-quality forage in the early winter (Cumming et al. 1996; Peek 1998; Courtois et al. 2002; Maier et al. 2005; Potvin et al. 2005). These areas may provide a refuge for moose because wolf travel is impeded by deep, unconsolidated snow (Huggard 1993) that is characteristic of early winter snow pack conditions in this region.

Moose and wolves had a low degree of spatial separation in all other seasons. Moose are the primary prey of wolves in this system (Seip 1992), and therefore would select habitat types that matched the habitat selection patterns and highest densities of moose in order to maximize their foraging efficiency (Hebblewhite 2006). Overlap in habitat use and elevation has also been documented between moose and wolves in other studies (Seip 1992; Cumming et al. 1996; James et al. 2004).

In the late winter, moose and wolves used landcover categories in similar proportions with the exception of forests-other (Douglas fir, deciduous, pine). Although the strength of differences in proximity to low-use roads were weak, moose used areas closer to roads more than wolves, possibly to increase their travel efficiency on hard-packed snow surfaces. Areas around roads may also represent areas with reduced predation risk for moose, if wolves avoid these areas to reduce their risk of mortality from human hunting and poaching (Kunkel and Pletscher 2000). Roads are also often built to access timber harvesting, which are located near high quality forage habitats and with nearby hiding cover ideal for moose (Kunkel and Pletscher 2000; Dussault et al. 2005). In snow-free seasons, there were small increases in relative use by moose of spruce/subalpine fir forests, decreased use of cutblock areas, and movements away from low-use roads compared to wolves. These differences in resource selection by moose and wolves may reflect the migration of moose to higher elevations to take advantage of forage available in high-alpine dwarf shrub communities and wet subalpine forests (Edwards and Ricey 1956; Seip 1992). In contrast, wolves may be constrained to lower elevations because of activities surrounding denning and rendevous sites (Mao et al. 2005). These sites often occur at low elevations in close proximity to rivers (Ballard and Dau 1983; Huggard 1993). This response to wolf activity is seen in Yellowstone National Park, when elk select higher elevations, less open habitat, and more burned forests in the summer to avoid wolf activity centered around den and rendezvous areas (Mao et al. 2005). By selecting elevations above high wolf-use areas, moose can reduce their predation risk (e.g. Kunkel and Pletscher 2000). Spatial separation between moose and wolves may be lowest in the late summer when wolf packs resume their hunting forays after wolf pups are old enough to travel.

Limitations and assumptions

As with most resource selection studies, our ability to accurately predict resource selection may be affected by sample size, autocorrelation of relocations, pooling of relocation data, choice of study area size and boundaries, and number of habitats considered (Thomas and Taylor 2006; Alldredge and Griswold 2006). Telemetry data used to represent wolf resource selection could be improved by increasing sample sizes and sampling a broader distribution of wolf packs within the study area. The model representing wolf resource selection was weighted towards selection by the Goldstream pack, but we assumed that this selection was indicative of selection across wolf packs.

Three of 15 models had poor to moderate predictive ability. This could be due to selection of variables occurring at different scales than those included, exclusion of important variables, or the complete overlap of species resource selection. For example, in the moose and wolf comparison model, if there was complete overlap in resource selection, most of the variables would be highly correlated or not significant and a highly predictive model may not be found. The proportion of locations within another species buffer, did not always agree with the model results and was not a useful measure of spatial separation at fine scales.

CONCLUSIONS

Is the current anitpredator strategy of caribou sufficient to reduce wolf predation in a landscape with elevated moose populations, fragmented forest patches and the conversion of mature forests to early-seral stage forests? Lessard (2005) outlines the conditions by which mountain caribou can escape despensatory predation and extirpation. These conditions exist when there is habitat differentiation between caribou and moose, caribou are not limited by amount of older forests, there is high spatial separation between caribou and moose, moose density is higher than caribou density, and predators do not dominate the scale at which caribou and moose select habitats (Lessard 2005). Caribou population declines in British Columbia and Alberta (e.g. Seip 1992; Neufeld 2006) may be due to violations in these conditions, often found in altered habitats (Lessard 2005). In the north Columbia Mountains, all conditions may be satisfied in all seasons except spring and calving, where spatial separation is at its lowest between mountain caribou and moose. The majority of all predation events occur during calving and summer months in the study area (McLellan pers. comm), and province-wide (1984 – 2002; Wittmer et al. 2005), reflecting a possible failure of spatial separation as an antipredator strategy for caribou during these seasons. Seip (1992) also found that wolf predation occurred in the summer and early winter, and bear predation in the spring and early summer. The increase in the number of adult caribou mortalities attributed to wolves during the time period of this study (2003 – 2006), suggested a failure of spatial separation occurred. More data on caribou mortality sources after 2000 is required to confirm this hypothesis. Lessard (2005) also suggests that wolves may be scale dominant over prey because wolves defend large territories and have fast movement rates, therefore reducing the effectiveness of niche differentiation between caribou and moose.

Therefore, snow-free periods would pose the greatest risk of spatial overlap when movement rates of wolves are greatest.

Survival of mountain caribou in the north Columbia Mountains may depend on maintaining the integrity of spatial and temporal refuges and the connectivity between these refuges. For example, mountain caribou consistently selected older forests (>140 yrs) more than wolves and moose in all seasons. Wittmer (2007) found that mountain caribou killed due to predation have lower proportions of old forest and more mid-age forests in their home range when compared to live caribou. Therefore, these older forest age classes represent not only a source of arboreal lichen for mountain caribou, but a spatial refuge that minimizes predation risk from wolves. Any management or recovery scenarios should focus on maintaining important variables contributing to spatial separation and in seasons when the probability of overlap between these three species is most likely to occur.

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Table 1. Description of variables used in RSF models to determine differences in habitat selection between mountain caribou, moose and wolves in five seasons in the north Columbia Mountains, British Columbia between 2003-2006.

Variable		Variable type	Range of values	Description
Terrain				
	ASP	Categorical	North South	Aspect
	TRI	Continuous	0-0.38	Terrain Ruggedness Index
	SLP	Continuous	0-90 degrees	Slope
	ELEV	Continuous	345 – 3661 meters	Elevation
Habitat				
	LAND	Categorical	Cedar/hemlock Forest-other Spruce/Subalpine Fir Alpine Non-forest	Landcover type Forest-other includes forests with deciduous, pine spp. or fir as leading species. Non-forest includes non-commercial brush, cutblocks, burns and areas not currently forested.
	CRN	Continuous	0-100%	Crown closure defined as amount of ground area covered by tree crowns
	AGE	Categorical	1 (0-40) yrs 2 (41-100) yrs 3 (101-140) yrs 4 (141-650) yrs	Forest age
Human-use				
	RD_L	Categorical	1 (0-0.10) km 2 (0.10-0.50) km 3 (0.50-2.0) km 4 (>2.0) km	Distance to low-use gravel road and trail
	LOG	Categorical	1 (0-0.10) km 2 (0.10-0.50) km 3 (0.50-2.0) km 4 (>2.0) km	Distance to cutblock

Table 2. The results from the likelihood ratio χ^2 tests and appropriate degrees of freedom for each seasonal model for each species comparison. All models were significant with p-values <0.01.

Species Comparison	Early Winter		Late Winter		Spring		Calving		Summer	
	χ^2	df	χ^2	df	χ^2	df	χ^2	df	χ^2	df
Caribou-Wolf	1934.2	11	721.78	11	488.86	11	697.77	12	1631.43	10
Caribou-Moose	142.33	10	590.15	10	770.34	11	131.08	11	725.5	12
Moose-Wolf	59.99	4	81.21	7	636.05	14	639.97	10	21.13	3

Table 3. The number of telemetry locations (GPS and VHF) per season from moose, caribou and wolves from the north Columbia Mountains, British Columbia between 2003 – 2006 (EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer).

Season	Caribou	Moose	Wolf	Total
EW	2000	1435	305	3740
LW	2330	1139	305	3774
SP	1988	1048	962	3998
CA	681	359	962	2002
SU	3134	2206	962	6302

Table 4. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between mountain caribou and wolves in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Mountain caribou are coded as one and wolves are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Early Winter		Late Winter		Spring		Calving		Summer	
		β	SE	β	SE	β	SE	β	SE	β	SE
Forest age	0-40 yrs	**-1.760**	0.335	**-2.000**	0.713	0.339	0.292	-0.113	0.59	**-0.540**	0.317
	41-100 yrs*	**-**	-	**-**	-	-	-	-	-	**-**	-
	101-140 yrs	**1.110**	0.242	**1.710**	0.275	**1.230**	0.332	**1.050**	0.475	**1.590**	0.446
	141-680 yrs	**3.190**	0.537	**4.420**	0.633	**1.760**	0.389	**2.080**	0.511	**2.060**	0.382
Landcover	Cedar/hemlock*	**-**	-	**-**	-	-	-	-	-	**-**	-
	Forest-other	**-1.490**	0.555	0.429	0.623	0.460	0.456	0.606	0.581	0.385	0.609
	SX/subalpine fir	**1.840**	0.736	**1.720**	0.676	**1.440**	0.439	**1.730**	0.396	**1.420**	0.627
	Alpine	**4.450**	1.26	**5.460**	1.53	**2.690**	0.372	**2.380**	0.425	**3.060**	0.428
	Non-forest	0.016	0.352	-0.151	0.804	0.320	0.309	0.114	0.438	**-1.010**	0.322
Road_low	0.00-0.10 km	**-1.700**	0.712	**-2.300**	0.937	**-3.260**	0.324	**-3.020**	0.324	**-4.190**	0.409
	0.10-0.50 km	-0.716	0.433	-1.160	0.650	**-2.080**	0.217	**-1.990**	0.293	**-4.370**	0.324
	0.50-2.00 km*	-	-	-	-	**-**	-	**-**	-	**-**	-
	> 2.00 km	**1.700**	0.817	**1.760**	0.654	**2.000**	0.554	**2.060**	0.547	**2.890**	0.632
Aspect	North*	**-**	-	**-**	-	-	-	-	-	**-**	-
	South	**-1.110**	0.51	-	-	-	-	-	-	-	-
Crown closure		-	-	**-0.045**	0.0125	-	-	**-0.020**	0.001	-	-
TRI		-	-	-	-	**1.770**	0.546	**2.350**	0.499	-	-
k-fold rho (P)		0.782	(<0.01)	0.748	(<0.02)	0.745	(<0.02)	0.636	(<0.05)	0.795	(<0.01)

Table 5. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between mountain caribou and moose in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Mountain caribou are coded as one and moose are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Early Winter		Late Winter		Spring		Calving		Summer	
		β	SE	β	SE	β	SE	β	SE	β	SE
Forest age	0-40 yrs	**-1.920**	0.295	-0.022	0.937	0.324	0.650	-0.091	0.708	-0.465	0.290
	41-100 yrs*	**-**	-	-	-	-	-	-	-	-	-
	101-140 yrs	**0.601**	0.230	0.685	0.401	**1.220**	0.419	0.167	0.596	**0.850**	0.313
	141-680 yrs	**2.270**	0.300	**2.850**	0.693	**2.850**	0.418	**1.860**	0.520	**1.780**	0.548
Landcover	Cedar/hemlock*	**-**	-	**-**	-	**-**	-	**-**	-	**-**	-
	Forest-other	**-2.020**	0.819	1.100	1.050	-0.594	0.546	1.010	0.606	1.150	0.657
	SX/subalpine fir	1.240	0.663	**2.420**	0.930	0.443	0.679	0.535	0.550	0.288	0.665
	Alpine	**3.280**	0.950	**5.050**	1.370	**3.530**	1.020	**3.390**	0.851	1.220	0.995
	Non-forest	**-1.040**	0.297	-0.032	1.100	0.248	0.740	-0.313	0.551	-0.852	0.816
Road_low	0.00-0.10 km	-1.220	0.864	**-0.740**	0.249	-0.145	0.276	0.313	0.579	0.661	0.505
	0.10-0.50 km	**2.860**	0.467	**2.960**	0.643	**2.970**	0.363	1.230	0.642	**2.820**	0.330
	0.50-2.00 km*	**-**	-	**-**	-	**-**	-	-	-	**-**	-
	> 2.00 km	**5.030**	1.540	**6.400**	1.010	**7.320**	1.220	**7.180**	1.400	**5.540**	0.653
Aspect	North*	**-**	-	**-**	-	**-**	-	**-**	-	**-**	-
	South	-	-	-	-	**-1.120**	0.446	**-1.590**	0.432	**-0.950**	0.465
TRI		-	-	-	-	-	-	-	-	**2.120**	2.120
k-fold rho (*P*)		0.669	(<0.05)	0.685	(<0.05)	0.644	(<0.05)	0.653	(<0.05)	0.833	(<0.01)

Table 6. Coefficients and standard errors for the most parsimonious RSF model for differences in selection in five seasons between moose and wolves in the northern Columbia Mountains, British Columbia from 2003-2006. Coefficients in bold indicate significant variables in the models. Moose are coded as one and wolves are coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Early Winter		Late Winter		Spring		Calving		Summer	
		β	SE	β	SE	β	SE	β	SE	β	SE
Forest age	0-40 yrs	**-**	-	-	-	0.430	0.383	-	-	-	-
	41-100 yrs*	-	-	-	-	-	-	**-**	**-**	-	-
	101-140 yrs	-	-	-	-	-0.248	0.336	-	-	-	-
	141-680 yrs	**-**	-	-	-	**-1.420**	0.501	-	-	-	-
Landcover	Cedar/hemlock*	-	-	-	-	**-**	-	-	-	**-**	-
	Forest-other	-	-	**-1.060**	0.482	0.851	0.768	-0.062	0.734	**-**	-
	SX/subalpine fir	-	-	-0.563	0.681	**0.527**	0.256	**1.170**	0.527	**-**	-
	Alpine	-	-	-0.363	2.05	**-2.340**	1.03	-1.100	0.922	-	-
	Non-forest	-	-	-0.816	0.621	-0.208	0.424	**1.100**	0.308	-	-
Cutblock	0.00-0.10 km	**5.210**	0.771	-	-	**-1.720**	0.771	-1.510	0.96	-0.641	0.446
	0.10-0.50 km	**3.740**	0.756	-	-	**-1.450**	0.756	-0.910	0.793	**-1.220**	0.385
	0.50-2.00 km*	**-**	-	**-**	**-**	**-**	-	-	-	**-**	-
	> 2.00 km	**2.440**	1.030	-	-	**-4.480**	1.03	-1.490	0.889	0.172	0.383
Road_low	0.00-0.10 km	-	-	**1.450**	0.536	0.795	0.654	**-1.800**	0.580	**-**	-
	0.10-0.50 km	-	-	**1.710**	0.449	**1.400**	0.535	**-0.930**	0.353	**-**	-
	0.50-2.00 km*	**-**	**-**	-	-	**-**	-	**-**	-	**-**	-
	> 2.00 km	-	-	-1.360	1.060	-2.570	1.43	**-3.930**	1.27	-	-
Aspect	North*	-	-	-	-	-	-	-	-	-	-
	south	-	-	**-**	**-**	**1.160**	0.525	-	-	-	-
Slope		-0.041	0.0215	-	-	-	-	-	-	-	-
k-fold rho (P)		0.901	(<0.002)	0.141	ns	0.647	(<0.05)	0.572	(<0.1)	0.515	(<0.2)

ns = not significant

Table 7. The Exp(β) of the most parsimonious RSF models used in the interpretation of the differences in selection in five seasons between mountain caribou, moose and wolves in the northern Columbia Mountains, British Columbia from 2003-2006 (EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer). Significant variables are highlighted in bold. The first species in the comparison heading is coded as one and the second is coded as zero in the logistic regression analysis. Reference categories are labeled with an asterix (*).

Variable		Caribou and Wolf Comparison					Caribou and Moose Comparison					Moose and Wolf Comparison				
		EW	LW	SP	CA	SU	EW	LW	SP	CA	SU	EW	LW	SP	CA	SU
Age	0-40	**5.81**	**7.39**	1.40	1.12	**1.72**	**6.82**	1.02	1.38	1.09	1.59	-	-	1.54	-	-
	41-100*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	101-140	**3.03**	**5.53**	**3.42**	**2.86**	**4.90**	**1.82**	1.98	**3.39**	1.18	**2.34**	-	-	1.28	-	-
	141-680	**24.29**	**83.10**	**5.81**	**8.00**	**7.85**	**9.68**	**17.29**	**17.29**	**6.42**	**5.93**	-	-	**4.14**	-	-
Landcover	CW/HW*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Forest	**4.44**	1.54	1.58	1.83	1.47	**7.54**	3.00	1.81	2.75	3.16	-	2.89	2.34	1.06	-
	SX/BL	**6.30**	**5.58**	**4.22**	**5.64**	**4.14**	3.46	**11.25**	1.56	1.71	1.33	-	1.76	**1.69**	**3.22**	-
	Alpine	**85.63**	**235.10**	**14.73**	**10.80**	**21.33**	**26.58**	**156.0**	**34.12**	**29.67**	3.39	-	1.44	**10.38**	3.00	-
	Non-forest	1.02	1.16	1.38	1.12	**2.75**	**2.83**	1.03	1.28	1.37	2.34	-	2.26	1.23	**3.00**	-
Cutblock	0.0-0.1	-	-	-	-	-	-	-	-	-	-	**183.1**	-	**5.58**	4.53	1.90
(km)	0.1-0.5	-	-	-	-	-	-	-	-	-	-	**42.10**	-	**4.26**	2.48	**3.39**
	0.5-2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	> 2.0	-	-	-	-	-	-	-	-	-	-	**11.47**	-	**88.23**	4.44	1.19
Road_low	0.0-0.1	**5.47**	**9.97**	**26.05**	**20.49**	**66.02**	3.39	**2.10**	1.16	1.37	1.94	-	4.26	2.21	**6.05**	-
(km)	0.1-0.50	2.05	3.19	**8.00**	**7.32**	**79.04**	**17.46**	**19.30**	**19.49**	3.42	**16.78**	-	5.53	4.06	2.53	-
	0.5-2.0*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	> 2.0	**5.47**	**5.81**	**7.39**	**7.85**	**17.99**	**152.9**	**601.9**	**1510**	**1313**	**254.7**	-	3.90	13.07	**50.91**	-
Aspect	North*						-	-	-	-	-	-	-	-	-	-
	South	**3.03**					-	-	**3.06**	**4.90**	**2.59**	-	-	**3.19**	-	-
Crown Closure		-	**1.05**		**1.02**		-	-	-	-	-	-	-	-	-	-
TRI		-	-	**5.87**	**10.49**		-	-	-	-	**8.33**	-	-	-	-	-
Slope		-	-	-	-	-	-	-	-	-	-	1.04	-	-	-	-

Table 8. The degree of spatial separation (H = high, M = moderate, L = low) for three species comparisons in five seasons in the north Columbia Mountains, British Columbia.

Species Comparison	Early Winter	Late Winter	Season Spring	Calving	Summer
Caribou-Wolf	M	H	L	L	M
Caribou-Moose	L	M	H	H	L
Moose-Wolf	H	L	L	L	L
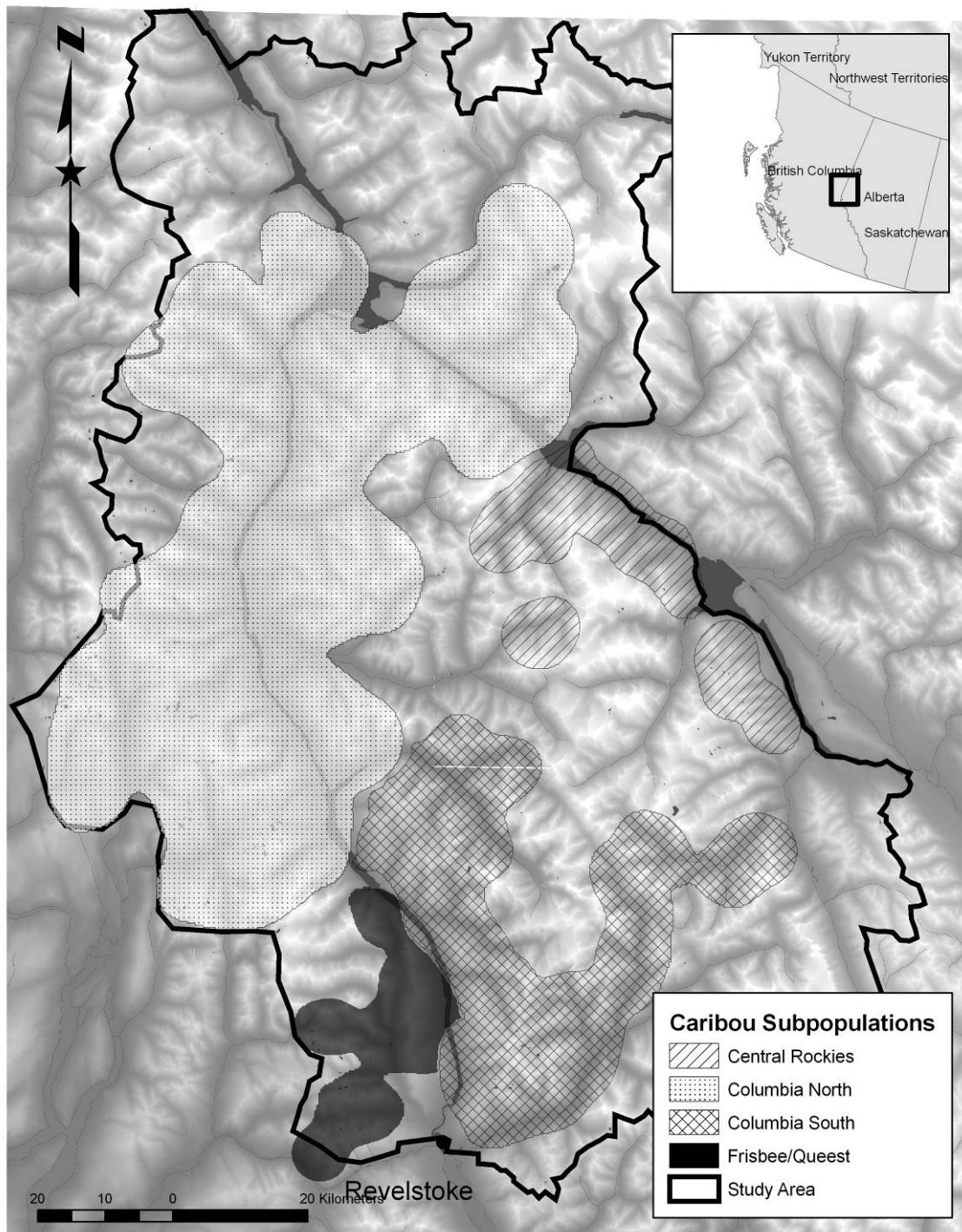
Figure 1. Outline of the study area encompassing the north Columbia Mountains, British Columbia, Canada. Mountain caribou subpopulations in the study area include Central Rockies, Columbia North, Columbia South and Frisbee/Queest (Witmer et al. 2005).
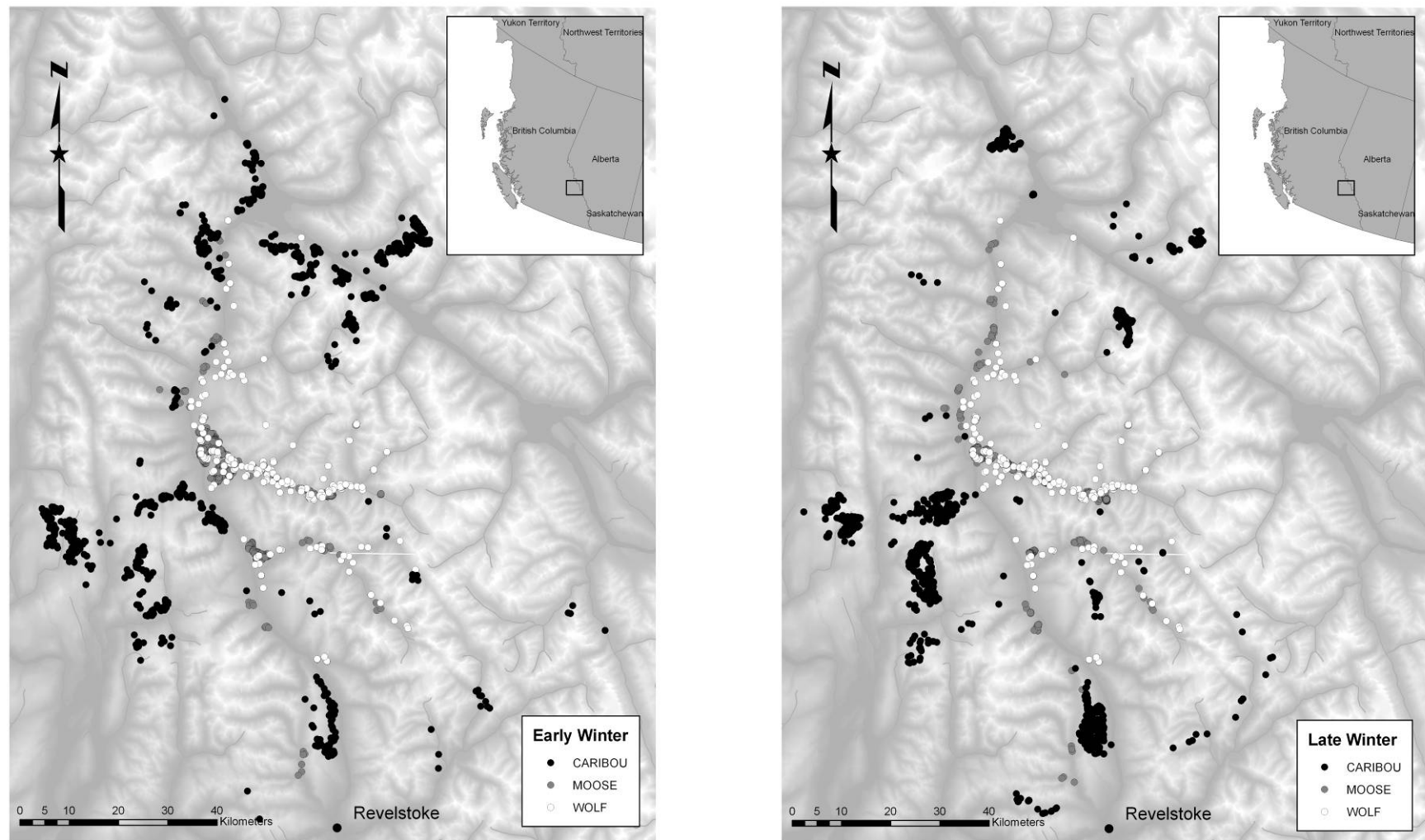
Figure 2. Telemetry locations (VHF and GPS) of mountain caribou, moose and wolves (2003 – 2006) in the northern Columbia Mountains, B.C. in the early winter (EW = Oct. 23 – Jan. 15) and late winter (LW = Jan. 16 – Mar. 31).
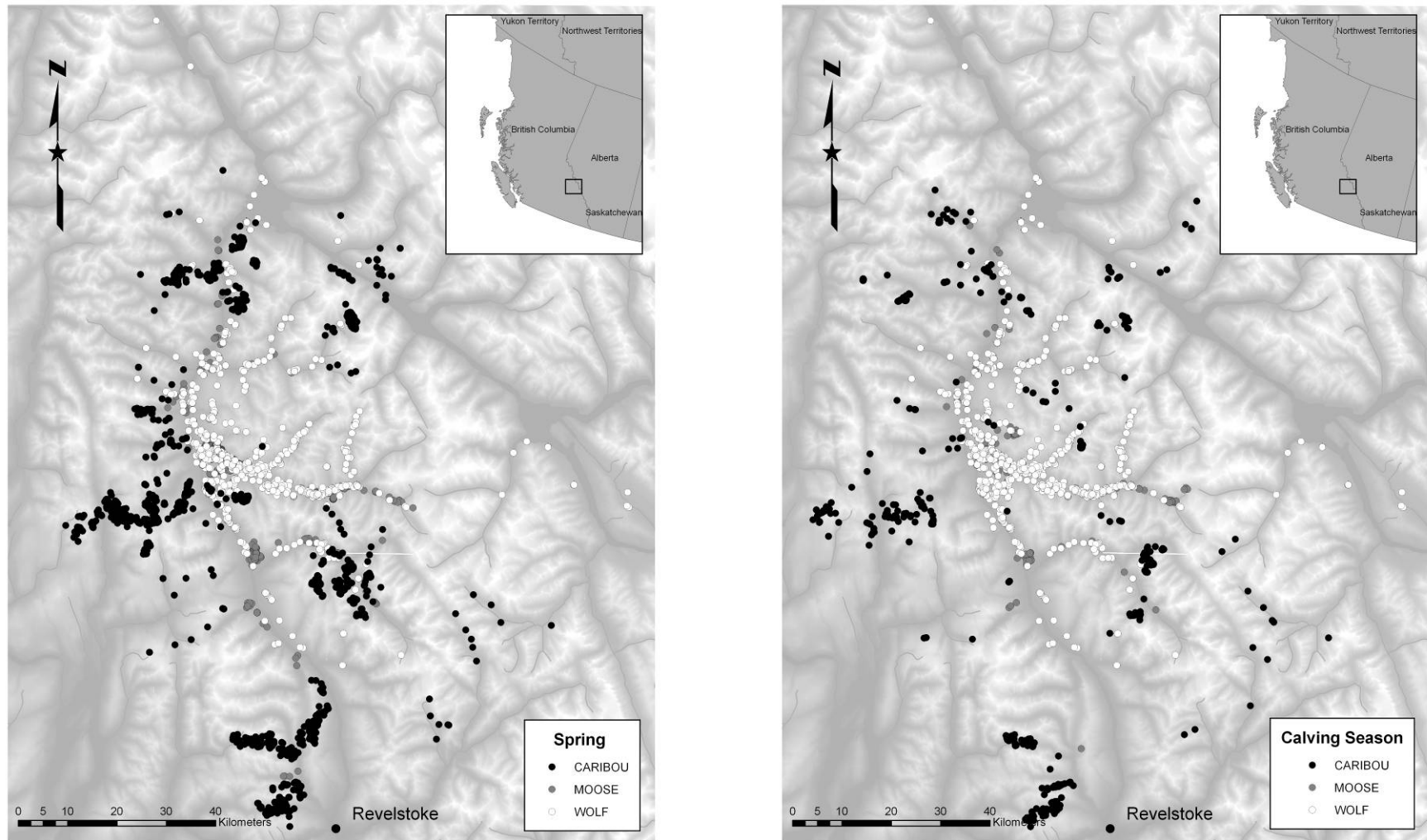
Figure 3. Telemetry locations (VHF and GPS) of mountain caribou, moose and wolves (2003 – 2006) in the northern Columbia Mountains, B.C. in the spring (SP = April 1 – May 23) and calving season (CA = May 24 – June 15)
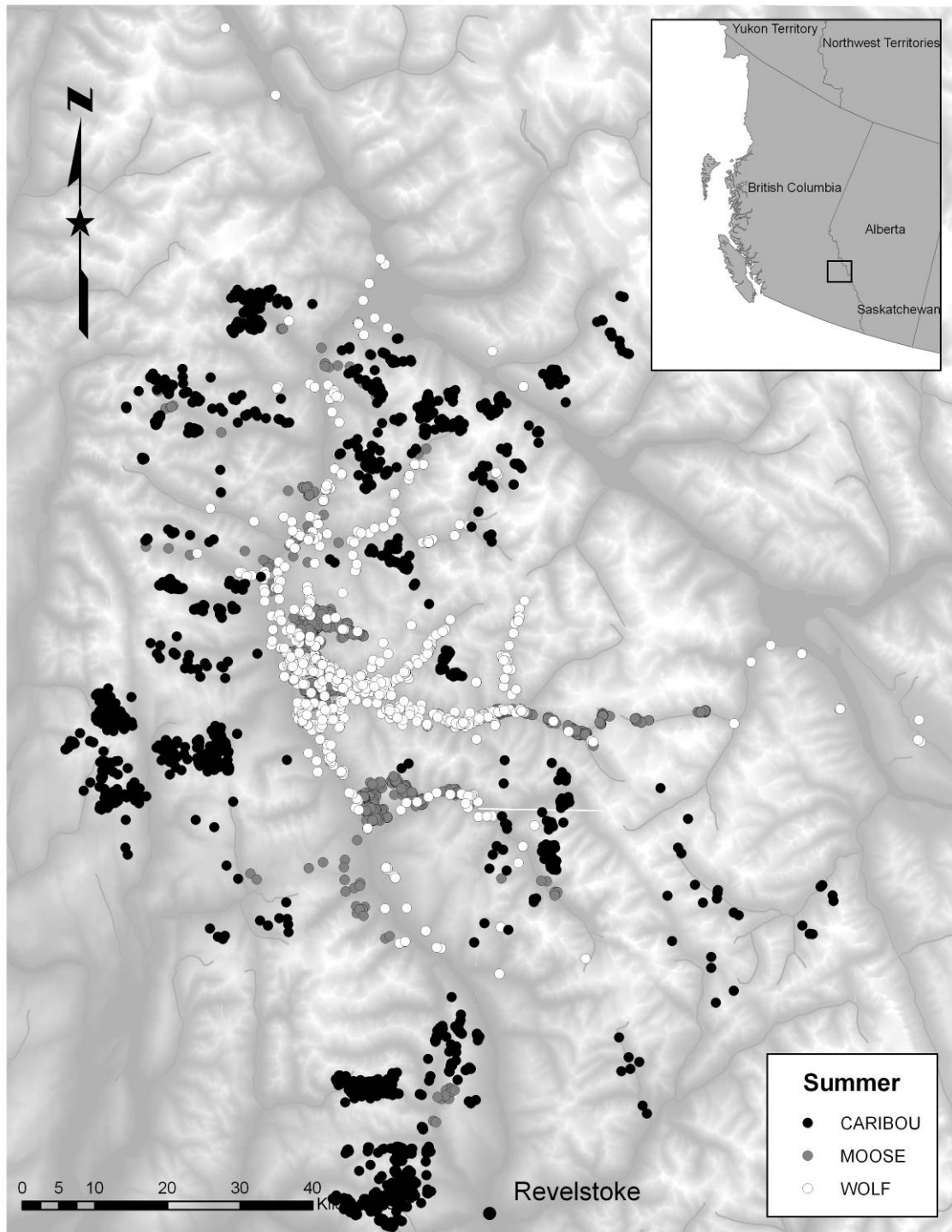
Figure 4. Telemetry locations (VHF and GPS) of mountain caribou, moose and wolves (2003 – 2006) in the northern Columbia Mountains, B.C. in the summer (SU = June 16 – Oct. 22).
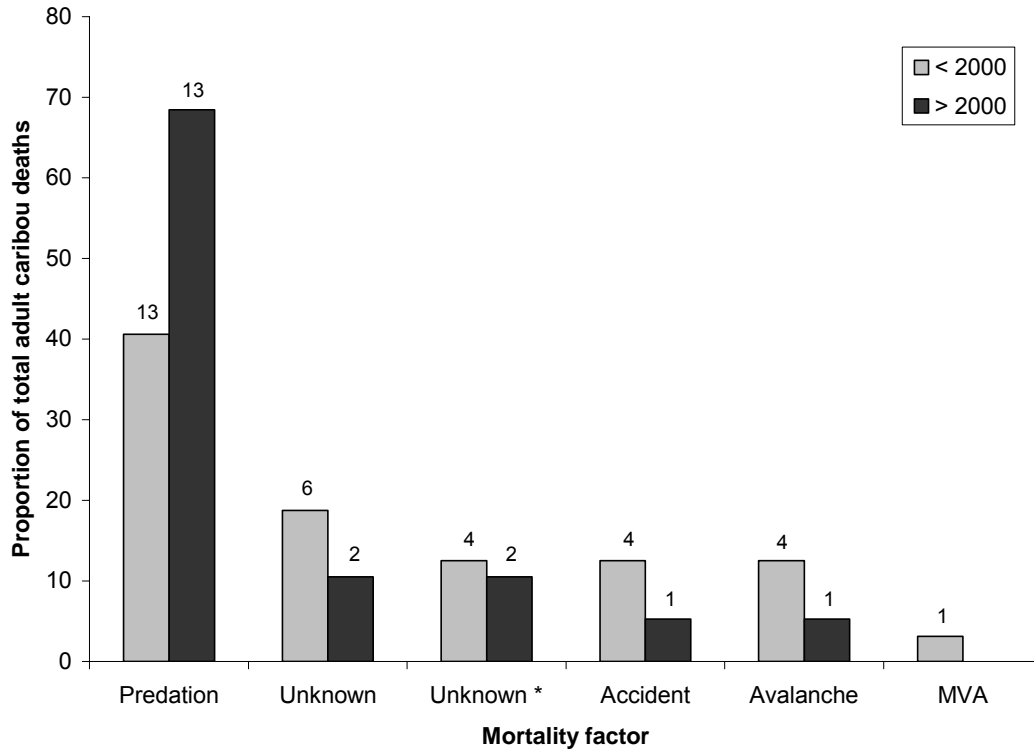
Figure 5. The proportion of total adult radio-collared mountain caribou mortality factors in the north Columbia Mountain study area, British Columbia from < 2000 (1992 - 1999) and > 2000 (2000 – 2006). Proportions were corrected for caribou sampling effort (number of caribou years) during each time period. The number above the bars indicated the raw number of mortalities within each mortality category. * Non-predation related unknown mortalities. MVA = motor vehicle accidents. Accident = natural disasters such as tree fall and rock crevasses.
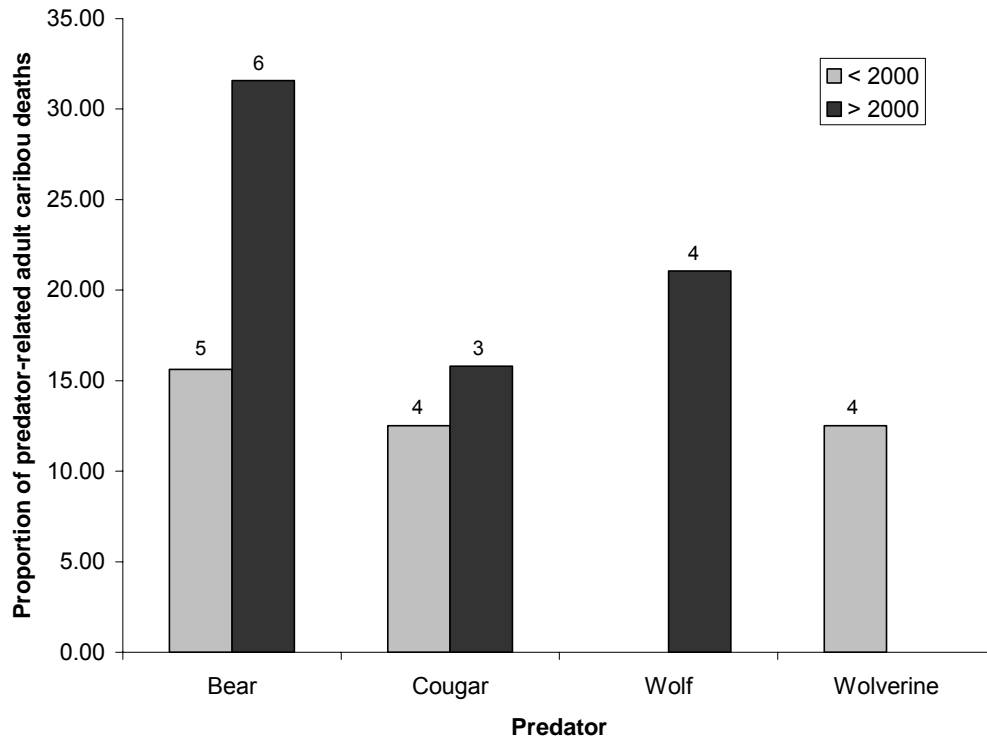
Figure 6. The proportion of predation-related adult radio-collared mountain caribou mortality factors in the north Columbia Mountain study area, British Columbia from < 2000 (1992 - 1999) and > 2000 (2000 – 2006). Proportions were corrected for caribou sampling effort (number of caribou years) during each time period. The number above the bars indicated the raw number of mortalities within each mortality category.

a)

b)

c)
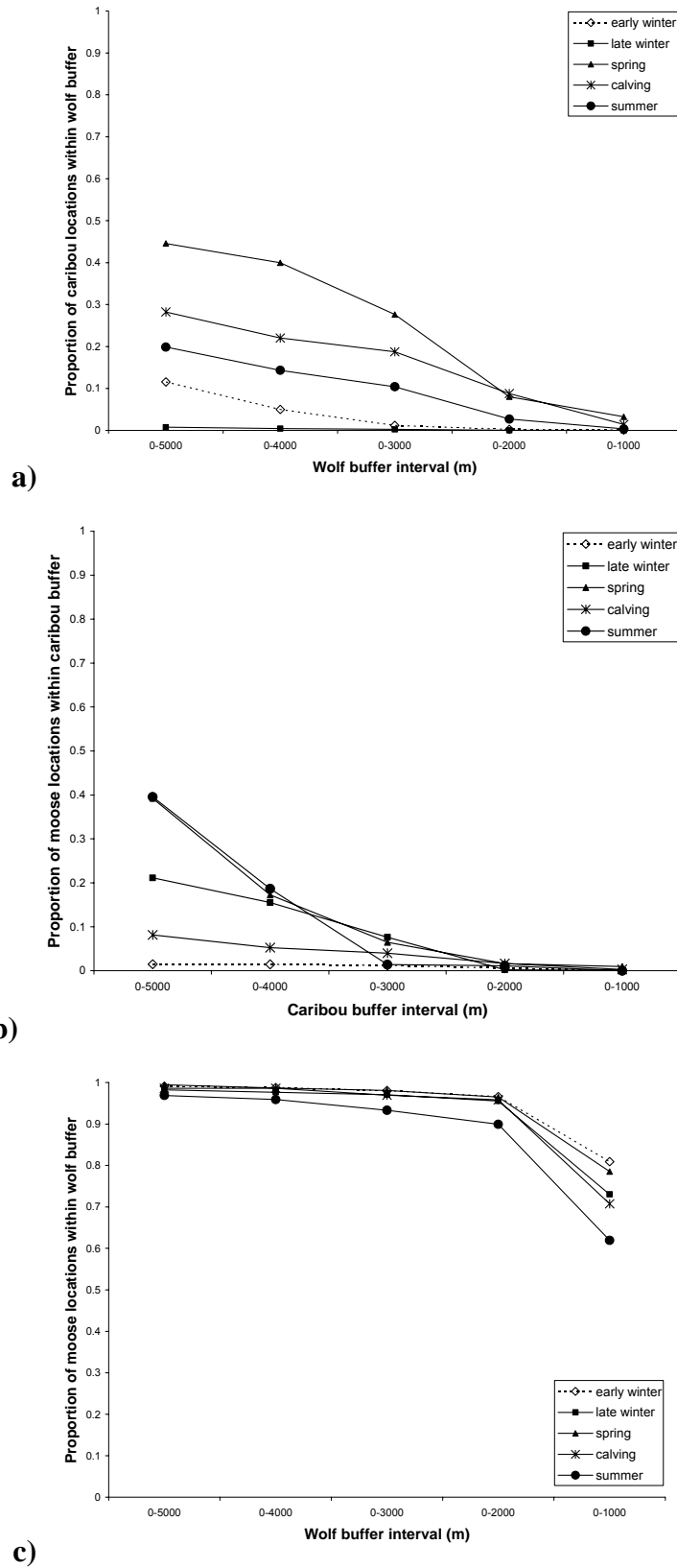
Figure 7. The proportion of telemetry locations for mountain caribou and moose falling within 1000 m buffers for five seasons in the north Columbia mountains, British Columbia from 2003-2006.

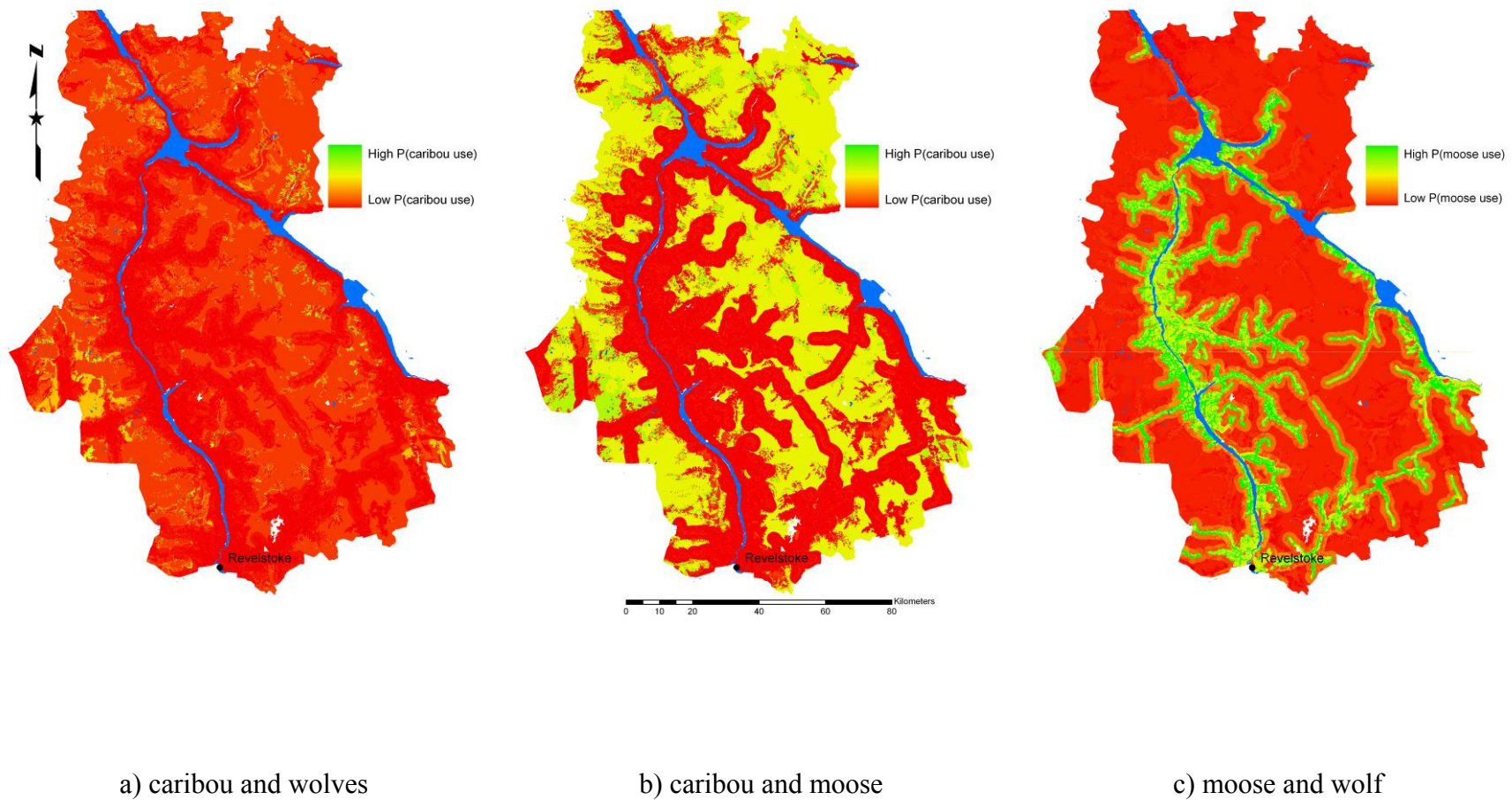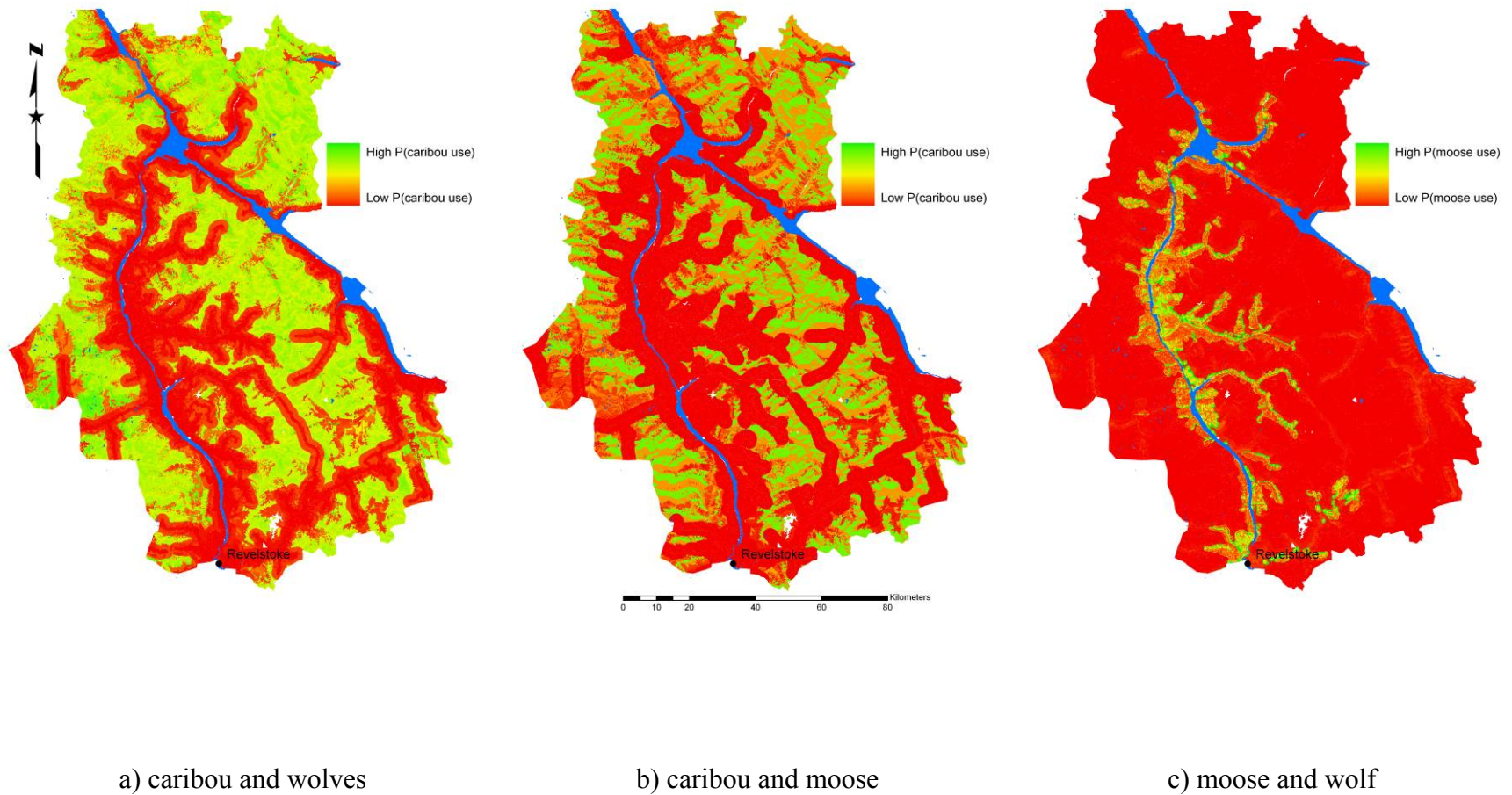a) caribou and wolves   b) caribou and moose   c) moose and wolf
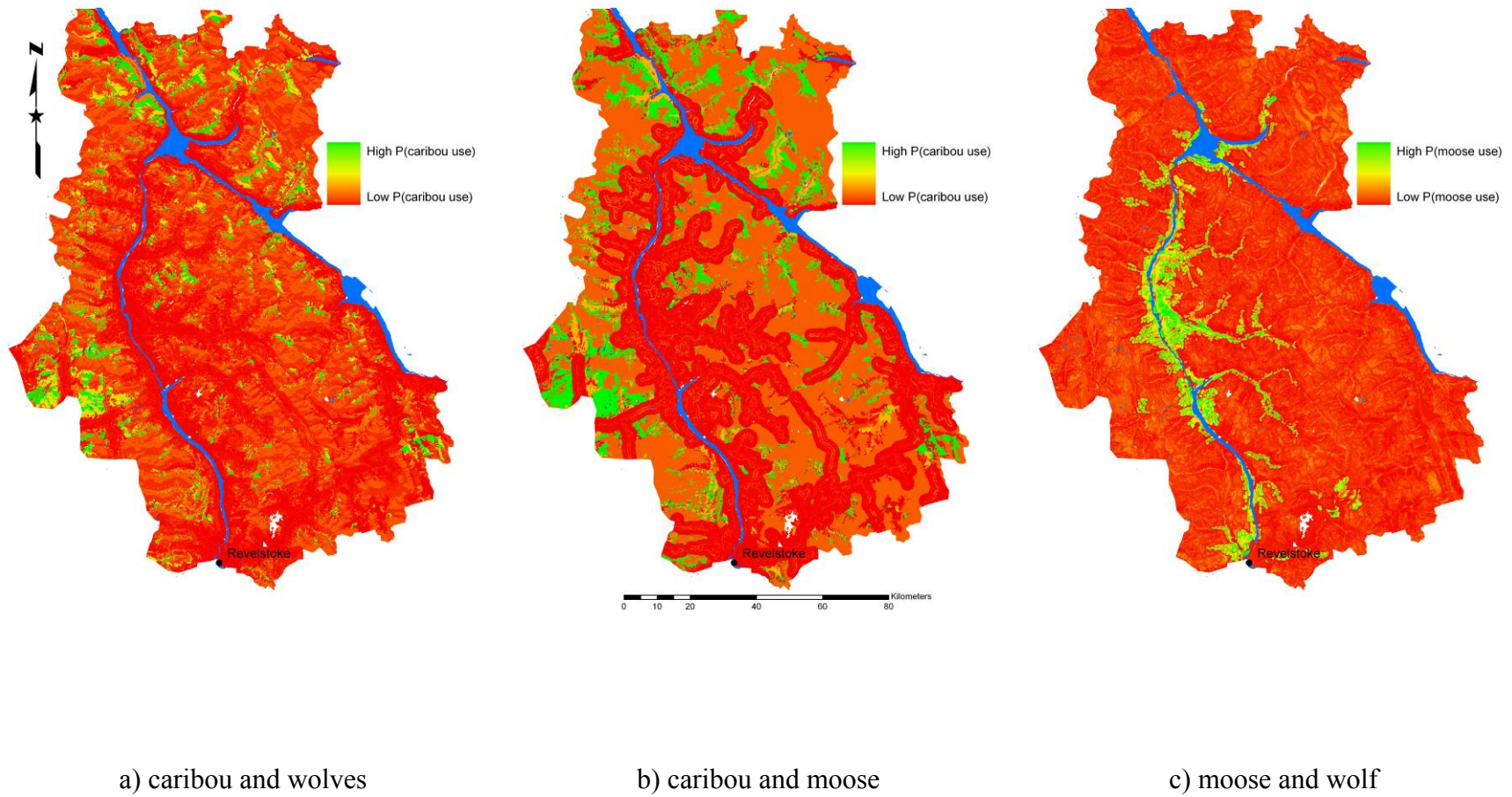
Figure 8. The difference in resource selection between mountain caribou, wolves and moose in the early winter season from 2003-2006 in the north Columbia Mountains, British Columbia.
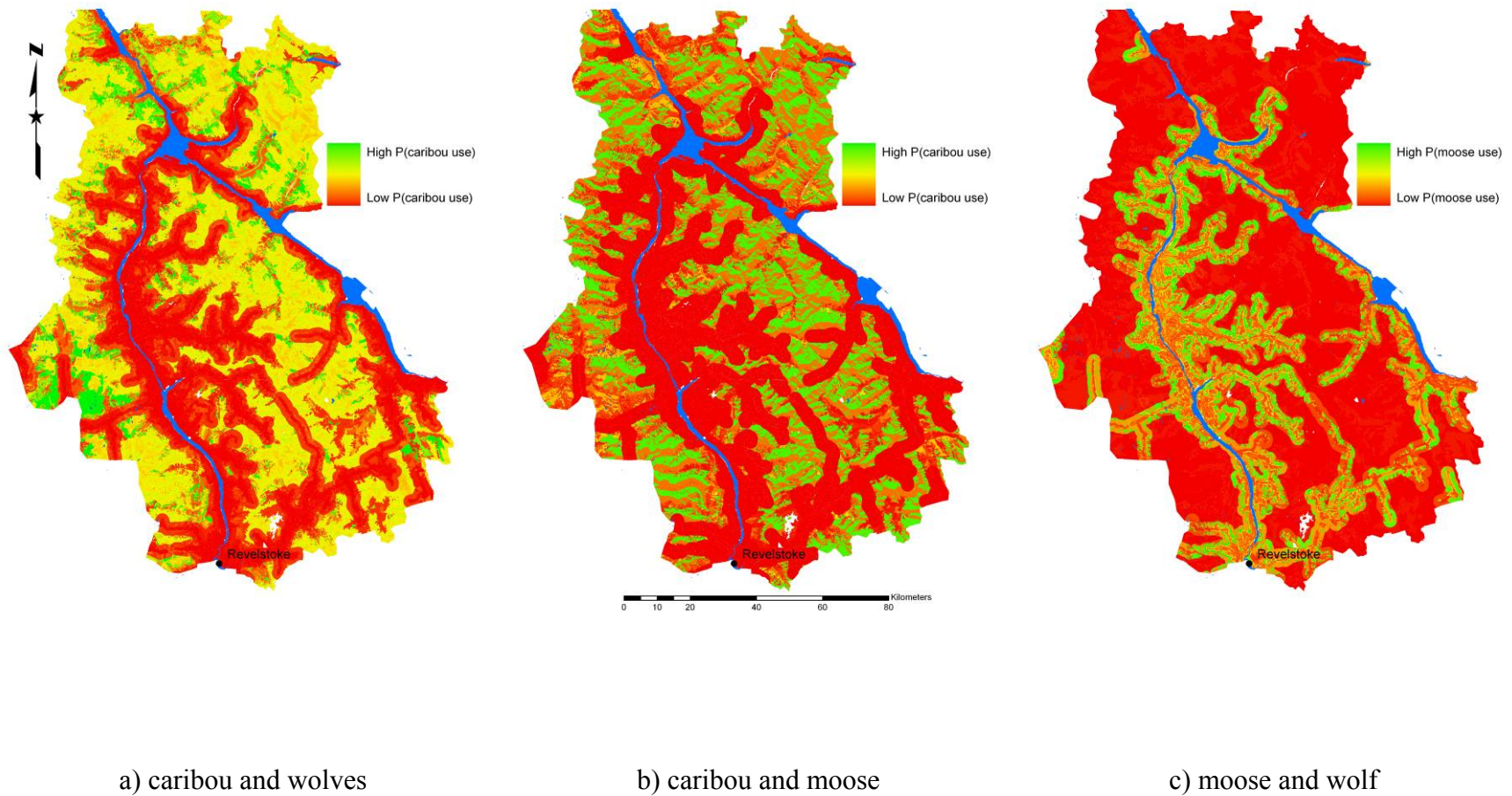
a) caribou and wolves   b) caribou and moose   c) moose and wolf

Figure 9. The difference in resource selection between mountain caribou, wolves and moose in the late winter season from 2003-2006 in the north Columbia Mountains, British Columbia.
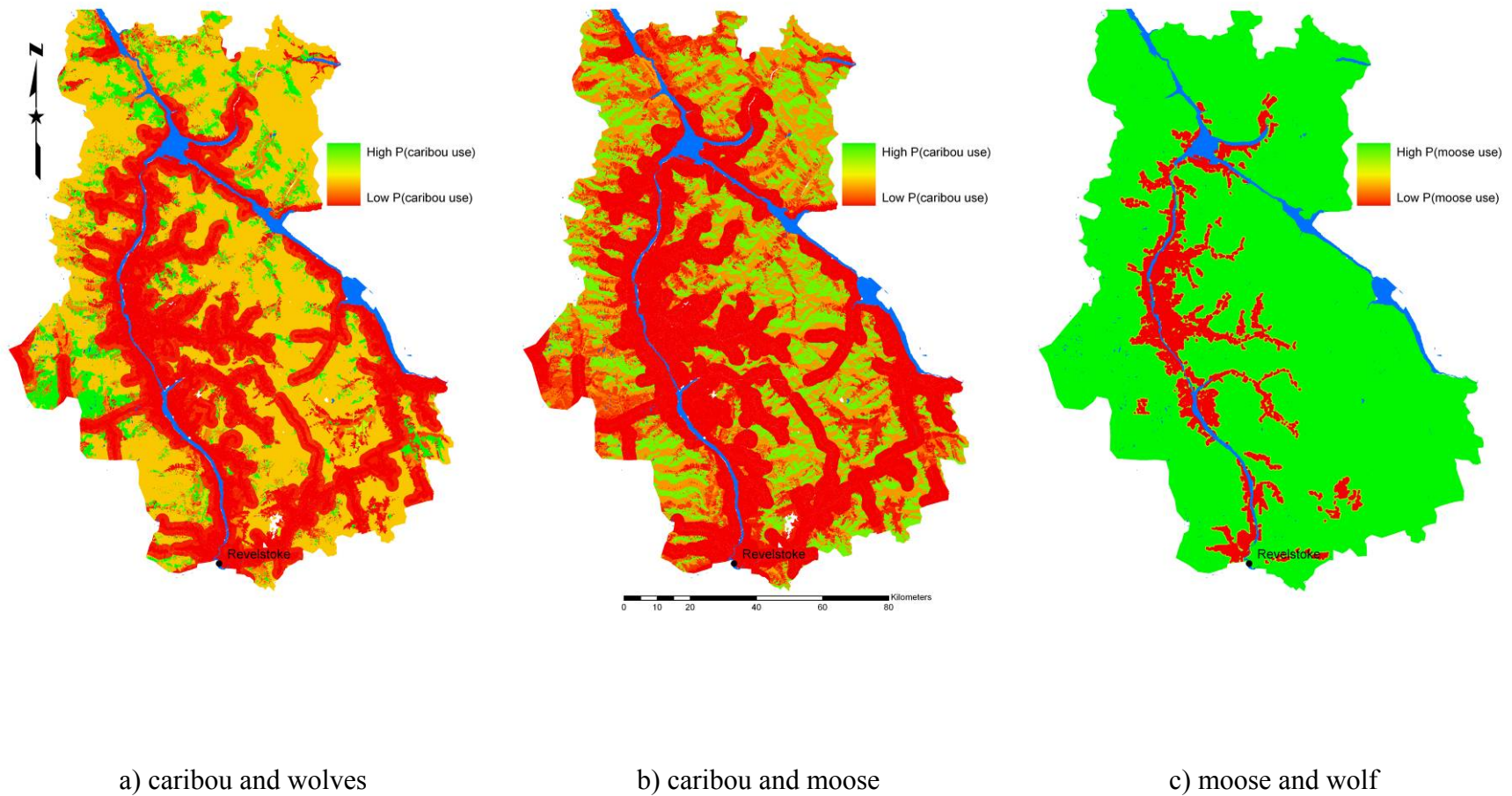
a) caribou and wolves   b) caribou and moose   c) moose and wolf

Figure 10. The difference in resource selection between mountain caribou, wolves and moose in the spring season from 2003-2006 in the north Columbia Mountains, British Columbia.

a) caribou and wolves

b) caribou and moose

c) moose and wolf

Figure 11. The difference in resource selection between mountain caribou, wolves and moose in the calving season from 2003-2006 in the north Columbia Mountains, British Columbia.
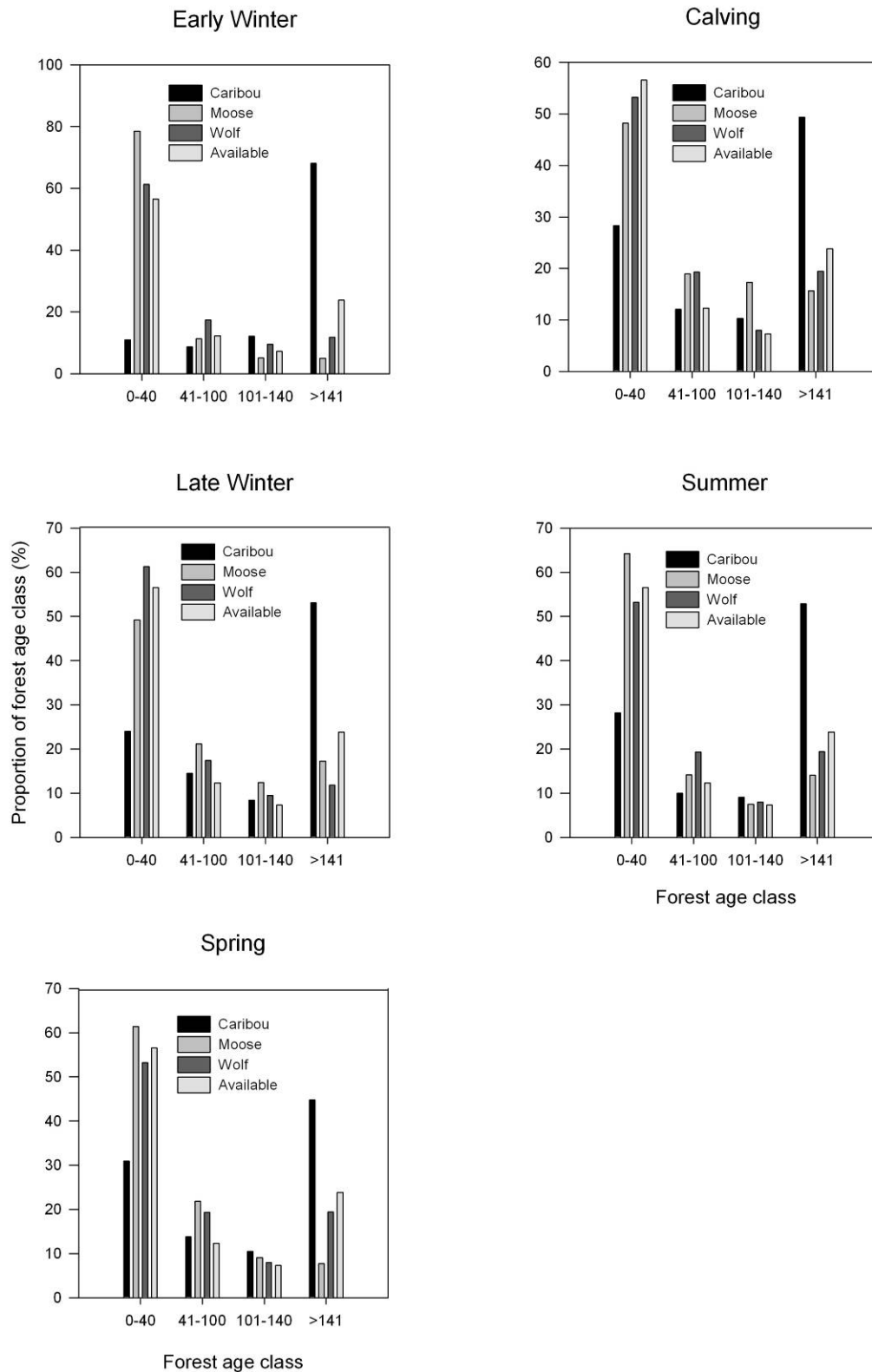
a) caribou and wolves   b) caribou and moose   c) moose and wolf

Figure 12. The difference in resource selection between mountain caribou, wolves and moose in the summer season from 2003-2006 in the north Columbia Mountains, British Columbia.

Figure 13. The available habitat and marginal use of forest age classes for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.
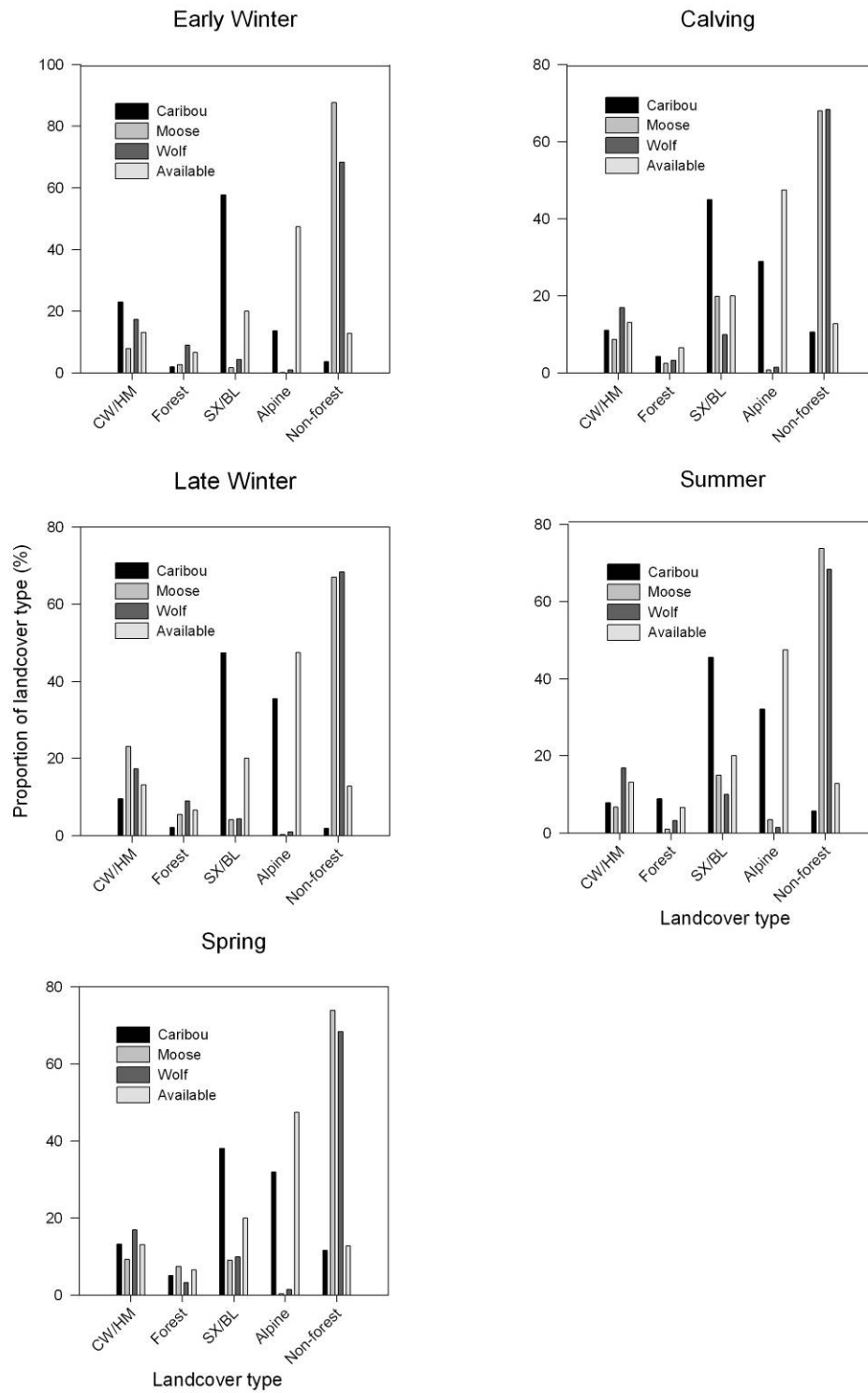
Figure 14. The available habitat and marginal use of landcover for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.
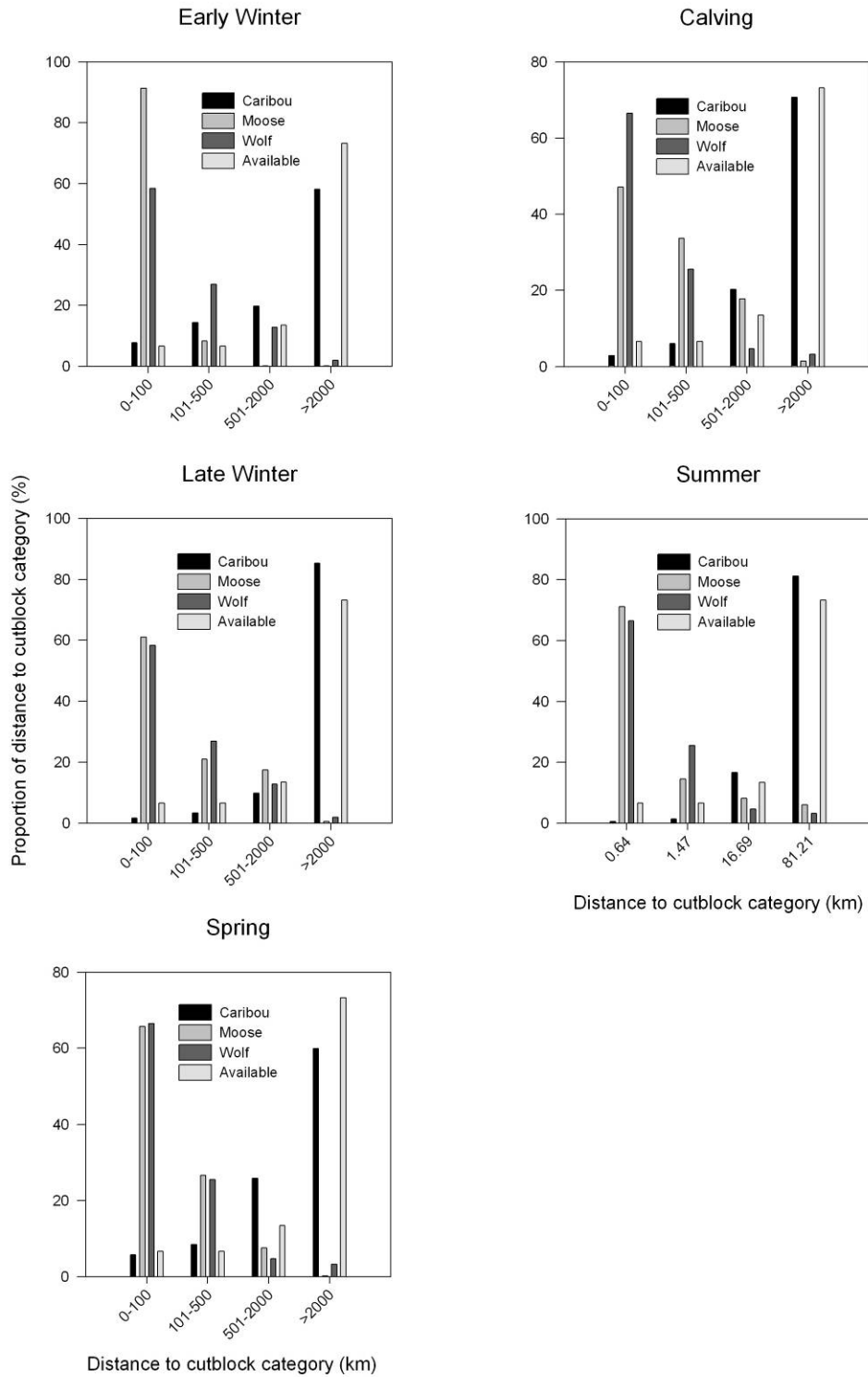
Figure 15. The available habitat and marginal use of distance to cutblock category for moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.
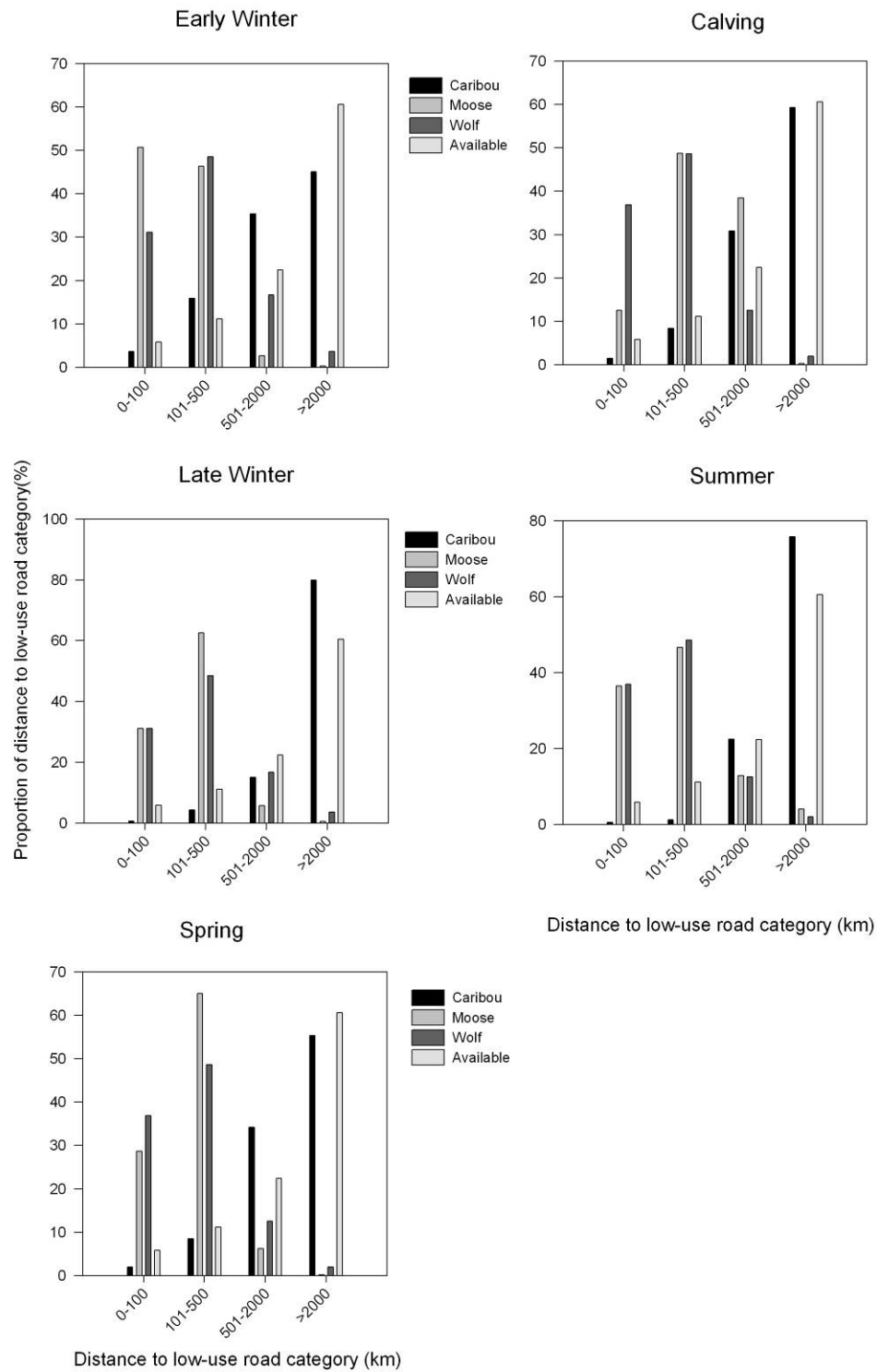
Figure 16. The available habitat and marginal use of distance to low-use road category for caribou, moose and wolves in the north Columbia Mountains, British Columbia from 2003-2006.