Assessing caribou survival in relation to the distribution and abundance of moose and wolves

Final report May 2017

Prepared for the BC Oil and Gas Research and Innovation Society (BC OGRIS)

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Executive summary

Our research focused on quantifying the relationships among caribou, moose, and wolves across gradients of anthropogenic disturbances and moose and wolf densities in northeast (NE) British Columbia (BC). We used fine-scale data provided by GPS monitoring, along with other available data, to explore three hypotheses by which anthropogenic disturbances may be influencing adult, female caribou survival. These mechanisms are predicated on the assumption that increased caribou-wolf encounters leads to decreased caribou survival. Increases in disturbances may increase moose densities leading to increased wolf densities, and thus, increased wolf-caribou encounters. Alternatively, increased disturbances may increase moose-caribou spatial overlap leading to increased spatial overlap with wolves and increased wolf-caribou encounters; and finally, increased disturbances might directly alter wolf distributions leading to increased spatial overlap with caribou and increased encounters.

To understand the influence of anthropogenic disturbances on moose, caribou, and wolf resource selection and spatial overlap, we first identified common, biologically relevant seasons for caribou, moose, and wolves, and established important vegetation and disturbance classes, along with other natural and anthropogenic landscape features. We settled on four seasons (i.e., birthing: May 16 – July 15; late summer: July 16 – October 31; early winter: November 1 – January 31; and late winter: February 1 – May 15) after considering seasonal behaviours and environmental conditions for each species and potential changes in vulnerability to predation for moose and caribou. After obtaining the Ducks Unlimited (DU) vegetation layer, we re-classified the 30 DU vegetation classes in to eight classes, but also tested the value of adding an additional class, marsh. We added four disturbance classes consisting of old and new burns and old and new cutblocks. Our examination suggested that these 12 vegetation and disturbance classes were appropriate for caribou, moose, and wolf resource selection models.

Prior to building resource selection functions in a use-available design, we modeled available locations for moose using the 90^{th} quantile of movement distances for each season. We found that 12-h movements of collared moose were longest during the birthing season (distinct from the actual parturition period) and shortest during late winter. We report male and female moose use and availability for vegetation and disturbance classes and compare these estimates to female caribou and wolf use and availability. Male and female moose consistently used hardwood swamps greater than they were available and treed bogs less than their availability. Caribou demonstrated an opposing pattern (lower use of hardwood swamps and higher use of treed bogs), while wolf use patterns mirrored those of moose. Burns and seismic lines are minor classes in NE BC making patterns of use versus availability difficult to decipher. Moose tended to use new cutblocks more than their availability and wolves used both new and old cutblocks in greater proportions than their availability. Caribou used old burns greater-than their availability during some seasons.

Next, we modelled resource selection for moose, caribou, and wolves. Selection and avoidance of vegetation and disturbance classes matched our comparisons of use and availability. Given the extensive network of linear features across NE BC, we were particularly interested in the role of roads and seismic lines in resource selection. Areas with higher densities of roads were selected by male moose during calving, but were not included in the best-supported resource selection model for male moose during late summer. High road density was avoided by male and female moose during all other seasons. Male moose more frequently selected for locations with high seismic line densities, while female moose tended towards avoidance. Caribou generally avoided high road and seismic line densities, and wolves demonstrated consistent selection for roads and seismic lines.

To examine the potential for anthropogenic disturbances to increase moose densities, we built linear regression models using previously estimated moose densities and several types of disturbances present in NE BC. We predicted that moose densities would be largely driven by vegetation class. Thus, we built competing candidate models, which included the proportion of hardwood swamps (selected by moose) and proportion of treed bogs (avoided by moose), along with one of six disturbance covariates. Disturbance covariates included the proportion of cutblocks, proportion of burns, proportions of burns and cutblocks, density (m/m^2) of roads, density (m/m^2) of seismic lines, and the density (m/m^2) of roads and seismic lines. Our best-supported model included a positive relationship between moose density and the proportion of hardwood swamps and a negative relationship between moose density and the proportion of treed bogs. Moose density was also positively correlated to the proportion of burns, but none of the other disturbance models outperformed the vegetation class only model (moose density = proportion of hardwood swamps and proportion of treed bogs).

As a first step to understanding the influence of anthropogenic disturbances on risk to caribou, we first explored associations between risk and landscape covariates (natural and anthropogenic). Our approach to assessing risk was a two-step process that included the risk of encountering a predator and the risk of being killed given that encounter. We modelled differences between caribou locations versus wolf-caribou encounters and encounters versus locations of caribou mortalities attributed to wolves. Based on that approach, caribou were more likely to encounter wolves near or in areas with higher densities of roads and seismic lines; there was no relationship, however, between linear features and the probability of being killed given an encounter. The probability of encounter also increased in areas with more hardwood swamps and treed bogs and at lower elevations. The probability of caribou being killed by wolves increased in areas with more conifer and hardwood swamps, but decreased in areas with more treed bogs and rich and poor fens in winter. In summer, areas with more edges between vegetation classes decreased the probability of caribou being killed, but areas with higher amounts of terrain roughness increased the probability of being killed given an encounter.

We then evaluated relationships between spatial overlap and risk by visually assessing the predicted spatial overlap (both caribou and moose, and caribou and wolves) between areas most frequently used by caribou and areas where caribou are killed by wolves. Caribou mortalities were more likely to occur in areas with greater amounts of overlap between caribou and moose (male and female) and caribou and wolves across all seasons. Comparisons between areas with high and low spatial overlap (both caribou and moose overlap, and caribou and wolf overlap) revealed that caribou locations with high spatial overlap were less likely to be in treed bogs or poor fens and more likely to have high levels of road and seismic line densities.

Finally, we modelled the probability of mortality for caribou in NE BC. Our focus was to specifically address our three hypotheses relating anthropogenic disturbances to caribou survival. First, increases in disturbances may increase moose and wolf densities and caribou-wolf encounters. Consequently, landscape covariates associated with higher moose densities should decrease caribou survival. Second, increased disturbances may increase caribou-moose spatial overlap leading to increased caribou-wolf spatial overlap and caribou-wolf encounters; therefore, locations more likely to be used by moose will decrease caribou survival. Third, increased disturbances might directly alter wolf distributions and increase spatial overlap and encounters with caribou. Thus, locations more likely to be used by wolves will decrease caribou survival.

We did not find support for our moose density hypothesis, but did find evidence supporting our hypotheses predicting that areas more likely to be used by moose and wolves will negatively impact caribou survival. Disturbance classes (burns and cutblocks) anticipated to increase moose density failed to demonstrate negative relationships with caribou survival. Consistent with our assessment of spatial overlap and locations where caribou are killed, caribou survival decreased in locations with higher predicted probabilities of moose and wolf selection. These findings, in conjunction with selection by moose (during certain seasons) and wolves for linear features, along with the consistent relationship between linear features and spatial overlap, support our hypotheses that linear features decrease caribou survival by increasing overlap with caribou and moose and caribou and wolves.

Collectively, these findings suggest that linear features are the primary anthropogenic disturbances impacting adult, female caribou survival in NE BC via the alteration of moose and wolf distributions. Although cutblocks have the potential to impact caribou survival through changes in moose and wolf densities, our analyses did not support this hypothesis, potentially because there are not many cutblocks in many parts of NE BC. Although we found seasonal variation in the response to linear features by moose and some seasonality in survival (highest survival in early winter), we were not able to fully explore seasonal variability in our caribou survival models due to a limited number of mortalities (n = 33) for our GPS-collared individuals.

Across all seasons, however, overlap with moose and wolves was associated with locations where caribou were killed by wolves and caribou survival models confirmed that caribou are at greater risk in locations more likely to be used by moose and wolves.

We recommend that steps should be taken to limit the number of linear features in or near caribou habitats (poor fens and treed bogs). Further, future development should follow best-practices for limiting the impact of necessary seismic lines via alterations in density, structure, or width. The extensive network of existing roads and seismic lines, however, warrants management actions to restore unused roads and seismic lines when possible. A better understanding of what constitutes restoration and risk prioritization for cores or ranges will be necessary to achieve desirable outcomes and maximize existing funding. Dependent on the ability to effectively restore areas of NE BC, more invasive management actions may be necessary to ensure caribou population viability.

Several additional considerations should be noted. Wolf predation was the primary, proximate cause of adult, female mortality in NE BC. Factors, such as forage quality (or quantity) or disease, however, may interact with predation risk, but additional research would be necessary to tease out these relationships. Further, adult, female survival is only one of many demographic parameters that may be limiting caribou population growth in NE BC. Decreased calf recruitment might be as or more influential than adult, female survival. Efforts should be made to harness existing data, perhaps in the form of an integrated population model, to identify limiting demographic parameters, drivers of those parameters if possible, and more accurate predictions of boreal caribou viability under future management scenarios.

Project overview and objectives

Project scope

Woodland caribou (*Rangifer tarandus caribou*) are listed as threatened or of concern under the Species at Risk Act in Canada. Declining numbers of caribou have been linked to habitat alterations and to complex predator-prey interactions. Predators can disproportionately affect one prey species when those predators are numerically linked to another more abundant prey species (e.g., DeCesare et al. 2010; McLellan et al. 2010). This interaction has relevance to caribou on the boreal landscapes of northeast (NE) British Columbia (BC) because wolves (*Canis lupus*) are the principal predator of caribou, but moose (*Alces alces*) are the primary prey of wolves. Further, current patterns of landscape change in the boreal may result in changes in moose distribution and abundance and related changes in wolf distribution and abundance (Culling and Cichowski 2017).

Our research focused on quantifying the relationships among caribou, moose, and wolves across gradients of anthropogenic disturbances and moose and wolf densities — we used fine-scale data provided by GPS monitoring to explore caribou, moose, and wolf distributions and evaluate drivers of adult, female caribou survival. Our first step was to quantify space-use by caribou, moose, and wolves and determine the influence of natural and anthropogenic landscape features on each species resource selection. We were then able to examine spatial overlap between caribou and moose and caribou and wolves, and predict the influence of anthropogenic disturbances on species overlap. This information provided us with a framework to generate and test hypotheses regarding the mechanisms by which anthropogenic disturbances might decrease caribou survival. These hypotheses are as follows:

i. Anthropogenic disturbances increase moose densities leading to increased wolf densities and increased wolf-caribou encounters and decreased caribou survival;

ii. Anthropogenic disturbances alter moose distributions leading to increased wolf-caribou encounters and decreased caribou survival; and

iii. Anthropogenic disturbances alter wolf distributions leading to increased wolf-caribou encounters and decreased caribou survival.

Project objectives

Using telemetry data from radio-collared moose, caribou, and wolves provided to the University of Northern British Columbia (UNBC), our moose-wolf-caribou interaction analysis determined:

1. if moose distribution and abundance is related to human-caused habitat change inside and outside of core caribou habitat?;
2. if wolf use of caribou habitat is related to moose distribution and abundance?;
3. if predator and prey abundance and behaviour interact to put caribou at increased risk?; and
4. what biotic, landscape, and anthropogenic attributes affect the survival of boreal caribou — with particular reference to those attributes that can be managed?

Project activities

The completed project addressed five activities:

A1) receive and analyze moose telemetry data;

A2) develop initial moose use/selection layers (existing data);

A3) develop initial caribou risk layers using existing data;

A4) refine caribou risk layers using incoming moose, caribou, and wolf data; and

A5) model caribou survival using all moose, caribou, and wolf data.

Here we report on all activities (by activity) undertaken over the course of the two-year project.

Activity 1: Receive and analyze moose telemetry data

Collaring approach and distribution of collars

Studies of habitat use and selection often restrict data collection to females. Our goal, however, was to understand how the presence of moose (likely through apparent competition) may influence risk for boreal caribou. Male moose (i.e., bulls) may be selecting different landscape features than female moose (i.e., cows) at some times of the year (e.g., after the rut when male body condition is low). Therefore, if we only documented locations and selection of cows, and wolves are responding to the location and selection of bulls after the rut, we could miss important aspects of the interaction among moose, caribou, and wolves. Concurrently, we did not want to lose an emphasis on female moose, because information about calving and calf recruitment (from a combination of progesterone tests, movement data, and aerial observations of collared cows) could reveal another season when wolves select locations to target vulnerable individuals. Consequently, our target for deploying collars was one-third bulls and two-third cows, which we maintained throughout the study.

Several factors could influence the link between presence and risk to caribou through apparent competition. Such factors may include relative densities of moose, caribou, and wolves, and the extent of natural and anthropogenic disturbance on the landscape. In order to maximize the spread across the different gradients potentially affecting the interactions among moose, caribou, and wolves, we chose to have moose collared in three areas: the Chinchaga RRA, Clarke Core, and Fortune Core in NE BC.

In total, 63 individual moose were captured by Diversified Environmental Services (under contract from BC FLNRO) and affixed with Vectronic Aerospace VERTEX Survey Globalstar collars set to transmit individual locations twice daily at 0300 and 1500 GMT. Three individuals were originally collared in March 2015 and then recaptured and recollared in January 2016 following collar failure. Collared individuals were distributed in or in close proximity to the Chinchaga Core (13 females; seven males), Clarke Core (15 females; seven males), and East Fortune Core (14 females; seven males; Table 1).

As of March 2017, 46 of the original 63 collared moose were still transmitting data. Fifteen moose have died and two additional females (one Chinchaga and one Clarke) have stopped transmitting locations. A male moose from the Fortune was killed by wolves immediately following capture and a female from the Clarke died in the spring during birthing. Five females (1 Chinchaga, 3 Clarke, and 1 Fortune) and two males (1 Chinchaga and 1 Fortune) were killed by wolves during winter 2015–2016. One female from the Fortune and one male from Chinchaga died of unknown causes in the spring of 2016 and were infested with a large number of winter ticks (*Dermacentor albipictus*). In the fall of 2016, a male from the Fortune was harvested, and during the winter of 2016-2017, two females from the Fortune and a male from the Chinchaga were killed by or suspected of being killed by wolves. Several individuals have undergone short forays into the Northwest Territories, and at present two individuals remain north of the BC border (Table 1).

Table 1. Current status and fate of GPS radio collars deployed in northeast British Columbia through April 2017.

Area	Collared		Mortality		In NWT		Failed GPS (Replaced)		Active	
	F	M	F	M	F	M	F	M	F	M
Chinchaga RRA	13	7	1	3			1(0)		11	4
Clarke Core	15	7	4				1(1)		11	7
Fortune Core	14	7	4	3	1	1	2(2)		10	4

We downloaded 40,997 moose locations through the Globalstar satellite system collected from March 2015 – December 2016 (Figure 1). The December 2016 cutoff was necessary in order to ensure sufficient time to meet objectives in accordance with project timelines. After previously determining that additional locations, not transmitted via the Globalstar satellite system, are stored on the collars (Mumma and Gillingham 2016), we directly downloaded location data (808 additional locations) from 11 of 14 collars collected from moose mortality locations. Eight of the 11 collars contained locations (10 – 255 additional locations) not transmitted via the Globalstar satellite system. These additional locations brought the fix rates above 90% for six of the eight collars (Table 1) providing further justification for the retrieval and direct downloading of collars from all moose mortalities. We did not directly download data for the male moose killed immediately after capture during the winter of 2015. The short duration between collaring and mortality precluded its inclusion in further analyses and the remaining two collars are still awaiting shipping from BC FLNRO Fort St. John office and were not included in our analyses.

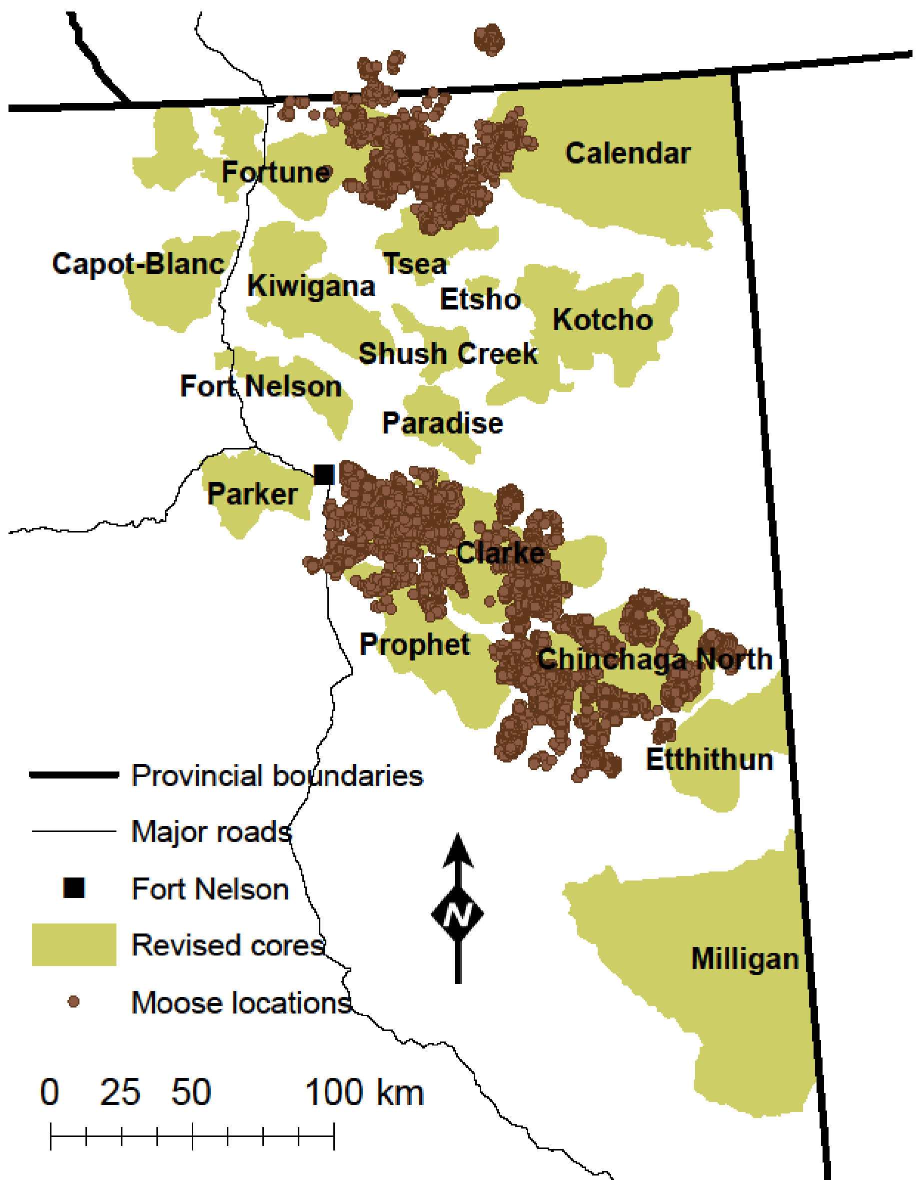

Figure 1. Distribution of moose telemetry fixes from March 2015 through December 2016 in northeast British Columbia. Bullets represent individual fixes for 62 (Table 1) male and female moose (not including male moose killed soon after capture in March 2015).

Because we needed to be able to screen data and continually update our models as new data became available, we developed programs to evaluate and view locations (currently in Google Earth) shortly after each download (Mumma and Gillingham 2016).

Telemetry screening tools

As described above (and in Table 1), there were 15 mortalities of collared moose during this study. In several cases, however, mortality-site investigations lagged weeks behind the mortality. The VERTEX collars are programmed to send a mortality email alert (and concurrently switch the collar to send several fixes at 30-min intervals) if minimal movement occurs between several consecutive fixes, but there are other animal movement and collar-performance patterns that may also be indicative of potential mortalities, warranting close monitoring or site investigation. Several such scenarios are listed in Table 2. For example, an abnormally long movement could be associated with an animal be chased by predators and

Table 2. Potential anomalous collar signals and movements that could be associated with potential mortality events.

Move and Fix Scenarios
Abnormally long movement between consecutive fixes
Long collar movement followed by no fixes
Long collar movement followed by little subsequent movement
Many consecutive missed fixes
Many consecutive short movements

a subsequent kill might place the collar in a position such that no fix can be received or transmitted for several days. Consequently, we developed an Excel macro that flags the scenarios outlined in Table 2 by monitoring for rapid fixes (associated with mortality messages in case the actual message is not sent or received), tracks fix rate, and then produces individual KML (i.e., Google Earth Markup language) files for each downloaded moose. The interface for the program (Figure 2) allows customization of the screening criteria (Figure 3). Individual KML files are colour-coded

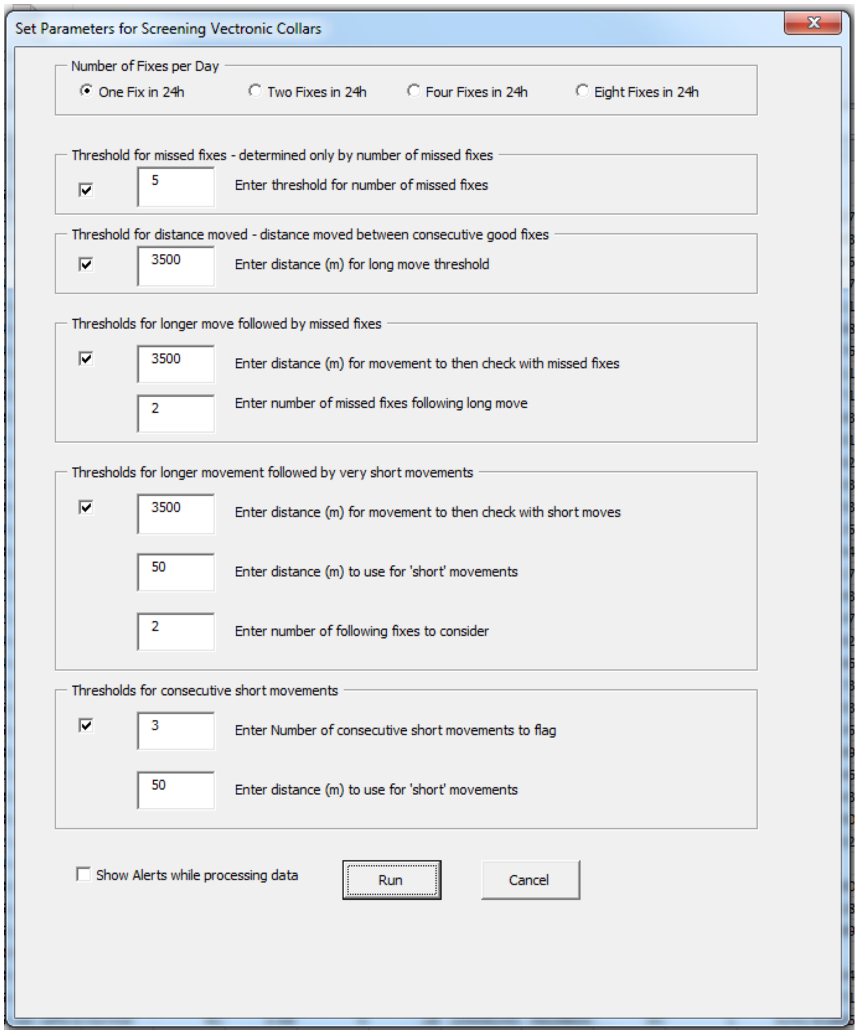

Figure 2. Screen capture of user-interface for screening Vectronic radio-collar downloads.

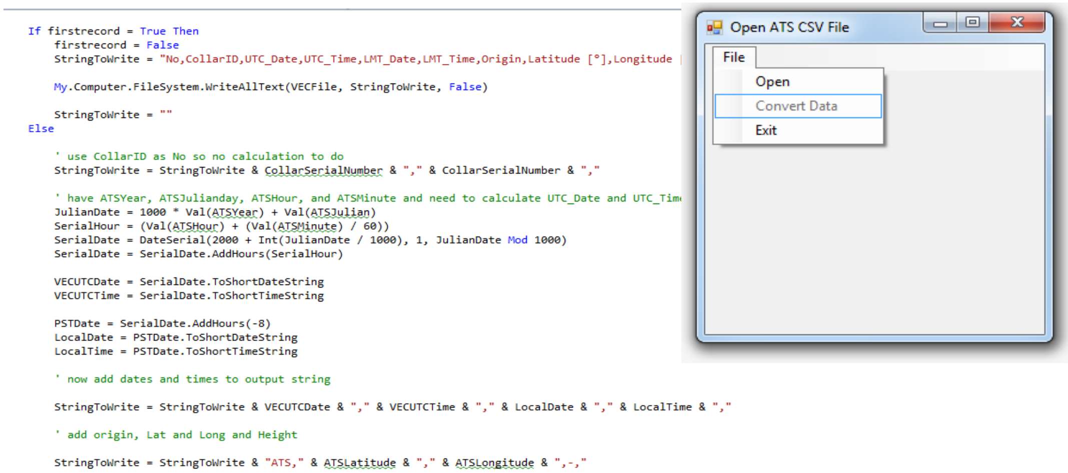

Figure 3. Screen capture of portion of program written to reformat ATS collar data into Vectronic collar format. Reformatted data can then be screened with the telemetry point screening program.

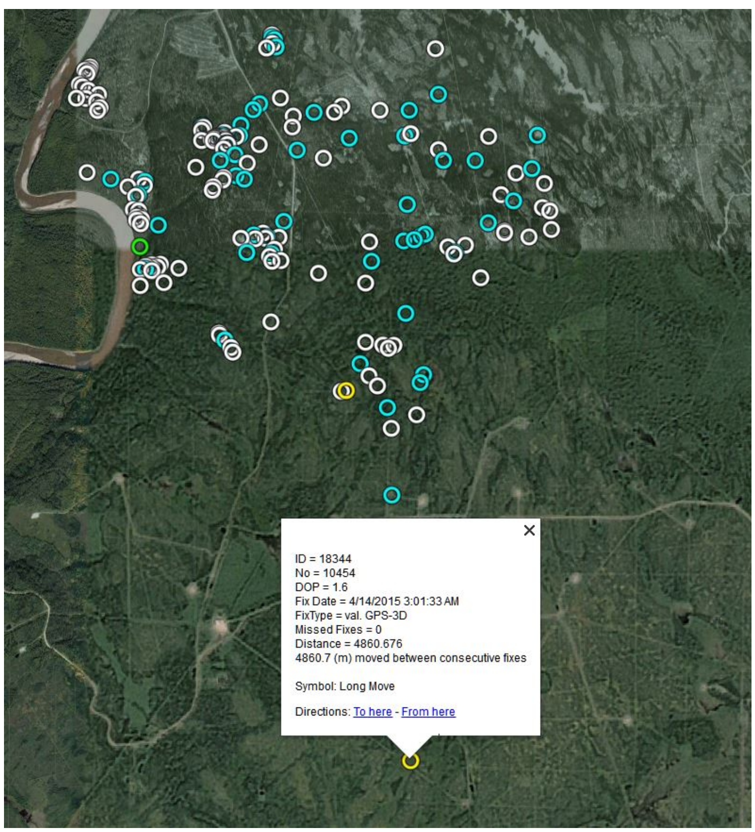

Figure 4. Portion of a KML file (viewed in Google Earth) for an individual collared moose. Different colour symbols are used to indicate long movements, missed fixes, and other scenarios (Table 2). Clicking on any symbol allows the user to view several attributes associated with that location.

for each type of flag (for moose) and document location attributes (see Figure 4). By using these combined tools, data could be quickly screened both by tabular inspection of flags and via examination of locations in Google Earth for anomalous (and potentially mortality related) movements. This combined approach has resulted in very rapid responses to mortalities in another ongoing study of moose (Kuzyk et al. 2016), but for a variety of reasons was not fully implemented in this project.

Collar fix rates

Obtaining a high fix rate (high number of animal locations out of the possible number of locations) is important to ensure unbiased estimates of habitat use — if animals in habitats with high canopy coverage have lower successful acquisition of GPS locations, for example, then there can be a bias in estimates of habitat use. In our initial screening of data for fix-rate success, we observed that the rate of successful fixes declined through September before improving from October onward (Figure 5). In addition, we also found that the average number of consecutively missed fixes had increased between March and September.

We proposed several hypotheses that might explain these trends including changes in the proportion of open habitats selected, an increase in movement distances between fixes, an on-average northward trend in animal locations affecting satellite dimensionality, and the influence of a few severely malfunctioning collars. We performed several analyses to test our various hypotheses. To determine if 'closed' (canopy) habitats were impacting fix rate success, we reclassified the 30 vegetative classifications of the Ducks Unlimited Vegetation Layer (Ducks Unlimited Canada 2013) into open and closed habitats in accordance with classification descriptions provided with those data layers. We then tested if there was a relationship between individual monthly fix rates and the proportion of open habitats used. In addition, we looked for relationships between individual monthly fix rate and the centroid of monthly fix latitudes for each moose and the average monthly consecutive-fix movement distance of each moose. We also visually evaluated monthly fix rate trends for each individual between March 2015 and September 2015. We did not detect any significant relationships between fix rate success and the proportion of open habitats used, latitudinal position, or movement distance,

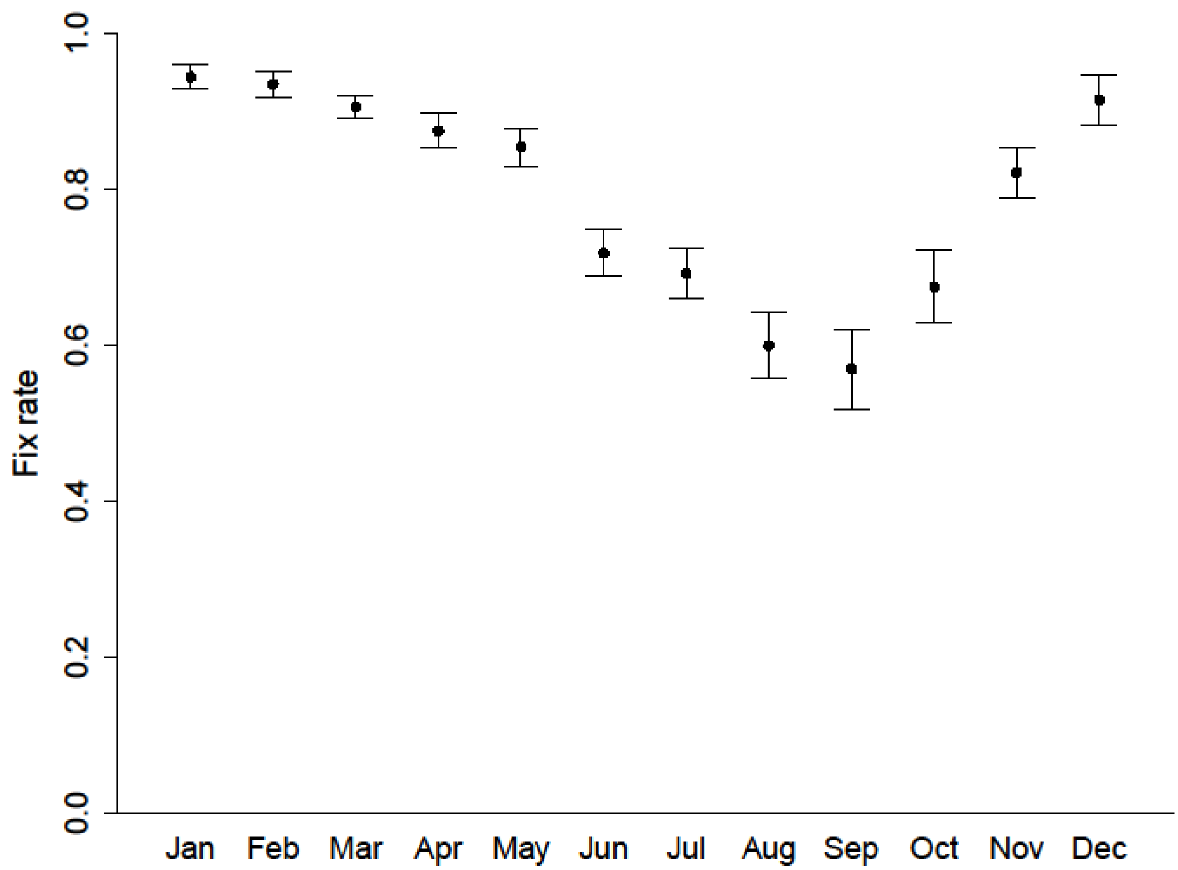

Figure 5. Mean (± SE) fix rate success (i.e., the proportion of possible fixes that were successfully recorded) as the study has progressed from April 2015 through December 2016.

and overall, the majority of individuals were undergoing a similar moderate decline in fix rate over time. We did, however, observe that generally individuals that spent >70% of their time in open habitats in a given month appeared to have fewer low monthly fix rates. More recently, we conducted a similar analysis of the same model of collar that has been deployed in central BC for approximately two years. In those data, we saw a similar drop in fix rate success during the summer months of both years followed by an increase in fix success during the fall and winter months. The most likely explanation appears to be that moose were spending more time in closed canopy areas in warmer months, which led to reduced fix rate success. Directly downloading collars recovered from moose mortalities, however, largely eliminated the seasonally low fix rates, because additional fixes are stored on the collars (so there were minimal issues with fix acquisition by the collars), but fail to transmit via the Globalstar satellite system (Mumma and Gillingham 2016). Because collars were only available for download following mortality and collar recovery or recapture, fix rates remain low for some living individuals during months with low fix rates.

Activity 2: Developing moose use/selection layers

Our first step to unraveling moose spatial patterns and their interactions with caribou and wolves was to define biologically relevant seasons that were applicable to all three species (Mumma and Gillingham 2016). Next, we established a means of defining availability and generated random available locations (Mumma and Gillingham 2016). We then defined our vegetation classes and explored their distributions at used and available locations (Mumma and Gillingham 2016). Finally, we determined additional landscape covariates hypothesized to drive selection patterns of moose (Mumma and Gillingham 2016) and built resource selection functions. We were particularly interested in the role of linear features on moose selection, given that roads and seismic lines are widespread across NE BC and might alter the amount of overlap between moose, caribou, and wolves.

Determining of seasons

Generally, individual selection patterns of moose vary seasonally in conjunction with animal behaviours (i.e., birthing, rearing of young, breeding, etc.), nutritional needs, and food availability (e.g., Gillingham and Parker 2008). We thought it was important to define several biologically relevant seasons in order to identify differences in selection throughout the year. Establishing seasons for this project posed a unique problem, because the research includes three species with an overall objective of understanding how the interactions among moose, caribou, and wolves influence caribou survival. Given this objective, we decided to establish identical seasons across species.

After consulting the work of other researchers, considering seasonal behaviours and environmental conditions for each species, and recognizing a need to assess potential changes in vulnerability to predation, we settled on four seasons (i.e., calving, late summer, early winter, and late winter). Each species gives birth in the spring marking a period when the vulnerability of young moose and caribou calves potentially modifies the behavior of adult females. Ungulate calves serve as an abundant prey for wolves that are concurrently constrained by their own rearing of pups. Although both moose and caribou demonstrate a birth pulse around the beginning of June, we set our calving period from May 16th to July 15th to capture the earliest date when calves of both ungulate species are born until the date when the vulnerability of late-born calves (calves born in mid-June) has declined (calves reach ~ one month of age — Gustine et al. 2006). This period also coincides with wolf pups becoming more mobile marking the beginning of our late summer season, which we defined from July 16th until October 31st. Late summer represents a snow-free season when young of the year are increasingly mobile and ungulate adults are maximizing consumption for the winter months ahead. Given the expectations of snow accumulation and ungulate body condition decline throughout winter, we thought it was important to define early and late winter seasons. We anticipated that early winter (November 1st – January 31st) would consist of moderate snow depths and relatively good ungulate body condition with the possible exception of mature ungulate males following the extensive energetic demands of the rut. We characterized late winter (February 1st – May 15th) as a period of increased snow depths and reduced ungulate body condition for both sexes.

Defining availability

Availability has been defined in a variety of ways in resource selection studies (e.g., Latham et al. 2013; Johnson et al. 2014). We chose to select a method that utilized information on movement to characterize locations that were truly available to a given individual without making assumptions associated with home-range based methods of determining availability. For each moose, we evaluated the distance moved between all 12-h consecutive locations (Figure 6) and determined the 90th quantile of movement distances for each individual by season (Figure 7). Those values represent the 'normal' range of moose movement distances, and therefore provide a means to define the area around each location from which a moose could have selected an alternative location. We buffered each moose location by the 90th centile movement distance for that individual during the corresponding season and then randomly selected five locations within the buffered area. The 90th movement centile ignores rare, abnormally long movements associated, but attempts to account for normal movements that could have been made around known fix locations. We implemented a similar approach when defining availability for caribou and wolves, although we reduced the buffer for wolves to the 80th quantile of movement distances, because of their propensity for occasional long movements that resulted in excessively large buffers.

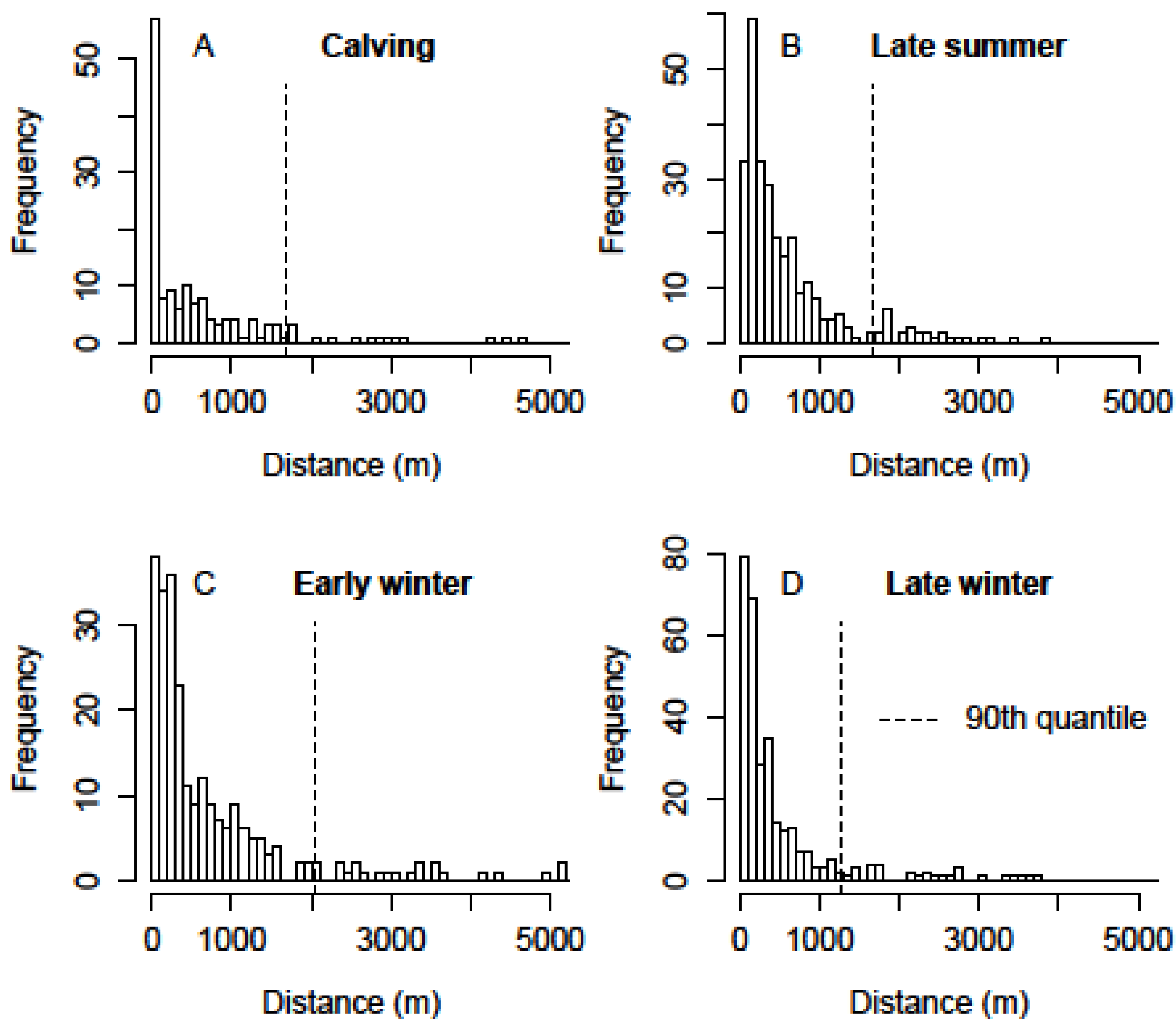

Figure 6. Frequency distributions and 90th quantiles of distances moved between consecutive 12-h fixes for one collared moose in northeast British Columbia by defined seasons.

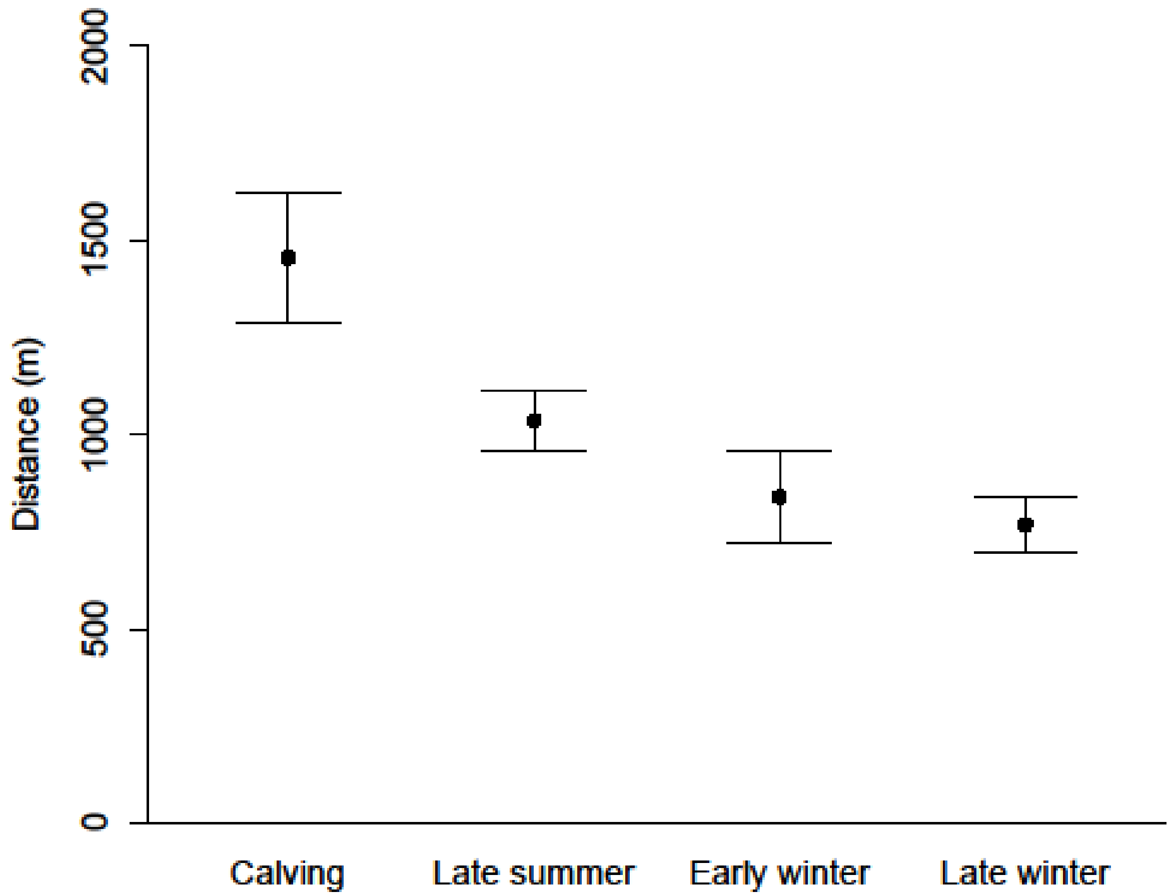

Figure 7. Mean (and 95% confidence intervals) of the 90th quantiles of distances moved for each individual radio-collared moose in northeast British Columbia by season.

Developing vegetation and disturbance classes

A first step in understanding moose distributions is to determine the influence of vegetation class on moose use. We signed an agreement with Ducks Unlimited Canada (hereafter DU) that allowed us to use their vegetation classification layer for the boreal region of British Columbia (Ducks Unlimited Canada 2013). Our covariates included eight categorical vegetation classes that were reclassified from the DU layer using the methods detailed by Demars (2015). These classes included conifer swamp, hardwood swamp, rich fen, poor fen, treed bog, upland conifer, upland deciduous, and other as our reference category. The other class included non-habitat (e.g., open water, anthropogenic, etc.) and minimally-present vegetation classes. We added four additional categorical disturbance classes (old burns, new burns, old cutblocks, and new cutblocks) using a combination of the Ducks Unlimited Canada layer and fire and cutblock layers downloaded from the BC data distribution service (DDS; available at https://apps.gov.bc.ca/pub/dwds/home.so). The earliest fires detected (1963) by the Ducks Unlimited Canada layer aligned with research indicating persistent changes in forest structure out to approximately 50 years post-disturbance (Kashian et al. 2005). We, therefore, identified old burns and cuts as disturbances occurring between 1963 and 1998 and new burns and cuts as disturbances occurring from 1999 to the present anticipating changes in forage quality and thermal and concealment cover between old and new disturbances (Fisher and Wilkinson 2005).

Moose vegetation and disturbance class use

Comparisons of vegetation class and disturbance class use by male and female moose followed similar trends. Both male and female moose consistently used hardwood swamps and rich fens in greater proportions than are available and treed bogs and poor fens in lesser proportions in comparison to their availability across seasons (Figures 8 and 9). Both sexes also tended to use uplands (i.e., conifer and deciduous) in greater proportions than were available during calving and late summer, but in lesser proportions than were available in the winter (early and late winter; Figures 8 and 9). Slight disparities were evident between male and female moose for conifer swamps, new burns, and cutblocks. Males used conifer swamps in slightly greater proportions than were available during calving and late summer, but lesser than were available in winter, while females consistently used conifer swamps less than their availability (Figures 8 and 9). The proportions of use and availability for disturbance classes were small making it difficult to extract definitive use-available differences, but it was apparent that males generally had higher amounts of used and available proportions of new burns and cutblocks (Figures 8 and 9), which they tended to use in greater proportions than were available (Figure 8). Females demonstrated an affinity for new cutbocks but not for new burns (Figure 9).

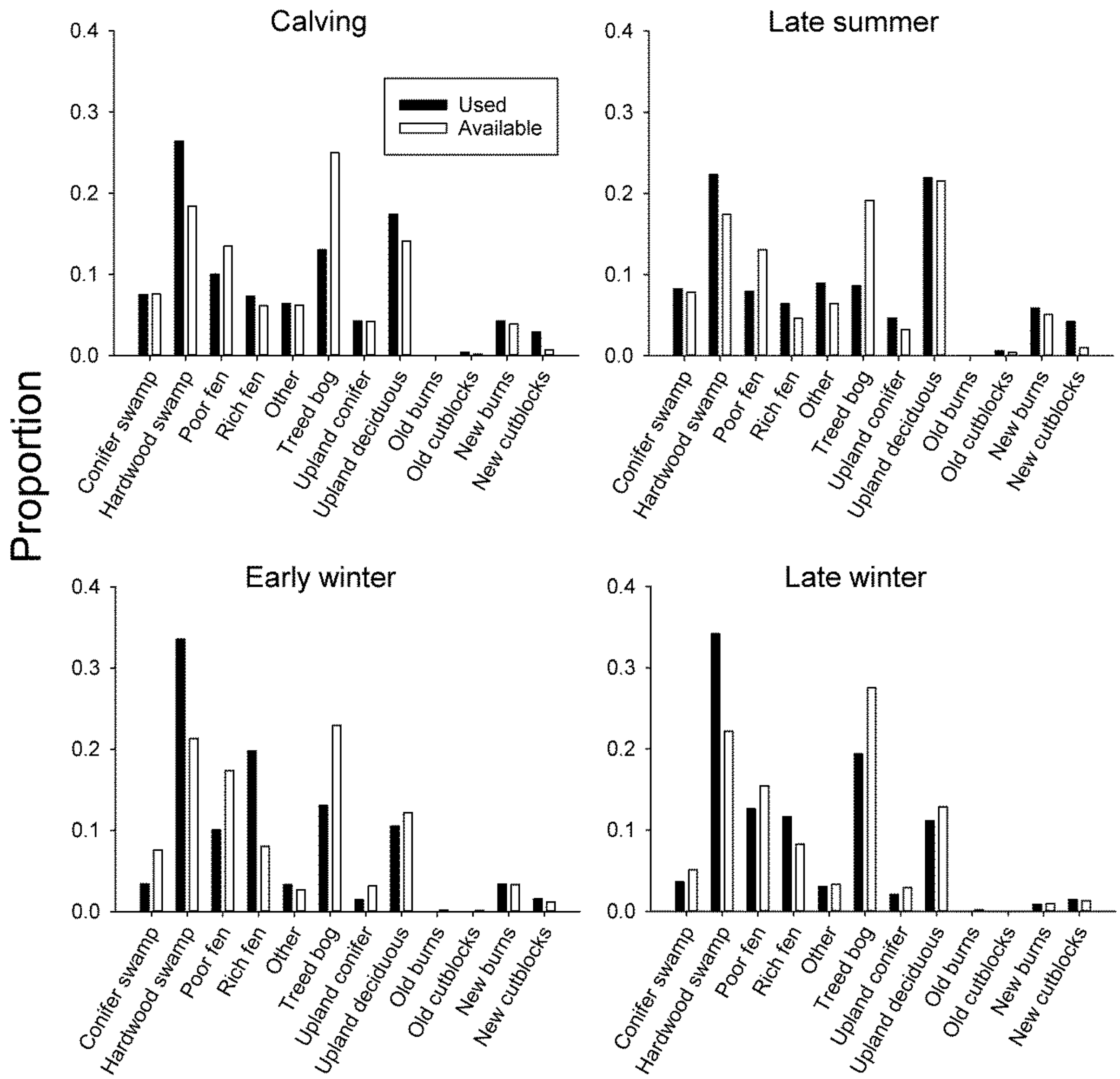

Figure 8. Seasonal use and availability of 12 vegetation and disturbance classes (see text) by collared male moose in northeast British Columbia.

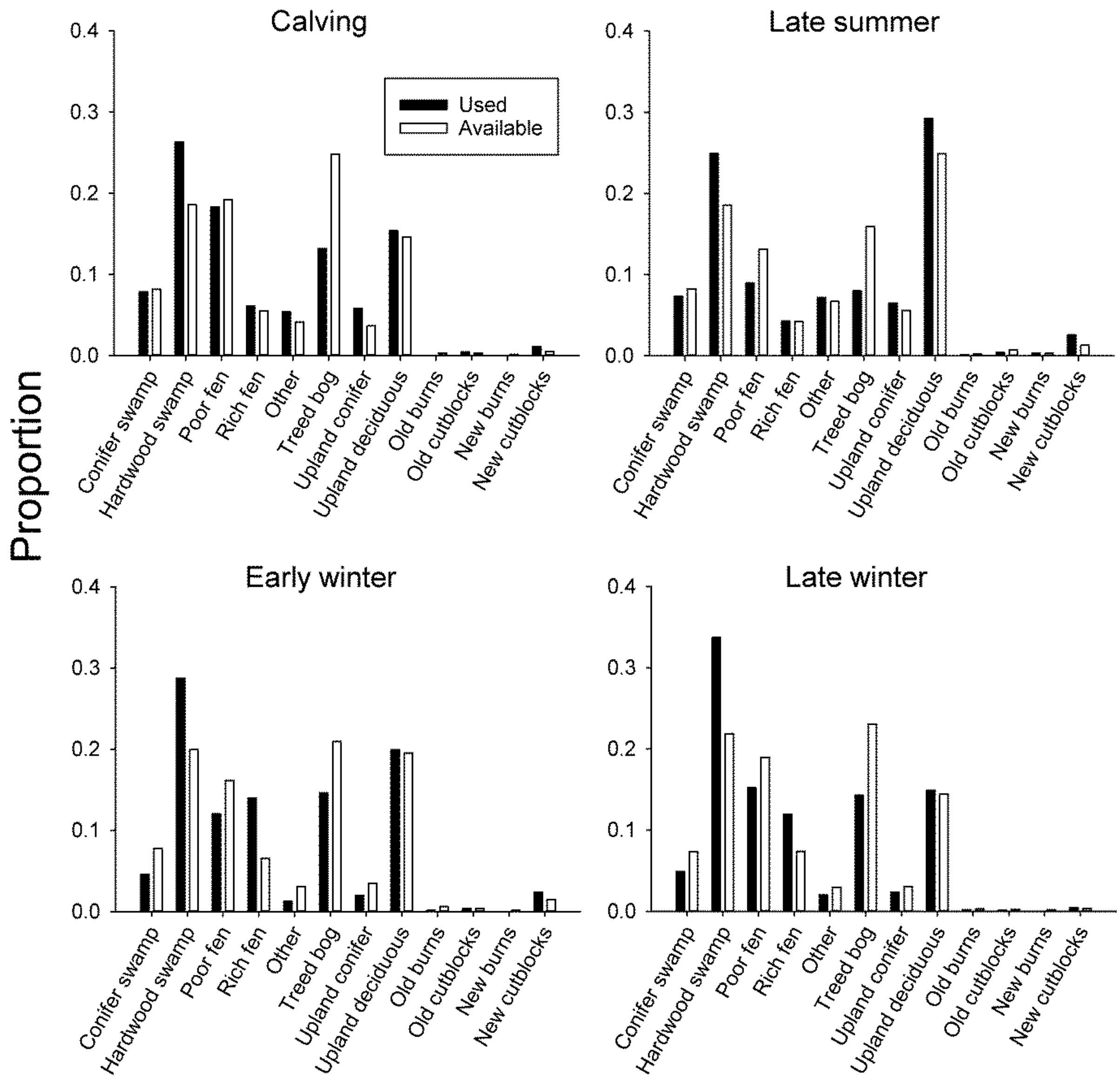

Figure 9. Seasonal use and availability of 12 vegetation and disturbance classes (see text) by collared female moose in northeast British Columbia.

<u>Comparing use between species</u>

We evaluated vegetation and disturbance class use by caribou and wolves in the same manner as moose. Comparisons of moose and caribou vegetation class use and availability revealed species differences between space-use at two different spatial scales. At a finer-scale, caribou used treed bogs and poor fens in greater proportions than are available and generally used all other vegetation classes less than their availability (Figure 10). Differences in the proportions of availability between moose and caribou revealed larger-scale differences in space-use. Caribou exhibited higher available proportions of treed bogs and poor fens, thereby indicating that they were broadly positioning themselves in areas with more treed bogs and poor fens and less swamps and uplands (Figure 10).

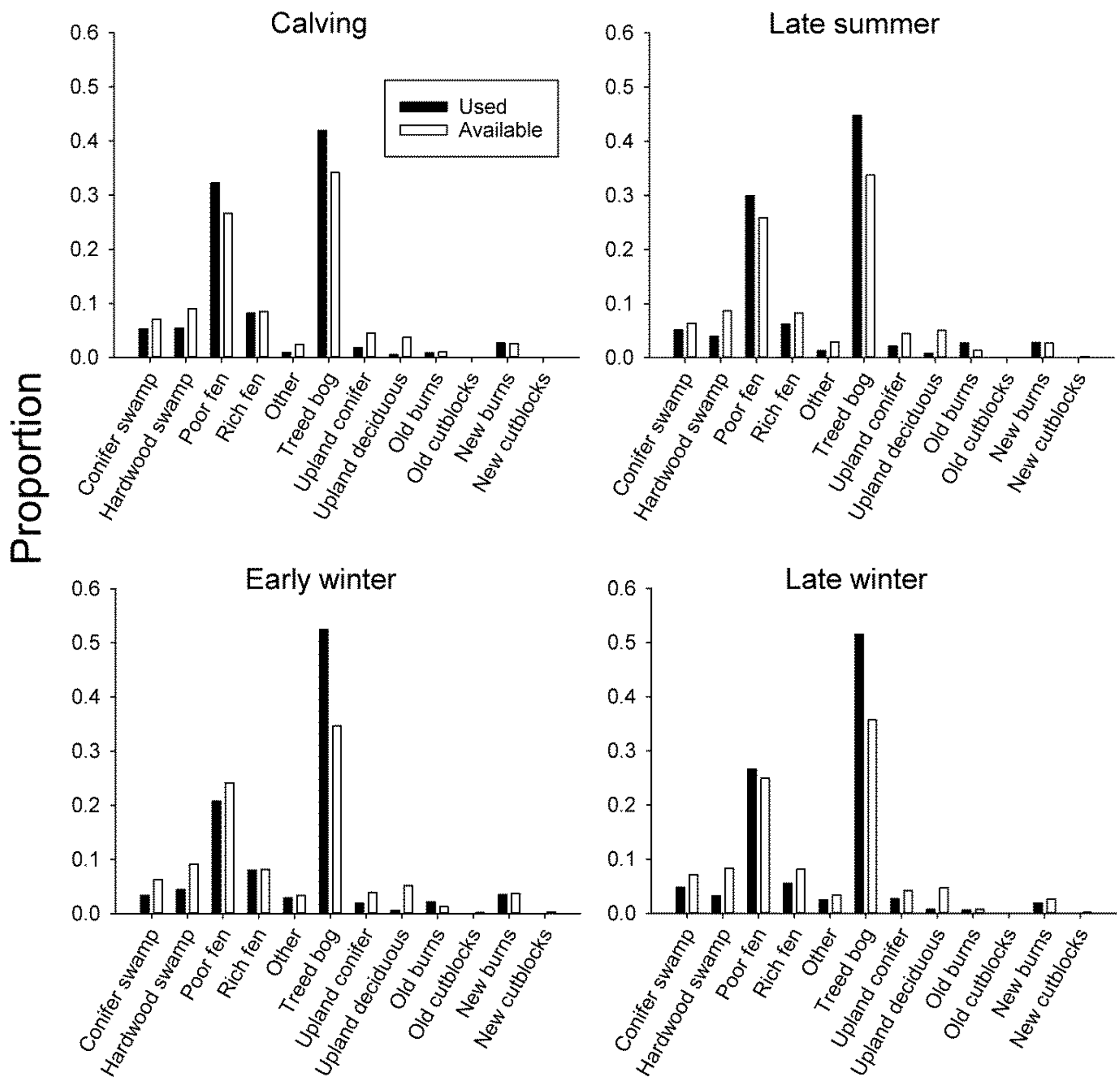

Figure 10. Seasonal use and availability of 12 vegetation and disturbance classes (see text) by collared female caribou in northeast British Columbia.

Wolf use largely mirrored that of moose with the notable exception of the other vegetation class, which wolves used in greater proportions than are available (Figure 11). This likely reflects wolf use of linear features that in some instances were characterized as anthropogenic by the DU layer and lumped into the 'other' vegetation class. The small proportions of available burns

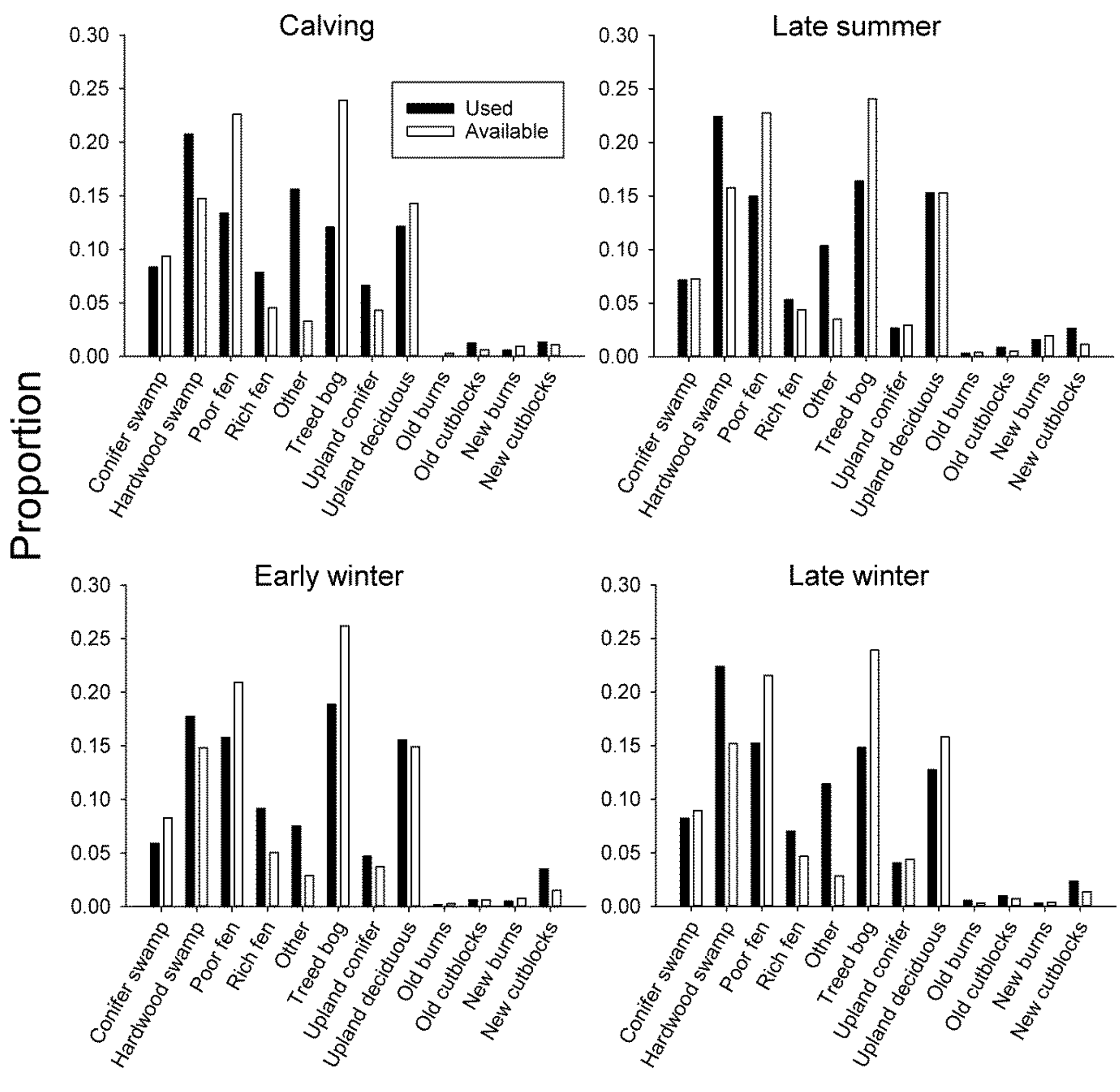

Figure 11. Seasonal use and availability of 12 vegetation and disturbance classes (see text) by collared wolves in northeast British Columbia.

and cutblocks made species comparison difficult, but caribou seemed to be using old burns in greater proportions than are available during some seasons (Figure 10) and wolves demonstrated an affinity for old cutblocks and new cutblocks (Figure 11), which is consistent with moose (Figures 8 and 9).

Moose resource selection functions

Prior to building resource selection functions, we determined additional landscape covariates hypothesized to drive selection patterns of male and female moose. These covariates were created using downloaded layers from the BC DDS and the BC Oil and Gas Commission (OGC; available at http://data-bcogc.opendata.arcgis.com/). Naturally occurring landscape covariates included elevation (BC DDS), terrain roughness within a 100-, 500-, and 1000-m buffer (standard deviation of slope; Grohmann et al. 2011), habitat richness (number of unique habitats within a 100-, 500-, and 1000-m radius), and distance to water (m). Additional anthropogenic covariates included the density of roads (m/km^2; 100-, 500-, and 1000-m radius) and density of seismic lines (m/km^2; 100-, 500-, and 1000-m radius; BC OGS). We used the density of linear features instead of distance to linear features, because we hoped to not simply capture wolf use of linear features, but also the potential for linear features to more broadly alter wolf distributions.

We used mixed-effects logistic regression to estimate resource selection functions (i.e., Johnson et al. 2006), including random intercepts for individual (package lme4, Bates et al. 2015), and performed our analyses in a hierarchal manner. We first ran univariate models to identify the best-supported buffer (100, 500, or 1000 m) for terrain roughness, habitat richness, density of roads, and density of seismic lines and determine if elevation was best modelled as a linear or quadratic relationship using Akaike's Information Criteria (Akaike 1998) for small sample sizes (AIC_c; Burnham and Anderson 2002; package MuMIn, Bartón 2015). We also used AIC_c to determine the most parsimonious characterization of burns and cutblocks. These characterizations were as follows: i) old burns, old cutblocks, new burns and new cutblocks; ii) all burns (old and new burns) and all cutblocks (old and new cutblocks); and iii) old seral (old burns and cutblocks) and new seral (new burns and cutblocks). We then used these and the remaining covariates to build competing hypotheses and selected the most parsimonious models (Burnham and Anderson 2002) for each season and sex using AIC_c. For several seasons, multiple models garnered support as evidenced by $\Delta AIC_c \leq 2$, which is the difference in AIC_c values between the top model and the model under consideration. The more complex models in these circumstances included all the covariates present in the simpler models and one additional covariate. Because AIC_c imposes a penalty of 2 AIC_c units for each additional covariate, we chose the more complex model as our top model only when delta AIC_c values were $<$1.95, thereby indicating that the additional covariate explained variance beyond the variance described by the simpler model. All statistical analyses were completed in program R (R Core Team 2015).

Vegetation classes selected by male moose included hardwood swamp and upland deciduous classes across all seasons and rich fens in early and late winter (Table 3). The best-supported characterization of burns and cutblocks for male moose during calving and late summer grouped old and new burns (all burns) and old and new cutblocks (all cutblocks; Table 3). In early and late winter, the best-supported models grouped old burns and cutblocks (old seral) and new burns and cutblocks (New seral; Table 3). Male moose selected burns and cutblocks during calving and late summer and selected new seral in early and late winter (Table 3). Male moose avoided old seral in early and late winter (Table 3). Male moose also selected for areas near water with high habitat richness and avoided steep slopes (Table 3). In calving and late summer, they selected for more terrain roughness, but avoided these areas in early and late winter (Table 3). They also selected for higher elevations during calving and lower elevations during all other seasons (Table 3). The response to male moose to roads and seismic lines varied among seasons. Male moose selected for higher road density during calving, demonstrated no response to road density during late summer and avoided high road density in early and late winter (Table 3; Figure 12). Conversely, they avoided areas with higher seismic line density during calving and selected for areas with higher seismic line density during all other seasons (Table 3; Figure 13).

Table 3. Best-supported male moose resource selection model (beta coefficients = β and standard errors = SE) for each season (calving, late summer, early winter, and late winter) in northeast British Columbia from March 2015–December 2016. Covariates are grouped within vegetation classes, disturbance classes, natural features, or anthropogenic features. Positive beta values indicate selection for a given covariate while negative beta values indicate avoidance. Distance water and elevation are in m. Density metrics are in m/km^2.

	Calving		Late summer		Early winter		Late winter	
Covariate	**β**	**se**	**β**	**se**	**β**	**se**	**β**	**se**
Vegetation classes								
Conifer swamp	-1.75E-01	8.67E-02	-1.43E-01	7.55E-02	-5.10E-01	1.40E-01	-2.21E-01	1.00E-01
Hardwood swamp	2.07E-01	5.57E-02	7.39E-02	5.15E-02	7.96E-01	1.10E-01	6.31E-01	7.03E-02
Poor fen	-4.61E-01	7.47E-02	-6.89E-01	7.42E-02	-2.55E-01	1.19E-01	-4.09E-02	7.70E-02
Rich fen	-8.69E-02	8.83E-02	1.04E-01	8.61E-02	1.22E+00	1.15E-01	4.98E-01	7.93E-02
Treed bog	-7.26E-01	6.75E-02	-8.85E-01	7.07E-02	-1.94E-01	1.16E-01	-1.50E-01	7.38E-02
Upland deciduous	2.31E-01	6.43E-02	1.82E-02	5.33E-02	2.77E-01	1.20E-01	1.05E-01	7.98E-02
Upland conifer	-1.42E-01	1.14E-01	1.87E-01	1.02E-01	-4.50E-01	1.78E-01	-2.11E-01	1.23E-01
Disturbance classes								
All burns	9.91E-03	1.28E-01	8.06E-02	9.69E-02				
All cutblocks	1.40	1.57E-01	1.20	1.14E-01				
Old seral					-1.85	9.11E-01	-8.19E-01	5.41E-01
New seral					5.81E-01	1.39E-01	2.07E-01	1.21E-01
Natural features								
Distance water	-2.99E-04	5.72E-05	-1.77E-04	5.23E-05	-2.12E-04	4.41E-05	-4.44E-05	3.54E-05
Habitat richness	2.32E-01	2.13E-02	1.89E-01	1.95E-02	1.12E-01	1.91E-02	1.20E-01	1.57E-02
Terrain roughness	8.13E-02	3.52E-02	1.29E-02	2.17E-02	-1.58E-02	1.85E-02	-6.05E-03	1.91E-02
Slope	-4.26E-02	1.55E-02	-3.83E-02	9.62E-03	-1.61E-02	9.76E-03	-1.93E-02	1.03E-02
Elevation	7.60E-05	7.05E-04	-1.46E-02	3.41E-03	-2.05E-02	4.77E-03	-9.61E-03	4.32E-03
Elevation^2			1.42E-05	3.47E-06	2.14E-05	4.79E-06	9.24E-06	4.38E-06
Anthropogenic features								
Road density	2.50E-05	1.06E-05			-6.02E-05	2.26E-05	-4.17E-05	2.22E-05
Seismic density	-9.99E-06	7.67E-06	8.14E-06	6.20E-06	1.36E-05	6.02E-06	1.15E-05	8.73E-06

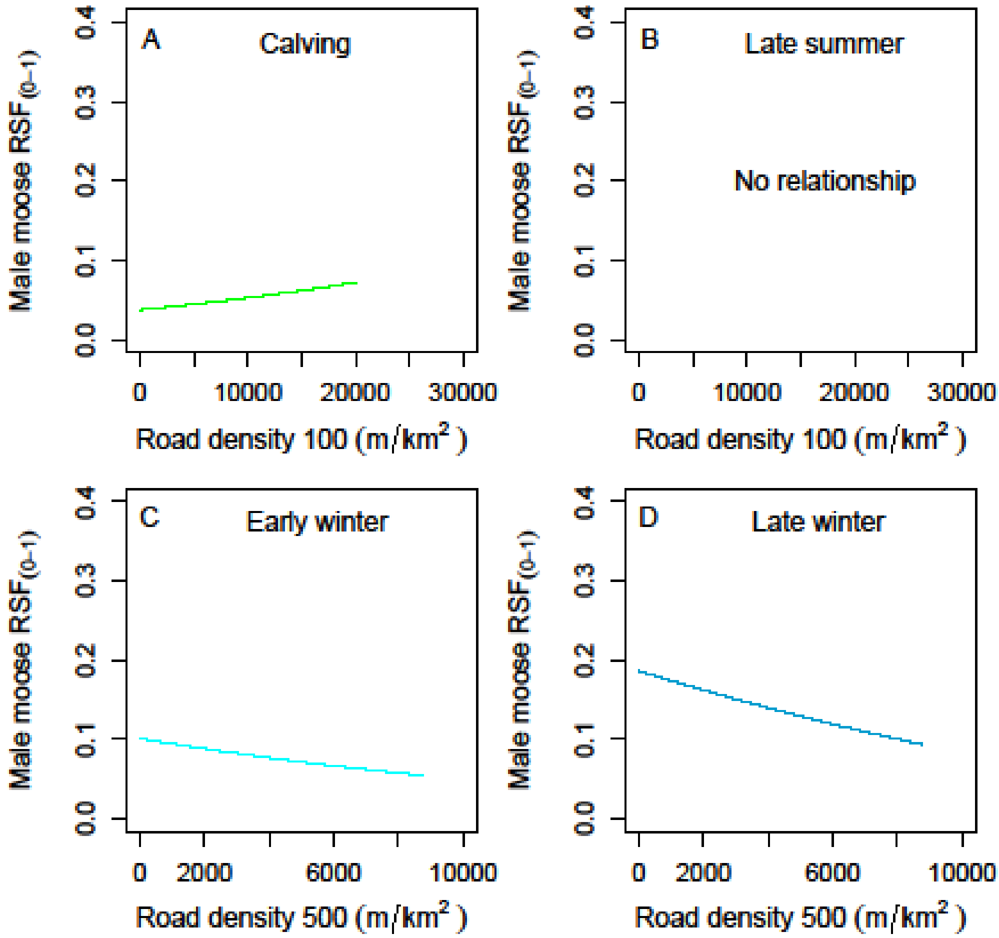

Figure 12. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by male moose as a function of road density for each season. The number (100 or 500) following road density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate road density model determined via AIC_c for each season.

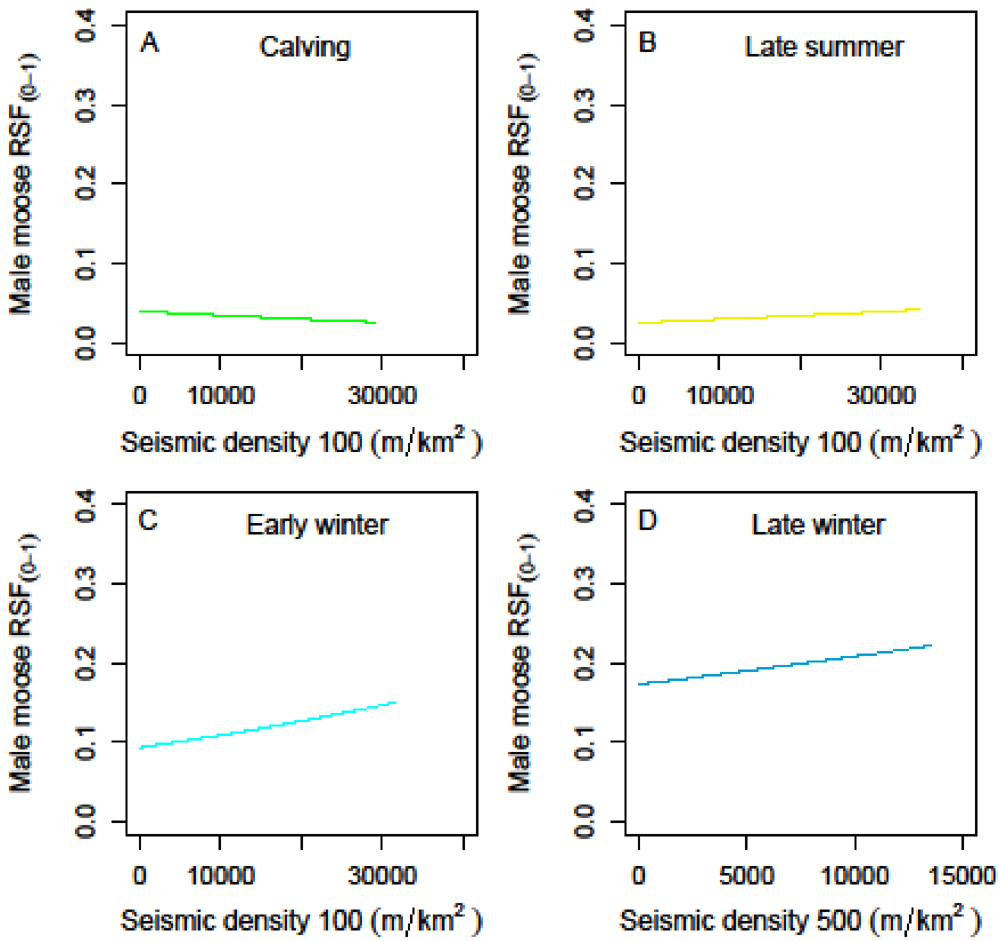

Figure 13. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by male moose as a function of seismic line (seismic) density for each season. The number (100 or 500) following seismic density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate seismic density model determined via AIC$_c$ for each season.

Female moose also demonstrated selection for hardwood swamp and upland deciduous vegetation classes across all seasons (Table 4). They avoided rich fens in late summer, but selected rich fens in the remaining seasons and demonstrated variable selection across seasons for poor fen and upland conifer vegetation classes (Table 4). The best-supported models combined all burns (old and new burns) and all cutblocks (old and new cutblocks) during calving, but included all four disturbance classes for the other seasons (Table 4). Old burns were avoided and selection was only demonstrated for new burns during late summer (Table 4).

Table 4. Best-supported female moose resource selection model (beta coefficients = β and standard errors = SE) for each season (calving, late summer, early winter, and late winter) in northeast British Columbia from March 2015–December 2016. Covariates are grouped within vegetation classes, disturbance classes, natural features, or anthropogenic features. Old and new burns and old and new cutblocks are combined in the calving model. Positive beta values indicate selection for a given covariate while negative beta values indicate avoidance. Distance water and elevation are in m. Density metrics are in m/km^2.

	Calving		Late summer		Early winter		Late winter	
Covariate	**β**	**se**	**β**	**se**	**β**	**se**	**β**	**se**
Vegetation classes								
Conifer swamp	-1.14E-02	8.02E-02	-1.27E-01	5.49E-02	-2.83E-01	7.77E-02	-1.74E-01	7.47E-02
Hardwood swamp	3.97E-01	6.84E-02	3.11E-01	4.36E-02	6.37E-01	5.85E-02	7.09E-01	6.22E-02
Poor fen	3.73E-03	7.07E-02	-4.14E-01	5.19E-02	-3.06E-02	6.44E-02	3.72E-02	6.50E-02
Rich fen	9.79E-02	8.50E-02	-6.30E-02	6.56E-02	1.05	6.50E-02	7.41E-01	6.73E-02
Treed bog	-5.52E-01	7.34E-02	-6.92E-01	5.31E-02	-6.78E-02	6.29E-02	-1.86E-01	6.52E-02
Upland deciduous	2.62E-01	7.31E-02	3.40E-01	4.34E-02	2.92E-01	6.15E-02	3.57E-01	6.56E-02
Upland conifer	5.66E-01	8.84E-02	2.12E-01	5.85E-02	-3.20E-01	1.01E-01	-5.09E-03	8.90E-02
Disturbance classes								
Old burns	-2.09	5.28E-01	-4.97E-01	2.84E-01	-1.15	3.17E-01	-3.00E-01	2.49E-01
New burns			2.53E-01	1.98E-01	-2.59E-01	4.00E-01	-1.16	4.72E-01
Old cutblocks	1.08E	1.40E-01	-2.44E-01	1.68E-01	5.12E-02	2.16E-01	-4.71E-01	3.25E-01
New cutblocks			9.10E-01	8.54E-02	7.80E-01	1.02E-01	5.70E-01	1.74E-01
Natural features								
Distance water	-7.71E-05	3.67E-05	-2.60E-04	3.32E-05	-1.01E-05	3.18E-05	5.62E-05	2.53E-05
Habitat richness	1.55E-01	1.43E-02	1.16E-01	1.07E-02	5.35E-02	1.29E-02	9.08E-02	1.08E-02
Terrain roughness	4.31E-02	1.45E-02	-1.91E-02	1.51E-02	4.33E-02	1.22E-02	1.18E-02	1.81E-02
Slope	-5.45E-02	7.46E-03	-4.00E-02	5.55E-03	-2.04E-02	6.17E-03	-6.21E-03	6.42E-03
Elevation	-1.32E-03	4.96E-04	-5.19E-03	1.95E-03	-4.61E-03	2.23E-03	-6.26E-03	2.92E-03
Elevation^2			5.50E-06	2.09E-06	5.08E-06	2.31E-06	6.17E-06	3.04E-06
Anthropogenic features								
Road density	-7.59E-05	1.02E-05	-6.75E-05	1.39E-05	-2.05E-05	6.64E-06	-6.41E-05	1.39E-05
Seismic density	-3.32E-06	4.46E-06	2.26E-06	3.49E-06	-3.96E-06	3.27E-06	-8.88E-07	2.99E-06

Cutblocks were selected with the exception of old cutblocks in late summer and late winter (Table 4). Female moose selected areas near water, except in late winter, and selected areas with higher habitat richness and terrain roughness, except in late summer (Table 4). They also avoided steep slopes and selected for lower elevations during calving and late winter, but demonstrated selection for low or high elevations (avoided intermediate elevations) during late summer and early winter (Table 4). In comparison to male moose, females showed fairly consistent avoidance of areas with high road and seismic densities (Table 4; Figure 14). Females did, however, select for high seismic density during late summer (Table 4; Figure 15).

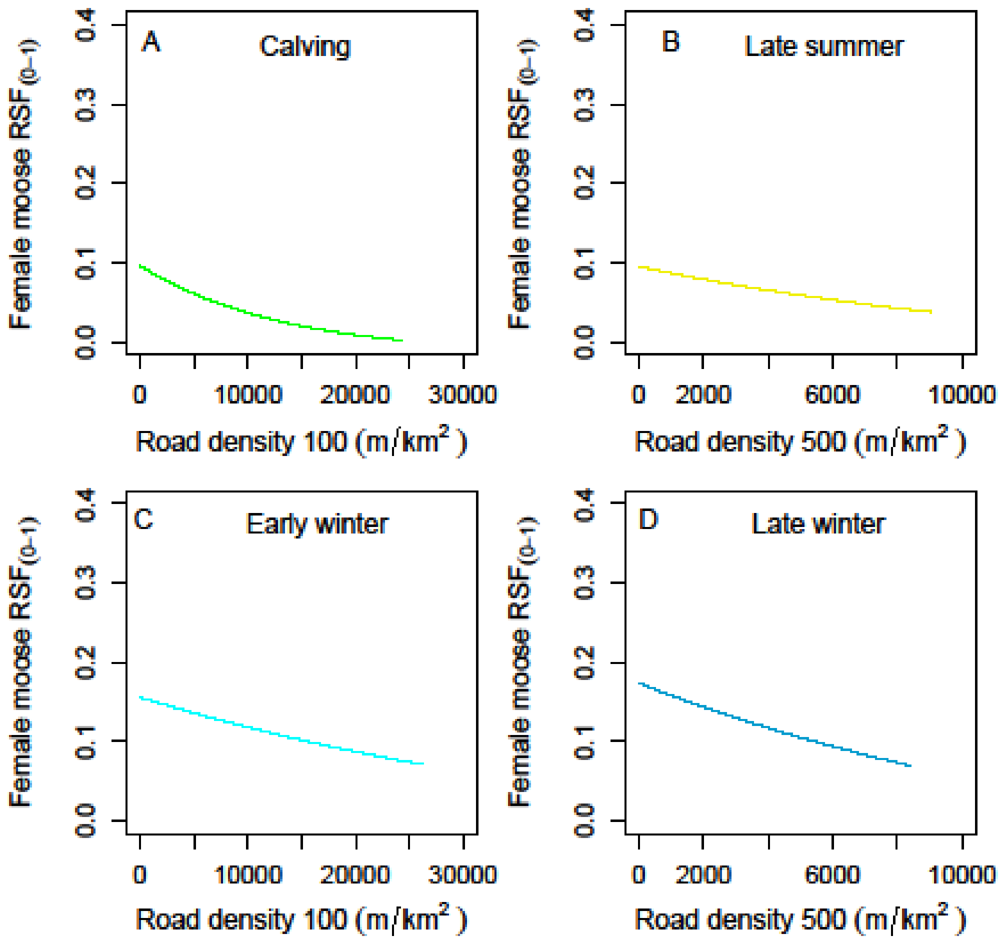

Figure 14. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by female moose as a function of road density for each season. The number (100 or 500) following road density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate road density model determined via AIC_c for each season.

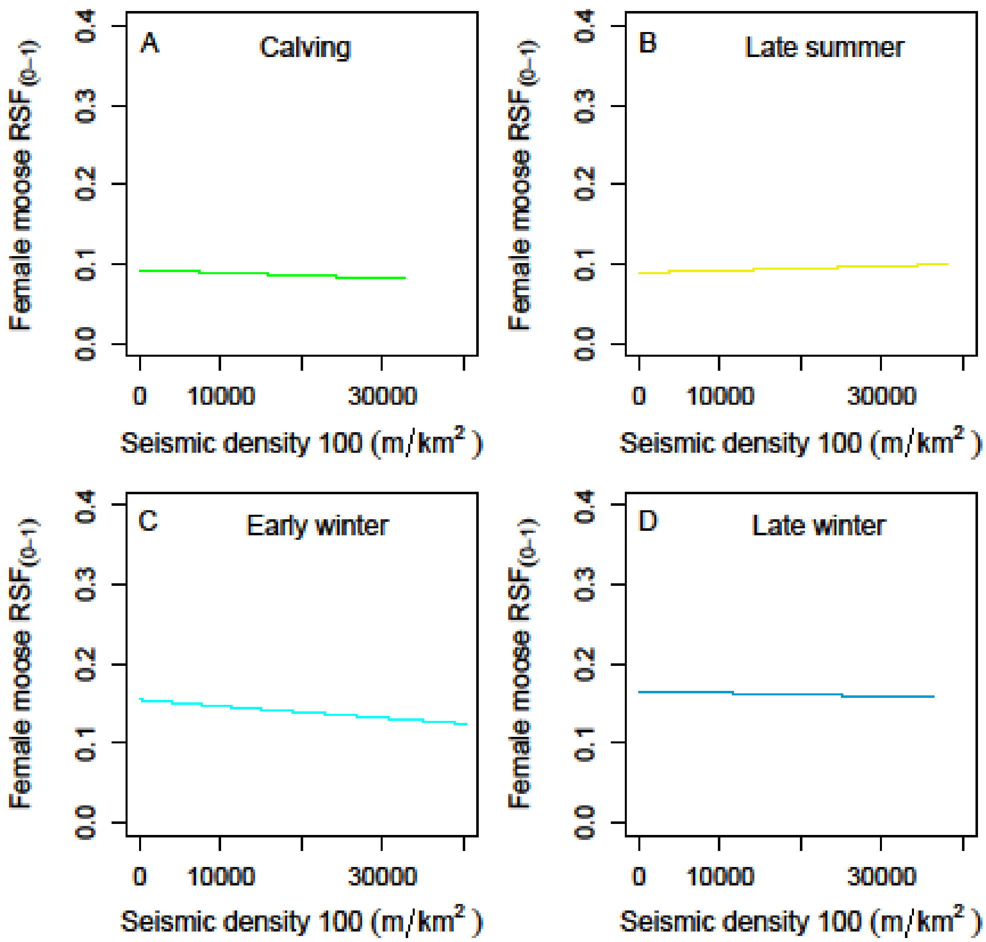

Figure 15. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by female moose as a function of seismic line (seismic) density for each season. The number (100) following seismic density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate seismic density model determined via AIC_c for each season.

Responses to linear features by caribou and wolves

To estimate caribou and wolf responses to linear features, we followed a similar methodology. We again used logistic regression to estimate resource selection functions and built competing models using many of the same covariates. We did not include tables of the best-supported caribou and wolf resource selection functions in the report, but we did plot the responses of caribou and wolves to roads and seismic lines. Caribou showed consistent avoidance of higher road densities across all seasons and avoided areas with higher seismic densities in all seasons, except late summer (Figures 16 and 17). In contrast, wolves selected higher road and seismic densities across all seasons with their selection for higher road densities having a greater impact on the relative predicted probability of selection (Figure 18 and 19).

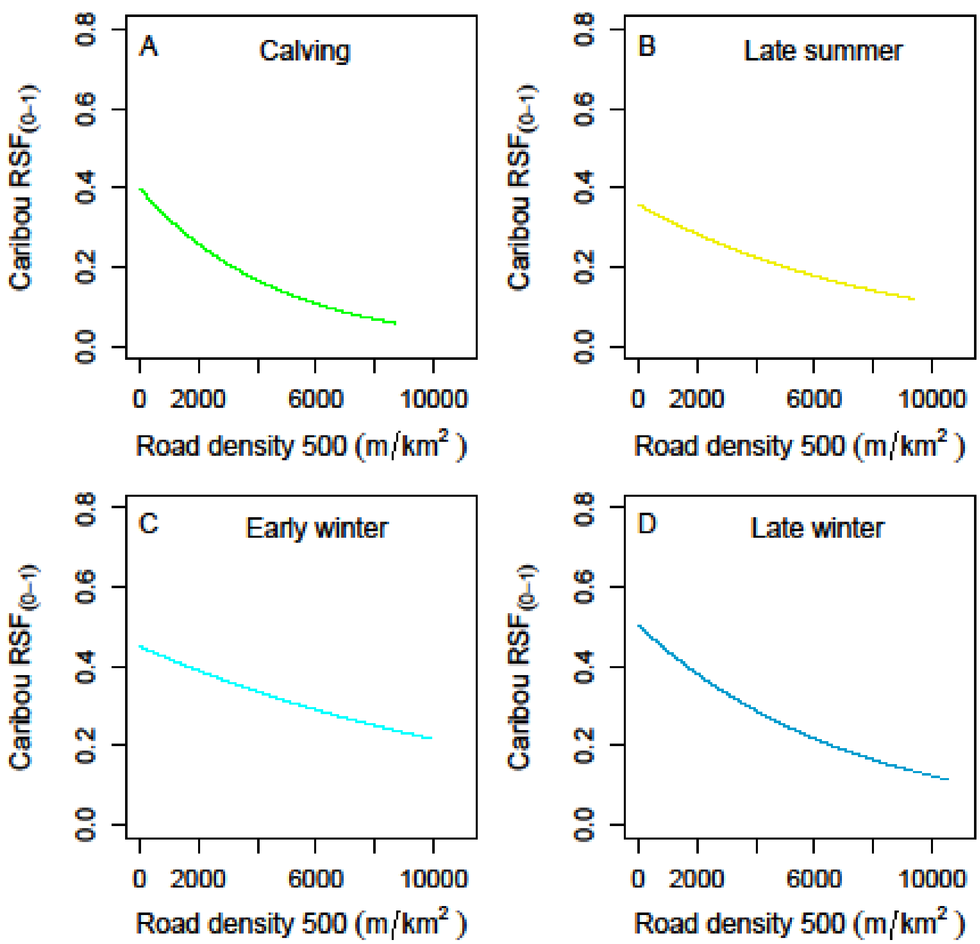

Figure 16. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by female caribou as a function of road density for each season. The number (500) following road density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate road density model determined via AIC_c for each season.

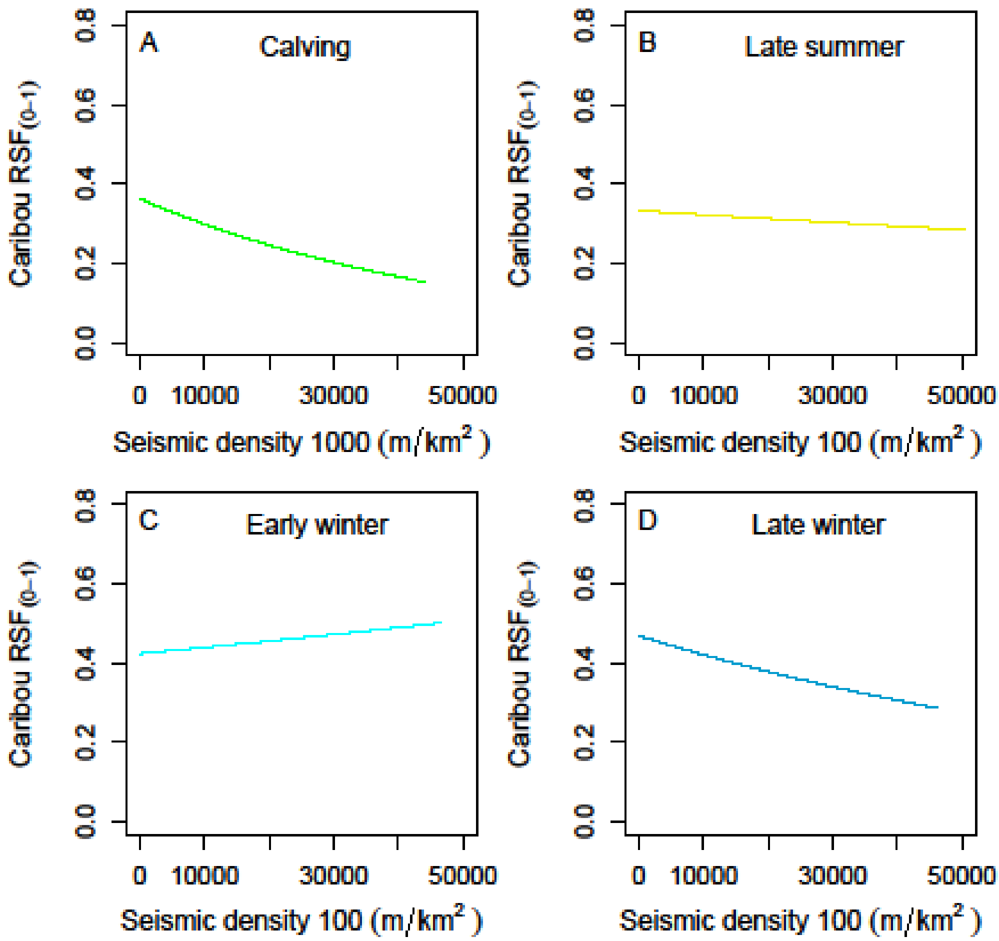

Figure 17. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by female caribou as a function of seismic line (seismic) density. The number (100) following seismic density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate seismic density model determined via AIC$_c$ for each season.

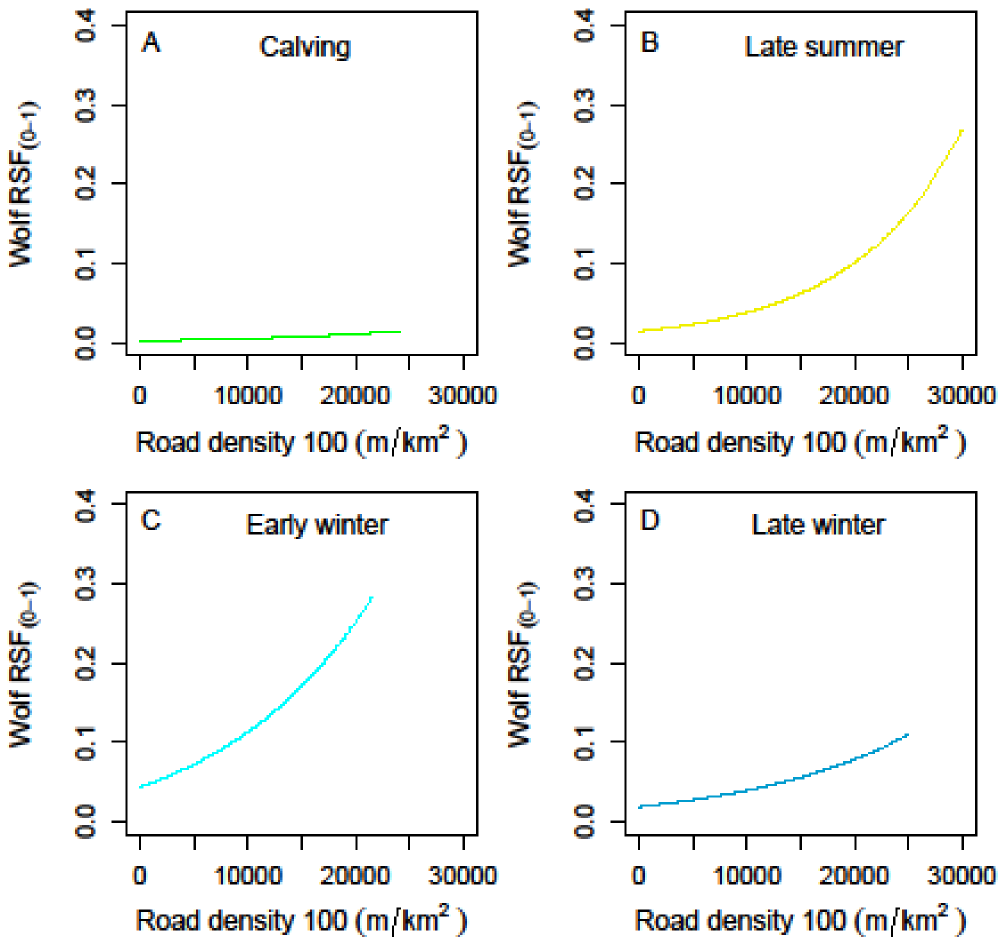

Figure 18. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by wolves as a function of road density. The number (100) following road density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate road density model determined via AIC_c for each season.

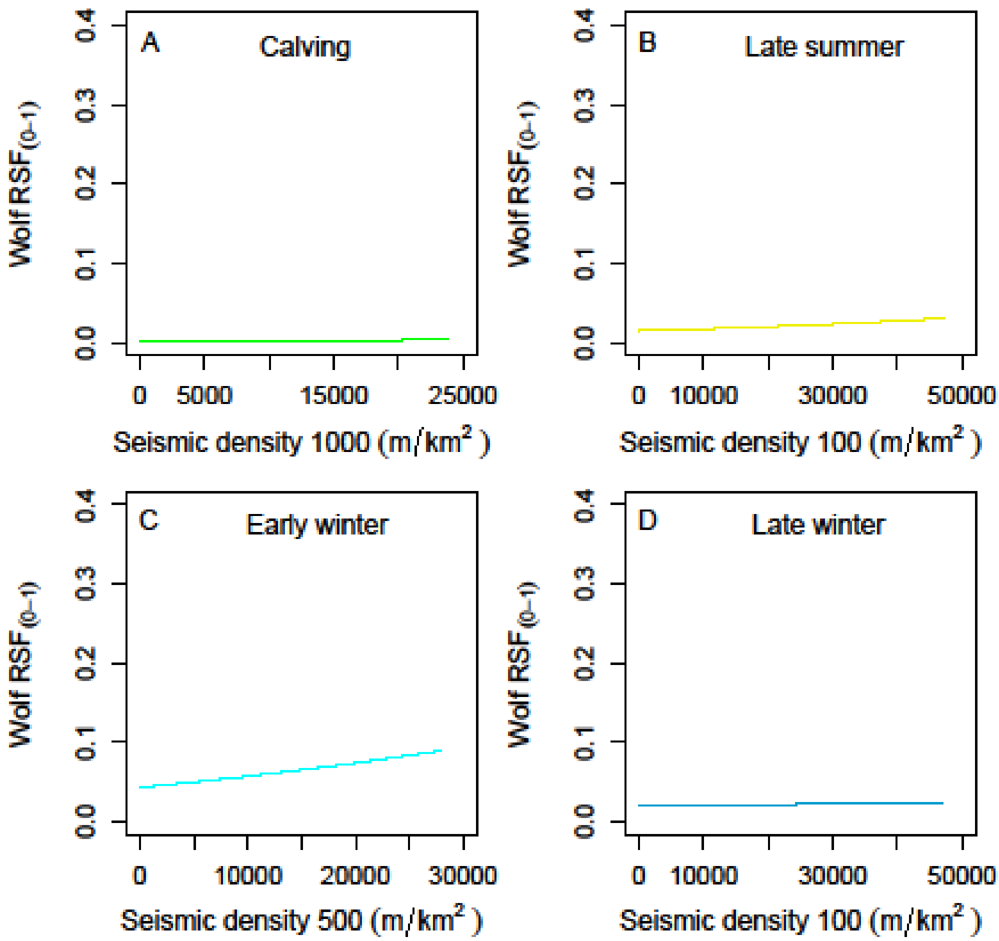

Figure 19. Relative predicted probability of selection of treed bog vegetation class (most frequently used vegetation class by caribou) by wolves as a function of seismic line (seismic) density. The number (100, 500, or 1000) following seismic density in the x-axis label indicates the buffer in m (see text) of the best-supported univariate seismic density model determined via AIC$_c$ for each season.

The contradictory responses of caribou and wolves to linear features are likely related. As wolves capitalized on the ease of movement and increased hunting efficiency provided by linear features (Dickie et al. 2017), caribou responded by avoiding the increased risk near linear features. Degradation of caribou forage, however, cannot be disregarded as an alternative or additional explanatory mechanism for caribou avoidance. Risk avoidance would also provide an explanation for the avoidance of linear features demonstrated by female moose. The inconsistent responses between roads and seismic lines by male moose are less easily explained.

Moose density as a function of disturbance

Our project was primarily focused on examining the influence disturbance has on moose and wolf distributions, in conjunction with the corresponding implications for caribou survival. The potential for disturbances to impact moose densities, however, may be equally important. Therefore, we used linear regression to evaluate if moose densities could be explained by different types of disturbances in NE BC. Moose densities (Figure 20) were estimated through surveys (McNay et al. 2013; Thiessen 2010) previously initiated and supported by BC FLNRO.

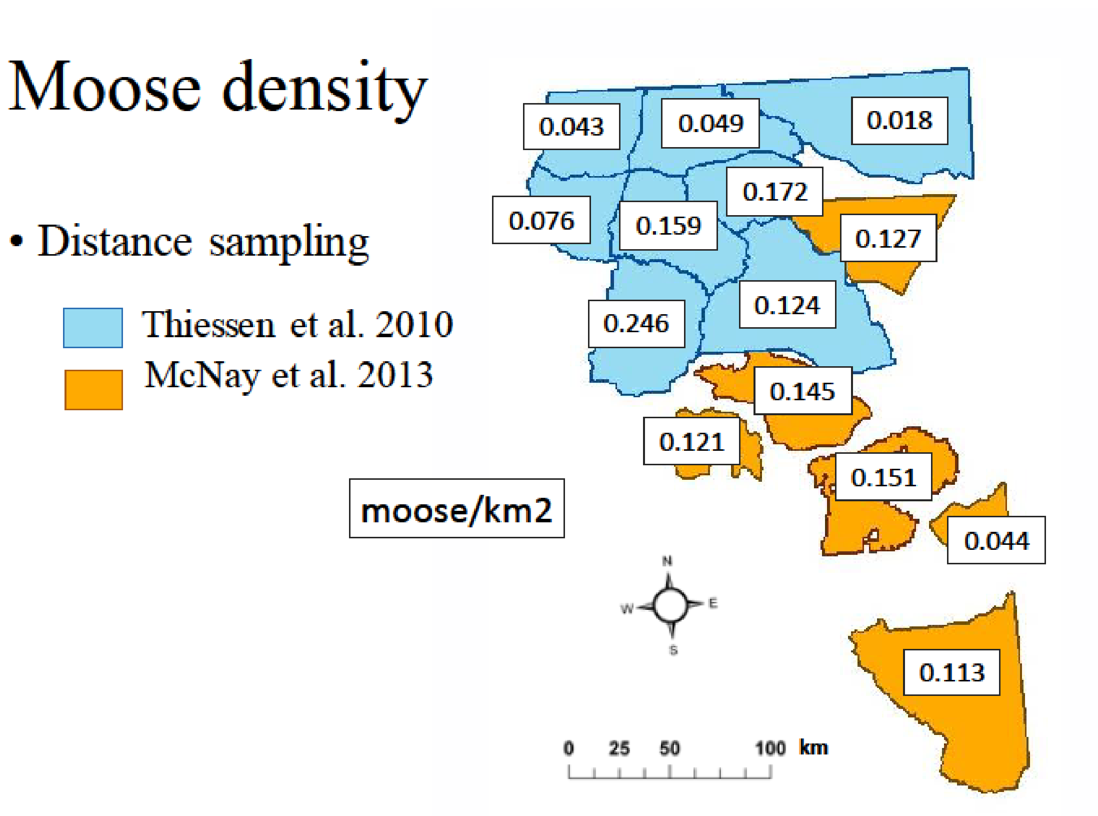

Figure 20. Moose densities (moose/km2) across northeastern British Columbia as estimated by McNay et al. (2013) and Thiessen (2010).

Although we were interested in understanding the impact of disturbances on moose density, we anticipated that moose density would be largely driven by naturally occurring vegetation classes. Thus, we built base, linear-regression models that included the proportions of a vegetation class (i.e., hardwood swamps) that is consistently selected by moose, and a vegetation class (i.e., treed bog) that is consistently avoided (Mumma and Gillingham 2016). We then added our disturbance covariates. These covariates included the proportion of burns, proportion of cutblocks, proportion of both cutblocks and burns, density (m/km^2) of roads, density (m/km^2) of seismic lines, and the density linear features (m/km^2; both roads and seismic lines). We used AIC_c to determine the best supported model. The only model that outperformed the habitat-only base model (proportion of hardwood swamp + proportion of treed bog) included the proportion of burns. As expected higher moose densities were found in areas with higher proportions of hardwood swamps, lower proportions of treed bogs, and higher proportions of burns (Table 5).

Table 5. Most parsimonious linear regression model for moose density in NE BC.

Covariate	β	SE
Intercept	0.097	0.048
Proportion of hardwood swamp	0.816	0.170
Proportion of treed bog	-0.500	0.320
Proportion of burns	0.439	0.168

R^2 = 0.545

The implications of this analysis are somewhat limited given the small number of density estimates, however, these results, if accurate, may have important implications. Research suggests that burn frequency in the boreal will be increased as a result of global climate change (Kasischke and Turetsky 2006), which would likely increase moose densities and exacerbate apparent competition between moose and caribou. Although cutblocks were not correlated with higher moose densities, logging in many areas of NE BC has been minimal and the highest proportion of cutblocks in any of the areas surveyed for moose density did not exceed 0.064

(6.4%). Uncertainty remains regarding the impact that increased logging in NE BC might have on moose densities and apparent competition.

Activity 2 synthesis

We hypothesized that anthropogenic disturbances may influence caribou survival via changes in moose and wolf distributions or densities. We built resource selection functions for moose, caribou, and wolves to evaluate the impact of anthropogenic disturbances on species distributions and linear regression models to examine the influence of disturbances on moose densities. We found that male and female moose mostly selected cutblocks. Areas with high road density tended to be avoided by male and female moose. Males generally selected and females generally avoided areas with high seismic line density. Caribou avoided high road and seismic line densities, except during early winter when seismic lines were selected. Wolves consistently selected high road and seismic line densities. Moose density was positively correlated with the proportion of hardwood swamps and burns, but negatively related to the proportion of treed bogs. These findings suggest that anthropogenic disturbances (i.e., cutblocks, roads, and seismic lines) are altering species distributions in NE BC, but do not indicate increases in moose density as a result of anthropogenic disturbance. Cutblocks likely increase habitat suitability for moose and wolves, but their current footprint in the boreal is limited. Roads likely decrease use by moose (in most seasons) and caribou, but increase use by wolves. Seismic lines likely increase use for male moose and wolves, but decrease use by female moose and caribou in most seasons. These responses have the potential to increase spatial overlap between moose, caribou, and wolves in certain seasons. Spatial overlap and its implications for caribou mortality are explored under Activities 4 and 5.

Activity 3: Develop caribou risk layers with moose, caribou, and wolf data

As a first step towards understanding the association among anthropogenic disturbance, spatial overlap, and predation risk for caribou, we explicitly evaluated the relationship between anthropogenic disturbance and predation risk. Predation risk can be characterized as the joint probability of encountering a predator and the probability of being killed by a predator following an encounter (Hebblewhite et al. 2005). Frequently, researchers model predator resource selection as an index of risk, which may be appropriate when the importance of the probability of encounter outweighs the probability of being killed given an encounter. The spacing-away strategy of caribou as a means to limit predator encounters (Demars et al. 2016) likely indicates that the risk of encounter is the more influential process as it pertains to caribou survival. We, however, were interested in modelling the two-step process of risk as a means to tease apart the drivers of both aspects of risk (i.e., risk of encounter and risk of being killed) with a particular interest in understanding the contributions of roads and seismic lines. Previous research suggests that wolves select for anthropogenic linear features because of ease of travel (Latham et al. 2011; Demars et al. 2016), thus increasing speed and hunting efficiency. Therefore, we anticipated that caribou-wolf encounters should be more frequent near roads and seismic lines, but we were unsure if roads or seismic lines would influence the probability of being killed given an encounter. We also anticipated that areas frequently used by moose (i.e., hardwood swamps) would increase the likelihood of caribou-wolf encounters.

Analyses of encounters and risk

We used locations (December 2012 – 2015) from 28 collared wolves and 104 collared caribou to identify nonlethal, potential wolf-caribou encounters as defined by a wolf location being within 1971 m (average 24-h caribou movement distance) of a caribou location within a 24-h period (Figure 21). Because of limited sample sizes, we combined our calving and late summer seasons (summer) and early and late winter seasons (winter). We used logistic regression to compare caribou locations to wolf-caribou encounters in order to determine landscape covariates that increased the probability of an encounter. To model the probability of being killed following an encounter, we used logistic regression to compare wolf-caribou encounters to caribou mortality locations assigned to wolves. When developing covariates to model the probability of being killed, we calculated metrics at a 100-, 500-, and 1000-m buffer to account for chase distances (Mech and Boitani 2007). We used AIC_c to identify the most parsimonious models (Burham and Anderson 2002) for the probability of encounter and probability of being killed. All statistical analyses were completed in program R (R Core Team 2015).

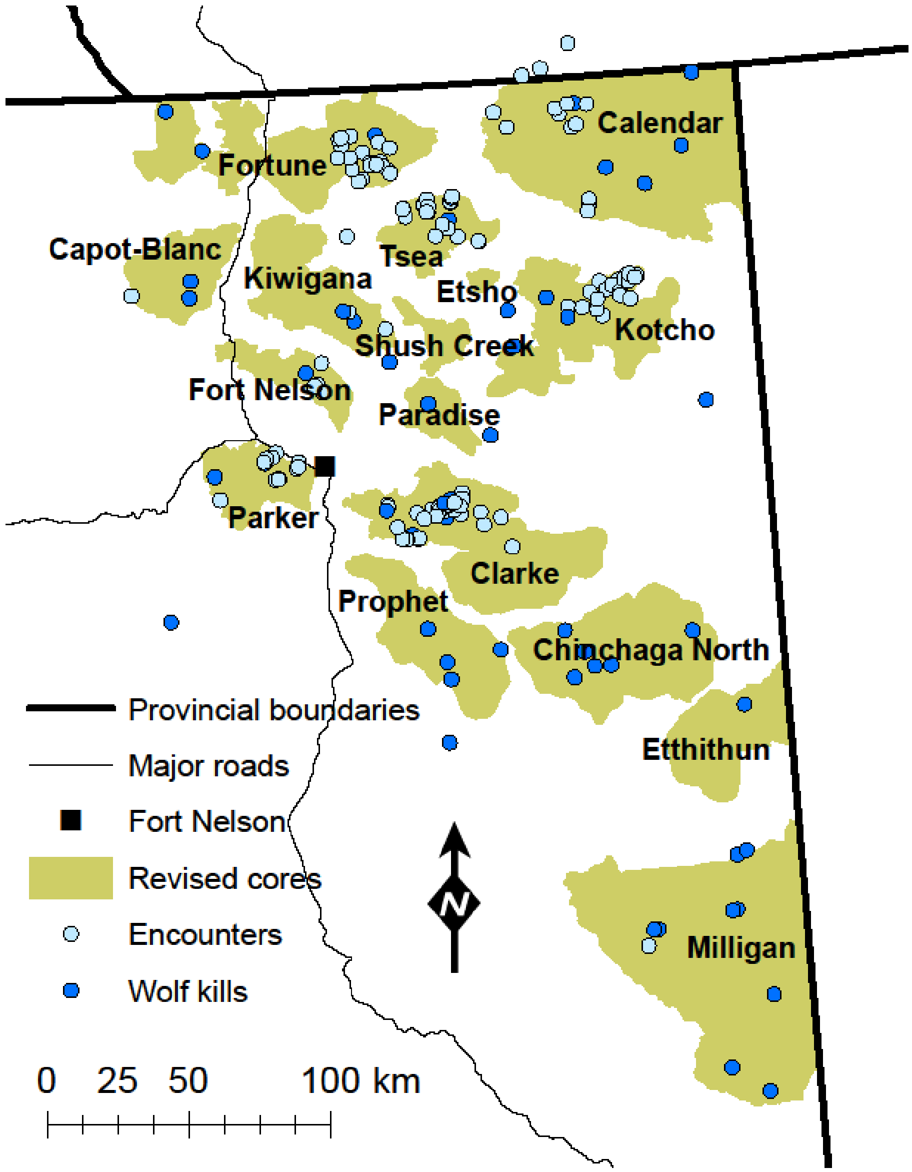

Figure 21. Locations of encounters (based on proximity of radio-collared wolves and caribou; see text) and caribou mortality locations attributed to wolves within the study area.

Landscape covariates associated with risk

Our analyses suggested that caribou were more likely to encounter wolves near or in areas with higher densities of roads and seismic lines, but we found no relationship between linear features and the probability of being killed given an encounter (Table 6). We also found that the probability of encounter increased in areas with more hardwood swamps and treed bogs and at lower elevations (Table 6). The probability of a collared caribou being killed by wolves increased in areas with more conifer and hardwood swamps, but decreased in areas with more treed bogs and rich and poor fens in winter (Table 6). In summer, areas with more habitat complexity (i.e., greater amount of vegetation class edges) decreased the probability of being killed, but areas with higher amounts of terrain roughness increased the probability of being killed given an encounter (Table 6). A 100-m buffer garnered the most consistent support for covariates of the probability of being killed indicating that this might be the most appropriate scale for this comparison.

Table 6. Covariates (and direction of effect) in the most parsimonious models of the probability of encounter and the probability of being killed given an encounter during summer and winter.

Probability of encounter	Summer	Winter
Proportion of hardwood swamp	Increased	Increased
Proportion of treed bog	Increased	Increased
Elevation	Decreased	Decreased
Density of roads	Increased	
Density of seismic lines	Increased	
Distance to roads		Decreased
Distance to seismic lines		Decreased

Probability of being killed	Summer	Winter
Proportion of swamps	Increased	Increased
Proportion of treed bogs		Decreased
Proportion of fens		Decreased
Habitat complexity	Decreased	
Terrain roughness	Increased	

Activity 3 synthesis

We hypothesized that roads and seismic lines may increase predation risk for caribou by increasing caribou-moose and caribou-wolf spatial overlap; thus increasing caribou-wolf encounters. We were unsure if anthropogenic linear features would have an influence on the probability of being killed given an encounter. We used logistic regression to compare caribou locations to potential caribou-wolf encounters (risk of encounter) and potential caribou-wolf encounters to caribou mortality locations attributed to wolves (risk of being killed given an encounter). We found that roads and seismic lines increased the risk of encounter, but did not impact the probability of being killed given an encounter. These results align with our hypotheses that anthropogenic features increase risk to caribou via spatial overlap and the encounter process (not the process of being killed given an encounter).

Activity 4: Refining caribou risk layers with moose, caribou, and wolf data

In refining our understanding of risk, we were interested in evaluating if increased spatial overlap between caribou and moose and caribou and wolves was associated with increased predation risk for caribou. We were also interested in identifying natural and anthropogenic landscape features that corresponded to areas of low and high caribou-moose and caribou-wolf spatial overlap. Our approach was to first calculate overlap metrics (Robinson et al. 2012) between caribou and male moose, caribou and female moose, and caribou and wolves. Overlap was calculated by deducting the predicted probability of selection ($RSF_{(0\text{-}1)}$) for male moose, female moose, or wolves from the predicted probability of selection for caribou (*caribou* $RSF_{(0\text{-}1)}$; EQ1) resulting in overlap values that ranged from -1 to 1. Values closer to 1 indicated areas selected by caribou with low overlap, values near 0 indicated high levels of overlap, and values near -1 indicated areas avoided by caribou with low overlap. For example, if a location had a

$$\text{EQ1.}\ Caribou\ and\ male\ moose\ overlap_{((-1)-(1))} =\ caribou\ RSF_{(0-1)} - Male\ moose\ RSF_{(0-1)}$$

predicted caribou RSF value of 0.7 and a predicted male moose RSF value of 0.1, the caribou-male moose spatial overlap at that location would equal 0.6 (0.7 – 0.1 = 0.6), indicating selection by caribou and a low spatial overlap.

To evaluate the relationship between spatial overlap (caribou and male moose, caribou and female moose, and caribou and wolves) and predation risk, we used locations (December 2012 – 2016) from 62 collared moose, 120 collared caribou, 30 collared wolves, and 69 caribou mortalities attributed to wolves. We binned overlap values for caribou, moose, and wolf locations by rounding to the nearest 10th (i.e., 1, 0.9, 0.8, etc.) and then tabulating the frequency of locations in each bin. We plotted those curves to provide a visual assessment of spatial overlap between caribou, moose, and wolves (Figures 22 and 23). We then calculated and binned overlap values for caribou mortality locations (attributed to wolves) and added them to each plot (Figures 22 and 23). To account for chase distances, we buffered each caribou mortality location by 100 m and calculated overlap at 10 randomly selected locations within each buffer. Under the assumption of apparent competition, we anticipated that overlap values for caribou mortality locations would be shifted toward areas with higher moose and caribou overlap. Alternatively, if wolves were primarily targeting caribou, then we would expect overlap values for caribou mortality locations to align with the distribution of overlap values for caribou locations, because we would presume that wolves would encounter and kill caribou in areas used most frequently by caribou. To identify relationships between landscape features and spatial overlap between caribou and moose and caribou and wolves, we calculated the median overlap values of caribou locations for each season and then summarized natural and anthropogenic landscape features for locations with overlap values above the median (low overlap) and below the median (high overlap).

<u>Spatial overlap and predation risk</u>

Our findings suggest that increased overlap between caribou and moose and caribou and wolves increases risk, and aligns with our hypotheses that fine-scale changes in moose and wolf distributions could reduce caribou survival. Caribou mortality locations (attributed to wolves) were within the distribution of caribou locations, but were shifted toward areas of increased overlap with male and female moose across seasons (Figure 22). This shifting demonstrates increased risk to caribou in locations more likely to be used by moose and aligns with our assumption that moose are the primary prey of wolves in NE BC. The locations of caribou mortalities were also shifted toward overlap with wolves (Figure 23) suggesting that altered wolf distributions, independent of altered moose distributions, could also increase risk and caribou mortality by increasing caribou and wolf encounters.

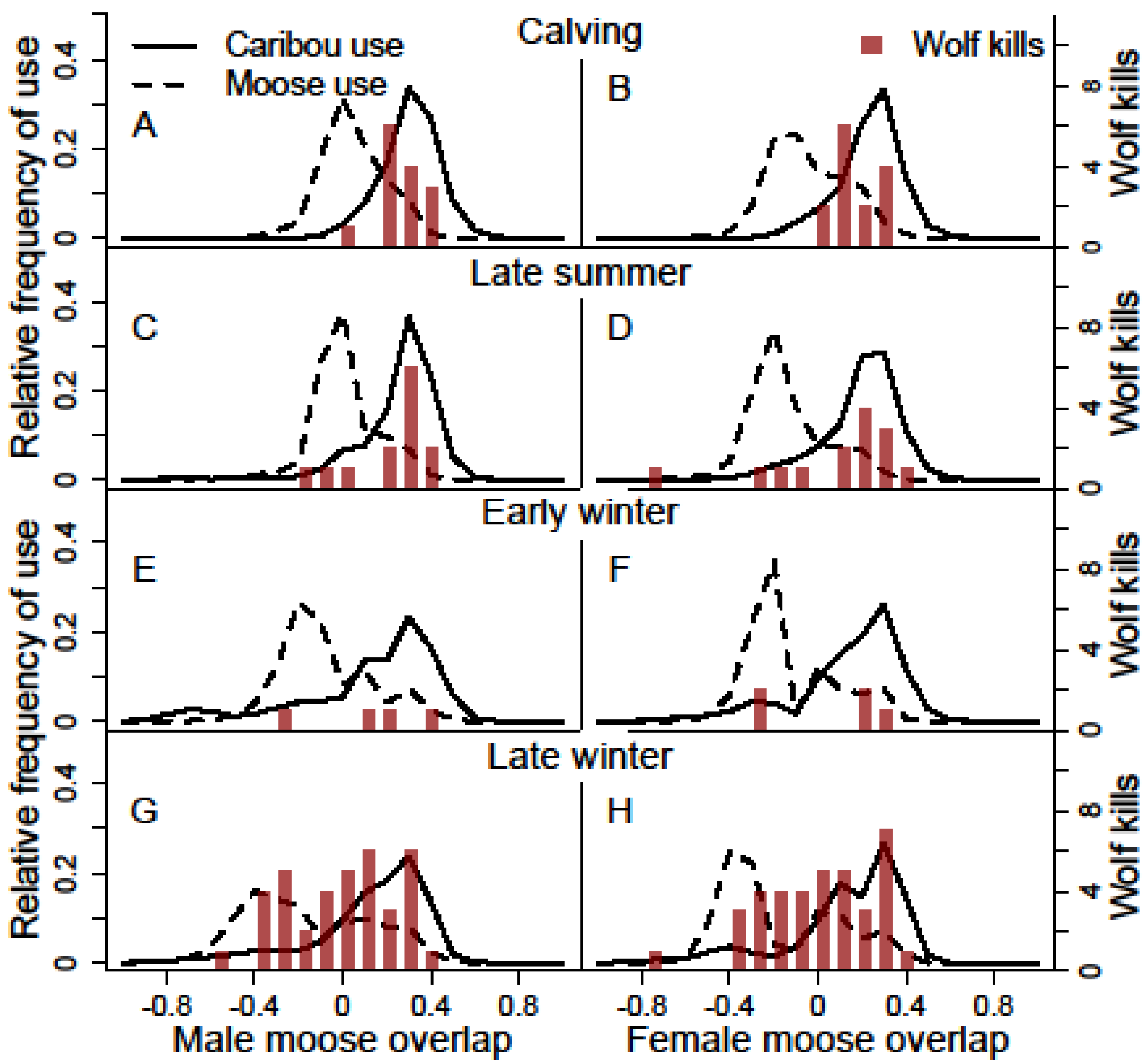

Figure 22. The distribution of moose (male – A, C, E and G, female – B, D, F, and H) and caribou locations in relation to caribou and moose overlap by season in northeastern British Columbia, along with overlap values for caribou mortality locations attributed to wolves.

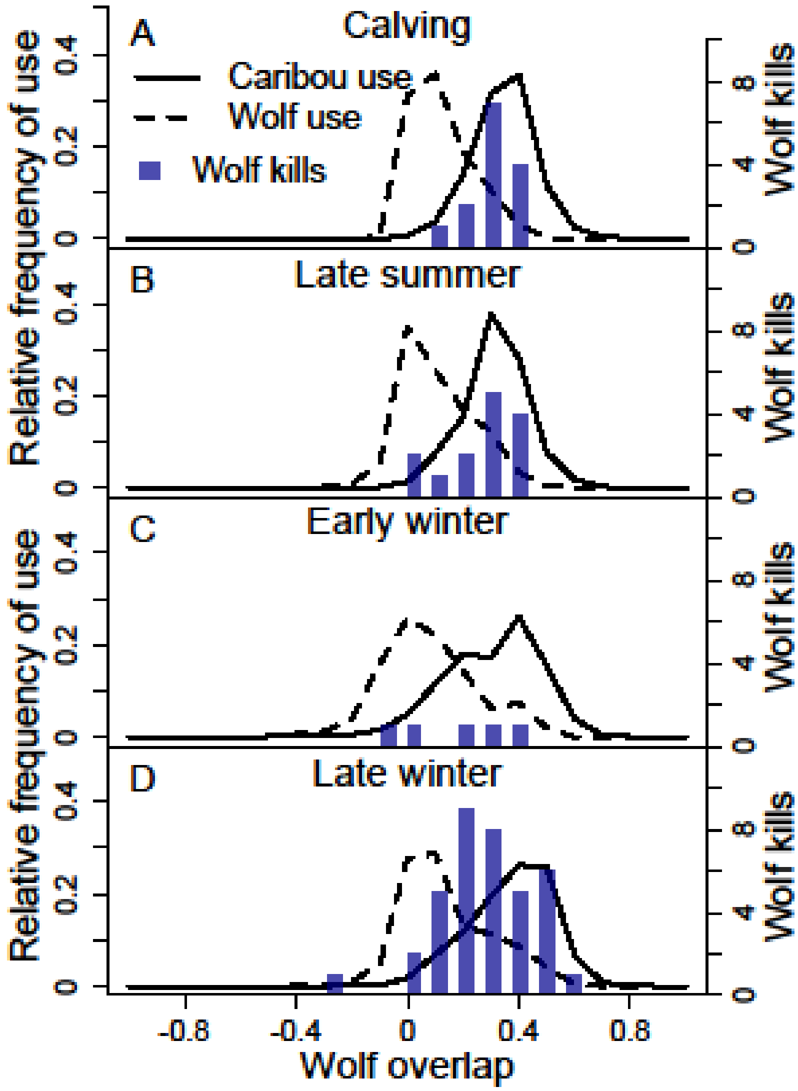

Figure 23. The distribution of wolf and caribou locations in relation to caribou and wolf overlap by season in northeastern British Columbia, along with overlap values for caribou mortality locations attributed to wolves.

Characterizing low and high spatial overlap

Landscape features characterizing low and high overlap between caribou and moose and caribou and wolves were similar. Consistent across seasons, areas with low moose and wolf overlap were more frequently in treed bogs than in areas with high moose and wolf overlap (Figures 24 – 26 and Appendix A: Figures A1 – A9). In contrast, other vegetation classes, except poor fens, were found in lower proportions for areas of low moose and wolf overlap. The proportions of

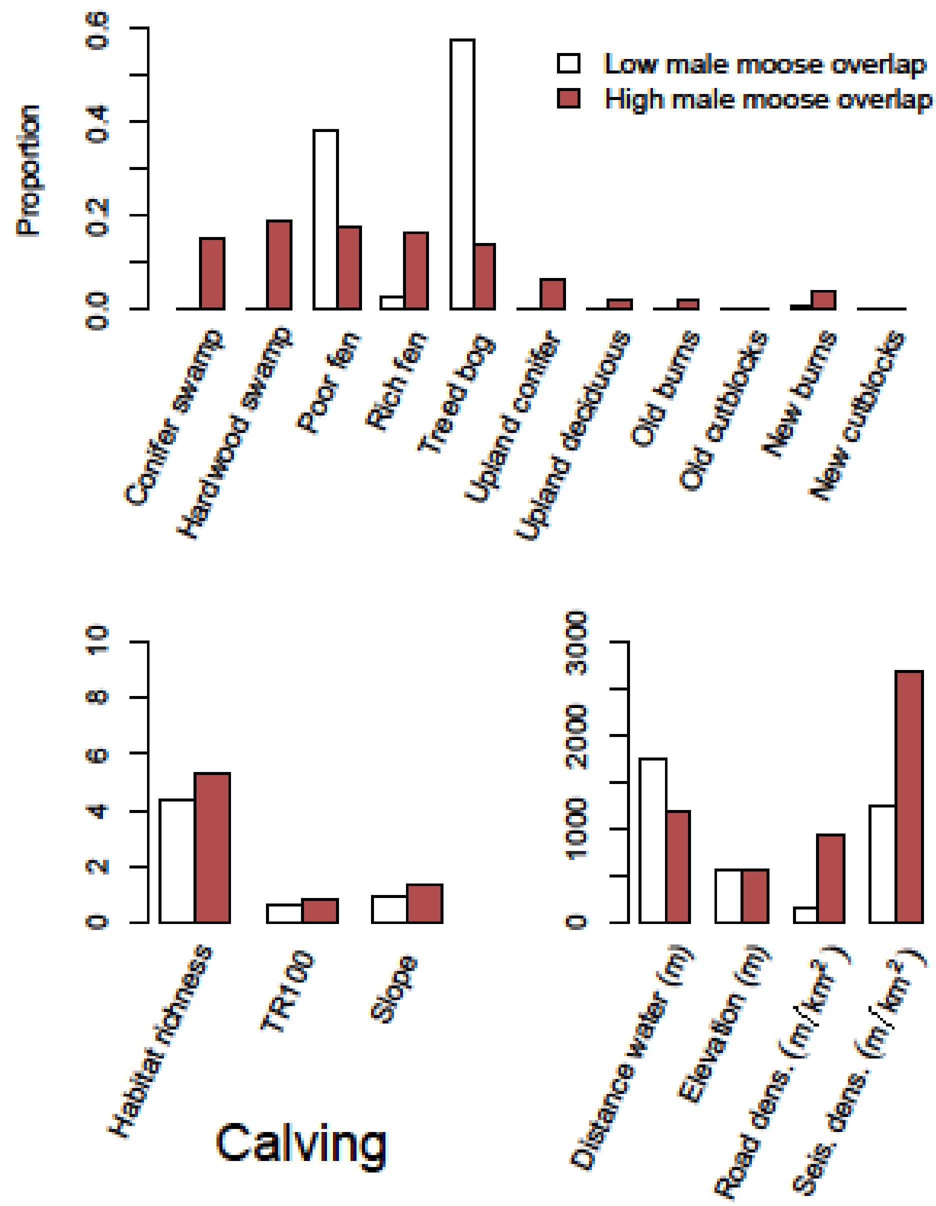

Figure 24. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and male moose in northeast British Columbia during calving. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

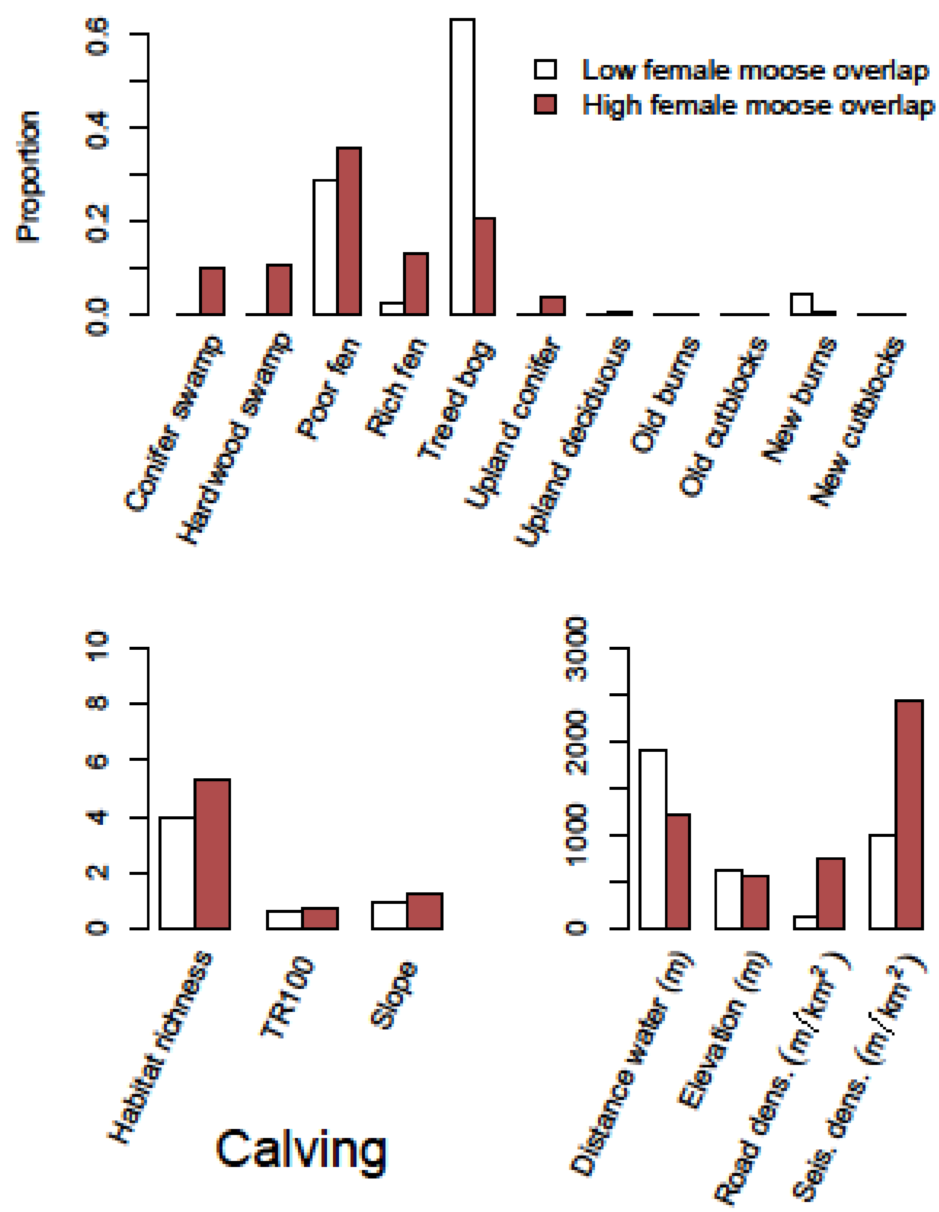

Figure 25. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and female moose in NE BC during calving. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

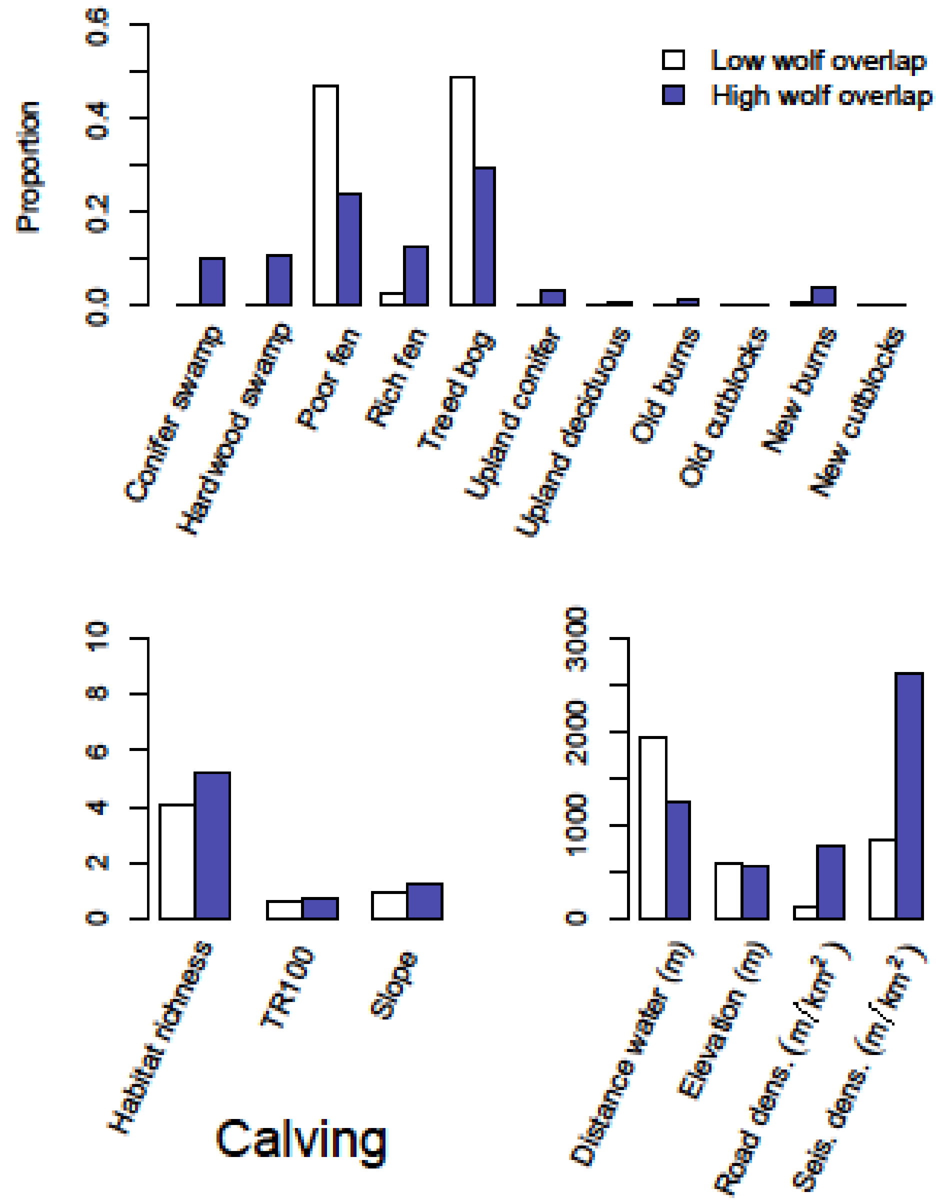

Figure 26. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and wolves in NE BC during calving. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

poor fens were also generally lower in areas of low moose and wolf overlap (Figures 24 – 26 and Appendix A: Figures A1 – A9), but not for male moose overlap during calving and wolf overlap during calving and late summer (Figure 24, Appendix A: Figures A7 and A8). The disturbance classes tended to be in lower proportions or equal proportions in areas of low moose and wolf overlap with the exception of old burns, which were higher in areas of low moose and wolf overlap during late summer and early winter, and new burns, which were higher in areas with low female moose overlap during calving (Figures 24 – 26 and Appendix A: Figures A1 – A9). Areas of low moose and wolf overlap also tended to have lower habitat richness, terrain roughness, and slopes and be further from water (Figures 24 – 26 and Appendix A: Figures A1 – A9). Lower elevations aligned with low moose and wolf overlap with the exception of the calving season and the late summer for wolf overlap (Figures 24 – 26 and Appendix A: Figures A1 – A9). Notably, lower road and seismic densities were attributed to low moose and wolf overlap, excluding female moose overlap during early winter (Figures 24 – 26 and Appendix A: Figures A1 – A9).

Activity 4 synthesis

We visually examined the influence of caribou-moose and caribou-wolf spatial overlap in relation to where caribou are killed by wolves. We also evaluated landscape features attributed to areas of predicted high and low spatial overlap. We found that caribou mortality locations were more likely to occur in areas with higher spatial overlap values for both male and female moose across seasons. Caribou mortality locations were also more likely to be in areas with higher spatial overlap with wolves. Areas with higher levels of overlap were consistent with species resource selection patterns (i.e., higher overlap in hardwood swamps and lower overlap in treed bogs). Most importantly, roads and seismic line densities were consistently higher in areas with high spatial overlap for both male and female moose and wolves across seasons. These results indicate that spatial overlap with moose and wolves increases risk for caribou and that roads and seismic lines are likely increasing spatial overlap and predation risk across the NE BC landscape.

Activity 5: Modelling caribou survival using all moose, caribou, and wolf data

Our work largely focused on evaluating if anthropogenic disturbances alter moose distributions and densities and how these potential alterations might influence caribou survival under an apparent competition framework. We hypothesized two primary mechanisms by which disturbances might exacerbate apparent competition. *First*, we theorized that cutblocks, along with burns, may increase moose forage quantity, thus increasing moose densities and leading to increased wolf densities. This numeric change in moose and wolf densities alone could lead to increased wolf encounters and decreased caribou survival. Our *second* theory was that roads, seismic lines, cutblocks, and burns may alter moose distributions and increase spatial overlap between moose and caribou. Subsequently, spatial overlap and encounters between wolves and caribou would be increased as wolves targeted areas used by moose that also overlapped caribou habitats. An alternative hypothesis, not related to apparent competition, by which anthropogenic disturbances could lower caribou survival, involves the direct influence of linear features on wolves. This *third* potential mechanism is based on roads and seismic lines altering wolf distributions and increasing wolf hunting efficiency (Dickie et al. 2017), thereby leading to increased caribou and wolf encounters and decreased caribou survival.

Prior to evaluating our caribou survival hypotheses, we assessed seasonal differences in caribou survival and the causes of caribou mortality. Latham et al. (2013) found that caribou survival was lowest during the spring and summer in Alberta. Although our research indicated that spatial overlap between caribou and moose and caribou and wolves increases risk across all seasons, we were interested in determining if there were particular seasons when caribou were most vulnerable to predation. In addition, our caribou hypotheses are predicated on wolves being the primary cause of caribou mortality, therefore we examined the cause of death for all collared caribou since December 2012.

To test our three caribou survival hypotheses, we used Cox-proportional hazard regression (Cox 1972; package survival, Therneau 2015) to model the probability of mortality (hazard). The probability of mortality is simply the inverse of survival, permitting us to draw inferences on the drivers of caribou survival. Our approach permitted staggered entry of individuals (Anderson and Gill 1982) and the inclusion of constant covariates (time-independent) and covariates that could vary over the course of an individual's lifetime (time-independent). The time-independent variables included such things as the predicted probability of selection by moose or wolves, thereby allowing us to capitalize on the fine-scale movement data provided by GPS-collared individuals. VHF-collared caribou lacked location data and were excluded from the analysis, thus limiting our sampling size and not allowing us to run separate models by season. These models estimate a baseline hazard function capable of proportional changes as a function of model covariates. We used a recurrent yearly start time (May 16) and end time (May 15) consistent with our seasons (start of calving and end of late winter). Because some individuals contributed multiple years to the analysis, we used robust 'sandwich' variance estimation to account for correlation (Cleves et al. 2008). Consistent with our *first* hypothesis, we included moose density as one of our covariates (Figure 20), but due to the coarseness of density estimates, we also included the proportions within the home range of several vegetation and disturbance classes. To estimate caribou home ranges, we first buffered the location of each individual by its 90th centile of movement distances for the corresponding season in the same manner that was used to establish availability (see Figure 27; Mumma and Gillingham 2016). We then estimated seasonal home ranges for each individual by merging the resulting circular polygons of each season for each individual (see Figure 27). We then calculated the proportion of hardwood swamp, proportion of treed bog, and the proportion of burns, which were all correlated to moose density (Table 5). We also calculated the proportion of cutblocks within each home range, given the potential for cutblocks to provide increased forage quantity for moose. To evaluate the influence that increased overlap with moose may have on caribou mortality (*second* hypothesis), we included the predicted probability of selection of male and female moose at each caribou location. Last, we included the predicted probability of selection for wolves and the distance to roads and seismic lines for each caribou location to evaluate our *third* hypothesis concerning the impact of linear features on wolf overlap and wolf hunting efficiency. We used these covariates to build competing models and selected the most parsimonious models using AIC_c. (Burnham and Anderson 2002). All statistical analyses were performed in program R (R Core Team 2015).

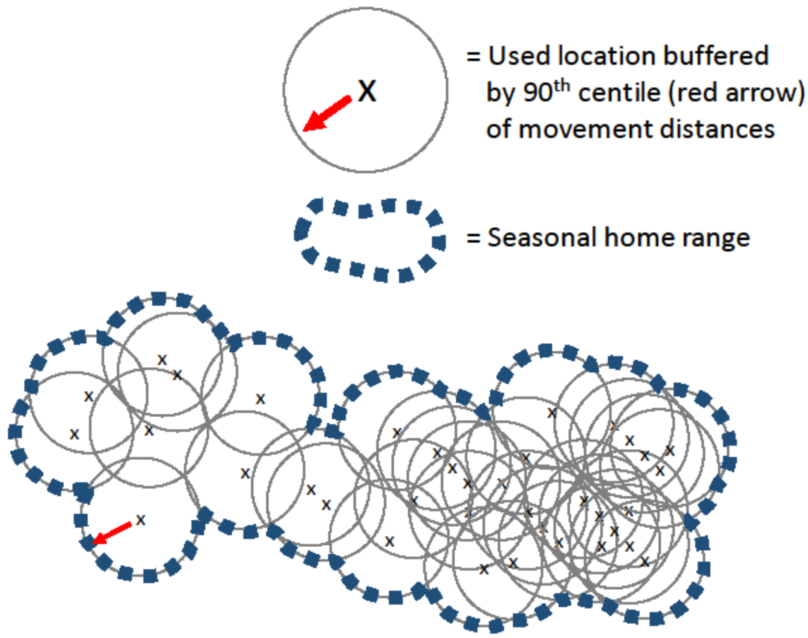

Figure 27. Seasonal home range was estimated for each individual by buffering the individual's used locations for each season by their corresponding seasonal 90th centile of movement distances and then merging the resulting circular polygons into a single home range.

Seasonal variation in survival and causes of mortality

We calculated daily survival rates for each season and year (early winter 2013 – late summer 2016) using 239 GPS- and VHF-collared caribou. We then converted daily survival rates to seasonal survival rates (standardized to our shortest season, calving 61 days) and calculated means and 95% confidence intervals for each season. The highest seasonal survival rate was in early winter (Figure 28). Confidence intervals for calving, late summer, and late winter overlapped, although late winter had the lowest mean value (Figure 28).

Ninety-three female caribou died since they were originally collared in December 2012 through December 2016. Mortality site investigations were conducted by Diversified Environmental Services (under contract from BC FLNRO). The primary cause of death was attributed to predation by wolves (Figure 28). There were 16 additional mortalities that were unable to be assigned a cause of death (Unknown, Figure 28). Wolverines killed two caribou and two caribou were harvested (Figure 28). Three caribou died as a result of poor condition and one individual died after another caribou's antler got tangled in its collar (Incidental, Figure 28).

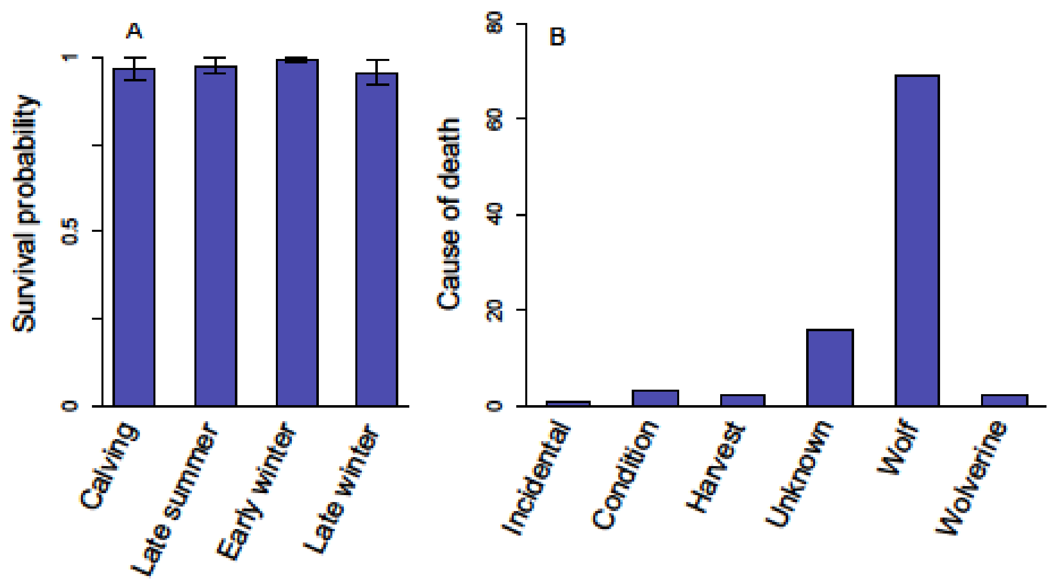

Figure 28. Seasonal survival probability (and 95% confidence intervals) standardized to the shortest season (calving 61 days) for 239 collared female caribou (A) and cause of mortality for 93 collared female caribou in northeastern British Columbia from December 2012 – 2016 (B).

Understanding survival using Cox-proportional hazard models

We used caribou locations (December 2012 – December 2016) from 120 GPS-collared caribou in Cox-proportional hazard models to evaluate drivers of caribou mortality in NE BC. Thirty-three GPS-collared caribou died during the study, primarily from wolves. We stratified our observations by range (Chinchaga range, Snake-Sahtaneh range, Westside range – Parker, Prophet, and Fort Nelson, Maxhamish range, and Calendar range) to account for variation not captured by our covariates. Positive beta coefficients for hazard models indicate an increase in the risk of mortality, while negative beta coefficients indicate a decrease in risk. The best supported model in our original model set, contained a positive beta coefficient (increased risk) for moose density. An assumption, however, of Cox-proportional hazard regression is that beta coefficients for each covariate are constant through time. Moose density violated this assumption, so we reran our competing models, excluding moose density.

In our final model set, several of our competing models had ΔAIC_c values less than 2 (Table 7; Burnham and Anderson 2002) indicating that there was support for all three models. All three models had negative beta coefficients (decreased risk) for the proportions (prop.) of hardwood swamps, treed bogs, burns, and cutblocks (Table 7). Both models also contained a positive relationship with distance to roads and a negative relationship with distance to seismic lines indicating that risk (probability of mortality) increases further from roads and closer to seismic lines (Table 7). Our best supported model also included a positive relationship (increased risk) to the probability of selection by wolves (wolf RSF; Table 7). Our second and third supported models substituted the wolf RSF covariate for the predicted probability of selection by male (male moose RSF) and female moose (female moose RSF; Table 7), respectively. Both male and female moose increased risk (positive beta coefficients) for caribou, but the influence was stronger for male moose. In order to visualize the influence of covariates on female caribou survival, we plotted survival curves as a function of burns and cutblocks (Figure 29), the distance to roads and seismic lines and wolf RSF values (Figure 30), and male and female moose RSF values (Figure 31).

Our first hypothesis predicted that burns and cutblocks would negatively influence caribou survival as a result of increasing moose and wolf densities. Under current conditions in NE BC, we did not detect a negative relationship between caribou survival and the proportions of burns and cutblocks, and in fact, detected a slightly positive influence (Figure 29). We do not have a clear explanation for these trends, and we are unable to forecast what impact an increasing footprint of burns or cutblocks could have on caribou survival in the future.

Consistent with our *second* hypothesis, there was a negative relationship between the probability of male and female moose selection and caribou survival (Figure 30). These results in conjunction with the responses by moose to anthropogenic disturbances during some seasons (Tables 3 and 4) indicate that anthropogenic disturbances in NE BC have likely altered the risk of

Table 7. Best supported Cox-proportional hazard (risk of mortality) models, excluding moose density, for female caribou in NE BC. Positive beta coefficients indicate increased risk, while negative beta coefficients indicate decreased risk. Proportion of = Prop., predicted probability of selection = RSF, number of parameters = k, Akaike's information criteria for small sample sizes = AIC_c, ΔAIC_c = change in AIC_c value relative to the top Model (Model 1).

Model	Prop. treed bog	Prop. cutblocks	Prop. burns	Prop. hardwood swamp	Male moose RSF	Female moose RSF	Distance road	Distance seismic	Wolf RSF	k	Log-likelihood	AICc	ΔAIC_c
1	-0.165	-6.79	-20.1	-2.73			5.35E-04	-2.23E-04	4.13	7	-121.109	256.2	0.00
2	-0.030	-6.59	-20.0	-2.50	0.841		5.27E-04	-2.21E-04		7	-121.292	256.6	0.37
3	-0.179	-6.63	-20.1	-2.83		0.286	5.16E-04	-2.22E-04		7	-121.501	257.0	0.78

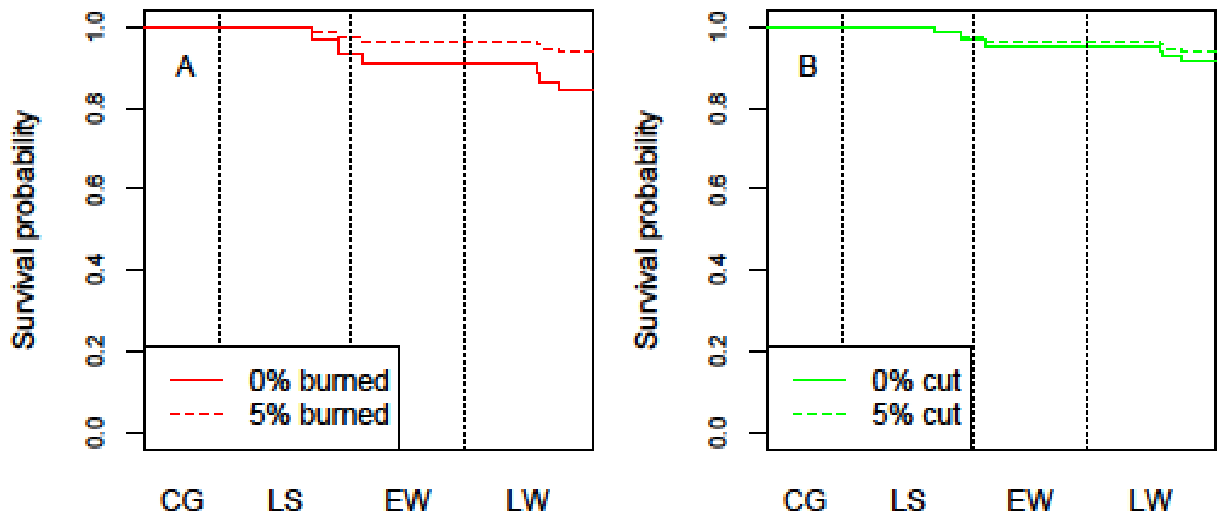

Figure 29. Caribou survival curves in response to the proportion of burns (A) and proportion of cutblocks (B) within the home range in northeast British Columbia. Calving = CG, late summer = LS, early winter = EW, late winter = LW

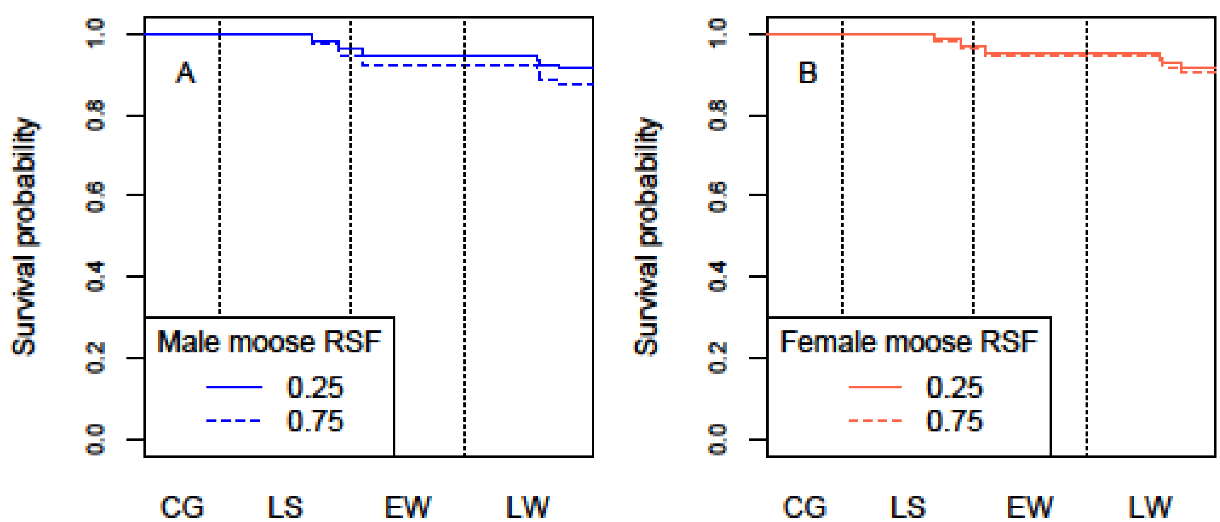

Figure 30. Caribou survival curves in response to the predicted probability of male (A, male moose RSF) and female moose selection northeast British Columbia (B, female moose RSF. Calving = CG, late summer = LS, early winter = EW, late winter = LW

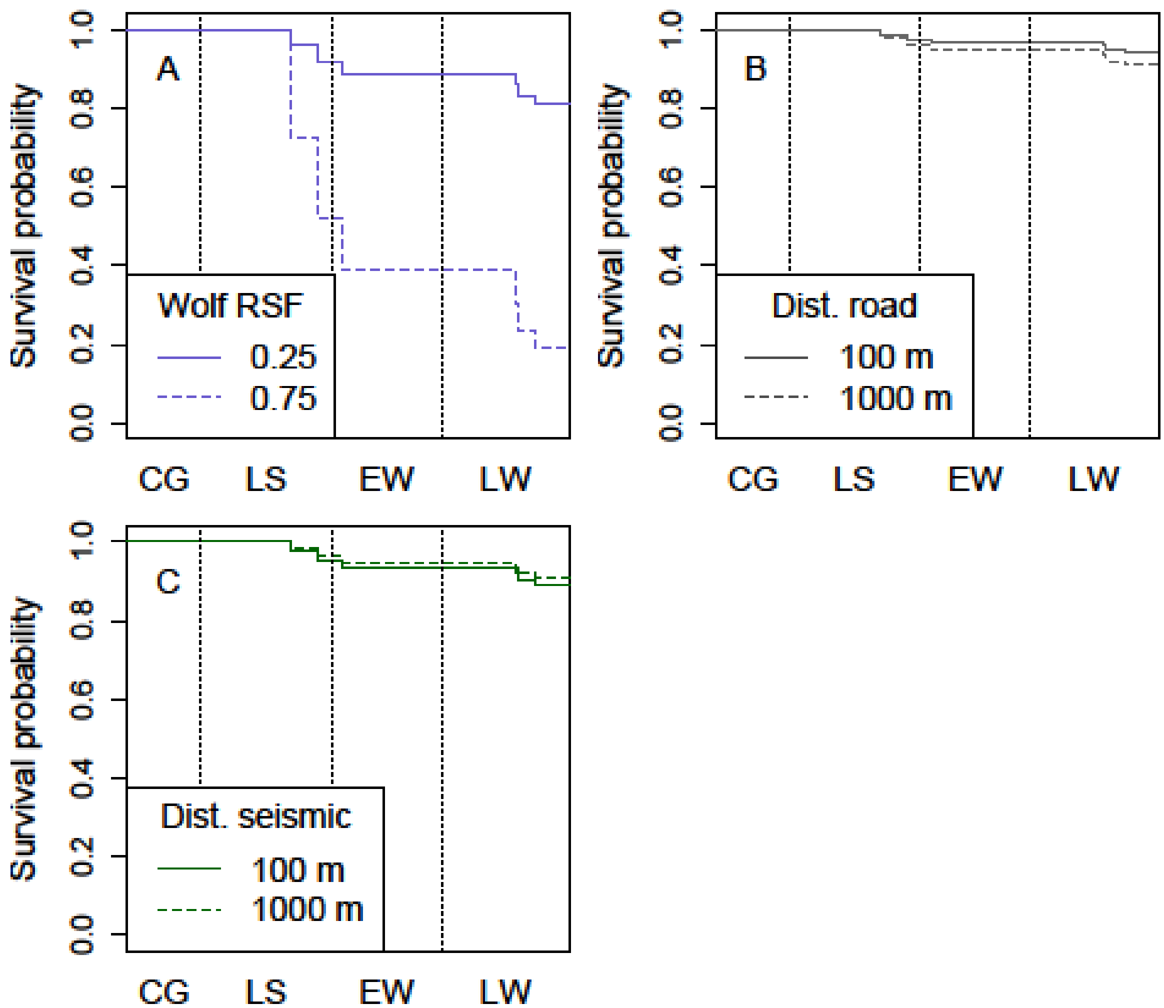

Figure 31. Caribou survival curves in response to the predicted probability of wolf selection (A, wolf RSF), distance (Dist.) to roads (B), and distance (Dist.) to seismic lines (C) in NE BC. Calving = CG, late summer = LS, early winter = EW, late winter = LW

predation for caribou by altering moose distributions. Given that moose responses to disturbances are not strictly positive (Tables 3 and 4), these alterations could increase or decrease overlap between moose and caribou, although areas of high moose and caribou overlap had higher densities of roads and seismic lines (Figures 24 – 26 and Appendix A: Figures A1 – A9). Beta coefficients for male and female moose (RSFs), however, were significantly lower than the beta coefficient for our wolf RSF covariate, which is also in our best supported model

(Table 7). Thus, our *third* hypothesis garners the highest level of support. Wolves consistently demonstrated positive responses to areas with high densities of roads and seismic lines (Figures 18 and 19) and locations with higher levels of predicted wolf use (wolf RSF) are negatively associated with caribou survival (Figure 31). Although areas near seismic lines were negatively associated with caribou survival, areas near roads were not (Figure 31). This might be explained by the consistent negative relationship between caribou and areas with high densities of roads (Figure 16), although a less strong, negative response is also present for seismic lines in three of four seasons (Figure 17).

Activity 5 synthesis

We hypothesized that caribou survival might be reduced as a result of increased moose densities or spatial overlap with moose and wolves. We used Cox-proportion hazard models to evaluate the influence of moose densities and moose and wolf distributions on caribou survival. We did not find support that areas predicted to have higher moose densities as a result of burns or cutblocks resulted in lower caribou survival. Our findings did, however, suggest that areas more likely to be used by male and female moose and wolves decreased the probability of caribou survival. Consistent with our hypotheses that caribou survival is decreased as a result of anthropogenic linear features increasing spatial overlap between caribou, moose, and wolves, caribou survival was decreased near seismic lines. Areas near roads, however, demonstrated a slightly positive influence on caribou survival. These results suggest that increases in overlap between moose and wolves will decrease caribou survival, but the opposing relationships detected for areas near seismic lines and roads create some uncertainty with regards to the mechanisms by which anthropogenic disturbances decrease caribou survival.

Extension plan and activities

Throughout our research, we liaised regularly with Megan Watters (FLNRO) in terms of mortality investigations and other project related issues – both via conference calls and during face-to-face meetings. These meetings included project-specific consultations with Megan, Steve Wilson (REMB Board), Kathy Parker (UNBC), and Chris Johnson (UNBC) and sessions regarding the direction of REMB-funded research, along with the strategic planning research activities. Additionally, we provided support roles through data and consultation to guide moose distance surveys completed by FLNRO staff and contractors in Region 7B (Peace) and Matthew Mumma participated with FLNRO on several RFP review teams related to contracts for moose data collection.

This research culminated in several presentations to date. Consistent with our extension plan, we presented a summary of our approach, findings, and implications (Title: Preliminary moose resource selection models by sex and their implications for wolf distributions in the boreal) in June 2016 as part of the REMB Spring Webinar Series. A link to this presentation is available on the extension page (http://www.bcogris.ca/boreal-caribou/extension) of the BC OGRIS website. We presented our work examining the risk of encounter and the risk of being killed (Title: Understanding the impact of linear features on predation risk and avoidance of wolves by boreal caribou) at the North American Caribou Workshop in May 2016 and (Title: Learning leads to increased risk in an altered landscape) at the Wildlife Society Meeting in October 2016. We presented our analysis of moose resource selection (Title: Anthropogenic drivers of moose resource selection and implications for the boreal ecosystem) at the North American Moose Workshop in September 2016. We also presented (Title: Understanding the influence of disturbance, moose, and wolves on boreal caribou) at the Boreal Caribou Researcher’s Workshop in Fort St. John in November 2016 (available on the extension page of the BC OGRIS website). Finally, we anticipate submitting several manuscripts for publication in peer-reviewed journals.

Conclusions and recommendations

This project examined the impact of disturbances on moose, caribou, and wolf distributions and spatial overlap, along with the cascading effects on adult caribou survival. We, therefore, have focused our conclusions and recommendations on the impacts of disturbances on the boreal system in NE BC, and specifically on how they contribute toward the testing of our three hypotheses.

i. Anthropogenic disturbances increase moose densities leading to increased wolf densities and increased wolf-caribou encounters and decreased caribou survival.

ii. Anthropogenic disturbances alter moose distributions leading to increased wolf-caribou encounters and decreased caribou survival.

iii. Anthropogenic disturbances alter wolf distributions leading to increased wolf-caribou encounters and decreased caribou survival.

Demars et al. (2016) suggested that increases in wolf densities are capable of having an overwhelming, negative impact on caribou survival by increasing the number of wolf-caribou encounters. We theorized (*first* hypothesis) that areas with higher amounts of early seral as a result of burns and cutblocks would increase moose densities, which would be predicted to increase wolf densities. Although caribou survival is likely decreased in areas with high moose densities, a link between logging and moose densities was not evident in our work. At present, the cutblock footprint in the boreal is not extensive, but selection by moose for new cutblocks may suggest that increased logging could increase moose and wolf densities in the future. Burns were positively correlated with moose densities and there may be other factors, such as long-term changes in climate, which have increased moose densities in the boreal, but management options for these large-scale factors are limited. Liberalized moose hunting has been implemented in other parts of BC, but desired outcomes (less wolves and increased caribou survival) remain uncertain (Gorley 2016).

Much of our research focused on fine-scale changes in male or female moose distributions that could lead to increases in spatial overlap between moose and caribou. We predicted that these changes might lead to increased overlap between wolves and caribou and decreases in caribou survival (*second* hypothesis). Selection by moose for new cutblocks suggest that these features could increase use by moose, but there infrequency across much of the boreal suggests that cutblocks are likely not, at present, having a significant influence on caribou-moose overlap. In contrast, roads and seismic lines are widespread across the boreal and we determined selection by moose (primarily by male moose) for areas with high densities of roads and seismic lines during some seasons. Densities of roads and seismic lines were also consistently higher in caribou locations predicted to have higher caribou-moose overlap and caribou survival was negatively related (more strongly for male moose) to locations predicted to be used more frequently by male and female moose. These findings support the underlying mechanism proposed by our *second* hypothesis and suggest that linear features decrease caribou survival by increasing spatial overlap between caribou and moose.

We were particularly interested in not simply confirming that wolves use linear features within their existing territories, but that linear features also have the potential to alter wolf distributions, leading us to model the density of linear features rather than the distance to or frequency of wolf locations on linear features. Our findings align with other studies that found strong selection for linear features by wolves (Latham et al. 2011; Dickie et al. 2017). The selection by wolves for areas with higher road and seismic densities, the consistent relationship between areas with high caribou-wolf overlap and high densities of linear features, and the decline in caribou survival in locations with high levels of predicted wolf use support our *third* mechanism by which anthropogenic disturbances may be decreasing caribou survival in the boreal.

Collectively, our results indicate that the primary anthropogenic disturbances impacting adult, female caribou survival under current conditions in NE BC are linear features, namely roads and seismic lines. The mechanisms include both the alteration of moose distributions and the indirect (wolves following moose) and direct (wolves selecting for areas with linear features) alteration of wolf distributions. Thus, the presence of anthropogenic linear features increases risk for caribou in NE BC. Caribou avoidance of roads and seismic lines is likely an effort to minimize predation risk, but this may also contribute to risk by concentrating caribou in areas away from linear features, thereby impacting the caribou spacing-away strategy (Demars et al. 2016). An alternative mechanism by which roads and seismic lines may influence caribou survival is through decreases in forage quality or quantity, which could interact with predation risk by reducing caribou body condition. Limiting the amount of roads and seismic lines in or near habitats (treed bogs and poor fens) frequently used by caribou would help prevent future increases in wolf-caribou overlap and adult caribou mortality. Current research evaluating the disparate impacts of seismic lines, dependent on seismic line dimensionality (MacNearney et al. 2016), will assist in lessening the effects of future development activities. The current footprint of roads and seismic lines in the boreal, however, may already be too extensive to assure population viability for all ranges (Wilson et al. 2010). Given the significant cost associated with linear feature restoration (Golder Associates 2016), we recommend a strategic approach that considers the extent of disturbance, future development plans, and the probability of ensuring population viability in order to target cores or ranges with high likelihoods of success and to maximize available resources. A better understanding of what constitutes restoration (DeWitt et al. 2016) will also be essential to achieve desirable outcomes. Dependent on the ability to effectively restore areas of NE BC, more invasive management actions (Sutherland et al. 2016) may be necessary to ensure caribou population viability.

It should be recognized that adult, female survival is only one of many demographic parameters that may be limiting caribou population growth in NE BC. Efforts should be made to utilize existing data in the form of an integrated population model to identify limiting demographic parameters, drivers of those parameters if possible, and accurate predictions of boreal caribou viability under future management scenarios. Low calf recruitment, resulting from low adult pregnancy rates or high calf mortality, may be as or more important than adult, female survival in limiting caribou population growth. Reduced adult caribou body condition as a result of decreased forage quality or quantity is an alternative mechanism by which disturbances could impact caribou population growth by decreasing caribou pregnancy or calf survival rates. Given that previous research attributed low calf survival to areas of high quality black bear (*Ursus americanus*) habitat (Demars 2015), additional research concerning the impacts of anthropogenic disturbances on black bear distributions and densities may also be warranted.

Acknowledgements

Support for this work is being provided by the BC Oil and Gas Research and Innovation Society (BC OGRIS) and the Research and Effectiveness Monitoring Board (REMB). Collar deployment and field monitoring of moose, caribou, and wolves were initiated and overseen by the BC Ministry of FLNRO in conjunction with Diversified Environmental Services (collaring and caribou mortality investigations), Ingebjorg Jean Mattson and Shifting Mosaics Consulting (moose mortality site investigation), and Caslys Consulting (collar monitoring). Indirect support was provided by the University of Northern British Columbia. We would also like to thank Ducks Unlimited Canada for allowing us to access their detailed habitat classification data.

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Appendix A

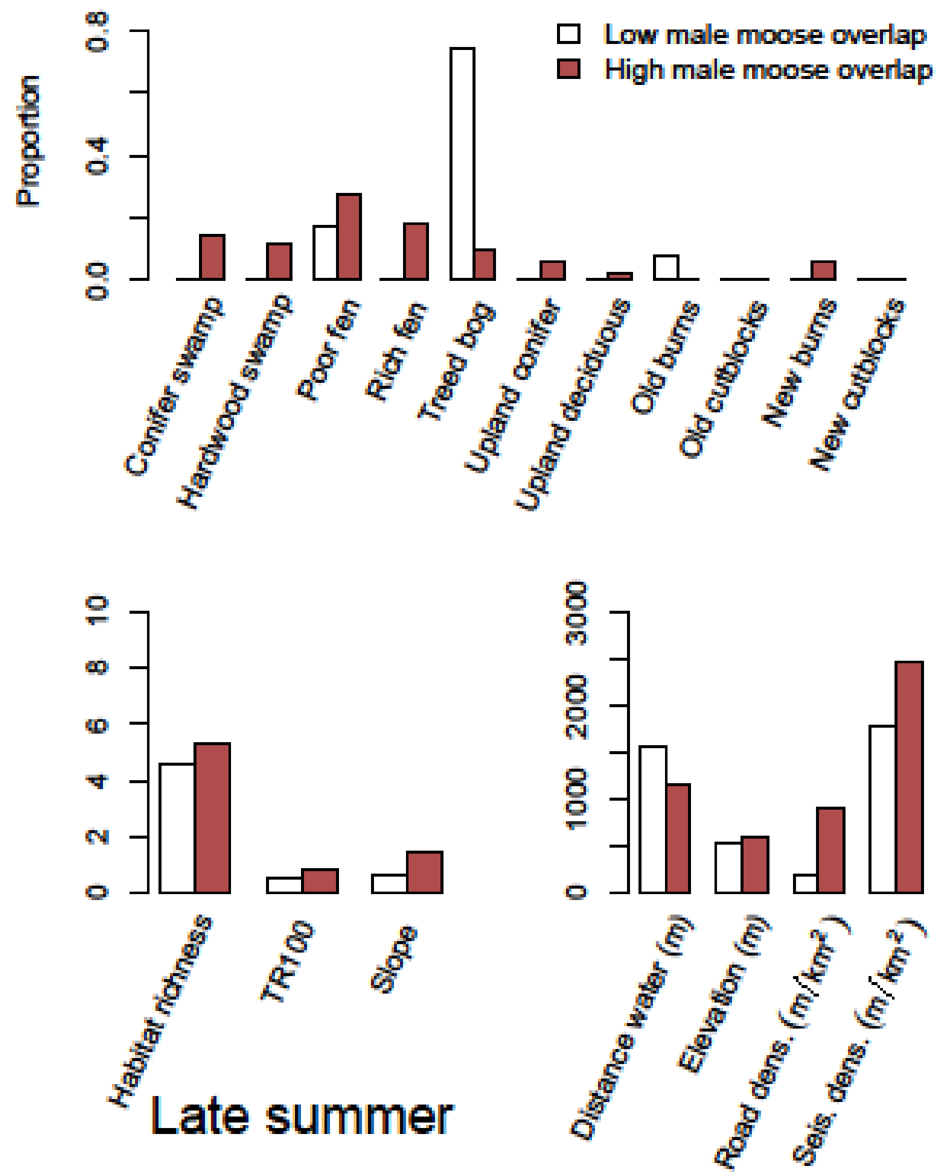

Figure A1. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and male moose in northeast British Columbia during late summer. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

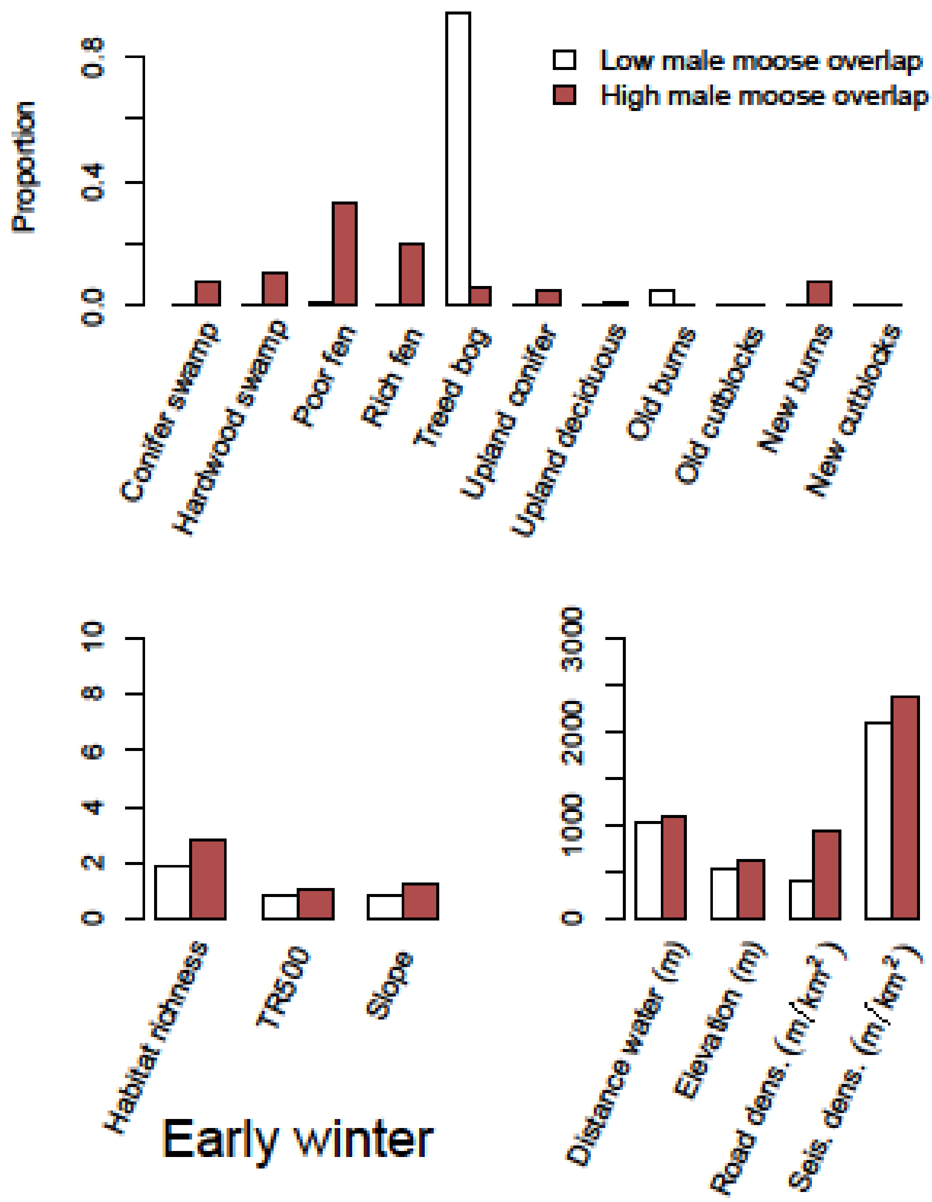

Figure A2. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and male moose in northeast British Columbia during early winter. Terrain roughness at a 500-m buffer = TR500, density = dens., seismic lines = seis.

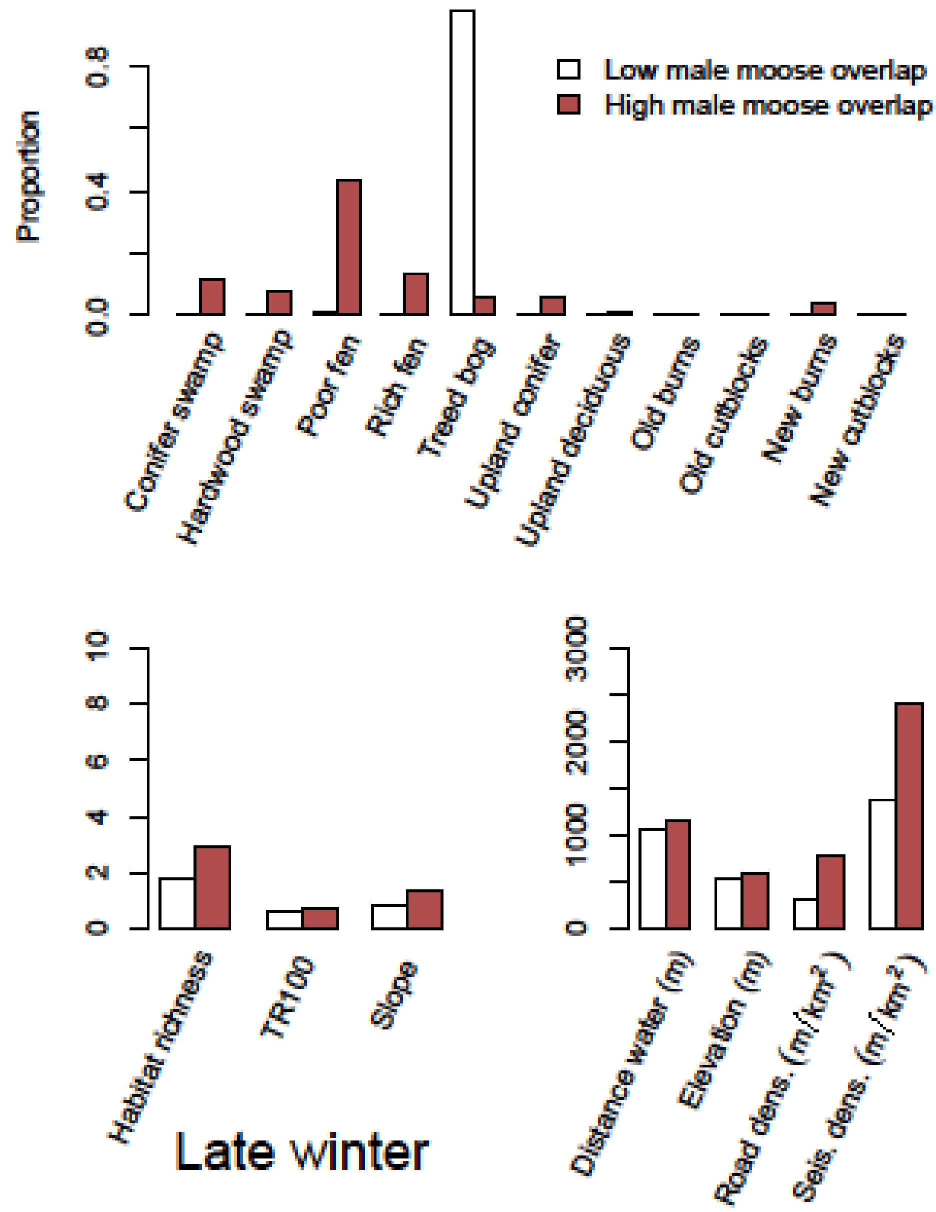

Figure A3. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and male moose in northeast British Columbia during late winter. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

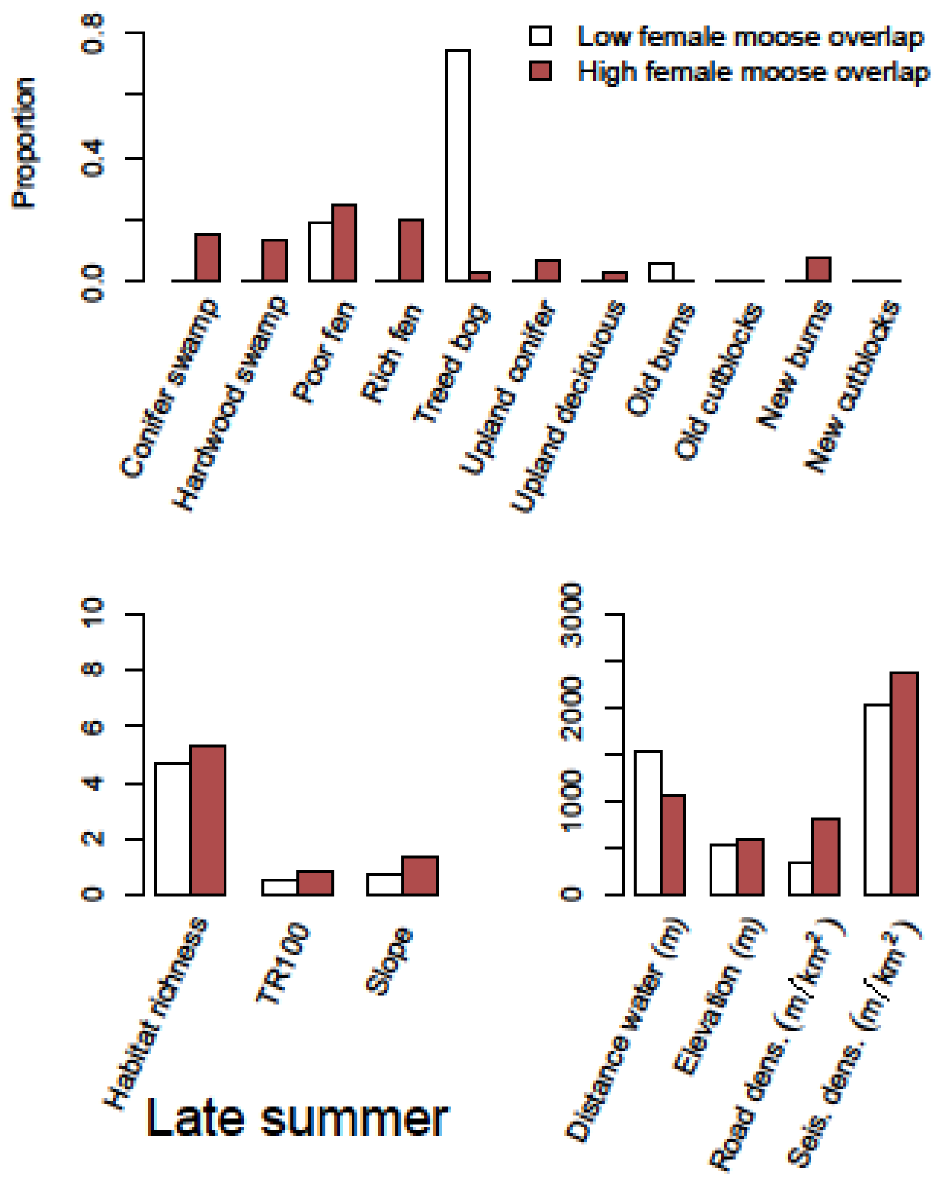

Figure A4. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and female moose in northeast British Columbia during late summer. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

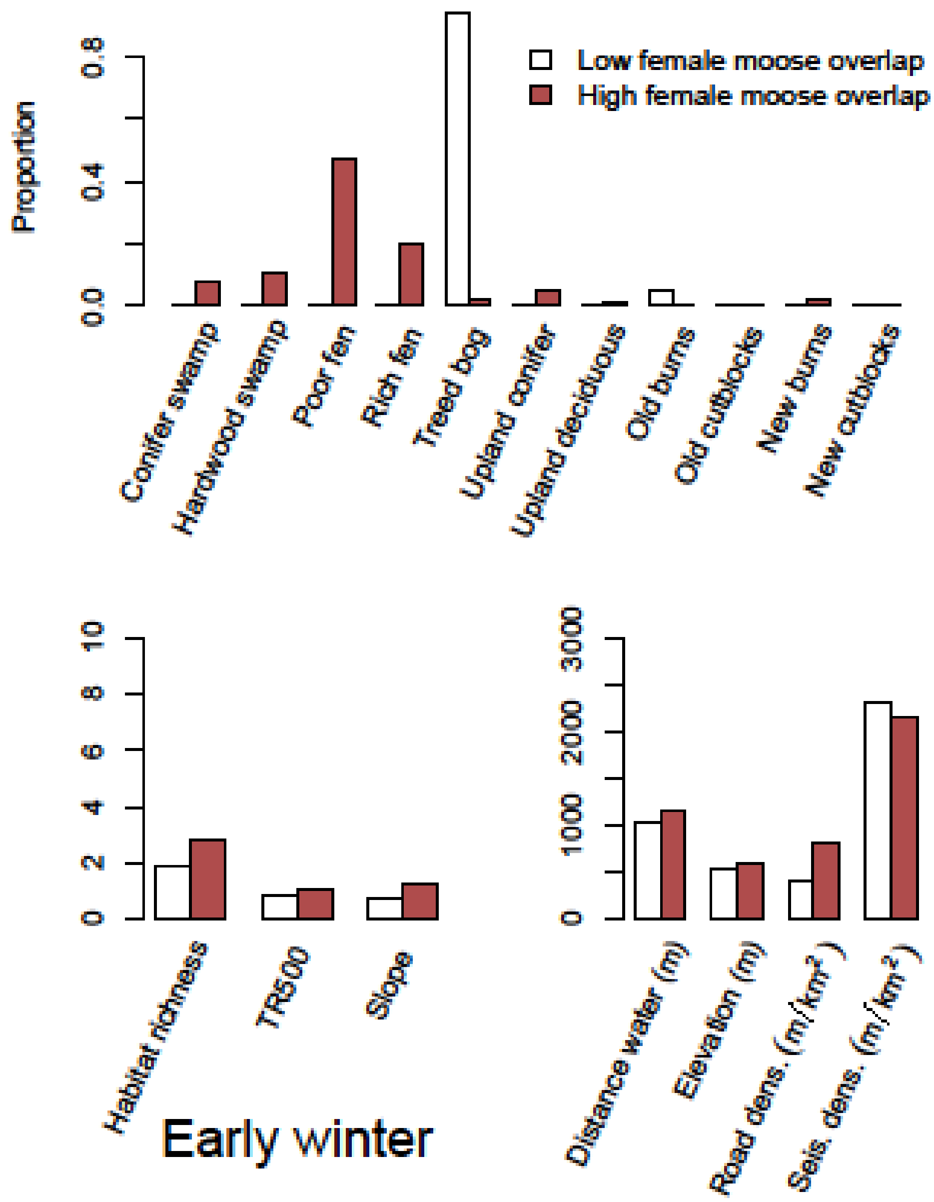

Figure A5. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and female moose in northeast British Columbia during early winter. Terrain roughness at a 500-m buffer = TR500, density = dens., seismic lines = seis.

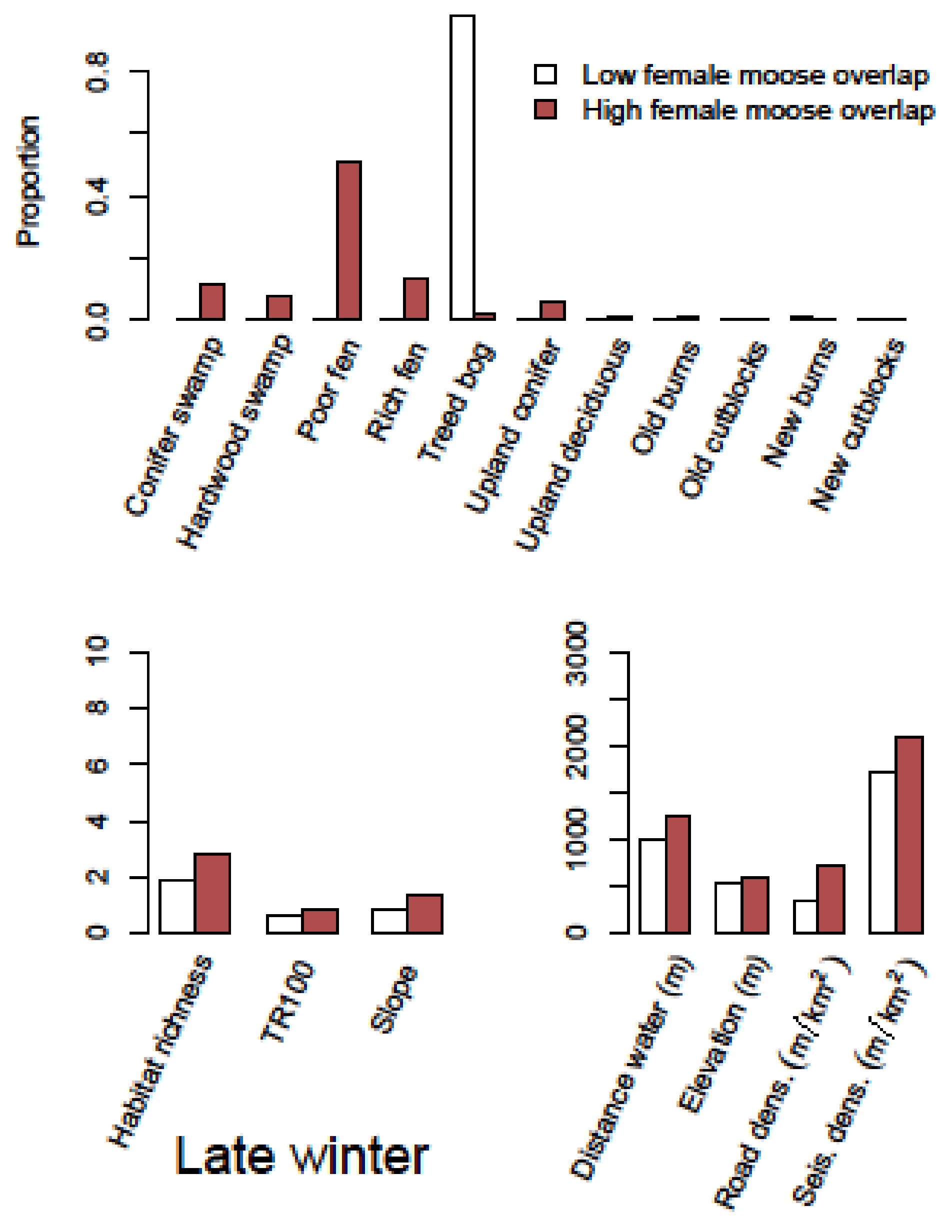

Figure A6. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and female moose in northeast British Columbia during late winter. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

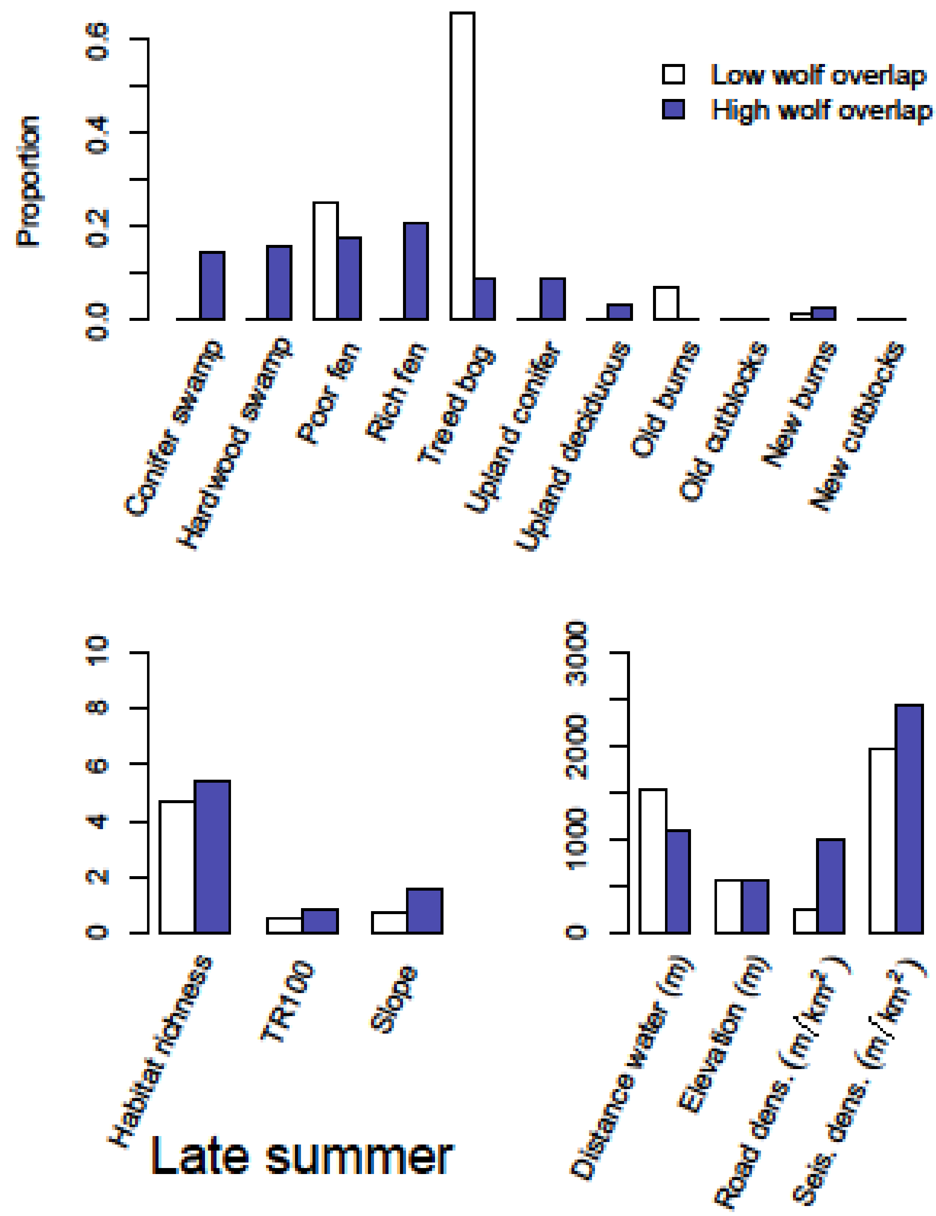

Figure A7. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and wolves in northeast British Columbia during late summer. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.

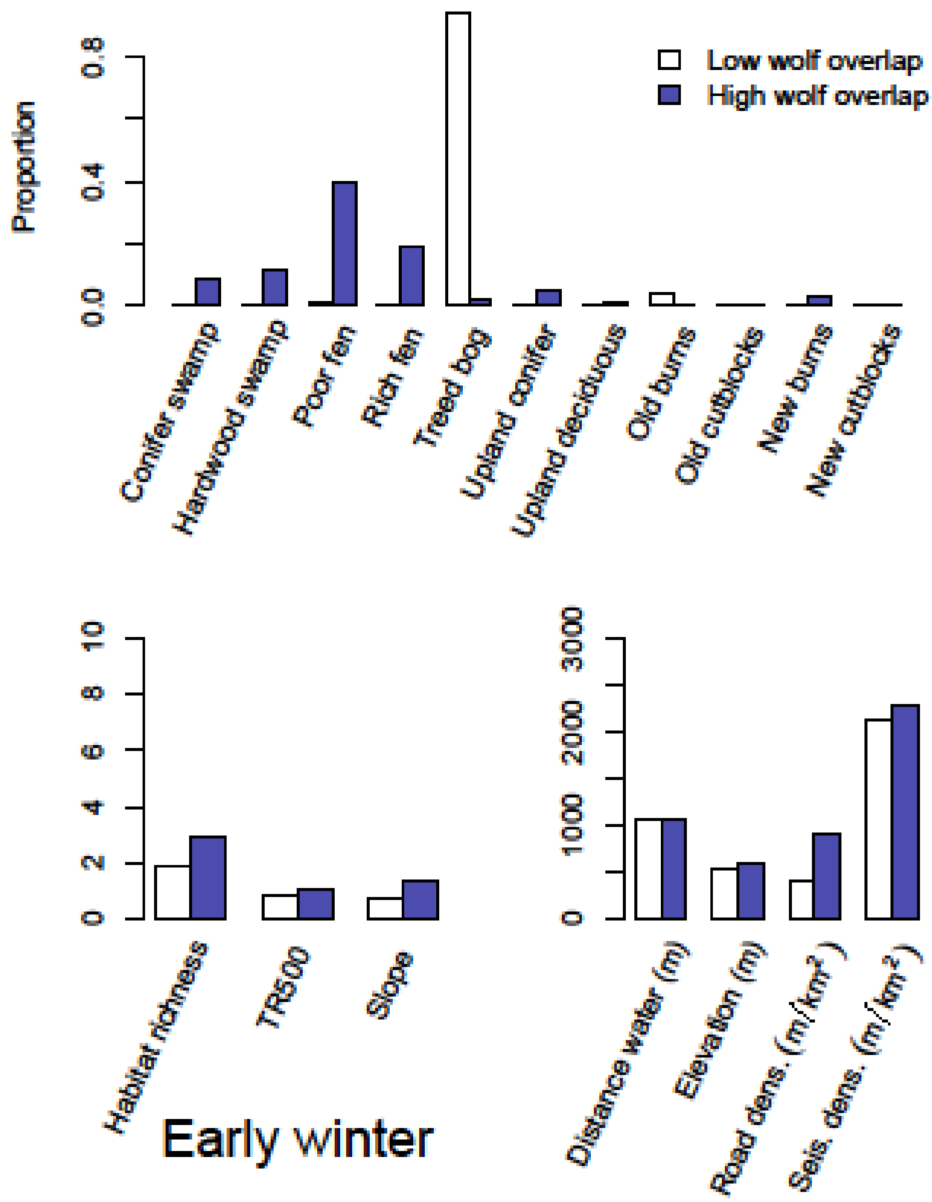

Figure A8. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and wolves in northeast British Columbia during early winter. Terrain roughness at a 500-m buffer = TR500, density = dens., seismic lines = seis.

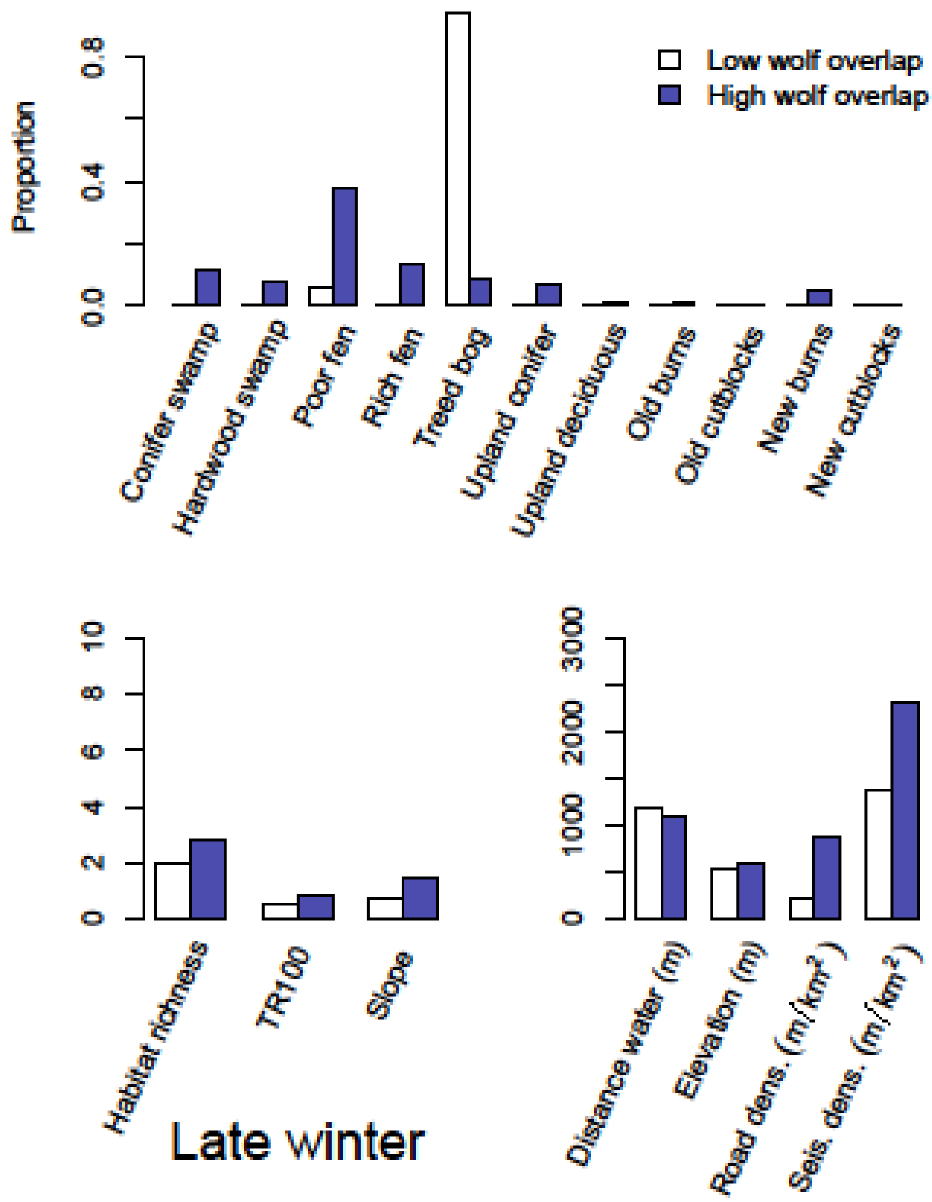

Figure A9. Comparison of landscape characteristics for caribou locations with low and high overlap between caribou and wolves in northeast British Columbia during late winter. Terrain roughness at a 100-m buffer = TR100, density = dens., seismic lines = seis.