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Spatial Factors Related to Mortality and Population Decline of Endangered Mountain Caribou

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ABSTRACT Mountain caribou are an endangered ecotype of woodland caribou (*Rangifer tarandus caribou*) that historically occurred throughout the high snowfall regions of southeast British Columbia and the northwestern United States. The decline in caribou is thought to be due to apparent competition where increases in early-seral conditions stimulate a numerical response in primary ungulate prey and their predators and these incidentally kill an unsustainable number of caribou. Based on the known location of death of 207 radio collared animals, we tested hypotheses pertaining to relationships between landscape composition and predator-specific mortality of mountain caribou at 2 ecologically based spatial scales. Relative to landscape conditions within subpopulation boundaries (level 1) or within home ranges (level 2), caribou were at greater risk of predation at low elevations particularly within otherwise complex terrain (i.e., valleys) with more variation in overstory canopy closure and greater road densities. Caribou vulnerability to bears was also positively related to the variation in overstory age. Cougar predation was not related to roads or terrain complexity but occurred more often in landscapes with warmer aspects and greater proportions of stands of <120 years. Wolf predation occurred primarily at low elevations at the broader scale and in association with roads at the finer scale. Our results indicate that caribou vulnerability to predation was a function of both static (e.g., terrain) and dynamic (e.g., overstory conditions) factors, but we did not find evidence that localized habitat fragmentation due to forest harvest influenced predation on caribou. This result is not inconsistent with the apparent competition hypothesis but suggests that habitat change largely functions at broader spatial scales involving landscapes that can be beyond those occupied by caribou, including the winter ranges of primary ungulate prey. These changes and the season-dependent dispersion of other ungulates and their predators may largely influence mortality risk to mountain caribou. Although roads and forest fragmentation are interrelated, roads may further contribute to caribou predation by increasing the efficiency of movement of some predators and thereby increasing encounter rates with caribou. © 2013 The Wildlife Society.

KEY WORDS apparent competition, bear, caribou, cougar, habitat fragmentation, mortality, predation, *Rangifer tarandus*, roads, spatial scale, wolf, wolverine.

Mountain caribou are an ecotype of woodland caribou (*Rangifer tarandus caribou*) and were historically distributed throughout the high snowfall regions of southeastern British Columbia, northern Idaho, northwest Montana, and northeast Washington. Mountain caribou in high-snowfall areas are distinguished from other caribou by a late-winter diet that consists almost entirely of arboreal hair lichens that are most abundant in old forests (Heard and Vagt 1998). For most of the winter, these caribou walk on top of a 2–5-m deep snowpack on high-elevation winter ranges to access these lichens in the canopy of conifers. At least 98% of the global population of this caribou ecotype now occurs within British Columbia, where they are considered Endangered (Conservation Data Centre 2002). Across their current geographic range, <2,000 of these animals were recently enumerated in 18 subpopulations (Wittmer et al. 2005*a*); 16 now remain, ranging in size from <10 to >500 individuals. Factors that have directly or indirectly precipitated recent range and population reductions pertain to the fragmentation and loss of old forests on which mountain caribou depend (Heard and Vagt 1998, Spalding 2000, Apps and McLellan 2006).

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In most mountain caribou subpopulations, unsustainable predation has been the proximate cause of population decline (Wittmer et al. 2005*a*). Although ultimate causal pathways appear complex, apparent competition (Holt 1977) is the hypothesis with most support (Bergerud and Elliot 1986; Seip 1992; Wittmer et al. 2005*a*, *b*). That is, caribou are subject to unsustainable predation as the numerical response of other ungulate species to increasing early-seral conditions leads to a numerical response of predators. The apparent competition hypothesis is also relevant to other woodland caribou populations across North America (e.g., Rettie and Messier 2000, James et al. 2004, McLoughlin et al. 2005).

The predator-prey systems within which mountain caribou exist include moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), and mountain goat (*Oreamnos americanus*). These are preyed upon by gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), and wolverines (*Gulo gulo*). In the northern part of mountain caribou range, wolves supported primarily by moose have a high predation rate on caribou (Seip 1992). In the south, deer and elk support cougar that prey on relatively small caribou subpopulations (Kinley and Apps 2001). Both grizzly and black bears prey on caribou across their distribution (Wittmer et al. 2005*a*). Most predation on mountain caribou likely is incidental given that most subpopulations have an insufficient number of caribou to be the primary prey for any predator species. Hence, the predation rate is unlikely to relax as subpopulations decline (Seip 1991, 1992; Wittmer et al. 2005*b*) or may even increase (McLellan et al. 2010), leading to their rapid extirpation.

Although unsustainable predation has been the proximate cause of caribou decline (Seip 1992; Wittmer et al. 2005*a*, *b*, 2007) due to the numerical response of predators to increasing prey, it is not clear if the functional response is also influenced by landscape conditions and associated changes due to clear-cut logging, powerlines, road building, and wildfires. In addition to increasing the density of primary prey and predators, human-induced landscape alteration can also shift the distribution of prey and their generalist predators (Oehler and Litvaitis 1996). Because most predation on caribou is during summer and fall (Seip 1992, Wittmer et al. 2005*b*), managers must determine if fragmenting summer and fall caribou habitat with early-seral conditions increases the distributional overlap of caribou with moose, deer, elk, and their predators (Latham et al. 2011) causing the incidental encounter and kill rate on caribou to increase (Bergerud and Elliot 1986, Seip 1992). Also, increased roading typical of landscapes with early-seral conditions can enhance the efficiency of cursorial predators such as wolves (James and Stuart-Smith 2000, Whittington et al. 2005). Alternatively, early-seral ungulates may be primarily limited by conditions of their winter ranges that, in mountainous terrain, are generally restricted to low elevations and often beyond the distribution of caribou. Enhancement of these winter ranges may increase caribou predation simply because of the numerical response of early-seral ungulates and their predators that naturally expand their range to overlap with caribou during summer and fall. Under this hypothesis, early-seral conditions within caribou summer and fall habitat will not affect the functional response and therefore the predation rate on caribou. Understanding the significance of creating early-seral conditions within summer and fall caribou habitat is important for wise conservation decisions across mountain caribou distribution.

Wittmer et al. (2007) found mountain caribou subpopulations in regions with a greater proportion of early- and mid-seral aged forests and at low population density were in most rapid decline. At a finer scale, they found caribou killed by predators had a lesser proportion of old forest in their multi-annual home ranges than did live caribou. Based on the findings of Wittmer et al. (2005*a*, 2007), we tested the hypothesis that caribou would be killed by predators more often in landscapes and specific locations modified by various human activities more than in pristine areas. More specifically, we predicted that 1) relative to where they survived, mountain caribou were killed by predators in landscapes with a high composition of early- (<60-yr) and mid- (61–120-yr) successional forests. However, we expected the interspersion of old and early-seral conditions was also relevant to predation risk. Thus, we also predicted that 2) both the distribution of the younger forest age classes relative to old (>120-yr) forests, and the variation in overstory conditions within the landscape would be greater where caribou died than where they survived. Finally, we expected that 3) the density of roads that can facilitate movement by cursorial predators would increase caribou vulnerability and we predicted landscapes where caribou died to have greater road densities than where they did not die. In addition to these dynamic variables affected by people, static variables pertaining to terrain conditions have been linked to caribou mortality risk (Seip 1992), and we accounted for the possible confounding influence of these factors in our analyses.

The likelihood of caribou mortality may be a function of both site-specific and broader scale landscape attributes influencing, for example, the degree of home range overlap with predators. We therefore considered 2 finer ecological scales in our analyses than reported by Wittmer et al. (2007) and employed a different design and response metric. Within subpopulations, we considered the composition of landscapes associated with specific caribou mortality locations relative to those known to have been occupied by caribou (level 1). Then, for each animal known to have died, we compared finer-scale conditions associated with mortalities to those where respective caribou survived (level 2), while controlling for variation in the survival time of individuals among landscapes.

STUDY AREA

Our analysis area encompassed the current range of mountain caribou in the deep snow areas of British Columbia (Fig. 1), comprising 146,310 km^2. It was characterized primarily by the wet and very wet subzones of the Engelmann Spruce—Subalpine Fir (ESSF) biogeoclimatic zone, the wet and very wet subzones of the Interior Cedar Hemlock (ICH)

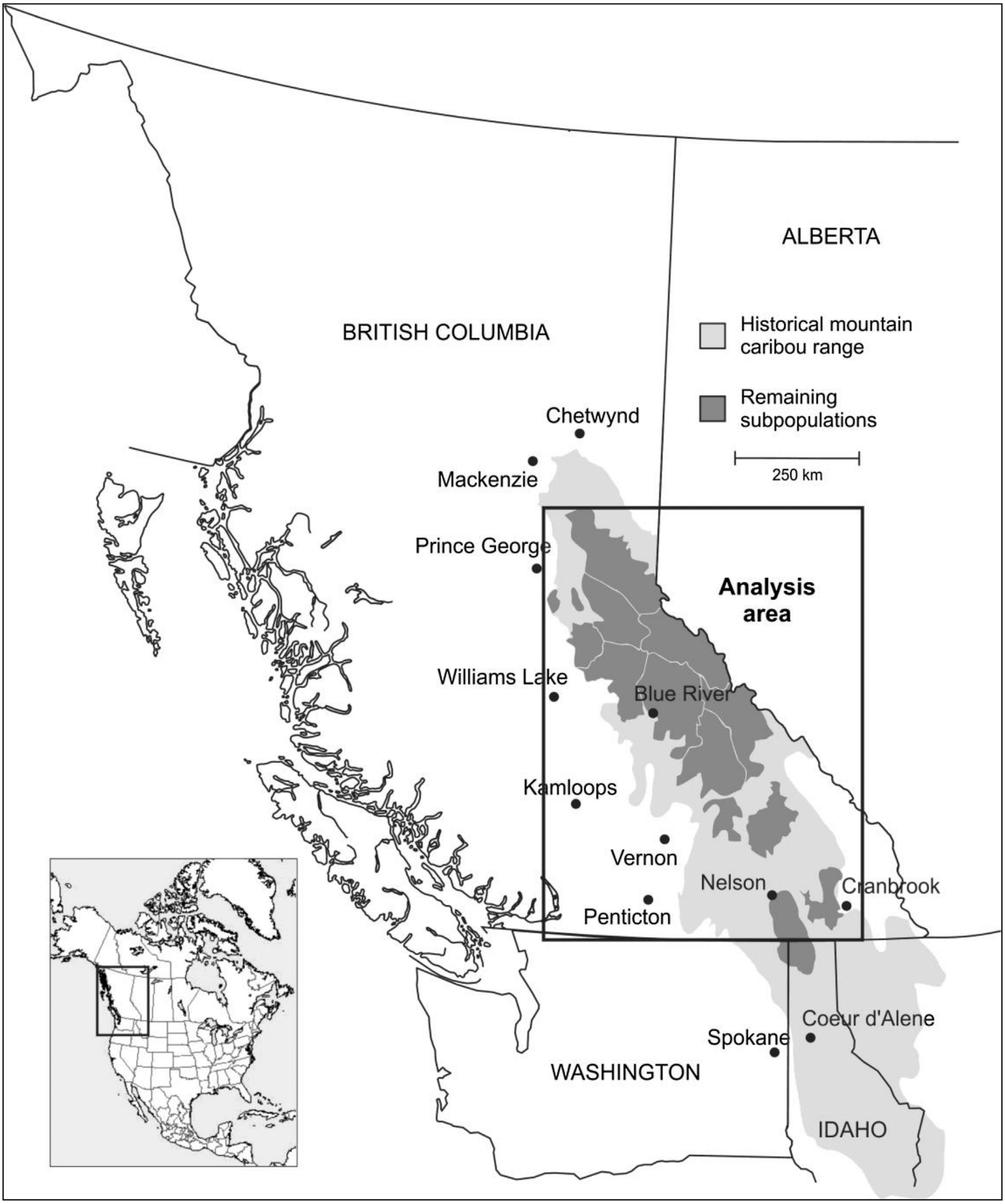

Figure 1. Analysis area for evaluation of spatial factors related to mountain caribou mortality risk in southeast British Columbia, Canada. The delineation of historical and current mountain caribou range is adapted from Spalding (2000) and Mountain Caribou Technical Advisory Committee (2002). Historical range specifically defined the analysis area within the box shown.

zone, and the very wet subzones of the Sub-Boreal Spruce (SBS) zone (Meidinger and Pojar 1991). Considerable precipitation from Pacific weather systems resulted in a deep snowpack in the mountains (>2 m) and a low frequency and extent of natural fire resulted in a natural forest condition dominated by old age classes (Jull et al. 1998). Elevations ranged from 350 m to >3,500 m. Human communities with populations of up to 10,000 existed within the study area, and included the city of Nelson and the towns of Valemont, Clearwater, and Revelstoke. Four major highways and several secondary highways intersected the study area. The analysis area encompassed all or parts of 18 distinct mountain caribou subpopulations (Wittmer et al. 2005*a*).

METHODS

Caribou Data

All extant mountain caribou subpopulations have been monitored using radio-telemetry for various periods beginning as early as 1984. In all studies, animals were captured using a net gun shot from a helicopter during late winter when caribou frequent high elevation, subalpine parkland habitats. Most animals (>85%; Apps et al. 2001, Wittmer et al. 2005*a*) are visible and available for capture at that time of year, and the distribution of sampled animals approximated the distribution of respective subpopulations. The data we used for our study represented 541 animals over 22 years and included both very high frequency (VHF)- and global positioning system (GPS)-collared animals. Observers conducted VHF radiotelemetry using fixed-wing aircraft at approximately 2-week intervals, whereas GPS collars obtained up to 8 GPS fixes per day. Individual animals were monitored for an average of 32 (±27, 1 SD) months. Sampling intensity varied among animals and studies, and 1 study determined that, prior to the use of GPS in telemetry aircraft, 95% of VHF radiolocations were accurate to within ±364 m ($\bar{x} = 148$; Apps et al. 2001). This is the maximum error reported or assumed across the independent sampling efforts from which our data are derived. Location fixes from GPS-collars were subject to screening for excessive spatial error (Moen et al. 1997).

All collars placed on caribou were equipped with motion-sensors. Collars emitting stationary signals were visited on the ground as soon as possible to confirm caribou mortality and investigate probable cause. Mortalities were classified based on field evidence and necropsy results that considered bone marrow, visceral, and rump fat deposits (Table 1). Predation was inferred from evidence of bleeding, struggle, or bite injuries. Non-predation deaths were classified as accident (e.g., avalanches, falls, falling trees), malnutrition, or human caused. Mortalities for which cause could not be confidently determined were classified as unknown.

Explanatory Variables and Spatial Scales

We assembled GIS-based habitat and human-use attribute data for our analysis area. We rasterized data at 100-m resolution and we derived 12 independent variables; we considered subsets of the variables for analysis at different ecological scales. We considered these variables to best represent independent factors relevant to our underlying hypotheses.

We derived forest overstory variables from current 1:20,000 forest inventory data (Resources Inventory Branch 1995) and 1:20,000 vegetation resources inventory data (Ministry of Sustainable Resource Management 2002). Relevant successional classes were represented by young and regenerating stands of <60 years and mid-aged stands of 61–120 years. To represent the interspersion of younger stands with old (>120 years) forests, we identified pixels comprising edge between respective age classes (between young and old stands, between mid-aged and old stands). Our stand-age cutpoints were subjective and may not best capture the variation in vegetation conditions most relevant to our hypotheses. The above variables also do not account for the influence of inherently non-forested habitats in the fragmentation of old forests. To deal with these limitations, we considered 2 further measures of landscape heterogeneity. Within defined landscapes, we measured the standard deviation of overstory age considering only potentially forested sites. We also considered the standard deviation of canopy closure accounting for both potentially forested and non-forested areas.

Table 1. Known mountain caribou mortality by subpopulation and category in British Columbia, 1985–2006. Because of the conservative criteria to determine cause of death, this table should not be used for cause-specific mortality comparisons.

Subpopulation	Animals monitored	Total mortalities	Human caused	Disease/ nutrition	Accident	Unknown	Predation bear	Predation wolf	Predation wolverine	Predation cougar	Predation unknown
Allan Creek	7	0	0	0	0	0	0	0	0	0	0
Barkerville	14	6	0	0	1	2	3	0	0	0	0
Columbia North	67	30	1	2	4	9	6	3	3	2	0
Columbia South	27	16	0	0	4	4	2	1	1	4	0
Duncan	5	3	0	1	0	0	0	0	1	1	0
Frisby Boulder	16	3	0	0	1	2	0	0	0	0	0
George Mtn.	2	1	0	0	0	0	0	0	0	0	1
Groundhog	13	7	0	1	1	3	0	1	0	0	1
Hart Ranges	22	5	0	1	0	3	0	1	0	0	0
Kinbasket	5	1	0	0	0	1	0	0	0	0	0
Monashee	2	0	0	0	0	0	0	0	0	0	0
Nakusp	34	12	1	0	1	6	4	0	0	0	0
Narrow Lake	2	1	0	0	0	1	0	0	0	0	0
North Cariboo	10	2	0	0	0	1	0	0	0	0	1
Purcells South	38	17	2	0	0	5	2	0	1	6	1
Purcells Central	10	2	0	0	1	1	0	0	0	0	0
South Selkirks	117	38	2	0	1	26	2	0	0	7	0
Wells Gray	162	64	0	6	8	25	8	15	1	1	0
Total	541	208	6	11	22	89	27	21	7	21	4

We derived terrain variables from 1:20,000 digital elevation data (Geographic Data BC 1996) and included elevation. We modeled terrain curvature as the maximum rate of change of a curve fit through each pixel in the context of its neighbors defined at a given scale (Pellegrini 1995). We derived the standard deviation of terrain curvature within a defined landscape radius as an index of terrain complexity. With this method, a complex landscape is one with high topographic variation commonly termed rugged. Because caribou usually avoid steep terrain (Apps et al. 2001), a complex landscape may influence caribou dispersion and thus vulnerability to predation as well as hunting efficiency of some predators. We also derived a variable that defined slope direction relative to the warmest (i.e., southwest) aspect, which may influence the winter distribution of ungulate prey other than caribou.

From 1:250,000 baseline thematic mapping data (Geographic Data BC 2001), we derived variables reflecting alpine, or vegetated areas above tree line, and avalanche habitats. Both habitat features are usually associated with open conditions and may (depending on site-specific conditions) contribute forage value for early-seral ungulates. Avalanche chutes are also known to provide concentrations of preferred bear plant-foods (Waller and Mace 1997, McLellan and Hovey 2001) and positively influence grizzly bear abundance (Apps et al. 2004). In contrast, alpine habitats are open and provide relatively distant line of sight from potential predators, and may improve caribou survival. From 1:20,000 planimetric and forest road databases (Surveys and Resource Mapping Branch 1992), we derived a road access variable potentially influencing human access and the distribution and predator-specific hunting efficiency.

We addressed variation in caribou mortality risk due to known predator species using data from 541 VHF- and GPS-collared caribou monitored across all subpopulations. We considered 2 spatial scales in our analyses (Fig. 2). At level 1, we considered the composition of landscapes associated with the location of each caribou mortality relative to those associated with all live caribou locations within respective subpopulations. Comparing mortalities only within respective subpopulations avoided the confounding influence of variation in regional conditions on caribou mortality rates. Specifically, we summarized landscape composition within a 7-km radius, roughly corresponding to a core home range area of 154 km^2. This, our broadest scale, is similar to the finest scale used by Wittmer et al. (2007), but they used a different design, a smaller sample of fewer herds, and they did not use the location of death.

At level 2, we compared conditions associated with the location of each caribou mortality to those of the individual's respective seasonal live locations. At this finer scale, we summarized landscape composition within a 350-m radius. We expected this radius to encompass most location error, particularly for data collected on live animals before the use of GPS in telemetry aircraft. To avoid spatial autocorrelation, we assigned to all live caribou locations (excluding initial locations) the time since the previous location to a maximum of 16 days. Apps and Kinley (2000) suggested that spatial independence between successive mountain caribou radio locations was achieved at 16 days. We then applied a temporal weighting factor to each live caribou location according to the proportion of the 16-day period comprising its respective sampling interval. At this scale of analysis, comparing mortalities only within respective animal home ranges avoided the confounding influence of broader landscape conditions on apparent site-specific relationships with caribou mortality risk. For each variable, at each scale, we extracted landscape attributes associated with dead caribou and live caribou data to a database.

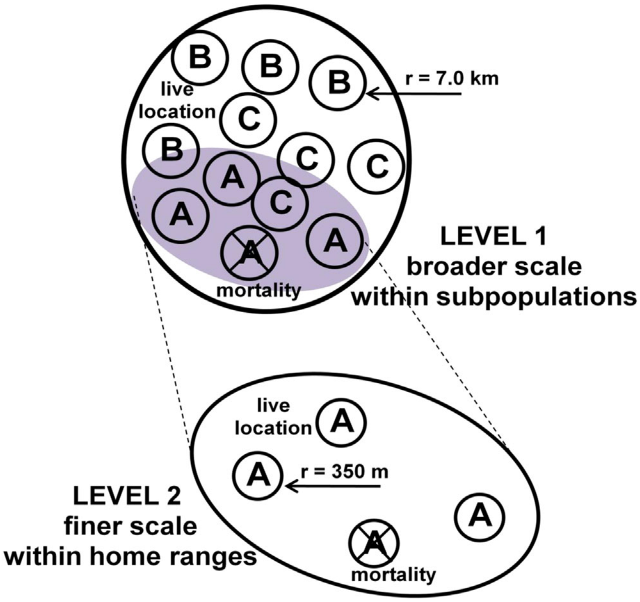

Figure 2. Schematic representation of scale-dependent analysis design. Level 1 compares caribou mortalities to live locations among all animals (e.g., A, B, C) within respective subpopulations, with landscape conditions sampled at a scale of 7 km around caribou locations. Level 2 compares caribou mortalities to live locations of respective animals only (e.g., A), with landscape conditions sampled at a scale of 350 m around caribou locations.

Seasonal habitat selection patterns by mountain caribou are characterized by shifts in elevation (Apps et al. 2001). We designed our analysis to control for differential landscape associations among caribou and their predators among seasons. Although empirically defined seasonal cutoff dates will differ slightly among subpopulations and years, we used 4 seasons with the following generic cutoff dates: early winter (ends 15 Jan), late winter (ends 15 Apr), spring (ends 30 Jun), and summer (ends 31 Oct). We compared caribou mortalities to live locations recorded only within the same season. In this way, we expected to avoid artifacts in our results that may have been due to seasonal differences in mortality risk.

Analysis

We excluded caribou mortalities known to be directly due to humans, disease or nutrition, and accidents because they were rare with small sample sizes compared to predation (Table 1). We expected some commonality in caribou predation risk due to different predator species. Therefore, in addition to considering predator-specific strata, we considered general relationships based on data pooled among known predators, and we pooled these data with mortalities of unknown cause. We expected that most of the unknown mortalities (43% of total sample) were in fact due to predation because non-predation causes, particularly accidents and human-caused deaths, are easier to determine and most known-cause mortalities were due to predation. Although 38–81% of caribou mortalities can be attributed to predation (Table 1), the actual proportion of caribou deaths due to predation likely is in the higher end of the range.

Our sample consisted of 145 animals whose deaths were due to predation or unknown cause (Table 1). We assessed differences in broad landscape composition around caribou mortality locations relative to caribou distribution within subpopulations (level 1), and differences in fine landscape composition at caribou mortality sites relative to sites used within home ranges (level 2). We initially explored differences between dead caribou and live caribou locations using single-sample t-tests to assess deviations from 0 and to screen covariates for consideration in multivariate modeling.

In the context of multiple landscape predictors, we analyzed cause-specific caribou mortality risk using generalized linear modeling. Our goal was to describe combinations of spatial factors that, given our data, best explain the distribution of dead caribou locations relative to live caribou locations for each stratum of cause-specific predation. That is, our response variable was the binary condition where a caribou was found either dead or alive. We considered only variables exhibiting at least marginal univariate relationships ($P < 0.2$) consistent with our predictions. We evaluated relationships among variables using linear regression tolerance statistics and by examining correlation matrices. Where problematic collinearity occurred (tolerance < 0.2 or $r > 0.7$; Menard 1995), we considered bivariate relationships and dropped variables of lesser univariate significance to avoid modeling spurious relationships (Rexstad et al. 1988, Anderson et al. 2001). Our hypotheses pertained to individual variables rather than definable multivariate models with theoretic support to the exclusion of others. Thus, competing specifically defined variable combinations in our analyses was impractical. Because the primary goal was variable ranking and identification, we considered all possible subsets among screened covariates as candidate models. We evaluated models with matched case-control logistic regression by using a stratifying variable that accounted for variation by subpopulation (level 1) or individual animal (level 2) within a Cox proportional hazards analysis (Hosmer and Lemeshow 2000). We gauged model parsimony and prediction using a modified Akaike's Information Criterion (AIC_c; Akaike 1973). To account for model uncertainty, we used Akaike weights to average parameter coefficients among all competing models according to the $\bar{\beta}$ (shrinkage) estimator (Burnham and Anderson 2002), such that model contribution was proportional to the evidence that each is best fit to the data. In light of concerns about uninformative parameters being included in selected models (Arnold 2010), we chose not to report model rankings and to base inferences on model-averaged standardized coefficients of individual variables. For each analysis stratum, we report model fit by way of a chi-square goodness-of-fit statistic (Zhang 1999) and also the area under the receiver operating characteristic curve (AUC; Manel et al. 2001, Pearce et al. 2002) corresponding to the proportion of cases where a greater probability of mortality is assigned to the dead caribou locations than to the average of matched live caribou locations.

RESULTS

Within subpopulations (level 1) and within home ranges of dead caribou (level 2), we selected a subset of potential explanatory covariates based on univariate associations and bivariate relationships. We did not pursue analysis of predation due to wolverine because of a lack of statistical power ($n = 7$ deaths), but relationships were apparent in explaining caribou death due to wolf, bear, cougar, all predators, and predation combined with mortalities of unknown cause. All top-ranked models fit the data better than random expectation, though level 1 models of predator-specific mortality performed better than those that pooled data (Table 2).

Multi-model inference suggested particular factors that influenced cause-specific risk of mortality among mountain caribou when considered in the context of broad (7-km radius) landscape conditions within subpopulations (level 1; Fig. 3) and fine (350-m radius) landscape conditions within seasonal home ranges (level 2; Fig. 4). The odds of caribou predation by wolves at level 1 increased 47% for every 100-m drop in elevation, and 16% for every 10-point increase in the terrain complexity index. At level 2, caribou were 5% more likely to be killed by wolves for every 1% increase in road

Table 2. Goodness-of-fit metrics and area under the receiver operating characteristic curve (AUC) of top-ranked models of cause-specific mountain caribou mortality within respective subpopulations (level 1) and home ranges (level 2) across British Columbia, 1988–2006.

	Level 1			Level 2		
Mortality cause	χ^2	***P*-value**	**AUC**	χ^2	***P*-value**	**AUC**
Wolf	9.6	0.011	0.71	10.6	0.005	0.71
Bear	12.5	0.002	0.79	26.8	<0.001	0.79
Cougar	16.8	<0.001	0.83	10.3	0.006	0.67
Predation-all	10.1	0.007	0.65	10.3	0.006	0.64
Predation-all and unknown	7.1	0.03	0.56	16.4	0.002	0.63

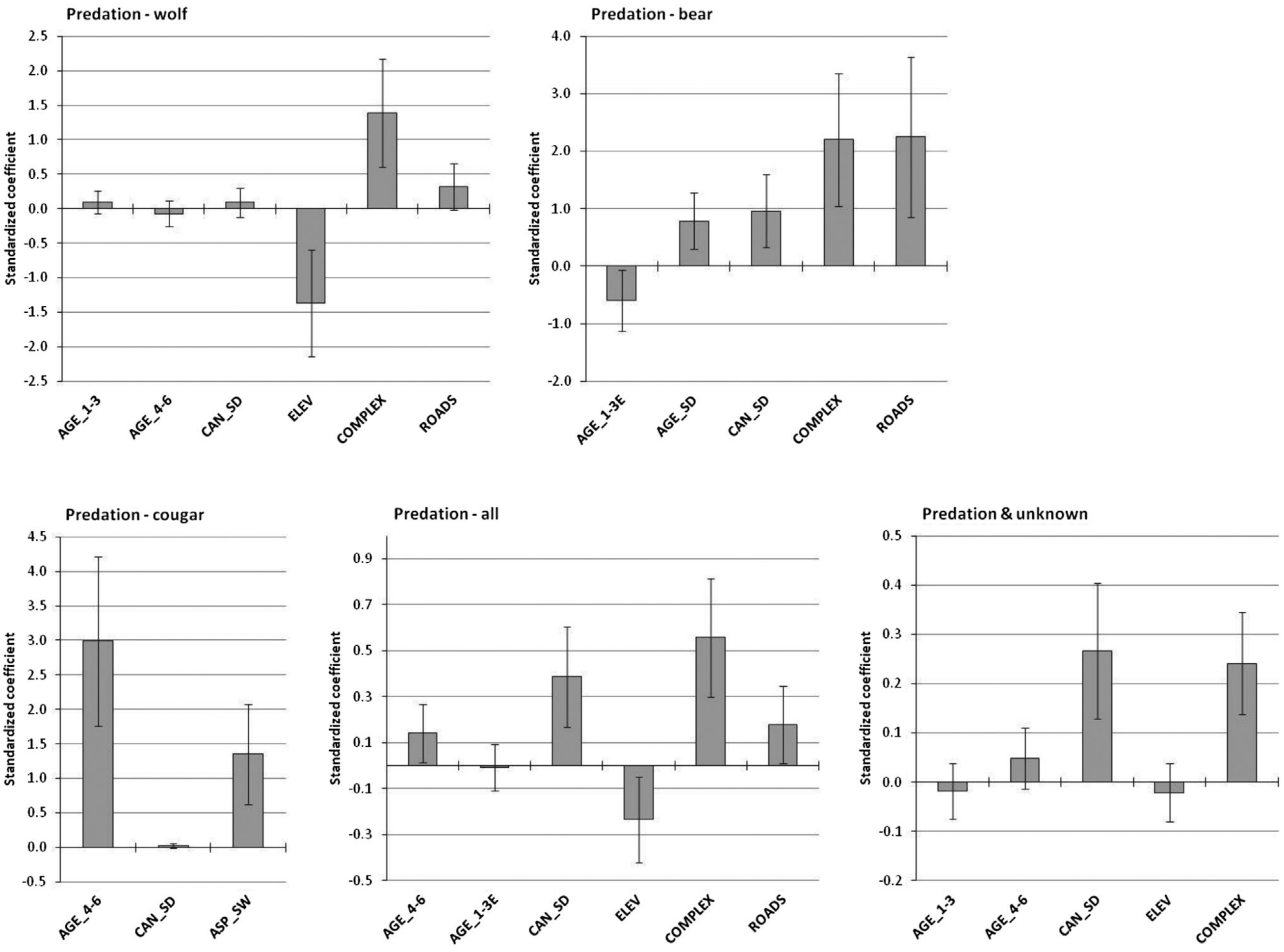

Figure 3. Multi-model-averaged standardized logistic regression coefficients (±SE) explaining cause-specific mortality risk of mountain caribou given landscape factors considered within respective subpopulations (level 1) across British Columbia, 1985–2006. Variables refer to overstory stands aged 1–60 years (AGE_1–3), overstory stands aged 61–120 years (AGE_4–6), edge between stands aged 1–60 years and >120 years (AGE_1–3–E), standard deviation of overstory stand age (AGE_SD), standard deviation of overstory canopy closure (CAN_SD), relative exposure to southwestern aspect (ASP_SW), elevation (ELEV), terrain complexity index (COMPLEX), and linear disturbance density (ROADS).

density. The odds of caribou being killed by bears at level 1 increased 25% for every 1% increase in road density, 29% for every 10-point increase in the terrain complexity index, 29% for each 0.5 standard deviation by which canopy closure varied in the landscape, and 4% for each 0.5 standard deviation by which overstory age varied in the landscape. At level 2, caribou were 17% more likely to be killed by bears for every 100-m drop in elevation, and 27% more likely for every 10-point reduction in the terrain complexity index. The odds of caribou predation by cougars at level 1 increased 35% for every 1% increase in stands of 61–120 years and 38% for every 1% increase in the average exposure to southwest aspects. At level 2, caribou were 69% more likely to be killed by cougars for every 100-m drop in elevation, and 6% more likely for every 1% reduction in the proportion of edge between old (>120 years) and young (<60 years) stands. Considering all sources of known predation, caribou at level 1 were 7% more likely to be killed for every 10-point increase in the terrain complexity index, 11% more likely for each 0.5 standard deviation by which canopy closure varied in the landscape, 11% more likely for every 100-m drop in elevation, and 2% more likely for every 1% increase in road density. At level 2, caribou were 33% more likely to be killed by any predator for every 100-m drop in elevation, and 1% more likely for every 1% increase in road density. Pooling all predation sources and mortalities due to unknown cause, caribou at level 1 were 16% more likely to die for each 0.5 standard deviation by which canopy closure varied in the landscape, and 3% more likely for every 10-point increase in the terrain complexity index. At level 2, caribou were 28% more likely to die by any cause for each 100-m drop in elevation.

Our hypotheses related to stand age and the amount of edge between young and old forests were not supported at either level 1 or 2. Once we accounted for other static factors, the total amount of early-seral conditions and the amount of edge between young and old forest did not explain where caribou were killed by any predator species at either scale. At the 2 spatial scales we considered, the only direct human

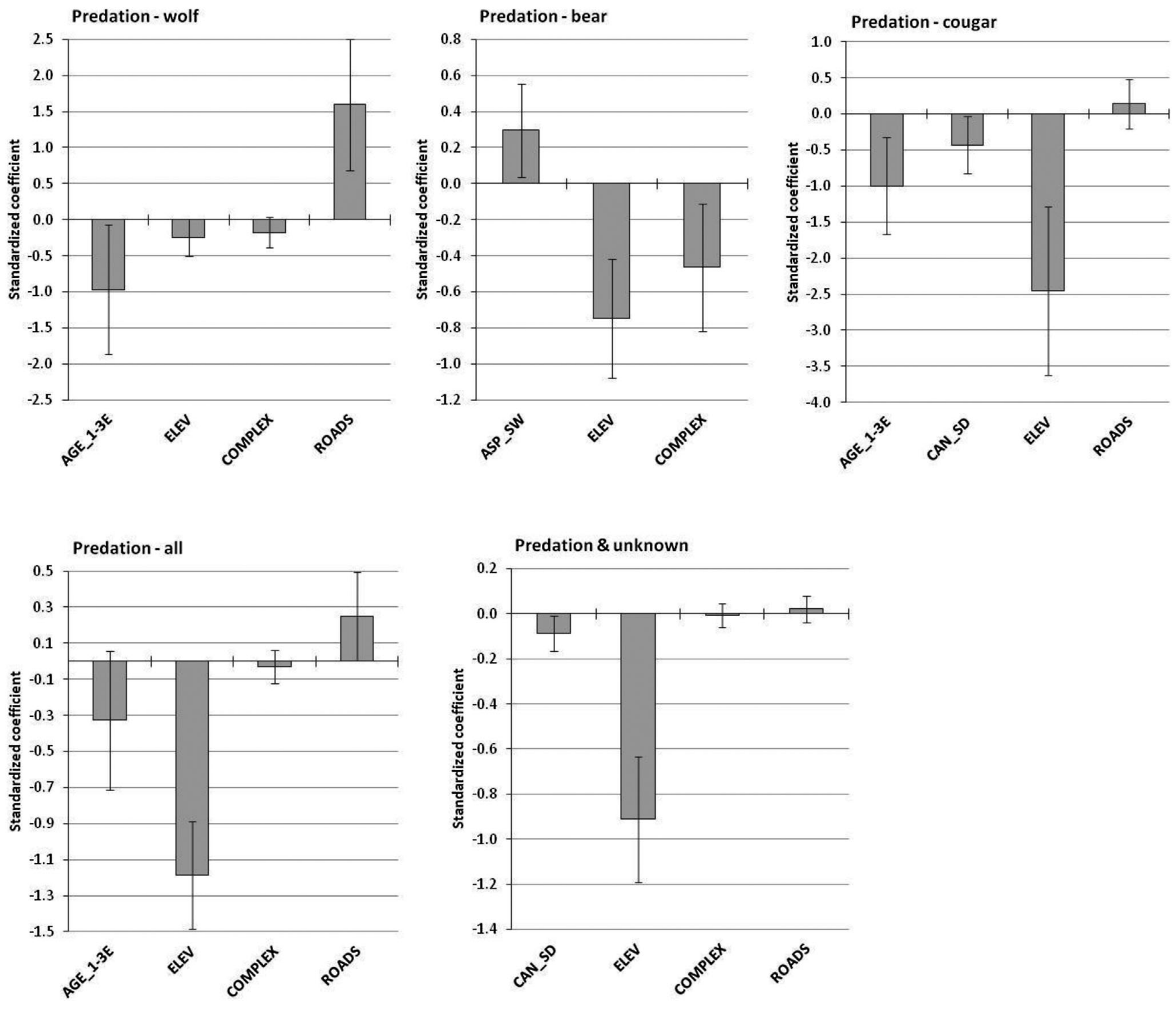

Figure 4. Multi-model-averaged standardized logistic regression coefficients (±SE) explaining cause-specific mortality risk of mountain caribou given landscape factors considered within respective home ranges (level 2) across British Columbia, 1985–2006. Variables refer to edge between stands aged 1–60 years and >120 years (AGE_1–3–E), standard deviation of overstory stand age (AGE_SD), standard deviation of overstory canopy closure (CAN_SD), relative exposure to southwestern aspect (ASP_SW), elevation (ELEV), terrain complexity index (COMPLEX), and linear disturbance density (ROADS).

factor apparently influencing caribou vulnerability to predation was roads.

DISCUSSION

Initially, we surmised that the vulnerability of mountain caribou to predation would be a function of spatial factors that influence landscape overlap with predators and factors that increase caribou susceptibility to those predators. Across seasons and scales, mountain caribou prefer habitats associated with old forests and gentle slopes (Rominger and Oldemeyer 1989, Apps et al. 2001, Apps and McLellan 2006). At the very low densities that most mountain caribou subpopulations are currently found, some loss of habitat may not have serious implications in the ability of caribou to meet forage requirements (Wittmer et al. 2005*b*), but caribou habitat selection or persistence may be largely influenced by predation risk, particularly at coarser scales (Ouellet et al. 1996, Stuart-Smith et al. 1997, Rettie and Messier 2000, McLoughlin et al. 2005).

Although multiple and potentially related factors are clearly relevant, our data do not support the prediction that caribou are more likely to die in landscapes with an abundance of early-seral conditions and edge created by logging, powerlines, or recent fires. This result suggests that, except for roads, habitat changes have had little effect on where caribou are killed by predators. During summer and fall, when predation on caribou is highest (Seip 1992, Wittmer et al. 2005*a*), caribou are found most often in higher elevation forests and subalpine parkland (Servheen and Lyon 1989, Apps et al. 2001). The number and distribution of early-seral ungulates, however, are likely limited by restricted, low-elevation winter habitat. During summer, moose, deer, and elk are likely to move to more open, higher-elevation forests and subalpine habitats where they overlap caribou regardless of logging there (Stotyn 2008).

Early-seral ungulates such as moose and white-tailed deer may select lower elevation habitats than do caribou in the summer. At broad scales, we found elevation influenced caribou vulnerability to predation. At finer scales, sites where caribou were killed by bears, cougars, or all predators combined were at lower elevations than where caribou more commonly occurred. Thus, when caribou move to lower elevations, they become more vulnerable to being killed by a predator regardless of whether the area has been heavily logged. Because caribou were more often killed by predators in relatively rugged terrain at the broader scale, caribou appear to have been most vulnerable in relatively narrow valleys rather than larger, wide valley or plateau areas. This trend held specifically for bears and cougars. Caribou were also vulnerable to wolves at low elevations but not in broad landscapes that were otherwise complex.

The only dynamic factor that clearly influenced where caribou were killed was roads, in association with which caribou were killed more often by wolves at the finer scale (level 2; 350-m radius). This result is consistent with roads being used as efficient travel routes for wolves and the negative impact of these features on caribou survival where wolves occur (Thurber et al. 1994, James and Stuart-Smith 2000, Whittington et al. 2005). Road networks are more likely to facilitate wolf predation on caribou where human access is low, given the avoidance by wolves of features with high human use (Whittington et al. 2005). Moreover, because wolves sometimes range more widely than other predators, they are likely to benefit simply from the presence of linear pathways that may or may not be associated with overall road densities that are relatively high at the broader scale (level 1) we considered.

The implications of roads to caribou vulnerability are not limited to predation by wolves. Bears killed caribou in landscapes with greater road densities at the broader scale (level 1; 7.0-km radius). We did not predict this result because grizzly bears generally avoid roads with some traffic (e.g., McLellan and Shackleton 1988, Mace et al. 1996). However, some bears use roads for travel, particularly at night when traffic is light (McLellan and Shackleton 1988) or when the roads otherwise have limited use (Wielgus et al. 2002, Ciarniello et al. 2007). Because of a generally low density of people across the remaining range of mountain caribou, most forestry roads receive little traffic except by forestry workers and virtually no traffic at night. Alternatively, because the relationship of bear predation with roads was apparent only at the broader (level 1) scale, it may partially relate to the greater forage value to bears of recent cutblocks that are usually in association with roads, and bears did kill caribou in broad landscapes with moderately high variation in stand age and canopy closure.

In contrast to their vulnerability to bears, caribou were apparently not as susceptible to cougar predation in landscapes with high heterogeneity in canopy closure. However, positive predictors did include an interspersion of mid-successional stands. This result may relate to the importance of overstory cover and stem density in providing stalking cover and ambush opportunities for cougars, but mid-successional stands may also be associated with ungulate wintering ranges. The positive relationship with relatively warm aspects also suggests that caribou are more vulnerable to cougars in proximity to wintering habitats of primary cougar prey, such as deer.

Because cougars were subject to a relatively liberal hunting harvest across most of our sampling years, we speculate that resident cougars were likely rare in landscapes with high road densities that facilitate vehicle access for hound hunters during winter. Because of the positive association between road access and logging, an interspersion of stands <60 years may have resulted in decreased cougar predation on caribou despite the value of early-seral conditions to the primary ungulate prey of cougars during the snow-free season.

MANAGEMENT IMPLICATIONS

Mountain caribou densities are too low to exclusively support predators such as wolves and cougar (1991, 1992; Katnik 2002). Where alternate prey sustain predators, and where these predators encounter caribou, sustained depression and extirpation of caribou populations can result (Seip 1992, Rettie and Messier 2000). Unsustainable predation rates have been recorded in declining subpopulations (Wittmer et al. 2005*a*, *b*) and 2 have been extirpated in recent years (Wittmer et al. 2007). Although predation has been the primary, proximate cause of mountain caribou population decline, the link to changes in the number and distribution of early-seral prey and predators has not been well documented (but see Latham et al. 2011). In this study, our results did not support the hypothesis that caribou would be killed in landscapes with an abundance of early-seral habitats primarily created by logging, or with an abundance of edge between early-seral and old forests. Other, more static factors such as elevation, terrain conditions, and variation in canopy cover influenced where caribou were killed by predators more than early-seral interspersion. However, even our broader scale of analysis did not encompass most winter ranges of early-seral ungulates that are the primary prey of the predators in the system. Where studied, early-seral prey numbers have increased dramatically adjacent to mountain caribou ranges, and these increases have correlated to increases in early-seral habitats on their winter ranges (Serrouya et al. 2011).

Relationships among habitat conditions, early-seral ungulate abundance and distribution, the numerical and functional responses of predators, and resulting predation on endangered mountain caribou are complex and far from being fully documented. Aside from roads, our results suggest that the population-level numerical response of predators to their primary ungulate prey, likely stemming from habitat enhancement within ungulate winter ranges, is more relevant to caribou mortality risk than the functional response of predators to habitat change within landscapes occupied by caribou. More work is clearly needed on these species and their interactions, but immediate management actions are necessary if caribou are to persist, particularly toward their southern distribution where populations are small and highly fragmented (Wittmer et al. 2005*a*). Although reducing logging and associated road building in higher elevation caribou habitat may reduce caribou predation over the long term to some degree, near-term management actions are required that reduce predators either directly or by also reducing the population size of early-seral ungulates on which they depend. Reducing the number of early-seral ungulates can be accomplished by hunting in some areas (Serrouya et al. 2011) but is unlikely in some remote areas (Seip 2008). Over the long-term, the greatest positive effect on caribou may be from stemming the continuous production of early-seral conditions by reducing or at least changing timber harvest practices in the winter ranges of early-seral ungulates. But benefits to caribou will not be realized for many years and some mountain caribou subpopulations are projected to extirpate sooner (Wittmer et al. 2010). A strategy to reduce the number of primary prey, predators, and timber harvesting will unlikely be acceptable to all citizens.

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