Caribou encounters with wolves increase near roads and trails: a time-to-event approach

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Summary

1. Caribou and reindeer *Rangifer tarandus* are declining across North America and Scandinavia in part from wolf *Canis lupus*-mediated apparent competition with more abundant ungulate prey species. While caribou generally persist in areas with low wolf density, wolf packs that overlap caribou ranges could trigger caribou declines. Moreover, anthropogenic linear features such as roads, trails and seismic lines are hypothesized to increase predation risk for caribou, yet few studies have examined the mechanistic effects of linear features or spatial overlap on wolf–caribou encounter rates and predation risk.

2. We used (a) time-to-event models of wolf–caribou encounters estimated from concurrent global positioning system (GPS) radio-collar data from wolves and caribou and (b) wolf resource selection models of travel locations, to determine the potential influence of wolf–caribou spatial overlap, linear features, elevation and season on encounter rates. Analyses were based on data from 35 adult female caribou and 37 male and female wolves from 11 wolf packs from Banff and Jasper National Parks, Canada, from 2002 until 2010.

3. Wolf–caribou encounter rates increased with high wolf–caribou overlap, proximity to linear features and lower elevations. Wolves strongly selected low elevations, especially during winter and spring. Selection for linear features as travel routes increased with elevation.

4. Caribou risk of encounter was highest during the summer and autumn when wolves spent the most time at high elevations. Most wolf-caused mortalities ($n = 12$) occurred during spring and summer.

5. *Synthesis and applications.* The presence of anthropogenic linear features and the amount of time wolves spend in caribou range could be equally as important as wolf density when prioritizing caribou recovery actions such as wolf or primary prey reductions or re-introductions. The use of GPS locations and time-to-event modelling offers a powerful tool for evaluating factors affecting predation risk of threatened and endangered species.

Key-words: Banff National Park, *Canis lupus*, linear features, predation risk, *Rangifer tarandus*, recovery, resource selection, spatial separation, species at risk, survival

Introduction

Predation risk affects the distribution, behaviour and trophic interactions amongst species (Brown, Laundré & Gurung 1999; Creel *et al.* 2007). Predation risk is the combined function of the ability of predators to find prey (encounter rates) and the conditional ability to kill prey given an encounter (attack rates) (Holling 1959; Hebblewhite, Merrill & McDonald 2005). Encounter rates have traditionally been measured using visual observations (Scheel 1993; MacNulty, Mech & Smith 2007), snow tracking (Hebblewhite, Merrill & McDonald 2005; Sand *et al.* 2006) or using theoretical models of predator–prey densities, group size and movement strategies (Fryxell *et al.* 2007; Mitchell 2009). The increasing use of global positioning system (GPS) radio-collars to collect fine-scale movement data on both predators and prey, however, has

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great potential to provide insights into the mechanisms of predation risk by allowing further examination of factors affecting both encounter and mortality rates (Merrill *et al.* 2010). Eriksen *et al.* (2008) examined observed and expected distances between wolf and moose *Alces alces* GPS collar locations to test whether or not wolves actively searched for moose. We build upon their approach using time-to-event modelling to examine factors affecting encounter rates between wolves and their endangered prey, woodland caribou.

Caribou and reindeer populations are declining through much of their range in North America and Scandinavia (Vors & Boyce 2009; Nellemann *et al.* 2010), and woodland caribou within the Southern Canadian Rockies are listed as threatened under Canada's Species At Risk Act (COSEWIC 2002). Many of the declines are thought to be driven by anthropogenic changes to landscapes resulting in wolf-mediated apparent competition between caribou and more abundant ungulate prey (Wittmer, Sinclair & McLellan 2005; DeCesare *et al.* 2010). There are two proposed mechanisms affecting wolf-mediated apparent competition for caribou. First, conversion of old forests into early seral stage forests increases habitat quality for primary prey such as moose (Serrouya *et al.* 2011) possibly resulting in increased wolf densities and lower caribou survival rates (James *et al.* 2004; Sorensen *et al.* 2008). Secondly, anthropogenic linear features such as roads or seismic exploration lines provide wolves with efficient travel routes into caribou range (James & Stuart-Smith 2000). Caribou counter predation risk near these features by avoiding roads and seismic lines (Dyer *et al.* 2001; Nellemann *et al.* 2001) yet still may have lower calf recruitment (Environment Canada 2009) and population growth rates in areas with high densities of linear features (Sorensen *et al.* 2008; but see Sleep & Loehle 2010). Both mechanisms occur in many caribou ranges where forest conversion and creation of linear features occur simultaneously. We focus on the wolf-mediated effects of anthropogenic linear features within a protected landscape containing little forest conversion. Despite the links between linear features and population-level declines, few studies have directly examined the mechanisms underlying how linear features, predator density and predator–prey overlap affect predation risk (James & Stuart-Smith 2000). Understanding mechanisms of anthropogenically enhanced predation risk is of vital conservation importance given the widespread declines in woodland caribou across their entire range.

Wolves are a dynamic and resilient species that have high growth potential but are also subject to high levels of human-caused mortality (Weaver, Paquet & Ruggiero 1996; Fuller, Mech & Cochrane 2003). Consequently, the density of wolves and their spatio-temporal overlap with caribou can vary greatly over time. While caribou have poor survival and recruitment rates in areas with high wolf density (Bergerud & Elliot 1986), it is not quantitatively clear how wolf–caribou overlap and variability in that overlap affects caribou demographic rates. This information is important for predicting the likelihood of caribou persistence (DeCesare *et al.* 2011) and for prioritizing recovery actions within caribou populations (McLellan *et al.* 2010; Schneider *et al.* 2010). For instance,

Banff and Jasper National Parks in Canada are considering translocation-based management as a means to recover declining or extirpated woodland caribou populations (DeCesare *et al.* 2011) but still need to assess how the amount of wolf–caribou overlap and interactions with primary prey would influence the likelihood of persistence.

Prey species reduce their risk of predation from learning predators by moving (Alonzo, Switzer & Mangel 2003; Mitchell 2009) and by occurring in areas with low probability of attack success (Creel *et al.* 2005; Laundré 2010). Woodland caribou reduce predation risk by occurring in low densities and in areas with few other prey species (Wittmer *et al.* 2005), but little is known about how these caribou, in the face of increasing wolf overlap, would fare in the predator–prey shell game (Mitchell 2009).

Here, we used time-to-event models (Cox proportional hazards) to determine the effects of wolf–caribou overlap, roads, trails and elevation on encounter rates: important components of predation risk (Hebblewhite, Merrill & McDonald 2005). We defined encounters as the spatio-temporal overlap between caribou and wolf GPS locations (Eriksen *et al.* 2008). We further tested the hypothesis that caribou spatially separate themselves from and avoid encounters with wolves by comparing encounters rates of concurrent wolf and caribou locations to a null model of encounter rates.

We also examined how the association between wolf travel routes and linear features (roads and trails) changed with elevation and season using resource selection analyses of wolf travel routes. Wolves clearly select linear features as travel routes (James & Stuart-Smith 2000; Whittington, St. Clair & Mercer 2005) and are more likely to kill ungulate prey near linear features (James & Stuart-Smith 2000). However, it is unclear how wolf selection for linear features and caribou predation risk are affected by rugged topography associated with higher elevations and deep snow depths during winter (Seip 1992). Therefore, we also assessed how wolves varied their selection for linear features, which is important for determining when and where linear features increase caribou predation risk. Together, our encounter rate and wolf movement resource selection analyses enabled us to better understand the fine-scale mechanisms affecting wolf–caribou encounters and potentially predation risk.

STUDY AREA

The study area included portions of Banff and Jasper National Parks of Canada (6858 and 11 228 km^2, respectively) along the eastern slopes of the Canadian Rockies (52°N, 117°W). The area is characterized by rugged topography with elevation ranging from 1000 to 3500 m, long cold winters and short summers (Holland *et al.* 1983). Forests are relatively open and dry, with lodgepole pine *Pinus contorta*-dominated forests in the montane ecoregion and Engelmann spruce *Picea engelmanii* and subalpine fir *Abies lasiocarpa*-dominated forests in the subalpine ecoregion (Holland *et al.* 1983). High elevation and alpine areas near the continental divide, where most caribou occur, receive the most precipitation and the deepest snow

depths. In addition to wolves, the predator community also includes mountain lions *Puma concolor*, grizzly bears *Ursus arctos*, black bears *Ursus americanus* and wolverine *Gulo gulo*. Wolf diet includes elk *Cervus elaphus*, moose, mule deer *Odocoileus hemionus*, white-tailed deer *Odocoileus virginianus*, bighorn sheep *Ovis canadensis*, mountain goat *Oreamnos americanus*, caribou and beaver *Castor canadensis*, in approximate order of importance in the diet.

Materials and methods

We collected GPS radio-collar (LOTEK, Aurora, ON, brands 3300, 4400) data from 35 adult female caribou and 37 male and female wolves from 11 packs from 2002 until 2010. Radio-collared wolves were at least 8 months old. Caribou were captured using helicopter net gun during winter, and wolves were captured using helicopter net gun and darting in winter, and foot-hold trapping in summer according to Parks Canada and University of Montana animal capture protocols (Animal Use Protocol 059–09MHWB-122209). GPS fix schedules ranged from fixes every 15 min to every 6 h, and effects of habitat-induced GPS bias on habitat models were minimal because of high fix rates around 85%. Data were collected from four caribou subpopulations including the Tonquin, Maligne and Brazeau in Jasper National Park and Banff in the northern portion of Banff National Park.

WOLF–CARIBOU ENCOUNTER RATES

We first examined the effects of wolves, linear features, elevation and differences in caribou subpopulations on wolf–caribou encounter rates using Cox proportional hazard models (Harrell 2001). Encounters were defined as when a wolf travelled within 1·285 km (median 6-h wolf step length) of a caribou location on the same year and calendar day (same-year encounter) or a different year and same calendar day (across-years encounter; analysis conducted to test hypotheses explained below) (Fig. 1). Our detection distance was likely to be within a wolf's sensory detection range (Mech & Boitani 2003) and was similar to a detection distance of 1·5 km for wolves in other studies (Muhly *et al.* 2010). Furthermore, the effects of the distance
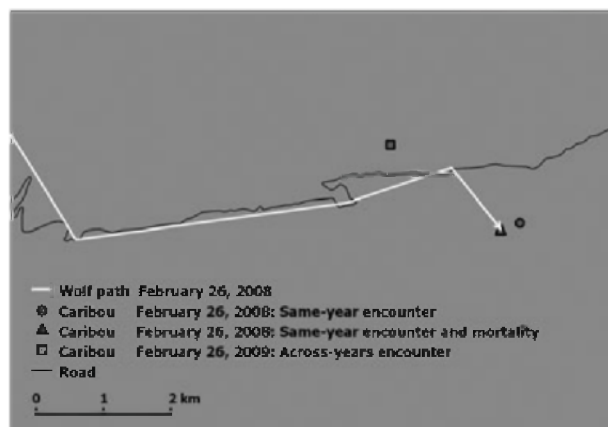

Fig. 1. Examples of wolf–caribou encounters showing a wolf movement path along a road and caribou locations resulting in a same-year encounter with no caribou mortality, same-year encounter resulting in mortality and an across-years encounter (same calendar day but different year), Jasper National Park.

threshold did not strongly affect univariate model coefficients (see Fig. S1, Appendix S1 in Supporting Information). Some wolves encountered caribou on successive days, but to ensure independence, we only classified the first day as an encounter.

We addressed encounter rates from the caribou's perspective using a temporal resolution of one caribou location per day. For each location, we determined whether or not an encounter occurred and calculated distance to nearest linear feature (road or trail; km), elevation (km), late winter wolf pack size, whether or not the wolf pack was transient, and a wolf–caribou utilization distribution overlap index (UDOI) (Fieberg & Kochanny 2005). UDOI is based on the product of two utilization distributions, usually ranges between zero (no overlap) and 1 (100% overlap of uniformly distributed locations) but can be > 1 and is thought to be the most appropriate metric of space-use sharing. When calculating the UDOI, we subsampled GPS data to a 6-h fix rate so that all animals had the same fix frequency. We calculated separate UDOIs for each season (summer = June–August; autumn = September–November; winter = December–February; spring = March–May). We limited the encounter analyses to GPS-collared wolves and caribou with a UDOI > 0·001 to include only animals that had a nonzero probability of encounter. We centred the explanatory variables on their median value (Harrell 2001) and performed univariate analyses to remove correlated ($r > |0·5|$ or variance inflation factor > 3) and uninformative variables. Linear features included all roads and trails used by the public within the parks. In winter, some but not all roads were ploughed and level of snow compaction varied greatly amongst trails. We considered wolf packs that formed for 1–3 years and then dispersed as transient wolf packs (Fuller, Mech & Cochrane 2003). These wolf packs could have disproportionately large effects on caribou because they often occur in lower-quality wolf habitats, which include higher elevation caribou ranges (sensu Kauffman et al. 2007). We compared competing models with all combinations of the remaining variables using Akaike Information Criterion (AIC), selected the top-ranked models with ΔAIC < 2 and averaged model coefficients and standard errors over the top-ranked models (Burnham & Anderson 2002).

We used Cox proportional hazard models to determine how wolves and linear features (roads and trails) affected caribou encounter rates. We used 1 June as a recurrent time of origin (Fieberg & DelGiudice 2009) because it is the start of a biological year when caribou are born and because the seasonal baseline hazard was not correlated with most annually changing explanatory variables of interest (J. Whittington unpublished data). We estimated the effects of wolves, linear features and topography on encounter rates using a generalized linear mixed model (GLMM) formulation of the Cox model (Whitehead 1980; Fieberg & DelGiudice 2009) with a Poisson distribution and a random intercept for each caribou (Yau 2001; Donohue & Xu 2010). We used natural splines with four fixed knots at the 0·05, 0·35, 0·65 and 0·95 quantiles of days since 1 June (Harrell 2001) to estimate the underlying baseline hazard.

The analyses used both same-year and across-years encounters. The across-years encounters provided a null model that allowed us to test the hypothesis that caribou evaded wolf encounters. To test this hypothesis, we compared models with and without the covariate from the same year (vs. across year) and its interaction with UDOI. The across-years encounters assumed that within their home ranges, caribou did not change their movements on a yearly time-scale to avoid wolf predation and that wolves did not change their movements on a yearly scale to search for caribou. However, if those assumptions did not hold and caribou adapted to real-time changes in wolf distribution, then we expected encounter rates for the same-year data to be lower than encounter rates for across-years data and that the

β coefficients from Cox models for the wolf–caribou overlap index would be lower for same-year analysis. Conversely, if wolves actively searched for caribou, then we expected encounter rates for the same-year data to be higher and β coefficients for the wolf–caribou overlap index to be higher than in the across-years data. Furthermore, the interaction between same year and UDOI allowed us to examine the effects of increasing overlap on predator–prey behavioural dynamics.

CARIBOU MORTALITY

We determined the cause of caribou mortalities by conducting aerial telemetry on a total of 53 caribou fitted with VHF or GPS radio-collars every 4–6 weeks. When radio-collars emitted a mortality signal, we investigated the mortality site and determined cause of death by looking for evidence of predation. We classified mortalities as wolf-caused or other based on signs of chase sequences, haematomas, carcass disarticulation, wolf tracks and wolf GPS data. We then assessed how season affected caribou vulnerability to predation by comparing the baseline hazards of encounter rates and wolf-caused caribou mortalities. We graphically compared the hazards because our limited number of known wolf-caused mortalities prohibited rigorous statistical comparisons.

WOLF TRAVEL RESOURCE SELECTION

We tested how wolf selection for linear features varied with elevation and season using resource selection function (RSF) models of wolf travel routes (Manly *et al.* 2002). We considered that wolves searched for prey while travelling (MacNulty, Mech & Smith 2007) and thus discriminated wolf travel from other states (resting, feeding on kills). We first rarefied the data into 2-h fix intervals and removed resting or feeding location where wolves spent > 6 h within a 300 m radius over 4 days (Webb, Hebblewhite and Merrill 2008). To test for selection of linear features, we compared attributes of wolf travel locations to an equal number of random locations within each individual wolf's home range estimated with a 95% adaptive kernel home range. We then developed a base RSF model with the explanatory variables known to strongly influence wolf movements (Whittington, St. Clair & Mercer 2005; Hebblewhite & Merrill 2008) and then compared five models with interactions between linear features (on or off a trail or road), elevation and season. We considered the three-way interaction between linear feature, elevation and season because one of our competing hypotheses was that wolf selection for linear features would increase in areas with difficult travel conditions such as in rugged topography at high elevations during winter. Explanatory variables used in the baseline RSF model were as follows: elevation (km), slope (degrees), southern aspects (−1 × cosine[aspect]), land cover (Hebblewhite & Merrill 2008) and distance to nearest edge (km). We defined edge as the border between forests and open land-cover classes (herbaceous, shrubs, deciduous, rock, water), and we used a decay term for distance $(1-\exp^{-2 \times \text{distance}})$ that was used for grizzly bears (Nielsen, Cranston & Stenhouse 2009). We used GLMMs with a logit link and a random intercept for each wolf, and we centred explanatory variables on their median value to improve model convergence. We generated models using data from 30 randomly selected wolves and validated the models with the remaining seven wolves using the area under the receiving operating characteristic curve (ROC) and the Spearman rank correlation coefficients between bin rank and area-adjusted frequencies of used locations (Boyce *et al.* 2002). All analyses were conducted using R 2.12.0 (R Development Core Team 2010) with the adehabitat (Calenge 2006), survival (Therneau & Lumley 2009) and lme4 (Bates & Maechler 2010) packages.

Results

WOLF–CARIBOU ENCOUNTER RATES

Eight of the 11 wolf packs (28 of the 37 wolves) had home ranges that overlapped with caribou home ranges. We recorded 58 independent same-year encounters of 9695 wolf–caribou days and 365 across-years encounters of 67 209 caribou wolf days. This resulted in daily same-year encounter rates of 0·6% (Banff = 1·8%; Brazeau = 1·0%; Maligne = 0·4%; and Tonquin = 0·5%) and daily across-years encounter rates of 0·5% (Banff = 1·8%; Brazeau = 1·1%; Maligne = 0·4%; and Tonquin = 0·5%). Forty-four per cent of the 35 caribou encountered a GPS-collared wolf, and the number of encounters per caribou ranged from 0 to 9. Most wolf–caribou encounters occurred during the summer and autumn (Fig. 2a,b).

Encounter rates increased with increasing UDOI and transient wolf packs (Tables 1 & 2). Encounter rates also increased when caribou travelled to lower elevations and areas near linear features (Fig. 3). The Banff and Brazeau subpopulations had higher across-years encounter rates than the Tonquin. The interaction between same-year data and UDOI suggested that as UDOI increased, encounter rates for same-year data were higher than for across-years data. Model coefficients estimated using the same-year subset of encounters data were similar in direction but had wider confidence intervals, probably owing to a smaller sample size, than coefficients estimated with both same-year and across-years data (see Table S1, Appendix S1
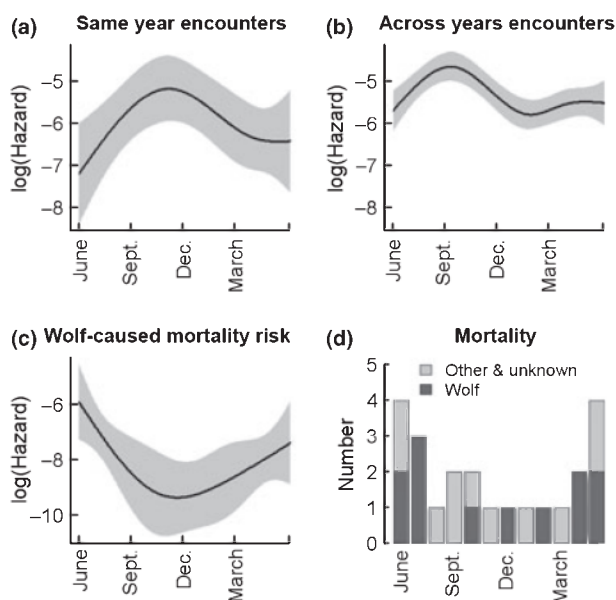

Fig. 2. Seasonal distributions of (a) same-year encounters between female caribou and wolves ($n = 58$), (b) across-years encounters ($n = 365$), (c) wolf-caused mortality risk for caribou ($n = 12$) and (d) caribou mortalities ($n = 23$), 2002–2010, Banff and Jasper National Parks. In the Cox proportional hazards encounters analysis, 1 June was used as the time of origin. Seasonal hazards were estimated using natural splines within a generalized linear mixed model, and shaded areas indicate 95% confidence intervals of the seasonal hazards. See text for more details.

Table 1. Top ranking models and Akaike weights (ω) for same-year and across-years wolf–caribou encounter rates (Cox proportional hazards) and wolf travel resource selection, 2002–2010, Banff and Jasper National Parks. Top ranking models were models with ΔAIC < 2·0 from the model with the lowest AIC value

Rank	Model	d.f.	ΔAIC	ω
Encounters	*423 encounters (58 same-year and 365 across-years) of 76904 wolf–caribou days*			
1	UDOI + region + transient + elev + dlinear	8	0·0	0·537
2	UDOI + same-year + region + transient + elev + dlinear + UDOI:same-year	10	0·3	0·463
Wolf travel RSF	*30 wolves and 29638 locations; Validate 7 wolves and 2224 locations*			
1	elev + slope + aspect-s + land cover + dist.edge + linear × elev × season	26	0	1

AIC, Akaike Information Criterion; RSF, Resource selection function; UDOI, utilization distribution overlap index; elev, elevation; dlinear, distance to nearest linear feature (km); aspect-s, −1 × cosine(aspect); dist. edge, $1-\exp^{(-2 \times \text{distance to nearest edge})}$(km); linear, on or off linear feature.

Table 2. Model averaged coefficients, standard errors and 95% confidence intervals from top-ranked models of wolf–caribou encounters from Table 1, 2002–2010, Banff and Jasper National Parks. Model estimates for the intercept and splines are not shown

Variable	B	SE	B·SE⁻¹	95% CI
Dlinear	−0·154	0·040	−3·8	−0·232, −0·076
Elevation	−1·277	0·278	−4·6	−1·822, −0·732
Region: Banff vs. Tonquin	1·374	0·387	3·5	0·615, 2·133
Region: Brazeau vs. Tonquin	0·820	0·243	3·4	0·344, 1·296
Region: Maligne vs. Tonquin	−0·027	0·235	−0·1	−0·488, 0·434
Transient	0·697	0·177	3·9	0·350, 1·044
UDOI	0·650	0·117	5·6	0·421, 0·879
Same-year	0·013	0·071	0·2	−0·126, 0·152
UDOI: same-year	0·248	0·121	2·0	0·011, 0·485

UDOI, utilization distribution overlap index.

Fig. 3. Cumulative probability of a wolf–caribou encounter with 95% confidence intervals for female caribou on and 5 km from linear features such as roads and trails, 2002–2010, Banff and Jasper National Parks. Ninety-five per cent of caribou locations occurred within 5·3 km from roads and trails.

in Supporting Information). There was also no effect of the number of wolves collared per wolf pack (mean = 1·4, range 1–3) on UDOI (J. Whittington, unpublished data).

CARIBOU MORTALITY PATTERNS

We recorded 23 mortalities from radio-collared caribou of which at least 12 were caused by wolves. Wolf-caused caribou mortalities occurred throughout the year, and most mortality occurred from April to July (Fig. 2c,d). Conversely, most encounters occurred during the late summer and autumn. Thus, the risk of mortality for adult female caribou was not directly proportional to their risk of encounter.

WOLF TRAVEL RESOURCE SELECTION

The top-ranked RSF model for wolf travel included a strong three-way interaction between being on or off linear features, elevation and season (Table 1, Table S2). Wolf selection for trails and roads increased with increasing elevation, especially during autumn, winter and spring (Table 3, Fig. 4). The wolves strongly selected lower elevations during winter and spring and used higher elevations more during summer and
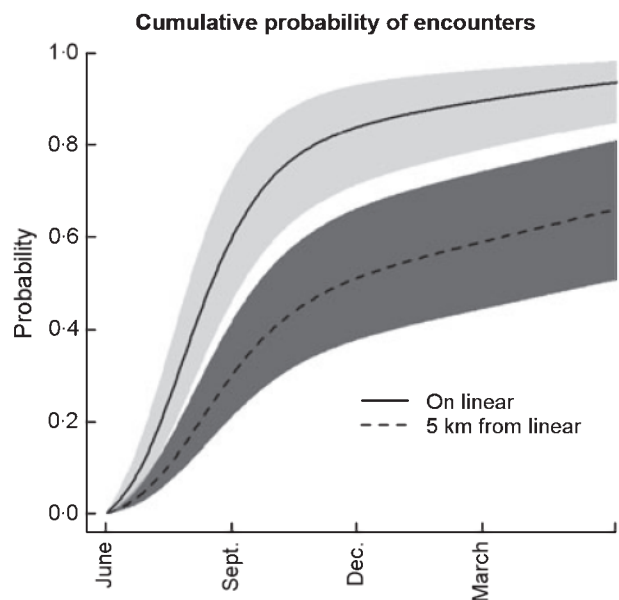
autumn, which was also when caribou had the highest risk of wolf encounter. The RSF model differentiated between the used and random locations well for both the model training (ROC = 0·80, Spearman rank correlation coefficient = 0·98) and withheld validation (ROC = 0·73, Spearman rank correlation coefficient = 0·91) data sets.
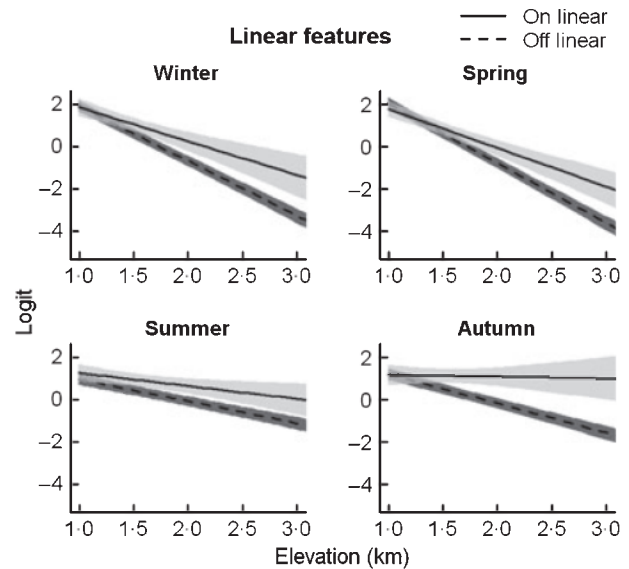
Discussion

Woodland caribou populations are thought to persist in areas with large-scale wolf densities lower than six wolves per 1000 km² (Bergerud & Elliot 1986). We found that encounter rates were driven by spatial–temporal overlap between wolves and caribou but not late winter wolf pack size. Moreover, the effect of overlap was stronger for the same-year data compared to our null model of across-years data. This suggests that during periods of high overlap, wolves win the predator–prey

Table 3. Resource selection function (RSF) model averaged coefficients, standard errors and 95% confidence intervals for wolf travel locations, 2002–2010, Banff and Jasper National Parks

Variable	B	SE	B·SE^{-1}	95% CI
Elevation	−1·039	0·075	−14·0	−1·185, −0·893
Aspect south	0·095	0·021	4·5	0·053, 0·136
Slope	−0·050	0·002	−29·7	−0·054, −0·047
Dedge	−1·209	0·062	−19·6	−1·330, −1·088
Land cover: reference conifer closed				
Barren	0·262	0·053	5·0	0·158, 0·366
Conifer open	0·159	0·045	3·6	0·071, 0·247
Herb high elevation	1·229	0·072	17·2	1·089, 1·369
Herb low elevation	0·752	0·101	7·5	0·554, 0·950
Mixed deciduous	0·448	0·107	4·2	0·238, 0·659
Shrub	0·773	0·060	12·9	0·655, 0·890
Water rock	0·155	0·075	2·1	0·007, 0·302
Season: reference summer				
Autumn	−0·003	0·045	−0·1	−0·092, 0·085
Spring	−0·190	0·041	−4·6	−0·270, −0·109
Winter	−0·144	0·047	−3·1	−0·236, −0·053
Linear	0·600	0·101	5·9	0·402, 0·799
Linear × elevation	0·424	0·247	1·7	−0·061, 0·908
Linear × autumn	0·281	0·166	1·7	−0·045, 0·607
Linear × spring	−0·170	0·149	−1·1	−0·461, 0·122
Linear × winter	0·039	0·166	0·2	−0·287, 0·364
Elevation × autumn	−0·352	0·100	−3·5	−0·548, −0·157
Elevation × spring	−1·795	0·097	−18·5	−1·984, −1·605
Elevation × winter	−1·552	0·105	−14·8	−1·757, −1·347
Linear × elevation × autumn	0·886	0·417	2·1	0·068, 1·703
Linear × elevation × spring	0·570	0·354	1·6	−0·123, 1·263
Linear × elevation × winter	0·563	0·404	1·4	−0·229, 1·353

Fig. 4. The influence of season and elevation on wolf resource selection for linear features (roads and trails) as travel routes, 2002–2010, Banff and Jasper National Parks. Shaded areas indicate 95% confidence intervals. Wolf selection for low elevations was strongest during winter and spring. Wolf selection for linear features increased with elevation, especially during autumn, winter and spring.

shell game and that caribou are unable to avoid encounters with wolves. Encounter rates with wolves increased when caribou moved near linear features and wolves showed strong selection for linear features, especially at high elevations near caribou range. The two results suggest that the addition of linear features into caribou range would likely increase encounter rates and predation risk. Snow compaction of linear features in caribou range could have an especially large effect in mid-winter when deep unconsolidated snow normally restricts wolves to the valley bottoms (Paquet *et al.* 2010). Our results support other studies where caribou face an increased risk of predation near linear features (James & Stuart-Smith 2000) and have lower recruitment rates (Environment Canada 2009) and potentially lower population growth rates in areas with a high density of linear features (Sorensen *et al.* 2008; but see Sleep & Loehle 2010).

Our subpopulation-specific encounter rates ranked similarly to estimates of subpopulation-specific survival rates (DeCesare *et al.* 2011). Banff, which historically had the smallest but now extirpated subpopulation (DeCesare *et al.* 2011), had the highest encounter rates. Encounter rates in Banff were three times higher than the Tonquin, which had the highest survival rates and the largest number of caribou. Thus, predicted survival rates for Banff translocation scenarios may be optimistic (DeCesare *et al.* 2011). The Brazeau also had higher encounter rates and lower survival rates than the Tonquin and now has < 20 caribou remaining. The Maligne had surprisingly similar encounter rates to the Tonquin given that it has lower survival

rates and < 10 animals remain. These results emphasize the conservation relevance of encounter rates as a useful measure of predation risk for threatened species.

Transient wolf packs encountered caribou more frequently than stable wolf packs. Transient packs have higher predation rates on caribou (Kojola *et al.* 2004), and translocation success of caribou to Idaho also appeared to depend on regional and temporally varying predator use of caribou range (Compton, Zager & Servheen 1995). Similarly, populations of others species such as bighorn sheep also appear to be driven by transient predators and stochastic predation events (Festa-Bianchet *et al.* 2006). Thus, transient predators, with a limited contribution to the viability of their own population, could have large effects on recovery actions for small populations. Unfortunately, little is known about patterns of density-dependent habitat selection by predators, but reductions in predator density overall would tend to reduce use of suboptimal habitat by transient predators (e.g. Kauffman *et al.* 2007).

Despite the importance of wolf overlap and resource selection for increasing encounter rates, and the close link between encounter rates and population growth rate (DeCesare *et al.* 2011), the seasonal distribution of encounter rates did not mirror the seasonal distribution of a limited sample of adult female mortalities. Most wolf–caribou encounters occurred during the summer and autumn, which is when wolves also showed the strongest selection for high elevations, whereas most wolf-caused mortality occurred during the spring and summer. Several biological mechanisms that mediate the risk of death given an encounter could explain the apparent discrepancy between risk of encounter and mortality. Annual variation in prey group size could reduce risk (McLellan *et al.* 2010), caribou could be in better body condition and better able to reduce

predation risk during summer, or wolf encounters with caribou could be incidental to wolf selection for other prey species during summer (Latham *et al.* 2011; Robinson *et al.* 2011, In revision). Similarly, caribou in our study could be more susceptible to predation given an encounter during late winter when snow crusts enable wolves to easily predate upon caribou. Finally, other cohorts of the population, such as calves, may be more susceptible to predation given an encounter (Gustine *et al.* 2006). The seasonal distribution of caribou mortality in other studies was similar to our distributions of encounter rates and wolf-caused mortality. Most wolf-caused caribou predation occurred during summer in Alberta (McLoughlin *et al.* 2003), Saskatchewan (Rettie & Messier 1998) and British Columbia (Kinley & Apps 2001; Wittmer *et al.* 2005). In Norway, wolf predation on reindeer occurred during summer, autumn and early winter but rarely in late winter (Kojola *et al.* 2004).

Our results suggest that when evaluating population persistence (Wittmer, Ahrens & McLellan 2010), ranking caribou populations for recovery (Schneider *et al.* 2010) or considering translocations to augment existing populations (DeCesare *et al.* 2011), wildlife managers need to consider not just the density of predators but also factors that influence the components of predation risk, especially encounters. The creation of linear features increased caribou risk of encounters and predation from wolves and potentially displace caribou from high-quality habitat (Nellemann *et al.* 2001; Vistnes & Nellemann 2008; Nellemann *et al.* 2010). Moreover, reclamation of linear features could increase habitat quality, improve conditions for recolonization of historic range (Nellemann *et al.* 2010) and reduce predation risk. Our approach for examining the effects of linear features and other factors on encounter rates and predation risk could have wide applicability to other threatened and endangered species.

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Supporting Information

Additional supporting information may be found in the online version of this article on page numbers indicated in the legend later.

Fig. S1. The effects of threshold distance on wolf–caribou encounter model coefficients and 95% confidence intervals (shaded area) for distance to nearest linear feature, elevation, transient wolf packs and UDOI.

Table S1. Wolf–caribou encounter rate model results estimated using the same-year subset of encounters data, year range, Banff and Jasper National Park, Alberta, Canada.

Table S2. Top ranking models and Akaike weights (ω) for all models considered for wolf travel resource selection, 2002–2010, Banff and Jasper National Parks.

Appendix S1. Model results for encounter analyses and wolf travel RSF examining the effects of using concurrent wolf and caribou GPS data, varying encounter distances and interactions with linear features.

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