Factors influencing the dispersion and fragmentation of endangered mountain caribou populations

Clayton D. Apps[a,*], Bruce N. McLellan[b]

[a]Resources and the Environment Program, University of Calgary, 2708 Cochrane Road NW, Calgary, Alta., Canada T2M 4H9
[b]British Columbia Ministry of Forests, RPO No. 3, P.O. Box 9158, Revelstoke, BC, Canada V0E 3K0

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ABSTRACT

Mountain caribou, an ecotype of woodland caribou, are endangered due to the loss and fragmentation of old forests on which they depend. However, a wider array of natural and human factors may limit caribou persistence and isolate populations, and understanding these may help to stop or reverse population declines by forecasting risk and targeting core habitat areas and key linkages for protection, enhancement or restoration. Across most of the historic range of mountain caribou, we conducted a bi-level analysis to evaluate factors related to the persistence of, and landscape occupancy within, remaining subpopulations. We used caribou location data from 235 radio-collared animals across 13 subpopulations to derive a landscape occupancy index, while accounting for inherent sampling biases. We analyzed this index against 33 landscape variables of forest overstory, land cover, terrain, climate, and human influence. At the metapopulation level, the persistence of subpopulations relative to historic range was explained by the extent of wet and very wet climatic conditions, the distribution of both old (>140 yr) forests, particularly of cedar and hemlock composition, and alpine areas. Other important factors were remoteness from human presence, low road density, and little motorized access. At the subpopulation level, the relative intensity of caribou landscape occupancy within subpopulation bounds was explained by the distribution of old cedar/hemlock and spruce/subalpine fir forests and the lack of deciduous forests. Other factors impeding population contiguity were icefields, non-forested alpine, hydro reservoirs, extensive road networks, and primary highway routes. Model outputs at both levels were combined to predict the potential for mountain caribou population persistence, isolation, and restoration. We combined this output with the original occupancy index to gauge the potential vulnerability of caribou to extirpation within landscapes known to have recently supported animals. We discuss implications as they pertain to range-wide caribou population connectivity and conservation.

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1. Introduction

Mountain caribou are an ecotype of woodland caribou (*Rangifer tarandus caribou*) and were historically distributed throughout the high snowfall region of southeastern British Columbia, northern Idaho, northeast Washington and northwest Montana. Mountain caribou are distinguished from other caribou ecotypes by a late-winter diet that consists almost entirely of arboreal hair lichens that are most abundant in old forests (Seip and Cichowski, 1996; Terry et al., 2000; Heard and Vagt, 1998). About 98% of the global population of mountain caribou occurs within British Columbia,

where they are considered "endangered" or "critically imperiled" (Hatter, 2000; Conservation Data Centre, 2002). Several factors may have caused historic population declines, including excessive hunting. But it is the fragmentation and loss of habitats, particularly old forests on which mountain caribou depend, that is thought to have directly or indirectly through changes in predation rates, precipitated recent range and population reductions (Seip and Cichowski, 1996; Heard and Vagt, 1998; Spalding, 2000; Stevenson et al., 2001; Wittmer et al., 2005a).

Across their current geographic range, the approximately 1900 remaining mountain caribou are found in 18 subpopulations ranging from 3 to about 525 animals (Wittmer et al., 2005a). Movements of radiocollared animals suggest little if any mixing among subpopulations and some likely are completely isolated, with small, declining numbers (Wittmer et al., 2005a). Within subpopulations there has been a concerted effort to characterize multi-scale habitat relationships such that probable caribou requirements can be integrated with resource management planning (e.g., Apps et al., 2001). Replication of similar analyses among regions has provided a foundation for understanding mountain caribou habitat preferences and variation among subpopulations (primarily with respect to climate and topography) and among seasons (primarily with respect to snow conditions) (Stevenson et al., 2001). However, the broader-scale factors that are expected to influence the persistence and distribution of mountain caribou subpopulations are hypothetical and have not been empirically evaluated. Spatial structure plays an important role in the dynamics, resiliency and viability of populations (Kareiva, 1990; Ritchie, 1997; Hanski, 1999; Wiegand et al., 2002), and understanding current and potential population distribution and the role of natural and human conditions is fundamental to the conservation of species at risk (Brown et al., 1995; Turner et al., 1995; Abbitt et al., 2000).

Several factors may influence the dispersion and fragmentation of mountain caribou populations and these may function differently across scales. Collectively, they determine the likelihood of mountain caribou persistence across the larger metapopulation (*sensu* Hanski and Ovaskainen, 2000). At very broad scales, the distribution of mountain caribou populations should conform to climatic and physiographic constraints, given the specialized foraging behavior and anti-predator strategies of this ecotype. However, caribou persistence may also be influenced by the distribution and juxtaposition of landscapes satisfying seasonal habitat requirements. Coupled with such natural restrictions, demographic isolation may be the result of potential human barriers, such as settled and agricultural landscapes, major highways, and hydro-electric impoundments. Within subpopulation bounds, habitat modification and fragmentation may increase caribou energetic demands, while elevating their vulnerability to generalist predators by concentrating caribou and promoting spatial overlap and interspersion of other ungulate species (Kinley and Apps, 2001; Katnik, 2002; Wittmer et al., 2005b). Associated road access to motorized vehicles can increase the risk of poaching and unintentional killing of caribou, but may also contribute to elevated predation by providing plowed or snow-compacted movement routes into caribou habitat (James and Stuart-Smith, 2000). Persistent back-country recreational snowmobile activity may elevate caribou stress leading to demographic consequences, or may displace caribou from preferred winter habitats (Simpson and Terry, 2000; Kinley, 2003).

Quantifying how the above factors or their correlates relate to the current distribution of mountain caribou can help us understand how subpopulations have or may become isolated, and evaluate the likelihood of natural demographic or genetic connectivity. Spatial predictions may inform the development of strategies to stop or reverse declines in the distribution and abundance of mountain caribou by forecasting population risk and targeting key population cores and linkages for protection, enhancement, or restoration. Further, understanding the likelihood of mountain caribou persistence across their range can serve to prioritize landscapes for population augmentation or reintroduction.

In this paper, we conduct a 2-stage inductive analysis to evaluate and describe factors associated with fragmentation among and within mountain caribou subpopulations across most of their historic range. Using radiotelemetry monitoring data for each subpopulation, we derive a spatial index reflecting the expected intensity with which landscapes are known to be currently occupied by caribou while accounting for inherent biases. At the "metapopulation level", we define existing subpopulation bounds from this index, and we compare landscape composition within occupied versus extirpated mountain caribou range. At the "subpopulation level", we evaluate factors that influence the intensity of landscape occupancy within subpopulations. Our analysis is descriptive and is intended to evaluate common factors that ultimately influence mountain caribou population dispersion and fragmentation among subpopulations and across their historic range.

2.　Study area

Our analysis area was defined by the southern two-thirds (i.e., south of 52°30′N) of historic mountain caribou range in southeastern British Columbia (Fig. 1), and comprised approximately 127,000 km². Following Spalding (2000), we defined historic mountain caribou range using the provincial ecosection classification (Demarchi, 1996). The analysis area is 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) zone, and the very wet subzones of the Sub-Boreal Spruce (SBS) zone (Meidinger and Pojar, 1991). These zones correspond to the Interior Wet-belt of the province, a highly mountainous region that receives considerable precipitation from pacific weather systems. A deep snowpack (>2 m) and a low frequency and extent of natural fire results in a natural forest condition dominated by old age classes, multi-layered structure, and abundant snags and coarse woody debris (Jull et al., 1998). Elevations range from 350 to >3500 m. Moose (*Alces alces*) are abundant in the northern portion of the study area while elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) are more abundant in the south (Wittmer et al., 2005a). Grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolverine (*Gulo*
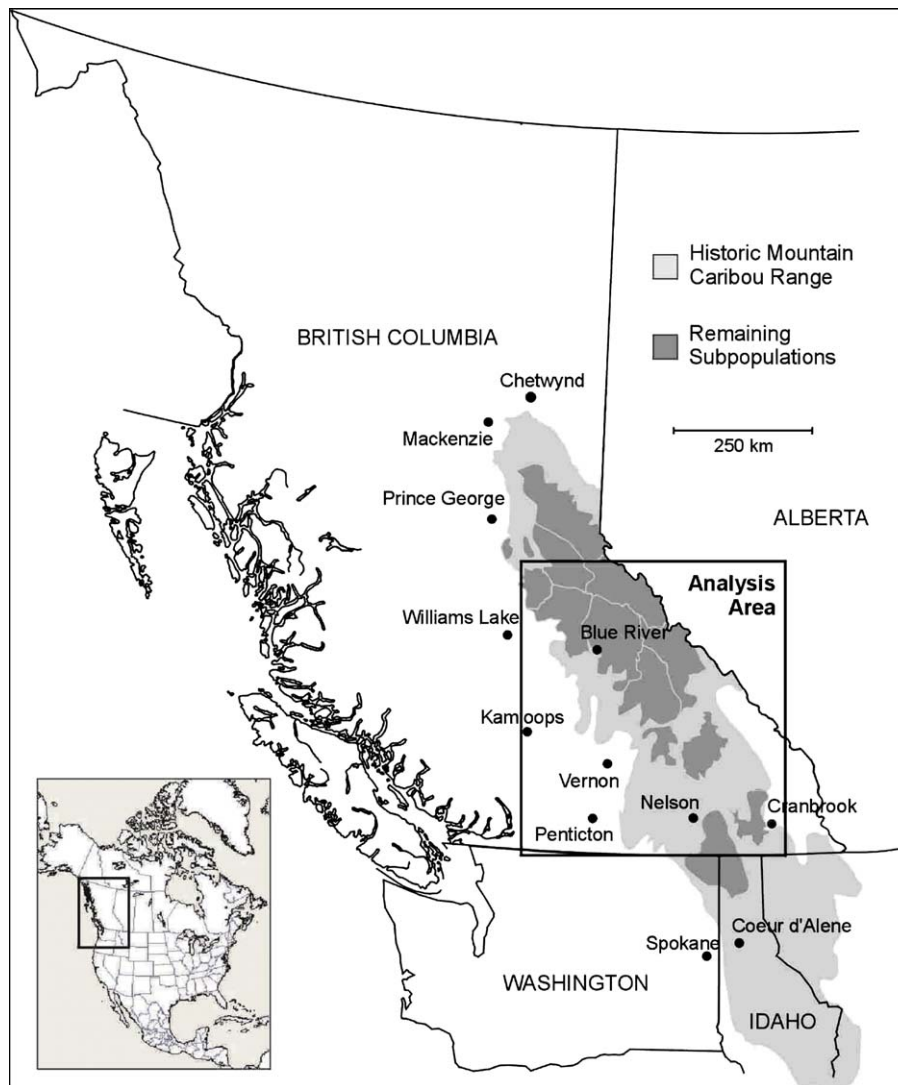
Fig. 1 – Analysis area for evaluating factors that influence mountain caribou population dispersion and fragmentation in southeast British Columbia, Canada, as adapted from Spalding (2000) and Mountain Caribou Technical Advisory Committee (2002).

gulo) are common predators across the distribution of mountain caribou while wolves (*Canis lupus*) are more common in the north and cougar (*Puma concolor*) more abundant in the south (Wittmer et al., 2005a). Human communities with populations of up to 26,000 exist within the study area, and include the cities of Nelson and Cranbrook and the towns of Valemont, Clearwater, Salmon Arm, and Revelstoke. Three major highways and several other secondary highways intersect the study area. The analysis area encompassed all or parts of 13 distinct mountain caribou subpopulations (Wittmer et al., 2005a).

3. Methods

3.1. Index of landscape occupancy by caribou

Mountain caribou have been monitored using radio-telemetry in several studies across their distribution. In all studies, animals were captured using a net gun shot from a helicopter during the late winter when the caribou frequent high elevation, subalpine parkland habitats. A high proportion of the population (>85%; Apps et al., 2001; Wittmer et al., 2005a) is visible and available for capture at that time of year, and the distribution of sampled animals is thus expected to approximate the distribution of subpopulations being studied. The data represented 325 animals over 20 yr. Datasets included VHF- and GPS-collared animals, and both the intensity and extent of monitoring varied among animals and studies. Using the collective dataset, we derive an index of landscape occupancy by caribou while correcting for inherent biases.

Mountain caribou foraging strategies are characterized by distinct patterns of elevation use among four recognized caribou seasons. Although seasonal transition dates may vary among years and subpopulations, Apps et al. (2001) defined multi-year seasonal cut-dates as: early winter (22 October–11 January), late winter (12 January–22 April), spring (23 April–28 May), and summer (29 May–20 October). Because we intended to address factors influencing population dispersion,

and not seasonal range affinities, it was important that data from individual animals were representative of annual space use. Given that the greatest range shifts are expected to occur between early-winter/spring and late-winter/summer (Apps et al., 2001), we assumed that data from individual caribou will represent each animal's annual occupation area if at least 5 temporally independent locations fell in either early-winter or spring and if 5 locations fell in either late-winter or summer, for a total of ⩾10 locations per animal. We assumed that caribou locations were temporally independent after an 8-day interval, because mountain caribou movements have been observed to asymptote at or before this period (Apps and Kinley, 1999; Apps and Kinley, 2000).

Our objectives were specific to the subpopulation level. Therefore, we calculated a weighting factor to ensure that each animal contributed equally in our analyses despite sample size differences among animals and study areas. The weighting factor was comprised of three subfactors. The first weighting subfactor (a) treated those locations temporally independent by ⩾8 days as 1, and assigned each of the remaining locations the proportion of 8 days spanned by its sampling interval. That is, $a = d/8$, where d is the number of days since the previous location to a maximum of 8 days.

The second weighting subfactor (b) ensured that locations for each animal summed to 1 within each season. That is, $b = 1/n_s$, where n_s is the total location sample for the animal in the respective season. The third weighting subfactor (c) accounted for the proportion of the year represented by the respective caribou season in which locations fell. That is, $c = (l_y/S_n)/l_s$, where l_y is the year length in days (i.e., 365), S_n is the number of caribou seasons (i.e., 4), and l_s is the respective season length in days. Subfactors b and c ensured that the temporal representation of data for each animal was balanced through the year, despite differential monitoring intensity among seasons. The final weighting factor (w) applied to each caribou location was derived such that the total weighted location sample for each animal summed to 1, which accounted for differential sample sizes among animals. That is, $w = (a \cdot b \cdot c)/\sum_i (a \cdot b \cdot c)$, where i is the individual study animal.

Within a geographic information system (GIS), we rasterized and summed weighted caribou locations across the analysis area using a 250 m^2 pixel resolution. We then averaged pixel values within the broader landscape using a GIS moving window routine (Bian, 1997). For this, we used a circular-window radius of 13.7 km, which approximates what has been
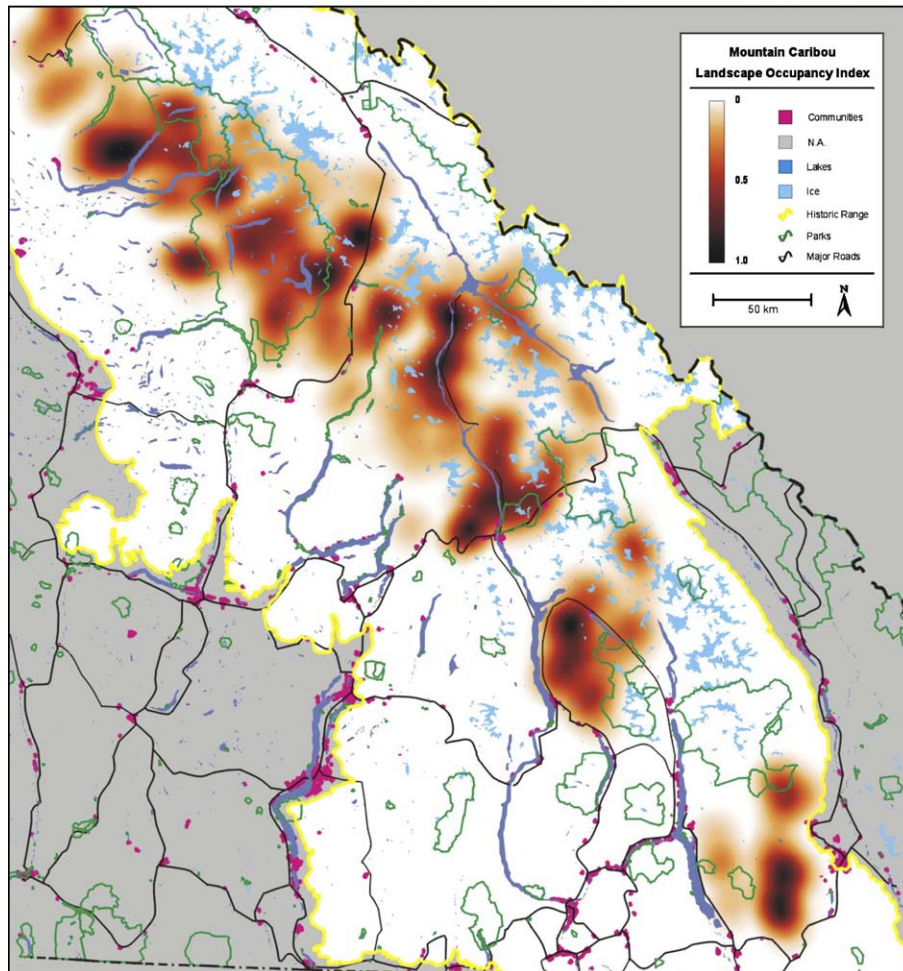

Fig. 2 – **Mountain caribou landscape occupancy index derived using weighted radiolocations sampled from 245 study animals across 13 subpopulations. The index reflects the certainty of landscape occupation by caribou during the period 1984–2004 as sampled from available radiotelemetry data.**

reported as the maximum (i.e., 95th percentile) movement of mountain caribou among independent locations (Apps et al., 2001). We carried out these steps independently for each study from which the caribou location database was built. We then standardized each resultant image (raster grid) to a $0 \rightarrow 1$ scale to account for differences in animal sample size among studies. Finally, using logical overlays, we combined images into one, assigning each pixel the maximum value among images. We refer to this output as an index of known mountain caribou landscape occupancy (Fig. 2).

3.2.   Explanatory variables

In a GIS, we assembled available habitat and human use attribute data from several sources, and we rasterized data at a 250 m resolution. For analysis, we derived 33 independent variables (Table 1) pertaining to hypotheses regarding factors and mechanisms that influence mountain caribou population dispersion and fragmentation. The habitat ecology of mountain caribou is seasonally influenced by overstory stand structure (Rominger and Oldemeyer, 1989; Rominger et al., 2000;

Table 1 – Independent landscape variables considered for analyses of mountain caribou population dispersion and fragmentation in southeastern British Columbia

Variable	Description
AGE_1–2	Overstory stand age 1–40 yr
AGE_3–5	Overstory stand age 41–100 yr
AGE_6–7	Overstory stand age 101–140 yr
AGE_8–9	Overstory stand age >140 yr
CANOPY	Overstory canopy closure (%)
SITE	Stand site productivity index
SPP_S-B	Spruce and subalpine fir composition (%)
SPP_C-H	Cedar and hemlock composition (%)
SPP_P	Lodgepole pine and white pine composition (%)
SPP_FD	Douglas-fir composition (%)
SPP_DEC	Deciduous species composition (%)
FOR_NP	"Non-productive" forest (%)
ELEV	Elevation (m)
SLOPE	Slope (%)
CURVA	Terrain curvature index
COMPLEX	Terrain complexity index
BTM_LAKE	Lakes and reservoirs (%)
BTM_AGRI	Agricultural lands (%)
BTM_ICE	Icefields (%)
BTM_ALP	Non-forested alpine (%)
BTM_OLD	Old ($\geqslant$140 yr) forest (%)
BTM_YNG	Young (<140 yr) forest (%)
BTM_BURN	Disturbance due to wildfire (%)
BTM_LOG	Disturbance due to logging (%)
BTM_URBAN	Urban development (%)
LINEAR	Linear human disturbance density (%)
HIGHWAY	Major transportation routes (%)
ROS	Recreation opportunity spectrum (1–7 remoteness index)
ROS_PRIM	Primitive and semi-primitive non-motorized recreation opportunities only
MOTOR_WI	Motorized recreation – winter (from RFI)
MOTOR_SU	Motorized recreation – summer (from RFI)
HELI-SKI	Helicopter skiing opportunities (from RFI)
BEC_W-V	Wet and very wet subzones of the ICH, ESSF, and SBS BEC zones

Terry et al., 2000; Apps et al., 2001; Kinley et al., 2003). Forest attributes are also relevant to the ecology of other ungulate prey species, the distribution of which may affect caribou predation risk. Thus, we expected that select forest overstory variables should relate to mountain caribou population distribution at broader scales, and we derived these from 1:20,000 forest inventory data (Resources Inventory Branch, 1995). Specifically, we considered four distinct stand age classes reflecting gross structural differences expected among dominant tree species in our analysis area, and which conform to the age class convention of the provincial forest inventory system (prefix AGE_ with 1–2, 3–5, 6–7, or 8–9). Canopy closure (CANOPY) depicted the ocular cover of the stand overstory. Site index (SITE) reflected forest productivity and is calculated with species-specific equations that incorporate stand age and height (Thrower et al., 1991). We considered overstory species composition (prefix SPP_ with S-B, C-H, P,FD, or DEC) including vegetated but non-forested sites (FOR_NP) for analysis because these variables relate to seasonal forage availability and are indicative of climatic variability (Apps et al., 2001). Individual or grouped species were included if their spatial composition was >3% of the analysis area.

Terrain features may influence the dispersion and connectivity of mountain caribou populations in several ways. Very rugged terrain can limit the distribution of landscapes supporting forest conditions preferred by caribou (Apps et al., 2001) and can also represent barriers to movement. The greater human accessibility of subdued terrain, especially at lower elevations, may facilitate greater human influence through industrial, recreational, transportation and settlement land uses. From an assemblage of 1:20,000 digital elevation data (Geographic Data BC, 1996), we derived variables of elevation (ELEV) and slope (SLOPE). Because elevations varied greatly among regions of the analysis area, we derived an index of terrain curvature (CURVA; Pellegrini, 1995) to indicate relative slope position independent of elevation. At finer scales, the complexity of terrain may mediate predation risk or human influence. Thus, we calculated a terrain complexity index (COMPLEX) as the standard deviation of terrain curvature values within a defined landscape radius (see Level 1 Analysis, below).

From 1:250,000 baseline thematic mapping data (Geographic Data BC, 2001), we derived variables reflecting general land cover types and uses that may partly explain caribou population distribution. This accounted for major hydrographic features, including lakes and reservoirs (BTM_LAKE). One variable (BTM_AGRI) considered various types of agricultural land use, including livestock grazing. Icefields (BTM_ICE) were defined by landscapes dominated by glaciers and permanent snow. Alpine areas (BTM_ALP) were those virtually devoid of trees at high elevations. Old (BTM_OLD) and young (BTM_YNG) forests were defined as those >6 m in height and either $\geqslant$ or <140 yr, respectively. Burned landscapes (BTM_BURN) were those generally devoid of trees due to wildfire in the past 20 yr. Logged landscapes (BTM_LOG) were those dominated by either clearcut or selective forest harvest. An "urban" variable (BTM_URBAN) depicted areas of concentrated human activity, including built up zones of industrial development or settlement and more isolated developments.

We obtained road access variables from 1:20,000 planimetric and forest roads databases (Surveys and Resource Mapping Branch, 1992). To the various road classes, we applied a weighting scheme previously used for inferring the relative impact of linear disturbances in wildlife habitat modeling (Apps et al., 2004), and we derived a variable (LINEAR) by calculating the density of features in surrounding landscapes of defined radius (see Level 1 Analysis, below). We treated major highways as a separate variable (HIGHWAY) because they may function as a barrier or filter to caribou movements.

Using 1:50,000 recreational opportunity spectrum data (Forest Practices Branch, 1998a), we derived a 7-class ordinal index of remoteness (ROS), ranging from primitive to urban. We also defined one variable (ROS_PRIM) that represented only primitive or semi-primitive, non-motorized recreation opportunities. Human motorized recreation may impact caribou persistence in a landscape (Simpson and Terry, 2000). We therefore used the recreation features inventory (Forest Practices Branch, 1998b) to identify landscapes commonly used by humans for winter motorized recreation such as snowmobiling (MOTOR_WI) and heli-skiing (HELI-SKI). We accounted for the landscape proportion preferred for summer motorized recreation as a separate variable (MOTOR_SU).

From the 1:250,000 biogeoclimatic ecosystem classification (Meidinger and Pojar, 1991), we extracted the "wet" and "very wet" biogeoclimatic subzones of the ICH and ESSF, and the "very wet" subzone of the SBS. This variable (BEC_W-V), which includes alpine areas encompassed by these zones, is intended to reflect the climatic conditions typically associated with a very low fire-return interval and a deep, consolidated late-winter snow-pack that are described as characterizing landscapes important to the mountain caribou ecotype (Stevenson et al., 2001; Mountain Caribou Technical Advisory Committee, 2002).

3.3. Metapopulation-level analysis

Using the variables described above, our broader, metapopulation-level analysis was a comparison of landscape attributes associated with the persistence of mountain caribou subpopulations to those where resident caribou presently are not known to occur within their historic range. Although the proportion of each subpopulation radiocollared did vary, we assumed that samples were representative of animal distribution within each. Therefore, we defined the spatial extent of subpopulations according to landscapes with a caribou occupancy index of >0. We then generated a systematic set of locations within historic caribou range using randomly located, 10 km grid intersections. Within a 13.7 km radius (as used in deriving the landscape occupancy index) surrounding each point, we found each variable's mean or proportional attribute value which we extracted to a database. For each variable, we compared attribute values at points that fell within and outside of caribou subpopulation boundaries, evaluating differences between the two groups using t-tests for independent samples. Due to the number of variables considered (33), we applied the Dunn–Šidák adjustment (Sokal and Rohlf, 1981) to ensure that all univariate tests were appropriately conservative (resulting $\alpha = 0.0015$). Our analyses were descriptive, and although we

were not testing conventional hypotheses, we considered the sign and strength of univariate statistics in ranking and describing relationships of individual variables with caribou population dispersion and fragmentation.

We employed generalized linear modeling to derive a resource selection probability function (Manly et al., 2002). Our goal was to describe the combination of broad factors that best explains the fragmentation of mountain caribou subpopulations given our potential explanatory variables. We considered only variables exhibiting at least marginal univariate relationships ($P > 0.25$), and we evaluated relationships among standardized variables using hierarchical cluster analysis (McGarigal et al., 2000) and linear regression tolerance statistics (Menard, 1995). Where problematic collinearity occurred (tolerance <0.2; Menard, 1995), we considered bivariate relationships and dropped variables of lesser univariate significance or estimated ecological relevancy, and thus we expected to avoid modeling spurious associations (Rextad et al., 1988; Anderson et al., 2001). We derived candidate models using multiple logistic regression (Hosmer and Lemeshow, 1989), while accounting for the potential influence of spatial autocorrelation in our data by including an autocovariate term representing the mean value of the 8 points adjacent to each sample (Augustin et al., 1996; Klute et al., 2002). We evaluated the parsimony relative to predictive efficiency of all possible subsets of candidate variables using Akaike's Information Criterion (AIC), and we selected the best-fit model as that with the minimum AIC (Burnham and Anderson, 1998). We gauged the predictive value of independent variables according to the change in model AIC with each variable removed. We further evaluated goodness of fit and predictive power using the Nagelkerke $R^2 (R_N^2)$ which approximates the proportion of variation explained by the model. As a threshold-independent measure of discrimination ability, we derived the area under the relative operating characteristic (ROC) curve, (c statistic; Norusis, 1999), which corresponds to the proportion of paired cases between the two groups in which a higher probability is assigned to cases where the event (i.e., a caribou subpopulation) has occurred (Manel et al., 2001; Pearce et al., 2002).

3.4. Subpopulation-level analysis

For our finer scale of analysis, at the subpopulation level, we examined how variables related to landscape occupancy by mountain caribou within defined subpopulations, such that we may better understand factors related to and possibly influencing current or emerging population fragmentation. Within landscapes with occupancy indices >0 (i.e., within subpopulations), we again sampled landscape composition at systematic random points using 10 km grid intersections. At each point, we extracted landscape occupancy index values and each variable's mean or proportional attribute value within a 13.7 km radius. We normalized the caribou occupancy index values using a square-root transformation (Sokal and Rohlf, 1981), and we evaluated linear relationships of caribou occupancy with each variable using Spearman-rank correlation coefficients. For generalized linear modeling, we applied least-squares multiple linear regression (Seber and Lee, 2003). Using methods consistent with our level-1

analysis, we used AIC for model selection, accounted for multicollinearity, and evaluated the importance of individual variables. We evaluated model goodness of fit and predictive power using analysis of variance and a coefficient of determination (R^2_N).

3.5. Geographic application of models

For both analysis levels, we spatially depicted best-fit models for prediction across our greater analysis area. This involved applying model coefficients to variables represented within the GIS using appropriate resource selection function equations (Manly et al., 2002). Given that the level-1 model output was probabilistic and the level-2 model output predicted caribou landscape occupancy index directly, both used the same predictive scale ($0 \rightarrow 1$, with level-2 predictions truncated at 1). Thus, we multiplied the models to derive single prediction of current potential mountain caribou population dispersion across the ecotype's assumed historic range.

Finally, we derived an index reflecting caribou vulnerability to short term extirpation within landscapes known to have supported animals during recent years. For this, we assumed that caribou currently inhabit landscapes with occupancy indices $\geqslant 0.3$ and the likelihood of occupancy decreases linearly with indices <0.3. For each pixel (i), we then modeled caribou population vulnerability (V_i) as:

$$V_i = O_i(\exp[O_i - Z_i]), \tag{1}$$

where O_i is the caribou landscape occupancy index, and Z_i is the predicted landscape occupancy potential.
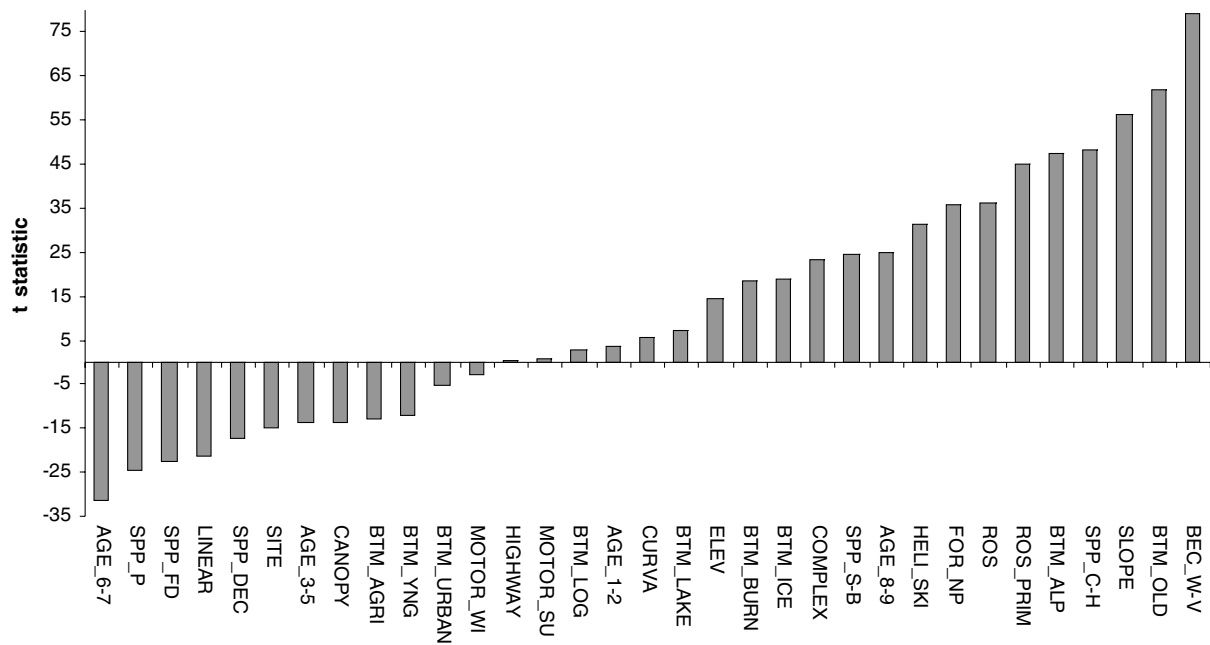

Fig. 3 – Univariate results of comparisons between the composition of landscapes currently occupied by mountain caribou and those unoccupied but within what is considered to be historic caribou range (metapopulation level). Variables are ordered according to t statistics, which reflect the strength and direction of association with caribou-occupied landscapes. All tests indicated significant differences (P < 0.0015), with the exception of lodgepole/white pine and Douglas-fir.

Table 2 – Variables and parameters of the best-fit (minimum AIC) autologistic regression model describing mountain caribou subpopulation persistence within historic range (metapopulation level)

Variable	Abbreviated description	β	SE	AIC Δ	Tolerance[a]
BEC_WV	Wet and very wet BEC subzones	3.46	0.11	536	0.31
BTM_ALP	Non-forested alpine	0.90	0.37	50	0.35
AGE_6–7	Overstory age 101–140 yr	−10.19	0.52	34	0.42
AGE_8–9	Overstory age >140 yr	1.023	0.27	531	0.60
SPP_C-H	Cedar/hemlock overstory composition	0.035	0.0037	12	0.55
CANOPY	Overstory canopy closure	0.088	0.0041	98	0.39
ROS	Remoteness index	0.36	0.015	786	0.71
MOTOR_SU	Motorized recreation – summer	−0.46	0.14	494	0.54
LINEAR	Road density	−1.98	0.32	12	0.38
Constant		−4.91	0.15		

The relative importance of each variable is indicated by the change in model AIC (AIC Δ) upon removal.
a Problematic collinearity is indicated by values <0.2 (Menard, 1995).

4. Results

Univariate relationships were apparent in comparing landscapes associated with persisting mountain caribou subpopulations to other landscapes within the ecotype's historic range (metapopulation level; Fig. 3). The occupation of landscapes by caribou was inversely related to the distribution of mid-successional closed-canopy forests of pine, Douglas-fir and deciduous composition. A negative association with linear disturbance densities and both human-settled and agricultural areas was also evident. Positive associations were strongest for the wet and very wet biogeoclimatic subzones, relatively steep and complex terrain at high elevations, and the distribution of non-forested alpine. Forest conditions were characterized by more old (>140 yr) forests of cedar/hemlock and spruce/subalpine fir composition. Landscapes

supporting caribou were remote from humans, although they were also positively correlated with optimal helicopter-skiing areas.

At the metapopulation level, mountain caribou subpopulation persistence was best explained ($R_N^2 = 0.62$) by 6 variables of the suite we considered (Table 2). The model successfully discriminated 83.3% of sample locations using a cutpoint of $P = 0.5$, and a higher persistence probability was correctly assigned to occupied landscapes in 91% of pairwise comparisons with landscapes currently unoccupied but within historic range.

In considering the degree of landscape occupancy by mountain caribou within subpopulations (subpopulation level), univariate habitat and human relationships were similar to those at the metapopulation level, but there were some notable differences (Fig. 4). Highways and agricultural landscapes showed
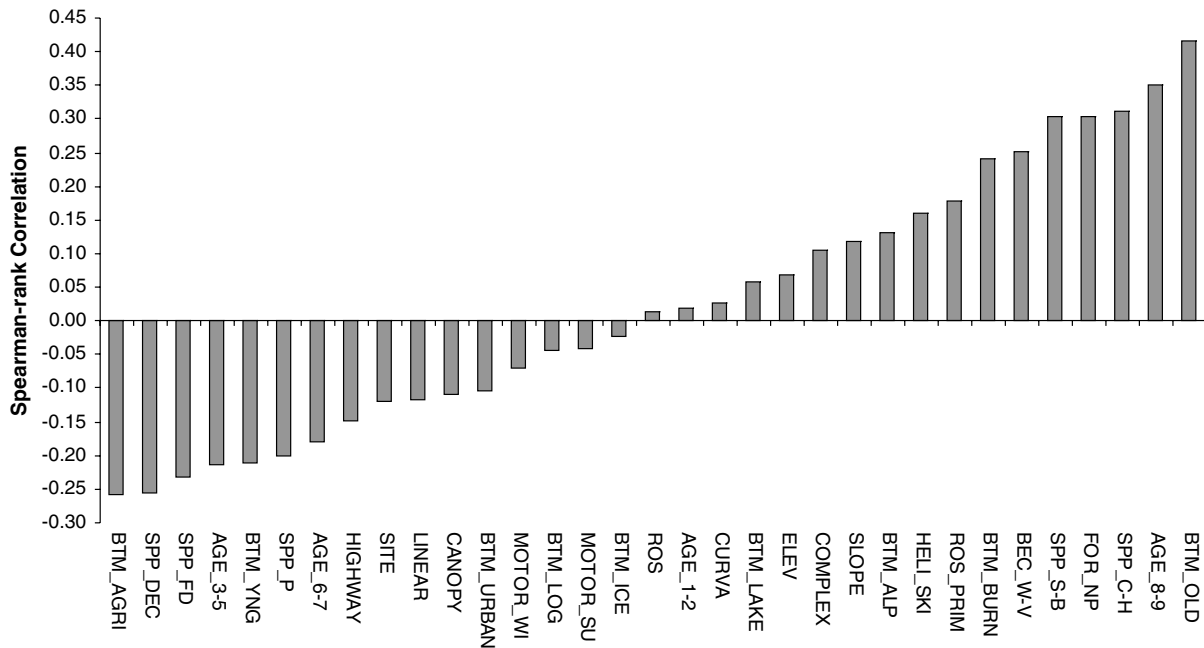

Fig. 4 – Univariate correlations between caribou occupancy index and landscape composition within areas defined as supporting mountain caribou subpopulations (subpopulation level). Variables are ordered by Spearman-rank correlation coefficients, which reflect the strength and direction of association. Significance of absolute values is: >0.03 (P < 0.15), >0.05 (P < 0.015), >0.07 (P < 0.0015).

Table 3 – Variables and parameters of the best-fit (minimum AlC) least-squares regression model describing landscape occupancy of mountain caribou within defined subpopulation bounds (subpopulation level)

Variable	Abbreviated description	β	SE	AlC Δ	Tolerance[a]
BTM_ALP	Non-forested alpine	−0.19	0.045	6	0.36
BTM_LAKE	Large lakes and reservoirs	−0.32	0.068	8	0.72
BTM_ICE	Icefields	−0.65	0.064	42	0.55
SPP_S-B	Spruce/subalpine-fir overstory composition	0.0045	0.00033	74	0.71
SPP_C-H	Cedar/hemlock overstory composition	0.0079	0.00040	158	0.87
SPP_DEC	Deciduous overstory composition	−0.032	0.0024	72	0.53
LINEAR	Road density	−0.43	0.0456	37	0.43
HIGHWAY	Major highway transportation routes	−2.72	0.4828	12	0.80
Constant		0.32	0.018		

The relative importance of each variable is indicated by the change in model AlC (AlC Δ) upon removal.
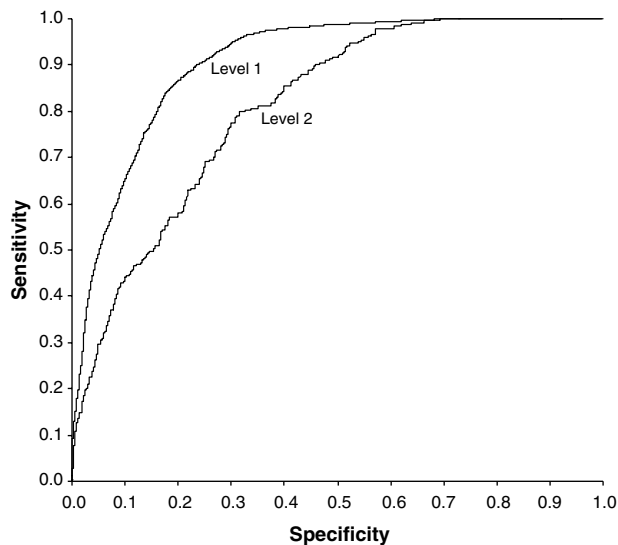a Problematic collinearity is indicated by values <0.2 (Menard, 1995).

Fig. 5 – Relative operating characteristic (ROC) curves for predictive models developed at each analysis level. The area under each curve corresponds to the proportion of pairs of sampling points with different observed outcomes in which higher probabilities are assigned to cases with rather than without the event. The event was defined as a sampling point falling within a defined subpopulation (metapopulation level) or within a landscape of caribou occupancy index >0.5 (subpopulation level).

negative associations that were more extreme relative to other variables, and old cedar/hemlock and spruce/subalpine fir forests exhibited relationships that were generally more positive than climatic or terrain conditions. At this level, landscape occupancy was best explained by 8 variables (Table 3) that accounted for 34% of the variation in caribou landscape occupancy within subpopulations. A higher predicted occupancy index was correctly assigned to landscapes with an actual occupancy index >0.5 in 81% of all possible comparisons within other landscapes within subpopulation bounds. Predictive models performed well at both analysis levels, but fit was marginally better at the metapopulation level (Fig. 5). Spatial depiction of combined model outputs estimates the potential distribution and connectivity of mountain caribou populations given the variables we were able to consider for analysis (Fig. 6). As derived in Eq. (1), the index of caribou population vulnerability (Fig. 7) reflects landscapes where caribou are known to occur, or at least have recently occurred, but are most vulnerable to short-term extirpation given current landscape conditions.

5.   Discussion

In comparing landscapes known to support mountain caribou subpopulations to other areas within their historic range (level 1), our results confirm general observations that this ecotype is strongly associated with biogeoclimatic zones that essentially define the "interior wet-belt" of British Columbia (Stevenson et al., 2001). These climatic conditions are themselves associated with steep, complex topography of relatively high elevation. Although mountain caribou prefer

gentle slopes at successively finer scales (Rominger and Oldemeyer, 1989; Terry et al., 2000; Apps et al., 2001), the association with high, rugged terrain at scales of population distribution may represent more than a fortuitous association with wet climatic conditions. Complex topography could be necessary for the juxtaposition of seasonally important habitats that mountain caribou access with elevation shifts rather than the horizontal movements and long migrations more typical of other caribou ecotypes and subspecies (Bergerud, 1996). Our results also confirm the known, broad associations of mountain caribou with old-growth forested landscapes of predominantly cedar/hemlock and spruce/subalpine fir composition, and alpine-forest ecotones of low timber-value productivity. Across a much finer range of scales, habitat selection analyses have demonstrated a direct preference by mountain caribou for similar old-growth forest conditions (Rominger and Oldemeyer, 1989; Terry et al., 2000; Apps et al., 2001; Johnson et al., 2004).

Because the historic range of mountain caribou is largely based on subjective evaluation of various occurrence records, the ecosection boundaries used to delineate it may only approximate the area that was consistently occupied by caribou prior to European settlement. In what, if any, portions of this range caribou occurrence was ephemeral is unclear. Therefore, in explaining present mountain caribou distribution, it is difficult to separate climatic and physiographic limitations from human influences; the distribution of existing subpopulations can be largely explained by inherent climatic and habitat potential, but other important predictors do pertain to human activity. Notwithstanding climatic conditions, subpopulations especially conform to the distribution of remaining old growth (age >140 yr) forests and are characterized by landscapes remote from human activity, with relatively low road densities and motorized recreational access.

Our subpopulation-level results address factors influencing mountain caribou landscape occupancy within existing subpopulation bounds. At this scale, population distribution was even more directly associated with the old-growth forest characteristics than described at the metapopulation level, while terrain and climatic conditions were less relevant. Negative associations at the subpopulation level that were consistent with metapopulation-level results included strong inverse relationships with agricultural lands, human settlement, and forest attributes typical of mid-successional (41–101 yr) conditions. To mountain caribou, these conditions provide little forage value in terms of arboreal lichen (Goward, 1998) and preferred shrubs and forbs (Terry et al., 2000; Rominger et al., 2000; Kinley et al., 2003). The density of some stands typical of this age range may also inhibit travel or increase caribou vulnerability to stalking predators such as cougars (Puma concolor), which represent an important proximate factor influencing caribou persistence in some subpopulations (Compton et al., 1995; Kinley and Apps, 2001; Katnik, 2002).

Human-induced landscape heterogeneity may lead to shifts in prey species composition and the distribution of generalist predators (Oehler and Litvaitis, 1996; Holt, 1997). Accordingly, it has been suggested that caribou predation risk is heightened by forest fragmentation that increases the number of other ungulate species and their predators while
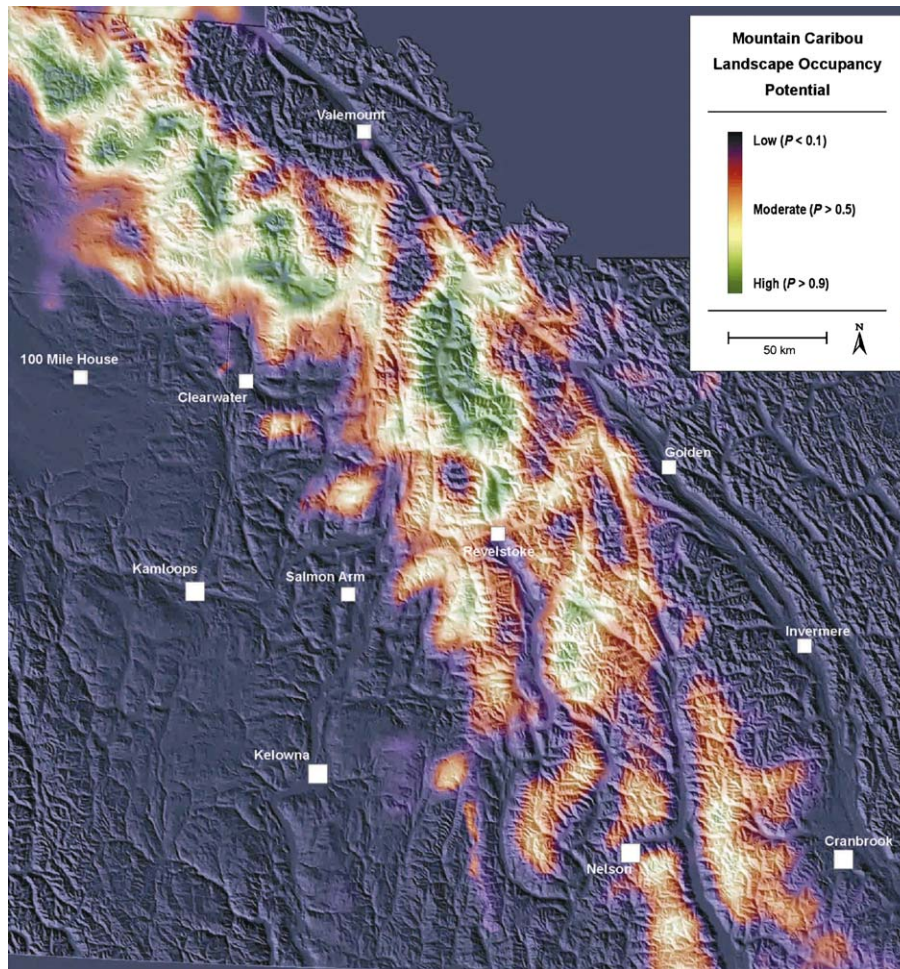
Fig. 6 – Final combined output from models predicting the likelihood of a persisting mountain caribou subpopulation (metapopulation level) and the spatial dispersion of animals within subpopulations (subpopulation level) across most of the geographic range of the ecotype in southeastern British Columbia. Prediction values can be interpreted as the probability of landscape occupancy by caribou resulting either in subpopulation persistence or demographic connectivity among subpopulations.

concentrating caribou and their movements (Bergerud and El-liot, 1986; Seip, 1992; Kinley and Apps, 2001; Wittmer et al., 2005a and Wittmer et al., 2005b) resulting in apparent competition (Holt, 1977). At our broad scale of analysis, we did not find that the distribution of very young forests (i.e., <40 yr) was related to caribou landscape occupancy. Where these very young forests are due to logging within caribou range, they are interspersed within late-successional forests, and their influence on caribou use is best addressed at finer scales of movement by individual animals (Apps et al., 2001). More-over, such conditions may be promoting unsustainable preda-tion rates but the effect on caribou landscape occupancy at the scale we have considered could be delayed by years if not decades as the predator–prey system changes, masking our ability to detect the effect. Wittmer (2004), however, did find adult female survival and subpopulation trend to be in-versely correlated with the amount of young forest (<100 yr) within subpopulation ranges. The strong association between landscapes where caribou no longer occur and the amount of mid-seral forests suggests that climatic changes after the "lit-tle ice age" (Pielou, 1991) may have contributed to the range

reduction of mountain caribou by an increase in wildfire fre-quency that removed caribou winter habitat and improved conditions for other ungulates and their predators.

It is clear that a combination of both natural and human factors best explain the dispersion of mountain caribou within subpopulations. As discussed, forest conditions are an obvious factor in determining caribou persistence, and populations appear to be naturally fragmented by large non-forested features such as icefields and extensive barren and alpine areas. As would be expected, major water bodies contribute to the fracture of populations, and in most cases these constitute reservoirs from hydro-electric impound-ment of the Columbia River. Present or emerging fragmenta-tion within subpopulations is also explained by road density and primary highway transportation routes. At finer scales, a feature such as the Trans-Canada Highway may represent a barrier, with permeability that varies depending on season, time of day, and adjacent habitat. However, at the broader scale of our analysis, human settlement and both the indus-trial and recreational access that highways facilitate may lead to human disturbance or forest conditions that are
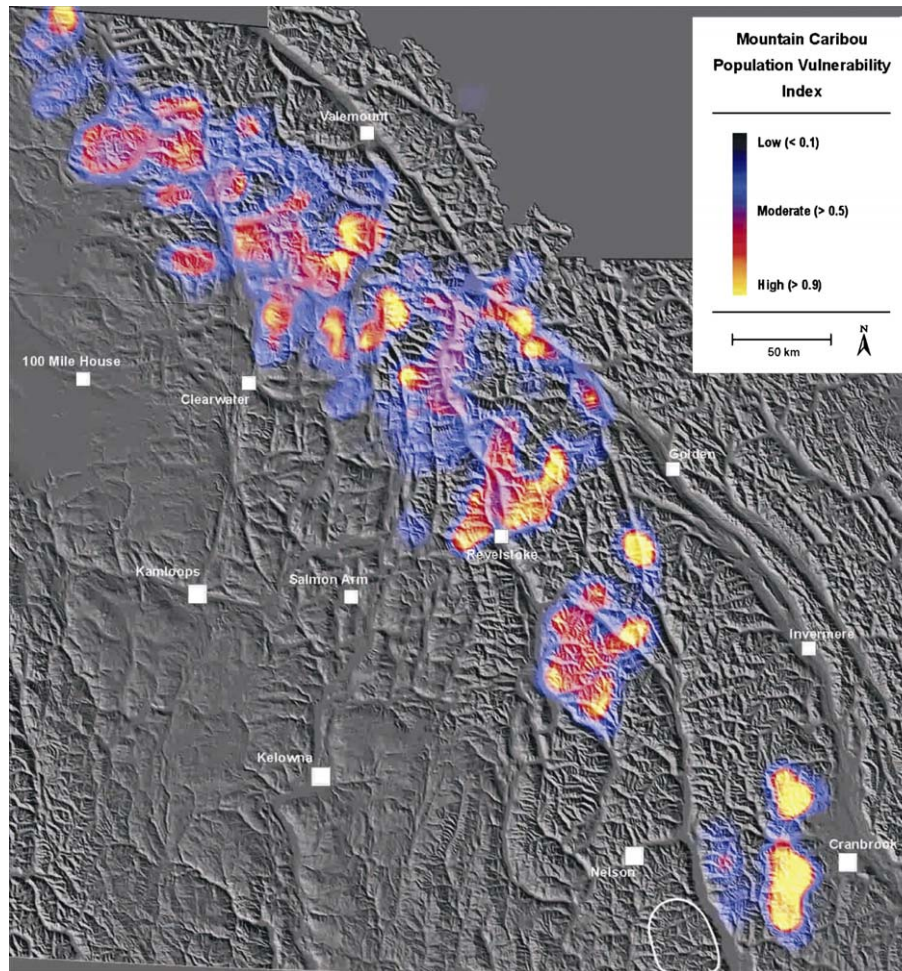
Fig. 7 – Potential vulnerability of mountain caribou to extirpation within landscapes where animals are known to have occurred. This index is a result of combining the caribou landscape occupancy index with the occupancy potential model according to Eq. (1). The white outline encompasses the Canadian portion of the translocated South Selkirk caribou subpopulation for which we did not have data.

either directly avoided by caribou or which promote unsustainable mortality. Associated impacts would also be expected from dense road networks. For example, landscapes of higher road density and old forest fragmentation in the southern Purcell Mountains were spatially related to an unsustainable rate of caribou mortality (Kinley and Apps, 2001). Other studies of woodland caribou have linked increased predation risk to linear disturbance density and associated forest development (Edmonds, 1988; James and Stuart-Smith, 2000).

Throughout our analysis area, the typical wildfire return-interval and resulting distribution of late-seral forests may have varied considerably over time. Although caribou persistence and population densities likely also varied considerably among landscapes, the permeability to movement and perhaps intermittent suitability of some landscapes may have facilitated enough dispersal to ensure the long-term persistence of peripheral subpopulations. Such natural, though not complete, isolation is supported by the results of microsatellite DNA analysis (K. Zitlau, University of Alberta, cited in Mountain Caribou Technical Advisory Com-

mittee, 2002) that indicates that the southernmost naturally persisting mountain caribou subpopulation (Southern Purcells; see Fig. 1) has significantly less genetic variation than a relatively large core subpopulation approximately 200 km to the north (Revelstoke). This result suggests a longer-term separation that is contrary to Spalding (2000)'s suggestion that current peripheral subpopulations have only been isolated through habitat fragmentation since the late 19th century. Peripheral populations of many species are often more isolated, receive fewer immigrants, and persist at lower but often varying densities (Gaston, 1990; Lawton et al., 1994; Brown et al., 1995). However, it is still likely that broad-scale population fragmentation has increased since European settlement, given that the current spatial distribution of several subpopulations are known to be smaller remnants of those known to have occurred historically (Spalding, 2000). This is evidenced by the predictive importance of human-related variables in selected best-fit models at both analysis levels. Moreover, the caribou is a naturally outbreeding species and elevated extinction risk can be expected where genetic diversity is reduced (sensu Frankham, 2005).

6. Conclusions

Within a risk-assessment framework (Harwood, 2000), the predictive model output resulting from our exploratory analyses (Fig. 6) represents a useful strategic planning tool for mountain caribou conservation at the scale of range-wide population distribution. Within potential subpopulations, model output can predict the degree of contiguity or fracture among and within core population areas. This capability can help prioritize core and linkage landscapes to meet goals of caribou population recovery, connectivity, and long-term persistence through the management of habitat and human activity at finer scales (e.g., Stevenson et al., 2001). Model predictions can also serve as an objective means to evaluate the need for, and conservation value of, population translocation and augmentation programs. However, interpreting output in this regard should be tempered with some caution given that the probability of species persistence does not increase linearly with habitat amount and quality (Harrison and Bruna, 1999).

As discussed, it is possible that landscapes within defined historic mountain caribou range facilitated episodic residency and dispersal among otherwise disjunct subpopulations. However, provincial forests have and continue to be intensively managed for timber values, under loose guidelines that reflect assumed natural disturbance regimes within coarse planning units (Ministry of Forests, 1995). When considered with other human factors, and the synergistic influence of climate change (Opdam and Wascher, 2004), isolated landscapes that currently do, or potentially could, support caribou subpopulations are less likely to receive natural immigrants over the long term. Without such periodic augmentation, they will be subject to the genetic and stochastic threats typical of small populations (Foley, 1997). Once extirpated, it may be more difficult to garner necessary public and political will to reverse human impacts and restore conditions necessary for the *potential* recovery of caribou through either dispersal or translocation. As is true for any species associated with a narrow range of habitat conditions, the role of long-term variation of landscape conditions in the biogeography of mountain caribou needs to be explicitly acknowledged in conservation strategies.

Acknowledgements

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