The effect of fire on spatial separation between wolves and caribou

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Abstract: Fire management is an important conservation tool in Canada's national parks. Fires can benefit some species, while others may be negatively impacted. We used GPS and VHF collar data for 47 wolves from 12 separate packs and 153 caribou from 5 separate herds, and resource selection analysis to model the effects of fire on these species' habitat and potential interactions. Resource selection modeling showed that wolves select for burned areas and areas close to burns, presumably due to the presence of primary prey (i.e., elk and moose), while caribou avoid burns. Fire reduced the amount of high quality caribou habitat (a direct effect), but also increased the probability of wolf-caribou overlap (an indirect effect). We delineated a spatial index of caribou "safe zones" (areas of low overlap with wolves), and found a positive relationship between the proportion of a herd's home range represented by "safe zone" in winter and population size ($P = 0.10$, $n = 4$). While currently-planned prescribed fires in Banff and Jasper reduced the amount of quality caribou habitat by up to 4%, they reduced the area of "safe zones" by up to 7%, varying by herd, location, and season. We suggest that conservation managers should account for the indirect, predator-mediated impacts of fire on caribou in addition to direct effects of habitat loss.

Key words: *Canis lupus*; fire; *Rangifer tarandus caribou*; resource selection; spatial separation; wolf; woodland caribou.

Introduction

Woodland caribou (*Rangifer tarandus caribou*) are classified in Alberta as *threatened* both provincially (under the Alberta Wildlife Act) and nationally (under the Species at Risk Act), and are declining likely due to resource extraction activities that are altering predator-prey dynamics (Alberta Woodland Caribou Recovery Team, 2005; Wittmer *et al.*, 2005). Human activities such as forestry are thought to increase densities of primary prey, which in turn increase densities of predators (Seip, 1992; Wittmer *et al.*, 2007). Moreover, linear features such as roads and seismic lines created by human development may enhance predator efficiency (James & Stuart-Smith, 2000). High levels of human development in Alberta from forestry and oil and gas development are related to declines in almost all provincial caribou herds (McLoughlin *et al.*, 2003; Sorensen *et al.*, 2008). Banff

and Jasper National Parks in Alberta (Banff and Jasper) have historically maintained populations of woodland caribou, although numbers in both parks have declined since the 1980s. The cause of declines within the national parks where resource extraction does not occur is unclear, but is also hypothesized to be related to predation.

Recovery of wolf (*Canis lupus*) populations in Banff and Jasper during the 1970s appears to have coincided with caribou declines (Hebblewhite *et al.*, 2010). A possible mechanism explaining this relationship is apparent competition; where secondary prey experience increased predation pressure due to a shared predator's response to primary prey (Holt, 1977; DeCesare *et al.*, 2010). Under the apparent competition hypothesis, increased predation pressure on secondary prey may be the result of an increased number of predators (numerical response), or increased spatial overlap between predators and secondary prey (aggregative response) (Holt & Lawton, 1994; Berryman & Gutierrez, 1999). Caribou are thought to have historically avoided the affects of apparent competition by minimizing spatial and temporal overlap with wolves; a strategy termed the Spatial Separation Hypothesis (Bergerud *et al.*, 1984; James *et al.*, 2004). In the National Parks, primary prey populations (i.e., elk (*Cervus elaphus*) and moose (*Alces alces*)) increased during decades of wolf control. As a result, following recolonization, wolves likely exceeded historically common densities and caused declines of caribou due to increased predation (Hebblewhite *et al.*, 2007b; Hebblewhite *et al.*, 2010). Persistence of caribou in Banff and Jasper may therefore be tied to densities of wolves and primary prey, as well as habitat-related spatial factors that affect overlap between wolves, primary prey, and caribou.

Parks Canada has an active fire management program with goals of restoring historic fire cycles, reducing the risk of catastrophic fires near townsites and adjacent provincial lands, and of managing mountain pine beetle outbreaks (Parks Canada, 2005). While fire can improve habitat for some species, it may be directly detrimental to species (such as caribou) that rely on older seral stage forests. For instance, southern mountain caribou in British Columbia prefer late-seral forests where the abundance of arboreal lichens is highest (Terry *et al.*, 2000; Johnson *et al.*, 2004). Previous studies of caribou resource selection within Banff and Jasper showed that caribou selected forest stands older than 75 years of age (Shepherd *et al.*, 2007). Rupp *et al.* (2006) used landscape-scale fire and climate simulations to show that increased fire frequency would have negative effects on the availability of winter caribou habitat in east-central Alaska.

Conversely, elk and moose both respond positively to the increased forage within burned areas (Tracy & McNaughton, 1997; Karns, 1998; Maier *et al.*, 2005; Mao *et al.*, 2005; Sachro *et al.*, 2005). Despite their reliance on old forests, Bergerud (1974) suggested that the direct loss of lichen forage due to fire or logging was not sufficient to cause observed declines in caribou populations. Fire may reduce caribou habitat quality directly through removal of lichen biomass. However, fire may also act to reduce caribou populations by altering apparent competition dynamics by increasing primary prey and predator densities and/or the spatial overlap of these species with caribou.

It may be possible to mitigate effects of fire on caribou by assessing how fire influences overlap between wolves and caribou and identifying areas of high overlap. Recent applications of resource selection function (RSF) modeling to predator-prey theory have suggested that RSF models can be used to estimate overlap using two independent RSF models. Therefore, we estimated wolf–caribou overlap in Banff and Jasper using wolf and caribou RSF models. Under the spatial separation hypothesis, we predicted that most predation would occur where the probability of overlap between wolves and caribou was greatest. Conversely, we identified areas with low probability of wolf and caribou overlap to delineate caribou "safe zones" where caribou had an extremely low probability of wolf-caused mortality. We then tested the indirect effects of fire on wolf-caribou overlap by measuring the effects of simulated prescribed fires and the resulting change in "safe zone" habitat. Finally, we compared the indirect effects of fire on safe zones to the direct loss of high quality caribou habitat due to fire. We predicted that fire would increase the amount of wolf–caribou overlap, effectively reducing the "safe zones" for caribou.

Study area

Our study area was defined by the movements of radio-collared caribou and wolves along the eastern slopes of the Canadian Rockies in Banff and Jasper National Parks (hereafter referred to as Banff and Jasper) in the province of Alberta and a small adjacent area of British Columbia, a combined area of approximately 67 000 km² (Fig. 1). Topography ranges from 896 m to 3739 m ASL in elevation, and climate is characterized by long, cold winters, and short summers with most precipitation occurring in spring. Banff is 6858 km² and Jasper is 11 228 km² in area. Vegetation is classified into three broad ecoregions: montane, subalpine, and alpine. The montane is dominated by lodgepole pine (*Pinus contorta*) interspersed
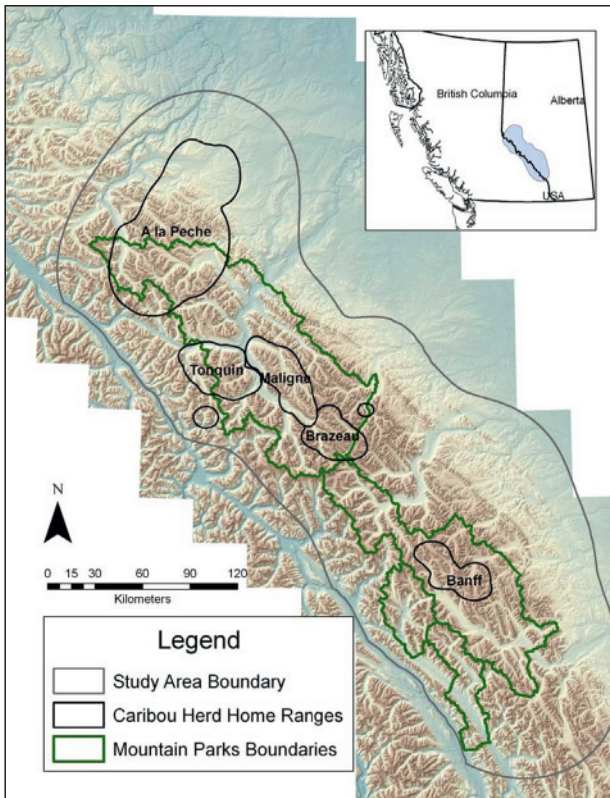
Fig. 1. Annual 99% adaptive kernel home ranges of five wood-land caribou herds utilizing Banff and Jasper National Parks, Alberta (2001 - 2008).

while the Maligne ($n=4$) and Brazeau ($n=9$) have declined to low population levels (DeCesare *et al.*, 2011).

The mammalian community of predators include wolves, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), and coyotes (*Canis latrans*). Ungulate species besides caribou include moose, elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Wolves rely primarily on elk as prey in the southern end of this ecosystem (Hebblewhite *et al.*, 2004), but shift towards moose along a north-south gradient as moose become more abundant (Kuzyk *et al.*, 2005; Franke *et al.*, 2006).

Methods

We captured and radio-collared wolves and caribou from 2001 to 2010 to obtain location data used to develop resource selection function models. Study animals were captured via leg-hold trap (wolves) or via helicopter net-gunning and darting by trained personnel (wolves and caribou), under approved university and government animal handling protocols (University of Montana Animal Use Protocol 059-09MHWB-122209). We outfitted adult animals with either very high frequency (VHF) or LOTEK (Aurora, ON) global positioning system (GPS) radiocollars (LOTEK models GPS 2000, 2200, 3300, 4400). GPS collar data was standardized to a 4-hour acquisition interval for both species with an average fix location error of 33 m (Hebblewhite *et al.*, 2007a).VHF-collared animals were located from fixed-wing or rotary-wing aircraft approximately once per month.

From 2001 to 2007, 40 female caribou from the 5 herds were captured and fit with GPS collars. From 1980 to 2007 an additional 113 caribou were fit with VHF collars. From 2002 to 2009, 28 wolves from 12 packs in Banff and Jasper were captured and fit with GPS collars, and an additional 19 wolves were fit with VHF collars during that same period. All GPS locations acquired prior to 2008 were used in model training. GPS locations acquired after 2007 were standardized to a single location per day, combined with all VHF collar locations, and used for model validation (see supplementary materials Tables 1, 2 and 3 for further information regarding telemetry data).

with Englemann spruce (*Picea engelmanii*) and willow (*Salix* spp.) areas, aspen (*Populus tremuloides*) parkland, and grassland. Sub-alpine and alpine ecoregions are comprised of Engleman spruce, subalpine fir (*Abies lasiocarpa*) and lodegepole pine forest interspersed with willow-shrub riparian communities, subalpine grassland, grading to open shrub-forb meadows in the alpine ecoregion (Holland & Coen, 1983).

Hewitt (1921) noted that caribou were historically "abundant" in the Canadian Rockies. Jasper may have sustained populations of mountain caribou ranging from 435 to 700 individuals into the early 1970s following decades of wolf control in Alberta (Stelfox, 1974; Gunson, 1992). Wolves recolonized Banff and Jasper in the early 1970s (Carbyn, 1974; Dekker *et al.*, 1995; Paquet *et al.*, 1996). Today, the mountain national parks support 4 extant caribou herds, containing an estimated population of 237 individuals (Fig. 1). In March 2009, all known individuals ($n=4$) in Banff were killed in an avalanche, and the herd was likely extirpated (Hebblewhite *et al.*, 2010). Of the remaining herds, the Tonquin ($n=74$) and A La Pêche ($n=150$) are thought to be stable or declining,

Resource Selection Functions

We developed seasonal resource selection functions (RSFs) for both wolves and caribou. We identified two seasons based on the elevational migration of caribou in the study area: winter (December to May) and summer (June to November) (McDevitt *et al.*, 2009). Recent studies have demonstrated that caribou populations are most influenced by factors operating at large-landscape scales (Rettie & Messier, 2000; McLoughlin *et al.*, 2005; Sorensen *et al.*, 2008), and that factors influencing caribou habitat should be investigated at large spatial scales (Environment Canada, 2008). Therefore, we evaluated caribou resource selection at the second-order scale, assessing the selection of home range resources within the regional landscape (Johnson, 1980). We evaluated selection using a used-available design by comparing the proportionate use of resources to their proportionate availability within a logistic regression framework (Hosmer & Lemeshow, 2000; Manly, 2002). We sampled availability using a 3:1 ratio of random available locations to telemetry locations. Random available locations were drawn from within the study area boundary defined by a 99% adaptive kernel (Worton, 1989) based on the combined locations of all study animals (Fig. 1). We used a generalized linear mixed-effects modeling (GLLAMM) framework to account for unbalanced sample sizes between individual radio-collared animals and to treat the individual animal as the most appropriate sample unit (Gillies *et al.*, 2006). The used-available design results in a relative probability function of selection because true unused locations are not sampled, but this relative probability is appropriate to rank habitat quality (Johnson *et al.*, 2006).

We overlaid caribou and wolf telemetry data on raster layers (30m resolution) in a geographic information system (GIS; ArcGIS 9.3) to quantify the underlying resources (habitat) associated with each location. Habitat variables included landcover (i.e., dominant vegetation), topography (i.e., elevation, slope, etc.), and human use (i.e., distance to infrastructure) (see supplementary materials Table 4 for complete description of all candidate variables).

To characterize vegetation we used seamless GIS coverages of forest crown closure (0–100%), landcover, and forest species composition (0–100% coniferous) for the entire study area developed with Landsat 5 Thematic Mapper (TM) or Landsat 7 TM sensor data (McDermid *et al.*, 2009). We also used the Normalized Difference Vegetation Index (NDVI) as a measure of the biomass of green forage biomass at a 250 m^2 scale obtained from Moderate Resolution Spectroradiometer (MODIS) data; NDVI has been shown to be related to ungulate and carnivore resource selection in recent studies (Pettorelli *et al.*, 2005; Hebblewhite *et al.*, 2008). However, because NDVI only indexes ungulate forage biomass reliably in open habitats, we only used NDVI in open habitats using the landcover model above to develop an open/closed mask for NDVI (e.g., Hebblewhite *et al.*, 2008). We used a digital elevation model (DEM) to derive layers of elevation, slope, and aspect.

As both caribou and wolves respond to human use and linear features (e.g., James & Stuart-Smith, 2000; Hebblewhite *et al.*, 2005b), we used vector geodatabases of towns, roads, seismic lines, and trails to create raster layers of the distance of each pixel to the nearest of each of these human-use linear or point features. Roads were classified as either primary (i.e., paved) or secondary (i.e., gravel) and a separate layer of the distance to each was created. A single trail layer was created by combining trails within the parks with seismic lines outside. We assumed that human use of both was similar and therefore that animal response to each would also be similar. Previous studies have shown that wolves selected areas close to edges and stream banks for travel (Hebblewhite *et al.*, 2005a; Bergman *et al.*, 2006). Therefore, we included GIS layers representing the straight-line distance to streams and forest edges.

Fire and stand age layers were obtained from Parks Canada for the National Parks, and from Alberta Sustainable Resource Development for areas outside the parks (White *et al.*, 2003; Van Wagner *et al.*, 2006). Caribou have been shown to avoid burned areas up to 50 years post burn, while primary prey use declines about that same time (Peck & Peek, 1991; Joly *et al.*, 2003). Therefore, we classified burns as any area where a fire had occurred since 1950, limiting the affects of fire to those within 50-60 yrs of our wildlife data collection.

We used a manual stepwise model building method described by Hosmer & Lemeshow (2000) to create "best" models that described the resource selection of both species. This pluralistic model building approach best reflects the balance between prediction and mechanism as achieved through regression-type models (Stephens *et al.*, 2005). Candidate variables were considered if biologically relevant, ecologically plausible, non-confounded, and uncorrelated at a correlation coefficient of $|r| < 0.5$ (Hosmer & Lemeshow, 2000). We considered both linear and non-linear (quadratic) responses to continuous variables for both species and used a combination of graphical and Akaike information criteria (AIC) based methods to determine how a response was best modeled. First, frequency histograms of used and

available distance locations were plotted then compared to the predicted values of a univariate model to graphically depict each species' response. Secondly, the AIC values of univariate models fit as a linear and quadratic response were compared in order to gauge if modeling as a quadratic improved fit (Burnham & Anderson, 1998). We followed the same procedure for all continuous covariates in which we expected potential non-linear resource selection patterns, including elevation (selection for intermediate elevations), distances to human activity, distance to burns, etc.

We used both within-sample and out-of-sample validation techniques to test the predictive ability of our models (Boyce et al., 2002). Within-sample validation first consisted of standard logistic regression diagnostics and goodness-of-fit measures including variance inflation factors (VIFs), classification tables and the area under the receiver operating characteristic (ROC) curves (Fielding & Bell, 1997; Hosmer & Lemeshow, 2000). We also used k-fold cross-validation to estimate Spearman's rank correlation (rho) statistics correlating model predictions to subsets of withheld data (Boyce et al., 2002). Finally, we used telemetry data, which we had withheld from model development entirely to asses model predictions again with Spearman's rank correlation (see supplementary materials Tables 1, 2 and 3 for description of data used in validation). This out-of-sample validation provided a robust measure of model performance (Fielding & Bell, 1997).

Overlap and probability of wolf predation on caribou.
We treated RSF models for caribou and wolves as habitat ranking models, and used them to assess wolf-caribou overlap by subtracting the caribou RSF from the wolf RSF (sensu Neufeld, 2006). Continuous RSF maps were categorized into 10 equal-area (km²) habitat bins based on the predicted values of random locations (Boyce et al., 2002). We estimated the wolf-caribou overlap index subtracting the binned wolf RSF model from the binned caribou RSF model. This generated a spatial overlap index from -10 to +10, where high values indicate high quality caribou habitat and low quality wolf habitat, and low values indicate low quality caribou habitat and high quality wolf habitat. We overlaid this index layer with our out-of-sample telemetry locations to graphically depict the frequency of use by each species across this overlap index. We used this overlay of withheld locations and overlap index to visually estimate a cut point at which high quality caribou habitat existed with little probability of wolf use, referring to these areas as caribou "safe zones". We hypothesized that most predation events would occur where the prob-

ability of overlap between wolves and caribou was greatest. We tested this hypothesis by obtaining the overlap index scores of suspected and confirmed wolf-caused caribou mortalities. Mortality locations were obtained from both collared caribou, and uncollared caribou discovered by parks staff when investigating wolf GPS locations, and those reported to Parks staff by the public.

Evaluating the direct and indirect effects of fire with burn scenarios
We modeled the direct and indirect effects of 3 future burn scenarios on caribou using Parks Canada's current prescribed fire plan, and two randomly located "wildfire" scenarios. The first scenario was created by simply adding all of the prescribed fires currently planned by Parks Canada within Banff and Jasper. Secondly, we simulated a single 1% wildfire within each caribou home range (interior wildfire), and thirdly, we simulated wildfires outside of caribou home ranges but within a 14-km buffer zone surrounding the home ranges (buffer wildfire). A 14-km buffer was chosen as it was the mean distance of avoidance of burns across seasons determined from our caribou resource selection results (see RSF results below).

In 2000, a wildfire was ignited by lightning in Jasper on the southeast corner of the Tonquin caribou herd's home range. The fire consumed 1028 ha of forest, or approximately 0.7% of the Tonquin caribou's range. Using this naturally occurring fire as a template of the extent of probable future events, we simulated wildfires in our GIS burn layers representing 1% of each of the five caribou home ranges. These burns were created by selecting at random the largest contiguous forest block with a stand origin closest to 1862, the mean stand origin of Parks Canada's current planned prescribed fires, and adding adjacent forest polygons until the desired burn size was achieved. GIS layers of planned prescribed fires were obtained for Banff and Jasper for use in simulations.

We projected our original RSF models onto landscapes created under each burn scenario and quantified changes in the amount of high quality caribou habitat and caribou "safe zones" within each herd's home range using Hawthtools Zonal Statistics (Hawth's Analysis Tools for ArcGIS v.3.27). To assess the direct effects of fire on caribou we quantified the change in the amount of high quality caribou habitat according to the caribou RSF model. We identified high quality caribou habitat using a caribou RSF bin rank of 8 or higher because 85% of all out-of-sample caribou telemetry locations occurred in habitat ranks of 8 or greater. To assess the indirect effects of fire

on caribou we quantified the change in the amount of caribou "safe zone". We quantified the relative change in the indirect effects of fire (safe zone loss) and direct effects of fire on caribou habitat (RSF loss) between herds, and fire type (planned prescribed fire, interior wildfire, or buffer wildfire) using a two-way analysis of variance (ANOVA) (Zar, 1999).

Population consequences of overlap between wolves and caribou

To test for the consequences of increased overlap between wolves and caribou on caribou population dynamics, we investigated the relationship between the amount of "safe zone" within each caribou herd ($n=4$) and herd-specific estimates of abundance, mean annual population growth rate, and adult female survival rates using data from complementary studies (Hebblewhite *et al.*, 2010; DeCesare *et al.*, 2011). Based on previous studies of spatial separation in mountainous terrain in BC (Seip, 1992), we expected that greater levels of spatial separation and larger areas of safe habitat would be positively correlated with larger caribou populations, higher caribou survival rates, and higher population growth rates. We tested this hypothesis by examining how the amount of winter, summer, and amount of seasonal change of safe zones affected these three demographic metrics across the 4 extant caribou herds using linear regression (Banff was excluded from this analysis as no demographic data existed for this extirpated herd).

A prediction of the apparent competition hypotheses is that caribou ranges with more "safe zone" habitat would have larger population size, higher adult female survival rates, and higher population growth rates due to increased spatial separation between wolves and caribou.

Results

Resource selection (RSFs)

In summer, wolves selected herb and shrublands at both high and low elevations (supplementary material Table 5). Burned areas were strongly selected as well as areas close to burns. Deciduous forests and alpine barren ground were avoided. Selection decreased with distance to stream banks. Wolves avoided secondary roads, while selection declined with distance from primary roads and trails showing selection for areas with human activity at this second-order scale. Geographically, wolf resource selection appeared to be a generalized function of low elevation valley bottoms throughout Banff and Jasper. The model ROC value of 0.89 showed excellent discrimination, and both within-sample k-fold cross-validation (rho = 0.99)

and validation using withheld out-of-sample data showed high predictive ability (rho = 0.98, $P < 0.01$).

In summer, caribou selected both low elevation and high elevation alpine herb and shrublands (supplementary material Table 5). Intermediate levels of greenness or NDVI in open habitats, presumably related to maximum forage quality (Hebblewhite *et al.*, 2008), were also selected. Caribou strongly avoided burned areas, even more strongly than the ice and rock landcover class. Caribou selection as a function of distance to burned areas was best modeled as a quadratic with use maximized at a distance of approximately 18 km. They selected moderate elevations with the highest probability of use at 1982 m. Our top summer caribou model accounted for approximately 50% of variation in summer resource use. The ROC value of 0.93 showed excellent discrimination of used/available locations. K-fold cross validation revealed excellent predictive capacity (rho = 0.99), however the model only adequately predicted withheld or out-of-sample locations (Spearman rank correlation rho = 0.67, $P = 0.03$)

In winter, wolves preferred open conifer forests, as well as low herb and shrublands (supplementary material Table 6). Burned areas were also strongly selected for, and selection declined linearly with distance to burn indicating selection for areas close to burns. Over and above their avoidance of high elevations, wolves also strongly avoided alpine areas and rock and ice during winter. Selection also declined with distance to stream banks and in open canopy forests. In winter, wolves selected for low-intermediate elevations (probability of use was highest at 1817 m). The model showed similar ability to discriminate between used and available locations as our summer wolf model, and validated well. The ROC value of 0.89 shows excellent discrimination. Both within-sample k-fold cross-validation (rho = 0.99), and validation using reserved out-of-sample data (rho = 0.98, $P < 0.01$) showed high predictive ability.

In winter, caribou selected for conifer forests and alpine herb and shrublands, while avoiding both low elevation and alpine barren ground (supplementary material Table 6). Burned areas were completely avoided, precluding a burn coefficient in the model (perfect predictability); however,; burned areas are included in the model intercept. Use based on distance to burned areas was best modeled as a quadratic function with use maximized at a distance of approximately 10 km. Our top winter model validated very well showing high ROC values (0.88), and outstanding within-sample k-fold (rho = 0.99) and out-of-sample Spearman rank correlation (rho = 0.98, $P < 0.01$).

Overlap and probability of wolf predation on caribou

We found the greatest number of wolf-killed caribou where their probability of spatial use was approximately equal to that of wolves, and therefore probability of overlap highest (Fig. 2). Overlap between wolves and caribou appeared to be negligible at overlap index values of positive 5 or above. We chose this overlap value of ≥ 5 as a cut-point to delineate caribou safe zones for the remainder of the analysis.

The seasonal strength of spatial separation by wolves varied between individual caribou herds as measured by the degree of safe zone within their home range. The A La Pêche had the greatest amount of safe zone habitat, followed by the Tonquin, Brazeau, Banff, and Maligne herds (Table 1). Spatial separation between wolves and caribou increased during winter for all herds, with the amount of safe zone at least doubling during that season.

Evaluating the direct and indirect effects of fire

The effects of fire on quality caribou habitat (direct effects) varied based on season, location of burn, and herd or home range size. ANOVA confirmed that the direct habitat-related effects of burn scenarios (prescribed, interior, buffer) on the percent of high quality habitat within caribou ranges were not significant (P = 0.978),
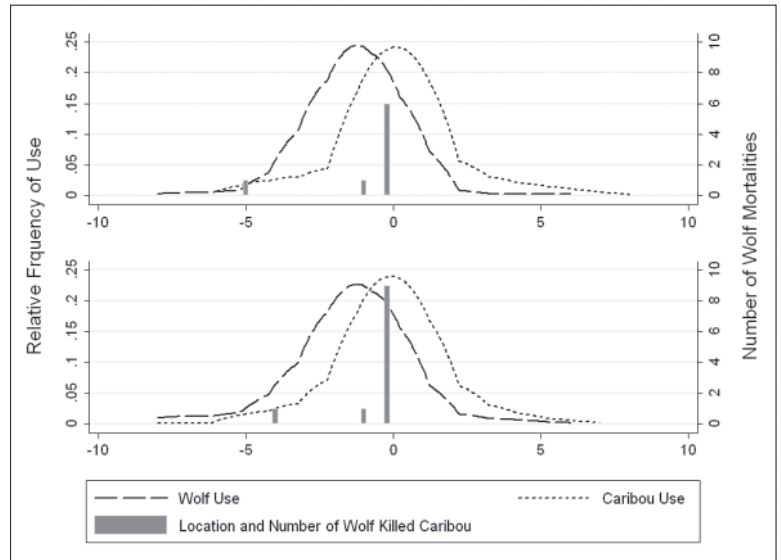

Fig. 2. Seasonal overlap of caribou and wolves showing relative probability of use as a function of the difference between summer (top) and winter (bottom) caribou and wolf resource selection models, and location and frequency of caribou mortalities (black bars). Note the X axis is the difference between binned RSF values of caribou and wolves, such that high values (10) represent safe areas for caribou, and low values (-10) represent high wolf use areas.

Table 1. Total area in km² and % of home range contained within safe zone habitat (with low wolf–caribou overlap) during winter and summer in the Canadian Rockies.

Herd	Season	Area (km²)	% of Home Range
A La Pêche	Summer	902.2	14.7
A La Pêche	Winter	1580.2	25.9
Banff	Summer	60.3	5.9
Banff	Winter	92.8	9.2
Brazeau	Summer	73.5	6.8
Brazeau	Winter	131.1	12.3
Maligne	Summer	1.2	0.1
Maligne	Winter	3.8	0.3
Tonquin	Summer	59.4	3.9
Tonquin	Winter	235.6	15.6

and that the main differences in habitat quality were driven by seasonal differences between winter and summer ($P<0.005$) (Table 2). Considering only the effects of direct habitat loss due to loss of high quality caribou habitat, currently planned prescribed fires showed proportional (1%:1%) reductions in habitat of the A La Pêche, Banff, and Maligne herds (Table 3). A 1 % interior burn within a herd's home range caused an average of 1% habitat loss in winter, but a 2.3% loss in summer. Also, logically, burns on the periphery of caribou ranges (within a 14-km buffer) had negligible effects on direct habitat loss (Table 3).

In comparison to the direct habitat-related effects of fires, the indirect predation risk effects of burns varied with season, herd, and type of fire (Table 3). ANOVA revealed much greater interaction between

Table 2. ANOVA results for the effects of burn scenarios, season, and herd status on the percentage of caribou ranges occurring in high quality caribou habitat from RSF models, measuring the direct effects of fire on caribou. Seasons were winter and summer, and burn scenarios were prescribed burns, interior area, and buffer area burns. No interactions were significant. Overall adjusted R^2 for the model was 0.831, $n=40$ landscape burn experiments.

	Partial SS	df	MS	F	P-value
Model	3.333	12	24.88	24.88	<0.0005
Season	3.227	1	192.77	192.7	<0.0005
Herd	0.102	4	1.53	0.218	0.218
Burn Scenario	0.003	3	0.06	0.06	0.978
Residual	0.519	31	0.0167		
Total	3.852	39			

Table 3. Percentage areal reduction (%) in habitat quality and amount of safe zone by herd following simulated 1% prescribed, within home range, and within buffer zone fires. Values greater than equal losses to the 1% fire are bolded, indicating indirect effects of fire were important.

Herd	% Habitat Loss			% Safe Zone Loss		
	Prescribed Fire	Interior Fire	Buffer Fire	Prescribed Fire	Interior Fire	Buffer Fire
Summer						
A La Pêche	**-1**	-2.7	-0.4	-2.2	-0.2	-0.1
Banff	-1.2	-4	<-0.1	-2	**-3.6**	-0.2
Brazeau	-0.6	-2.3	<-0.1	**-1**	-2.4	<-0.1
Maligne	-1.5	**-1.9**	-0.2	<-0.1	<-0.1	<-0.1
Tonquin	-0.5	-0.8	<-0.1	-0.2	<-0.1	<-0.1
Mean	-1	-2.3	-0.15	-1.1	-1.3	**-0.1**
Winter						
A La Pêche	-0.5	-1.2	**-0.2**	-7.4	-0.3	<-0.1
Banff	-0.3	-1.5	<-0.1	-2.7	**-3.8**	<-0.1
Brazeau	-0.4	-1.2	<-0.1	<-0.1	-4.6	<-0.1
Maligne	-0.5	-1.1	-0.1	<-0.1	-0.1	<-0.1
Tonquin	-0.4	<-0.1	<-0.1	<-0.2	<-0.1	<-0.1
Mean	-0.4	-1	-0.1	-2.1	-1.8	<-0.1

Table 4. ANOVA results for the effects of burn scenarios, season, and herd status on the percentage of caribou ranges occurring in safe zone habitat, measuring the indirect effects of fire on caribou mediated via increased wolf–caribou overlap. Seasons were winter, summer, and burn scenarios were prescribed burns, interior area, and buffer area burns. Both season*herd and burn*herd 2-way interaction were significant. Overall adjusted R^2 for the model was 0.985, $n=40$ landscape burn experiments.

	Partial SS	df	MS	F	P-value
Model	0.21	24	0.0088	107.71	<0.0005
Season	0.035	1	0.0348	427.28	<0.0005
Herd	0.151	4	0.0376	462.26	<0.0005
Burn Scenario	0.002	3	0.0007	8.81	0.0013
Season*Herd	0.018	4	0.0045	55.37	0.0021
Burn*Herd	0.005	12	0.0004	5.07	0.08
Residual	0.001	15	0.0001		
Total	0.211	39	0.0054		

season, burn scenarios, and herds such that the effects of fires differed substantially between burn scenarios and herds (Table 4). The single greatest effect on a herd was a 7% loss in winter safe zone within the A La Pêche home range resulting from a currently planned prescribed fire (Table 3). Similar to habitat loss, however, the greatest impact appears to be from fires located directly within the interior area, with the Banff and Brazeau herds showing 2-5% losses of safe zone following fire (representing 1% of that herd's home range). Fires in the buffer zones surrounding the caribou home ranges had little effect on the amount of safe zone within (Table 3).
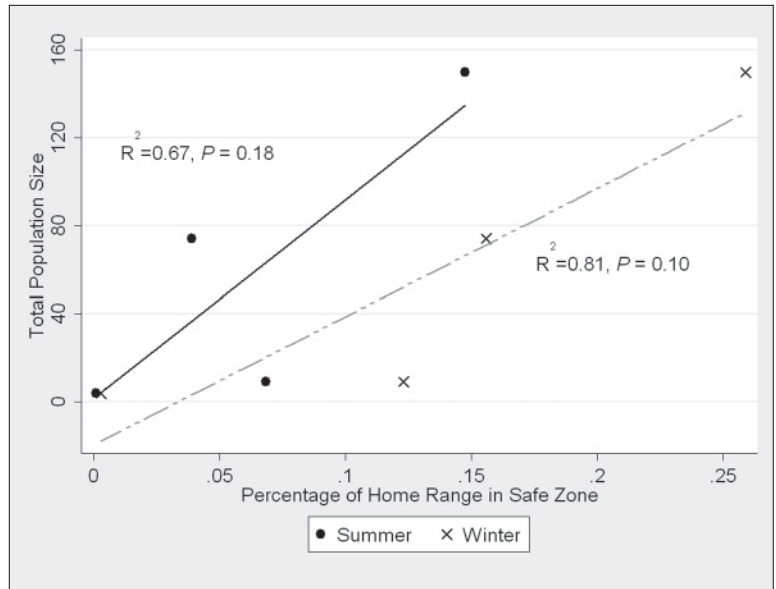

Fig. 3. Habitat-population relationships between percentage of home range consisting of safe zone within each caribou herd, and estimated population size of the caribou herd during winter and summer.

Population consequences of spatial separation between wolves and caribou

There was a positive relationship between the proportion of a herd's home range represented by "safe zone" and population size among the 4 caribou herds, although the relationship was marginally significant during winter ($P = 0.10$, $n=4$) but non-significant during summer ($P = 0.18$, $n=4$) (Fig. 3). There were similar positive effects of spatial separation on adult female caribou survival rates and population growth rate, although neither relationship was significant. Expressing separation as the proportion (%) that the safe zone increased during winter also showed that as spatial separation increased during winter, survival and population growth rate increased. These relationships may be biologically significant however a lack of sample size ($n=4$) limited statistical power.

Discussion

Our results suggest that spatial separation from wolves at broad, landscape scales is an important strategy for caribou to avoid mortality, and that fire will increase the amount of overlap between wolves and caribou with potentially negative consequences for caribou populations. Our support for the spatial separation hypothesis agrees with the results of many previous studies of caribou resource selection (Apps et al., 2001; McLoughlin et al., 2005; Wittmer et al., 2005) that indicated that, for example, "…the spatial distribution of woodland caribou largely reflects a behavioral response to risk" (Fortin et al., 2008). Our results show that the highest probability of caribou and wolf overlap occurs in areas where each species has an equal probability of use (i.e., areas near zero in terms of RSF difference), and it is in these same areas where the majority of wolf-caused caribou mortalities occur (Fig. 2). McLoughlin et al. (2005) showed similar results from boreal caribou in northern Alberta. Therefore, identifying areas of overlap between wolves and caribou is an important factor when considering how changes in landscape configuration induced by fire could affect wolf movements and caribou predation risk.

Our resource selection models show selection of landscape variables similar to the findings of past research on both species (e.g., Apps et al., 2001; Hebblewhite & Merrill, 2008). In summer, caribou and wolves showed similar selection for both low and high elevation (alpine) herb and shrub landcover classes; for wolves, this is presumably in response to increased prey availability. In winter, wolf selection for low elevation shrub and herb landcover classes, in conjunction with caribou selection for alpine herb and shrub, may create an elevational separation between the species; while selection by both for open conifer forests provides opportunity for overlap in that landcover type.

Wolves selected for burned areas in both seasons, while caribou avoided burns in both seasons (complete avoidance in winter), ostensibly suggesting that burns would be areas of strong separation between wolves and caribou. However, due to the linear response of wolves to distance to burned areas, their probability of use is increased not only in the burned area itself, but also in the surrounding areas. It follows that if a burn occurs in preferred caribou habitat, the probability of overlap between the two species increases by a greater proportion than simply the size of the fire.

Despite the limitations of having only 4 caribou herds to examine between-herd demographic consequences of spatial separation, our results support the demographic benefit of spatial separation from wolves over very large spatial scales. Total population size was positively correlated with the percentage of safe zone within a herd's home range during winter (P=0.10, n=4). The seasonal, but not total, estimates of spatial separation were weakly correlated with survival, lambda, and population size. Taken together, these results support the results from other studies that showed large patches of low predation risk caribou habitat are required for the long-term persistence of Boreal and Mountain populations of woodland caribou in Canada (Lessard, 2005; Wittmer et al., 2005; Courtois et al., 2007; Fortin et al., 2008). These results also support the results of recent demographic population viability models by DeCesare et al. (2011) that show almost certain extirpation of the caribou herds with low spatial separation (Maligne and Brazeau herds), but continued persistence and growth of the Tonquin herd which has more safe habitat.

We investigated the direct habitat loss and indirect predation risk effects of fire on caribou using spatial simulations of planned prescribed and natural fires. The direct effects of fire on caribou habitat itself were minimal. Burning 1% of a caribou home range reduced the abundance of high-quality caribou habitat throughout the range by an average of 2% in summer and 1% in winter. The direct effects of fire were unaffected by the position of the fires in the interior of the caribou range.

In contrast, the indirect effects of prescribed and natural fire on caribou were often greater than the direct effects, and varied across herds and burn scenarios. Fire in caribou range increased wolf use of the burned and surrounding area which in turn resulted in a decrease in safe habitat. On average, burning 1% of the landscape reduced the amount of safe habitat by ~2%, and this effect was most pronounced for fires occurring in the interior of their home ranges, and especially for a prescribed burn planned in the A La Pêche caribou home range (Table 3). This suggests that spatial arrangement of burns will be critical for evaluating effects of prescribed burn plans on caribou.

In the Canadian Rockies, we found caribou tended to select areas along the continental divide at higher elevations dominated by old-growth spruce and subalpine fir and with low fire frequency (Van Wagner et al., 2006). In contrast, wolves tended to select lower elevation, more early seral habitats that historically would have been spatially separated because of fire history (White et al., 2003; Van Wagner et al., 2006), probably contributing to the viability of caribou. Regardless, our results show that when fire overlaps current caribou habitat, there is increased overlap

with wolves, and that that has potential population consequences. Given the *threatened* status of southern mountain woodland caribou, maintenance of current caribou populations and distribution is an important management objective. Our results suggest Parks Canada managers should seek to spatially separate fires from caribou ranges when trying to restore both caribou populations and fire on the landscape—two potentially conflicting objectives. This is especially true because of potential changes to fire cycles due to fire suppression, climate change, and increased drought in Rocky Mountain areas (Schoennagel *et al.*, 2004).

Our fire scenarios did not consider a range of potential fire sizes or configurations evaluated in other wildlife-fire modeling efforts (Turner *et al.*, 1994). Even so, our results are conservative because we modeled the effect of only burning 1% of a caribou range, which equated to fire sizes of 10-61 km^2. Within the last decade, several fires in our study area were larger than the 1% burns we evaluated. With the potential for increased fire frequency resulting from the interacting effects of climatic change, historic fire suppression, and increased fuel loads (Brown *et al.*, 2004; Schoennagel *et al.*, 2005; Rupp *et al.*, 2006), large stand-replacing fires are possible in and adjacent to caribou ranges. Linking our caribou and wolf spatial overlap models to probabilistic and dynamic landscape fire simulations as used in Alaska (Rupp *et al.*, 2006) would be useful for evaluating the susceptibility of caribou in the National Parks to future fires.

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Supplementary tables

S-table 1. Number of radiocollared caribou monitored in Banff and Jasper National Parks, and total number of locations used in model development and validation.

Season	Herd	Model Training		Model Validation	
		Animals	Locations (mean, range)	Animals	Locations (mean, range)
Summer	A la Peche	10	8895 ($\bar{x}$=889, 212 - 2031)	72	924 ($\bar{x}$=13, 1 - 192)
	Banff	2	2125 ($\bar{x}$=1062, 954 - 1171)	2	31 ($\bar{x}$=15, 12 - 19)
	Brazeau	6	4521 ($\bar{x}$=735, 154 - 1523)	11	94 ($\bar{x}$=8, 3 - 13)
	Maligne	9	9329 ($\bar{x}$=1036, 187 - 2417)	10	94 ($\bar{x}$=9, 1- 22)
	Tonquin	8	4974 ($\bar{x}$=621, 152 - 1590)	17	204 ($\bar{x}$=12, 1 - 18)
Winter	A la Peche	15	11868 ($\bar{x}$=791, 341 - 1964)	78	1193 ($\bar{x}$=15, 1 - 245)
	Banff	2	1957 ($\bar{x}$=978, 880 - 1077)	2	36 ($\bar{x}$=18, 11 - 25)
	Brazeau	6	5220 ($\bar{x}$=870, 612 - 1244)	12	185 ($\bar{x}$=15, 3 - 27)
	Maligne	9	9336 ($\bar{x}$=1037, 374 - 2377)	8	95 ($\bar{x}$=11, 6 - 29)
	Tonquin	8	5058 ($\bar{x}$=632, 87 - 1553)	17	299 ($\bar{x}$=17, 3- 72)
		75		229	

S-table 2. Number of animals from each wolf pack monitored during summer in Banff and Jasper National Parks, and total number of locations used in summer model development and validation 2002 - 2009.

Park	Pack	Model Training		Model Validation	
		Animals	Locations (mean, range)	Animals	Locations (mean, range)
BANFF	Bow Valley	1	932 ($\bar{x}$= 932, N/A)	0	N/A
	Ranch	3	1859 ($\bar{x}$= 619, 561 - 675)	0	N/A
	Cascade	2	1218 ($\bar{x}$= 609, 164 - 1054)	0	N/A
	Red Deer	4	2037 ($\bar{x}$= 509, 193 - 775)	0	N/A
	Wildhorse	1	770 ($\bar{x}$= 770, N/A)	0	N/A
JASPER	Medicine	4	767 ($\bar{x}$= 191, 26 - 464)	3	60 ($\bar{x}$= 20, 2 - 32)
	Berland	1	625 ($\bar{x}$= 625, N/A)	0	N/A
	Brazeau	4	657 ($\bar{x}$= 164, 8 - 604)	1	1 ($\bar{x}$= 1, N/A)
	Maligne	1	319 ($\bar{x}$= 319, N/A)	2	3 ($\bar{x}$= 1.5, 1 - 3)
	Signal	4	760 ($\bar{x}$= 190, 3 - 328)	5	212 ($\bar{x}$= 42, 1 - 118)
	Sunwapta	2	1037 ($\bar{x}$= 518, 439 - 598)	4	316 ($\bar{x}$= 79, 2 - 158)

S-table 3.   Number of animals from each wolf pack monitored during winter in Banff and Jasper National Parks, and total number of locations used in winter model development and validation 2002 – 2009.

Park	Pack	Model Training		Model Validation	
		Animals	Locations (mean, range)	Animals	Locations (mean, range)
BANFF	Bow Valley	1	39 ($\bar{x}$= 39, N/A)	0	N/A
	Ranch	3	1472 ($\bar{x}$= 490, 253 - 813)	0	N/A
	Cascade	4	1261 ($\bar{x}$= 315, 31 - 961)	0	N/A
	Red Deer	4	1734 ($\bar{x}$= 433, 217 - 743)	0	N/A
	Wildhorse	3	1067 ($\bar{x}$=355, 103 - 544)	0	N/A
JASPER	Medicine	4	1859 ($\bar{x}$= 464, 110 - 734)	4	33 ($\bar{x}$= 8, 4 - 15)
	Berland	1	361 ($\bar{x}$= 361, N/A)	0	N/A
	Brazeau	4	2616 ($\bar{x}$= 654, 314 - 933)	2	71 ($\bar{x}$= 35, 3 - 68)
	Maligne	1	602 ($\bar{x}$= 602, N/A)	3	14 ($\bar{x}$= 4, 2 - 7)
	Rocky	1	132 ($\bar{x}$= 132, N/A)	1	2 ($\bar{x}$= 2, N/A)
	Signal	6	1879 ($\bar{x}$= 313, 6 - 595)	7	251 ($\bar{x}$= 35, 1 - 107)
	Sunwapta	2	1384 ($\bar{x}$= 692, 489 - 895)	6	361 ($\bar{x}$= 60, 4 - 186)

Variable	Variable Type	Range of Values	Description
Topography			
North	Categorical	0.1	North aspects from 315° to 45°
South	Categorical	0.1	South aspects from 135° to 225°
East	Categorical	0.1	East aspects from 45° to 135°
West	Categorical	0.1	West aspects from 225° to 315°
Flat	Categorical	0.1	No aspect (slope = 0)
Slope	Continuous	0–6827%	Percent slope (equivalent to 0 – 90°)
Elevation	Continuous	553–3955m	Elevation in meters
Landcover			
Alpine Barren	Categorical	0.1	Barren ground between 2200 and 2700m.
Alpine Herb	Categorical	0.1	Alpine meadows above 2200m.
Alpine Shrub	Categorical	0.1	Shrub communities above 2200m.
Burn	Categorical	0.1	Areas burned 1950 to present.
Closed Conifer	Categorical	0.1	Coniferous forest with >50% canopy closure and >70% conifer composition.
Deciduous Forest	Categorical	0.1	Deciduous dominated forests <30% coniferous.
Ice and Rock	Categorical	0.1	Permanent ice, snow and alpine rock above 2700m.
Low Barren	Categorical	0.1	Barren but possible still productive ground below 2200m.
Low Herb	Categorical	0.1	Grasslands below 2200m
Low Shrub	Categorical	0.1	Shrub stands below 2200m.
Mixed Forest	Categorical	0.1	Forests >30% and <70% coniferous.
Open Conifer	Categorical	0.1	Coniferous forest with <50% canopy closure and >70% conifer composition.
Wetlands and Water	Categorical	0.1	Water and wetlands at all elevations.
Bank Distance	Continuous	0–6951m	Distance to water's edge from both directions.
Burn Distance	Continuous	0–105670m	Distance to any burn occurring after 1950.
Edge Distance	Continuous	0–15531m	Distance to boundary between open and closed canopy from either direction.
Hard Distance	Continuous	0–6728m	Distance to the closest hard edge.
NDVI	Continuous	0–8759	Mean NDVI in open habitats
Open Distance	Continuous	0–15557m	Single direction distance to open canopy (i.e. value within open canopy is 0)
Human Use			
Primary Road Distance	Continuous	0–48247m	Distance to paved road.
Secondary Road Distance	Continuous	0–56075m	Distance to gravel road.
Trail Distance	Continuous	0–40972m	Distance to trails inside the parks and cutlines outside.
Water Distance	Continuous	0–6951m	Single direction distance to water.

S-table 5. Wolf and Caribou summer resource selection function (RSF) model for Banff and Jasper National Parks. Covariates without coefficients were non-significant in our stepwise model selection process and thus categorical variables (landcover type and aspect) without coefficients are included in the model intercept. For distance variables a positive coefficient shows avoidance (i.e., use increases with distance) while negative coefficients show selection (i.e., use decreases with distance). Squared variables are quadratic terms. All variables included in the models were significant at a level ≤ 0.01

Variable	Wolf Summer		Caribou Summer	
	Coef.	Std. Err.	Coef.	Std. Err.
LANDCOVER				
Burn	1.177	0.0656	-3.967	0.7119
Closed Conifer			-0.221	0.0303
Ice and Rock			-2.627	0.1004
Deciduous Forest	-0.527	0.2151		
Low Elevation Barren Ground			-0.976	0.0553
Low Elevation Herb	0.547	0.0671	0.954	0.0458
Low Elevation Shrub	0.605	0.0504	0.8	0.0393
Open Conifer	0.966	0.0429		
Alpine Barren	-0.444	0.0939		
Alpine Herb	1.239	0.1007	1.743	0.0449
Alpine Shrub	1.234	0.1368	1.486	0.0599
Mean NDVI			5.25E-04	2.21E-05
Mean NDVI^2			-9.61E-08	3.98E-09
Distance to Burn	-0.00012	3.16E-06	2.14E-04	5.24E-06
Distance to Burn^2			-5.84E-09	1.86E-10
Distance to Stream Bank	-0.00063	3.72E-05		
TOPOGRAPHY				
Elevation	0.0134	0.0004	0.0103	0.0003
Elevation^2	-0.000003	1.20E-07	-2.59E-06	8.17E-08
Slope	-0.051	0.0011	-0.05	0.0007
East Aspects	0.338	0.04	-0.441	0.0278
South Aspects	0.463	0.0417	-0.283	0.0279
West Aspects	0.188	0.0434		
North Aspects			-0.182	0.0282
HUMAN USE				
Distance to Primary Road	-0.00007	2.38E-06	1.31E-04	4.45E-06
Distance to Primary Road^2			-5.97E-09	1.40E-10
Distance to Secondary Road	0.00006	1.28E-06	1.83E-04	3.45E-06
Distance to Secondary Road^2			-1.98E-09	7.17E-11
Distance to Trail	-0.0003	1.02E-05	3.20E-05	1.44E-05
Distance to Trail^2			-2.88E-08	1.74E-09
(Model intercept)	-12.49	0.374	-15.1	0.282

S-table 6. Wolf and Caribou winter resource selection function (RSF) models for Banff and Jasper National Parks. Covariates without coefficients were non-significant in our stepwise model selection process and thus categorical variables (landcover type and aspect) without coefficients are included in the model intercept or constant term. For distance variables a positive coefficient shows avoidance (i.e., use increases with distance) while negative coefficients show selection (i.e., use decreases with distance). Squared variables are quadratic terms. All variables included in the models were significant at a level ≤ 0.01.

Variable	Wolf Winter RSF Coef.	Wolf Winter RSF Std. Err.	Caribou Winter RSF Coef.	Caribou Winter RSF Std. Err.
LANDCOVER				
Burn	0.543	0.0559		
Ice and Rock	-2.171	0.2749	-4.123	0.2045
Closed Conifer			0.338	0.0247
Open Conifer	0.748	0.0376	0.892	0.0316
Alpine Barren Ground	-0.671	0.1073	-0.566	0.0412
Alpine Herb			1.016	0.049
Alpine Shrub			1.144	0.0638
Low Elevation Barren Ground			-1.064	0.0503
Low Elevation Shrub	0.421	0.0423		
Low Elevation Herb	0.544	0.053		
Distance to Burn	-0.00014	2.94E-06	0.00025	5.44E-06
Distance to Burn^2			-1.30E-09	2.64E-10
Distance to Stream Bank	-0.0007	3.45E-05		
Distance to Open Canopy	-0.0013	6.25E-05		
Distance to Hard Edge			0.0024	9.84E-05
Distance to Hard Edge^2			-2.40E-06	1.10E-07
TOPOGRAPHY				
Elevation	0.015	0.0005	0.01	0.00018
Elevation^2	-4.00E-06	1.35E-07	-3.00E-05	5.02E-08
Slope	-0.038	0.0009	-0.039	0.0006
East Aspects	0.189	0.0303	-0.467	0.0206
South Aspects	0.24	0.0318	-0.316	0.0223
Flat Aspects			0.194	0.0398
HUMAN USE				
Distance to Secondary Road	6.03E-05	1.15E-06	0.0002	2.76E-06
Distance to Secondary Road^2			-3.00E-09	5.90E-11
Distance to Trail	-0.00024	8.19E-06	-0.0001	3.53E-06
Distance to Primary Road	-5.60E-05	2.04E-06		
(Model intercept)	-11.72	0.369	-12.69	0.155