MULTISCALE HABITAT MODELING FOR MOUNTAIN CARIBOU IN THE COLUMBIA HIGHLANDS AND NORTHERN COLUMBIA MOUNTAINS ECOREGIONS, BRITISH COLUMBIA

Prepared by

Clayton Apps, RPBio[1]

and

Trevor Kinley, RPBio[2]

For

Wildlife Section
Ministry of Environment, Lands and Parks
Williams Lake, British Columbia

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[1]Aspen Wildlife Research • 2708 Cochrane Road NW • Calgary, AB • T2M 4H9 • aspen@cadvision.com
[2]Sylvan Consulting Ltd. • RR5, 3519 Toby Creek Road • Invermere, BC • V0A 1K5 • sylvan@rockies.net

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ABSTRACT

Mountain caribou are a threatened ecotype of woodland caribou dependent upon old forests within the “interior wet belt” of British Columbia. Mountain caribou habitat values must be considered in forest management planning, requiring an understanding and ability to predict their habitat associations across multiple spatial scales. We pooled caribou location data derived from 5 sources to analyze caribou habitat selection across 4 seasons, 4 spatial scales, and for both a “Highland” and a “Mountain” physiographic zone in the Columbia Highlands and Northern Columbia Mountains ecoregions of British Columbia. Habitat variables were derived from 1:20,000 digital forest overstory and terrain data and our analysis employed a previously described scale-dependent design.

Within each zone and season, univariate habitat selection differed across scales, suggesting that spatial scale is an important parameter in understanding and describing caribou-habitat relationships in the analysis area. Seasonal differences in habitat selection were also apparent but were more pronounced in the Mountain zone than in the Highland zone.

Across seasons in the Highland zone, caribou generally preferred relatively rugged, higher elevation broad landscapes composed of oldgrowth subalpine fir. At most scales and across seasons, Highland caribou avoided landscapes of higher site index, younger stand age classes, and pine, Douglas-fir, and deciduous species composition. They especially preferred more open broad landscapes of higher alpine composition during late winter, and northeast aspects were preferred at the broadest scale during summer.

Caribou in the Mountain zone preferred higher elevations only during late winter and summer, and preferred low elevation broad landscapes of oldgrowth cedar and hemlock and lower alpine composition during early winter. Landscapes of higher cedar, hemlock, pine, deciduous, and Douglas fir composition were avoided at most scales during late winter and summer, and younger stand age classes were avoided at various scales across seasons. Subalpine fir was preferred across seasons, but less so during spring. Although caribou in the Mountain zone preferred broad landscapes that were relatively rugged during late winter, spring and summer, gentle terrain was highly preferred at the finest scale during late winter and summer. These caribou also preferred northern aspects at broader scales during summer.

Caribou in both zones were less selective for gentle terrain and productive forested sites than in the more rugged and wet “Revelstoke study area”. Caribou associated with a transitional zone encompassed within the Columbia Highlands ecoregion exhibited habitat selection similar to those of the Mountain zone, and this should be reflected in habitat management within that area.

We derived predictive multivariate habitat models for each season and zone that were significant in discriminating caribou from random locations and which accounted for habitat associations across scales. Applied within a GIS, models represent decision-support tools for strategic-level forest management planning.

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INTRODUCTION

Mountain caribou, an ecotype of woodland caribou (*Rangifer tarandus caribou*) are “red-listed” in British Columbia, meaning they are considered threatened. Fragmentation and decline of populations has occurred throughout their historic range, which is associated with the “interior wet belt” of the province (Stevenson et al. 1994, Simpson et al. 1997). Legislation now stipulates that requirements of rare species, including mountain caribou, be considered in forest management planning (Forest Practices Code of British Columbia Act 1993). This necessitates prescriptive guidelines for application at strategic and operational planning levels. The conservation efficacy of such measures depends on our understanding of mountain caribou habitat associations and requirements at multiple spatial scales. These are expected to differ among subpopulations, reflecting variations in physiography, climate, vegetation, and human impacts.

Mountain caribou range may have declined throughout the province since the onset of European settlement, and extensive logging at lower elevations in the Quesnel Highland and Cariboo Mountains coincided with a population decline in that region during the 1980s (Young and Roorda 2000). Maintaining habitat values for mountain caribou is now a primary objective of the Cariboo-Chilcotin Land Use Plan (BC Government 1996). To support this goal, the Quesnel Highland Caribou Project was initiated in 1993 and collected 6 years of extensive data (Ibid.). One of the objectives of this program was habitat model development to identify and conserve caribou habitat through protection, forest harvest modification, and maintaining or enhancing connectivity.

In this report, we bring together caribou monitoring data from the Quesnel Highland, Cariboo Mountains, Shuswap Highland, Bowron Valley and adjacent ecosections, straddling two ecoregions. We analyze habitat selection across four seasons and four spatial scales and compare differences among ecoregions. We then derive predictive models that integrate caribou habitat preferences across spatial scales for each caribou season and ecoregion. Our increased understanding of caribou-habitat associations and resulting spatially explicit models will allow probable caribou requirements to be considered in forest and land management at strategic and operational planning levels.

STUDY AREA

The analysis area is located in east-central British Columbia, east of Williams Lake (Figure 1). It is central within mountain caribou range, encompassing most of Wells Gray, Cariboo Mountains, and Bowron Lake provincial parks, as well as the communities of Wells, Clearwater, Blue River and Avola.

The analysis area falls within the Southern Interior Mountains ecoprovince (Demarchi 1996) and includes parts of 2 ecoregions (Appendix 2: Map1). The Columbia Highlands ecoregion (hereafter called the Highland zone) consists of the Quesnel Highland, Shuswap Highland and Bowron Valley ecosections. The Northern Columbia Mountains ecoregion (hereafter called the Mountain zone) consists of the Cariboo Mountains and the Northern Kootenay Mountains ecosections. The Mountain zone rises abruptly from the Rocky Mountain Trench in the east to a rugged mountain block including many glaciers. In contrast, the Highland zone has rolling terrain, although it becomes more rugged where it meets the Mountain zone. Both zones receive abundant precipitation, with the Mountain zone being within the wettest area in the interior of British Columbia (Demarchi 1996). The main focal area for this analysis includes the Quesnel Highland, Bowron Valley and Cariboo Mountains ecosections. Within the Bowron Valley and Quesnel Highland ecosections, caribou winter ranges are generally continuous, associated with rounded, subalpine mountain tops. Within the more rugged Cariboo Mountains ecosection, high elevation winter ranges are more restricted and discontinuous in nature (Young and Roorda 1998). A “transitional zone” has been identified that occurs within the Quesnel Highland ecosection but where caribou habitat use appears to be more characteristic of the Cariboo Mountains ecosection. This zone is generally defined by that section of the Quesnel Highland east of the north arm of Quesnel Lake and south of the east arm to Clearwater Lake (J. Young, MELP, pers. comm.).

The majority of the analysis area consists of 3 biogeoclimatic zones (Meidinger and Pojar 1991). The lowest elevations are within the Interior Cedar-Hemlock (ICH) zone, in which western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) are dominant climax tree species. Middle elevations occur within the Engelmann Spruce – Subalpine Fir (ESSF) zone. Climax species in the ESSF are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). The Alpine Tundra (AT) zone is non-forested, including glaciers and exposed bedrock, and occurs at the highest elevations. It is more extensive in the Mountain zone than the Highland zone. In drier portions of the Highland zone, the ICH is replaced by the Sub-Boreal Spruce (SBS) zone, which has hybrid white spruce (*P. engelmannii x glauca*) and subalpine fir as dominant climax species. Seral stands of lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and Douglas-fir (*Pseudotsuga menziesii*) are common, particularly in the SBS. Forest harvesting has occurred over large portions of the study area outside of parks, particularly at lower elevations.

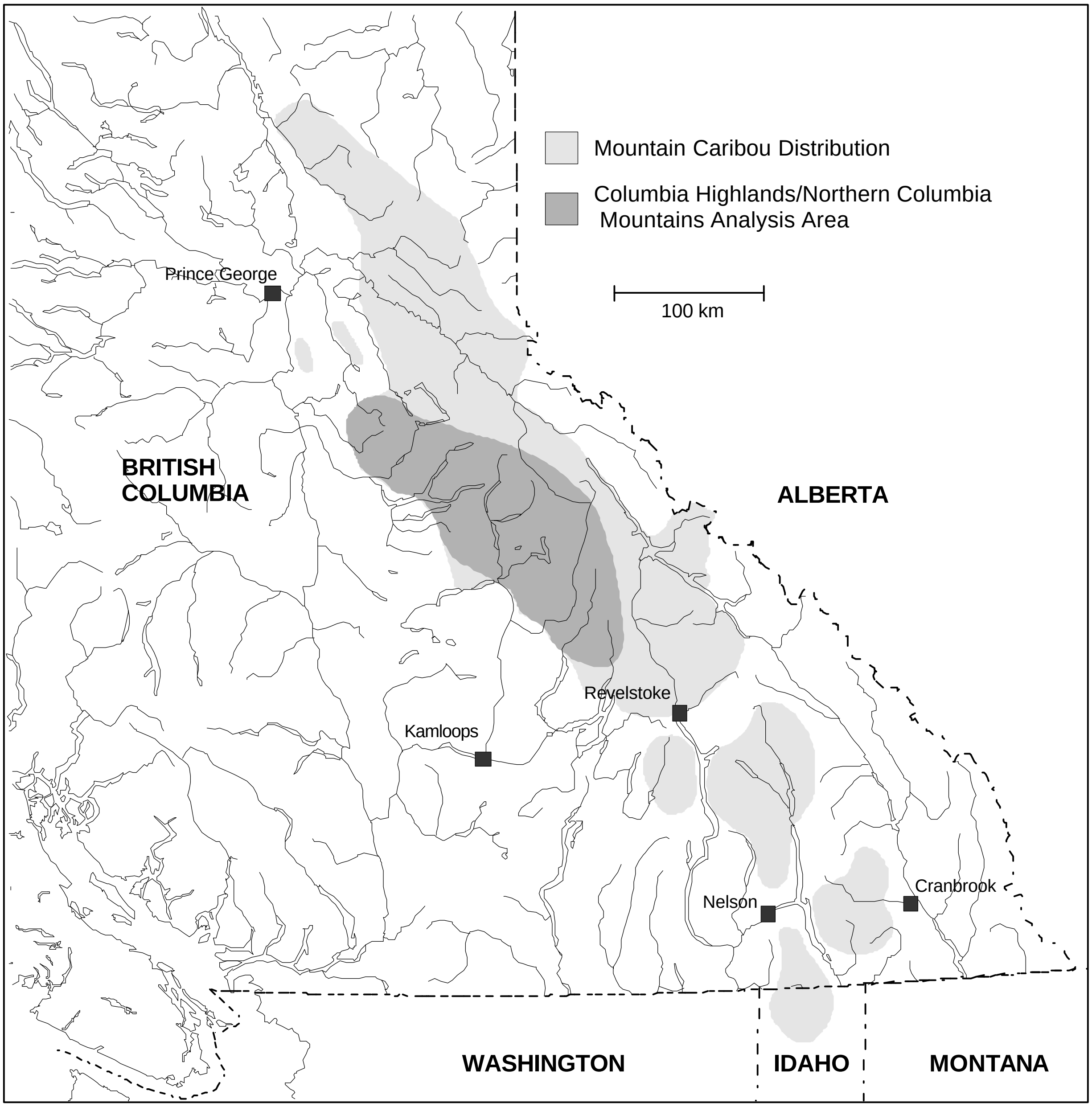

Figure 1. Current mountain caribou distribution and the Columbia Highlands/Northern Columbia Mountains analysis area.

METHODS

Caribou Location Data

We obtained caribou location data from several sources, representing different areas, monitoring periods, and sampling methods. All study animals were captured by net-gunning from helicopters in open, subalpine habitats during late winter. Data were collected using aircraft telemetry for very high frequency (VHF) collars, or by periodically downloading data from global positioning system (GPS) collars. Williams Lake MELP (J. Young) provided the 1993 – 1999 VHF dataset collected for the Quesnel Highland Caribou Project (Young and Roorda 2000). They also provided data collected for the Quesnel Lake area during 1984 – 1988 (Seip 1992) and for Wells Gray Park during 1986 – 1989 (Seip 1990). Kamloops MELP (M. Burwash) provided GPS location data, the post-processing and screening of which are described Apps and Kinley (1999). Kamloops MELP provided an additional VHF dataset collected during 1997 – 2000, which has not been previously analyzed. The total pooled dataset from these sources represented 6649 locations of 158 different caribou during 13 years (Table 1). The datasets covered an extensive geographic distribution that is assumed to approximate that of the population within the study area (Appendix 2: Map 1).

The median sampling interval for VHF caribou locations ranged from 10 – 25 days among datasets. However, as described by Apps and Kinley (1999), the original North Thompson GPS location dataset was randomly subsampled to daily locations to avoid autocorrelation at the finest scale of analysis. Relative to other datasets, this resulted in a high location sample but from few animals over a short time frame. To ensure that results reflected a balanced representation among animals and years, we weighted the daily locations from the Thompson River GPS dataset such that each sample unit was a weekly location.

We converted all data to a common reference system for this analysis (UTM, Zone 10, NAD83). We then stratified data according to 4 caribou seasons defined by Simpson et al (1997): Early Winter ending 15 January, Late Winter ending 15 April, Spring ending 31 May, and Summer ending 31 October. Seasonal cut-dates are expected to generally correspond to changes in foraging strategies as influenced by snow conditions, and correspond to marked elevation shifts in some populations (Stevenson et al. 1994, Simpson et al. 1997).

Table 1. Caribou location datasets used for multi-scale habitat analyses within the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 - 2000.

Dataset	Described by	Monitoring Period	Animal Sample	Median Sampling Interval (days)	Assumed Spatial Accuracy (± m)	Season[1]				Total
						EW	LW	SP	SU	
Quesnel Highland	Young and Roorda (2000)	02/93 – 05/99	43	13	117[2]	706	794	369	844	2713
Quesnel Lake	Seip (1992)	02/84 – 04/88	32	10	500[3]	242	452	292	794	1780
Wells Gray	Seip (1990)	03/86 – 03/89	31	17	500[3]	205	353	197	630	1385
North Thompson GPS	Apps and Kinley (1999)	04/96 – 12/98	12	7[4]	180[5]	60	44	42	113	259
North Thompson VHF	- -	03/97 – 01/00	40	25	Unknown	105	49	2	176	332
TOTAL			158			1318	1692	902	2557	6469

[1] Mountain caribou seasons defined by Simpson et al. (1997): early winter (EW) ends 15 Jan.; late winter (LW) ends 15 Apr.; spring (SP) ends 31 May; summer (SU) ends 31 Oct.

[2] Based on test collar data provided by J. Young, MELP, Williams Lake

[3] Based on locations being recorded on a 1 km grid

[4] GPS fixes were originally obtained up to 8 times per day, but this dataset was randomly subsampled to daily locations and then weighted to the equivalent of weekly samples.

[5] Based on screening performed by A. Norquay, MELP, Kamloops prior to analysis (Apps and Kinley 1999)

GIS Habitat Data

We assembled habitat data in a GIS for an approximately 35,000 km^2 area encompassing all caribou location data. Data were compiled from 1:20,000 digital forest inventory planning files (FIP; Resources Inventory Branch 1995) and Terrain Resource Information Management files (TRIM; Surveys and Resource Mapping Branch 1992) and were rasterized to 100 m resolution (cell size), equivalent to the minimum mapping unit. Forest inventory data for Well Gray Provincial Park were derived from an earlier system of polygon mapping and classification and are assumed to be of lower quality than those available for other lands within the study area. Other data sources were 1:250,000 National Topographic System (NTS) and provincial jurisdictional and ecosection files. From all data sources, we derived habitat variables associated with forest stand overstory and terrain attributes (Table 2).

Several attributes thought to be important to mountain caribou may relate to stand age in a non-linear manner (Stevenson et al. 1994). We therefore derived 4 stand age classes reflecting gross structural differences expected among dominant tree species in the region, and which conform to the age class convention of the provincial forest inventory system. The CANOPY variable depicted the ocular cover of the stand overstory. The SITE variable reflected site productivity based on stand age and height as calculated by species-specific equations (Thrower et al. 1991). We considered overstory species composition for analysis because it may relate to seasonal forage availability and will indicate climatic variability. Individual or grouped species were included if their spatial composition was > 3% of the total analysis area. Non-forested ALPINE encompassed all habitat types above treeline, including rock and ice. Terrain variables included elevation (ELEV) and slope (SLOPE). Relative to surrounding pixels, slope curvature (CURVA) measured the maximum rate of change of a curve fit through each pixel along the direction of aspect (profile curvature; Pellegrini 1995). For example, slope change will be greater near peaks, ridges, saddles or gullies. Aspect was represented by two continuous (0→100) variables depicting north→south (SOUTH) and east→west (WEST) aspects (Apps et al. 2000). For example, direct south aspects reflected values of 100 for south and 50 for WEST, direct east aspects reflected 50 for SOUTH and 0 for WEST, and direct northwest aspects reflected 25 for SOUTH and 75 for WEST. A terrain ruggedness index (TERRAIN) was derived by adapting a technique (Beasom et al. 1983) for GIS using 1:250,000 elevation contours, yielding a continuous (0→100) variable that is relative to the scale of contour data and pixel size. For example, an index of 100 would represent a landscape with at least one contour passing through each pixel, while an index of 0 would represent a landscape with no contours passing through any pixels. We defined a 100 m edge around all lakes as potential "seepage" sites (SEEPAGE), which we expected would influence stand structure and composition. All GIS applications employed the raster-based software *Idrisi 3.2* (Clark Labs 1999).

Table 2. Independent variables considered for analyses of mountain caribou habitat selection within the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 - 2000. All variables are ratio-scale, and represent either the mean or proportional composition within a surrounding landscape.

Variable	Description
AGE_1-2	Overstory stand age 1 – 40 yr (%)
AGE_3-5	Overstory stand age 41 – 101 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 index
B_SPP	Subalpine fir (*Abies lasiocarpa*) composition (%)
S_SPP	Spruce (*Picea* spp.) composition (%)
C_SPP	Western redcedar (*Thuja plicata*) composition (%)
H_SPP	Western hemlock (*Tsuga heterophylla*) composition (%)
P_SPP	Lodgepole (*Pinus contorta*) and white (*P. monticola*) pine composition (%)
FD_SPP	Douglas-fir (*Pseudotsuga menziesii*) composition (%)
DEC_SPP	Deciduous species composition (%)
ALPINE	Alpine tundra composition (%)
ELEV	Elevation (m)
SLOPE	Slope (%)
CURVA	Slope curvature index
SOUTH	North→south aspect (0→100)
WEST	East→west aspect (0→100)
TERRAIN	Terrain Ruggedness Index (0→100)
SEEPAGE	Potential seepage sites (%)

Scale-Dependent Analysis Design

Our analysis design conformed to Thomas and Taylor's (1990) study design 2, with inferences relevant at the population level. We considered the study animals a representative sample of the population, and we pooled location data among caribou, as is appropriate where few locations are obtained from many animals (Manly et al. 1993).

We adopted the scale-dependent analysis design described by Apps et al. (2000). Spatial scale in ecology is characterized by the geographic extent of analysis and the spatial resolution of data. We analyzed caribou-habitat associations at 4 spatial scales, corresponding to successively smaller landscapes of used and available habitat. At each analysis level, we adjusted the resolution of habitat variables by aggregating data (Bian 1997) using a moving window routine (*MapWalker 2.0*; Hovey 1999). Pixels thus reflected each variable's mean value or proportional composition within a surrounding circular landscape. Landscape composition was sampled at each caribou location and at a paired location of fixed distance but random azimuth from each caribou location (Figure 2). At level 1, the broadest scale of analysis, caribou and paired random locations were separated by 13.7 km. Apps et al. (2000) considered this to be the largest area potentially available to their radiocollared caribou, within their approximate 2 week sampling interval, because 95% of their sequential radiolocations were within this distance. We applied a multiplier of 0.4 to this distance to define the radius of the circular landscape around caribou and random locations, over which habitat composition was scaled (Figure 3). At levels 2 - 4, random locations were generated at distances equivalent to the landscape radius at the previous level, and habitat composition was again scaled to 0.4 of this distance. Although the 0.4 multiplier was arbitrary, it ensured that the radius used to scale habitat composition at level 4, the finest scale of analysis, matched the assumed 95% radiotelemetry error of Apps et al. (2000; Figure 3). Moreover, the proportion of used landscape to available area was equal at all levels, and used landscapes did not overlap with respective random landscapes. We assumed that the 0.35 km radius used to scale habitat composition at level 4, the finest analysis scale, would encompass most location error within the pooled dataset. Although we expect that the true location for some data will fall outside this error zone, we chose to accept the lower statistical power to detect habitat selection, relative to sample size, that will result from a random misassignment of habitat attributes for these data. In particular, despite the ±500 m error, level 4 habitat selection may still be detected from Seip's (1990, 1992) data because random locations occurred at a fixed distance of 900 m, markedly greater than the expected location error. This allowed the majority of the dataset to be analyzed at an appropriately fine scale, and facilitated comparison with analyses of other caribou subpopulations, for which these scales have previously been adopted (e.g. Apps et al. 2000). Lands for which forest cover data were not available, and lakes defined within FIP data, were not considered part of the landscape when aggregating data using the moving window routine.

At each analysis level, we extracted attributes associated with caribou and random landscapes to a database. However, the Quesnel Lake and Wells Gray datasets were collected approximately 10 years before the current forest cover inventory date. Therefore, prior to extracting attributes for these locations, we modified stand variables to better reflect conditions at the time those data were collected. We back-projected stand age by 10 years and, where disturbances occurred within 10 years prior to the forest inventory date, we interpolated overstory attributes from immediately adjacent undisturbed stands.

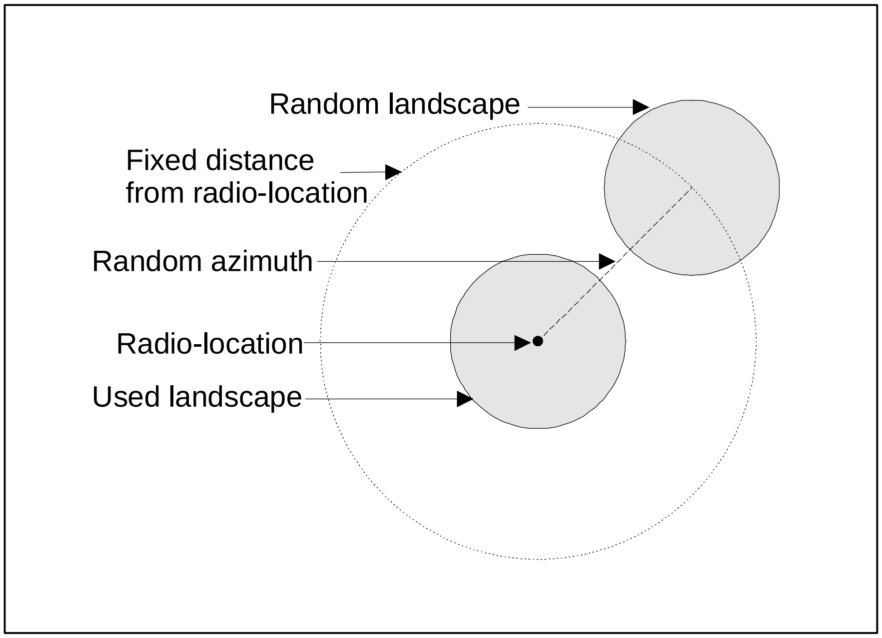

Figure 2. Scale-dependent design for analyzing caribou habitat selection in the Columbia Highlands and Northern Columbia Mountains, British Columbia.

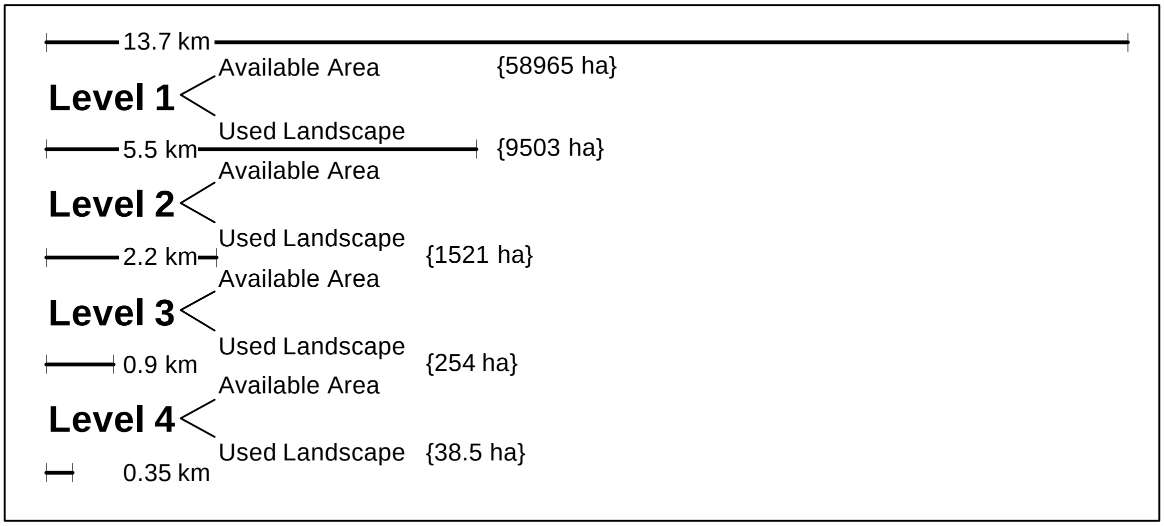

Figure 3. Hierarchical scales considered in analyzing caribou habitat selection in the Columbia Highlands and Northern Columbia Mountains, British Columbia. Scales were defined by radii of available areas and landscape composition. The radius of "available area" was the distance from caribou radiolocations at which landscapes were randomly sampled. The "landscape" radius was that within which habitat composition was defined.

Comparisons and Statistical Analyses

As described above, we stratified caribou location data into four seasons. For each season, we then compared caribou habitat selection between the Highland zone, the Mountain zone, and a transitional zone somewhat characteristic of both (see Study Area). Results of these analyses guided subsequent habitat model development.

At each scale and season, and for each variable, we used ANOVA to compare, among zones, mean differences between caribou used and paired random locations. Where variation was significant, we used Bonferroni pairwise multiple comparison tests to determine which zones differed. According to these results, we then split or grouped our univariate analyses by zone and used *t* tests to assess the differences in landscape composition between caribou used and random locations within each zone. Due to the number of variables considered, all univariate tests were appropriately conservative ($\alpha = 0.0005$).

After pooling data from the transitional zone with one of the other two zones, we compared seasonal habitat selection within each to that of the Revelstoke study area (Apps et al. 2000). That study area is also within the North Kootenay Mountains ecosection. Although habitat selection was analyzed as part of separate project (Ibid.), the methods were the same as used in this analysis, making data and results comparable. As previously described, we used ANOVA and Bonferroni multiple comparison tests to compare, among the Mountain zone, Highland zone and Revelstoke study area, mean differences between caribou used and paired random locations.

Finally, we derived multivariate seasonal habitat selection models for the Highland and Mountain zones. We applied multiple logistic regression (MLR) to derive probabilistic resource selection functions (Trexler and Travis 1993, Manly et al. 1993) across all 4 spatial scales and for each caribou season. Landscapes used by caribou and random landscapes represented the dichotomous dependent variable. However, the design differed from the scale-dependent univariate analyses in that paired random locations occurred at distances ranging from 0.9 – 13.7 km, spanning the 4 spatial scales. We did not transform variables because logistic regression does not require the assumption of multivariate normality among predictors (Hosmer and Lemeshow 1989). We employed forward stepwise selection using the likelihood-ratio test (Ibid.) to derive the most parsimonious variable combinations that best discriminated caribou used landscapes from random landscapes. We evaluated the improvement of fitted models over null models according to the reduction in (-2)loglikelihood ratios, and we evaluated the significance of variable coefficients using chi-square tests of Wald statistics (Ibid.). Variables included in best-fit models were examined for multicollinearity using linear regression *Tolerance* statistics (Menard 1995). Where problematic collinearity occurred (tolerance < 0.2; Ibid.), we inspected Pearson correlation coefficients to identify offending variables. Of highly correlated pairs, variables that were less significant in univariate analyses were excluded from the next iteration of model selection. We continued this iterative process until tolerance values associated with best-fit models were ≥ 0.2. We applied the software SPSS 7.0 for all statistical procedures (SPSS Inc. 1996; Norusis 1994).

RESULTS

Univariate analyses indicate that caribou selected some variables differently among the Highland, Mountain and transitional zones (Table 3). Among variables, seasons and scales, habitat selection was significantly different between Mountain and Highland zones in 78 of 352 comparisons. Habitat selection differed between the transitional zone and the Highland zone and between the transitional zone and the Mountain zone in 41 and 26 of 336 comparisons respectively. These overall results, coupled with specific results for key variables, suggest that data within the transitional zone should be pooled with that of the Mountain zone for subsequent analyses.

Within each of the two zones, habitat selection varied across scale and by season for most variables (Tables 4 and 5). For each zone, we illustrate differences in the mean composition of caribou used and random landscapes across scales in Appendix 1.

Comparisons of seasonal habitat selection among the two zones and the Revelstoke study area indicate significant differences among most variables and seasons. Seasonal habitat selection differed among areas for most variables (Table 6).

For the Highland zone, all best-fit seasonal MLR models were significant ($\chi^2 > 75.5$, df ≥ 7, $P < 0.0001$), with overall classification success of used and random locations (cutpoint $P = 0.5$) ranging from 60.7% - 68.6% (Table 7). For the Mountain zone, all best-fit seasonal MLR models were significant ($\chi^2 > 80.4$, df ≥ 7, $P < 0.0001$), with overall classification success of used and random locations (cutpoint $P = 0.5$) ranging from 61.3% - 66.5% (Table 8). Models predict the probability (P) that any particular site represents the scale-dependent conditions that characterize mountain caribou habitat. For both zones, the predictive subset of variables that best described caribou habitat selection represented most scales for each seasonal model (Tables 7 and 8). Model performance across cutpoint probability values suggested that optimal discrimination occurred at approximately $P = 0.5$ for early winter, late winter, spring, and summer within both the Highland and Mountain zones (Figures 4 and 5). The application of zone-specific best-fit MLR models to the GIS database is portrayed in Maps 2 – 5 (Appendix 2).

Table 3. Differential seasonal and scale-dependent caribou selection for forest overstory and terrain variables among 2 ecosection zones and a "transitional" zone in the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 - 2000. A positive sign[a] indicates that higher values of that variable were preferred more or avoided less in the first of the 2 compared zones. A negative sign indicates that higher values of that variable were preferred less or avoided more in the first of the 2 compared zones.

		Early Winter [b]				Late Winter				Spring				Summer			
Variable	Comparison [c]	1[d]	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
AGE_1-2	H - M	- -	- - -	-	o	- - -	- - -	o	o	- - -	-	o	o	- - -	- - -	- -	o
	H - t	-	o	o	o	-	o	o	o	-	-	o	o	- - -	o	o	o
	M - t	o	o	o	o	+++	+++	o	o	+	o	o	o	+	+++	o	o
AGE_3-5	H - M	o	-	o	o	-	- - -	o	o	- - -	o	o	o	- - -	- - -	o	o
	H - t	- -	-	o	o	-	- -	o	o	- -	-	o	o	o	o	o	o
	M - t	o	o	o	o	o	o	o	o	o	o	o	o	+++	++	o	o
AGE_6-7	H - M	o	o	o	o	o	o	o	o	- -	o	o	o	- - -	- - -	-	o
	H - t	o	++	o	o	o	o	o	o	o	o	o	o	-	- -	o	o
	M - t	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
AGE_8-9	H - M	o	o	-	o	++	+++	+	o	+++	o	- -	-	+++	+++	+++	+
	H - t	o	- -	o	-	+	o	o	o	+	o	o	o	o	o	o	o
	M - t	o	o	o	o	o	- - -	- -	o	o	o	o	o	- - -	- - -	- - -	-
SPP_S	H - M	o	-	-	-	+	-	o	o	o	o	-	-	+++	o	o	o
	H - t	o	- -	-	o	o	- - -	- -	-	o	-	o	- -	o	-	-	-
	M - t	o	o	o	o	o	o	o	o	o	o	+	o	- -	- -	- -	o
SPP_B	H - M	+++	o	o	o	+++	+	o	o	+++	o	o	o	+++	+++	+	o
	H - t	+++	++	o	o	+++	o	o	o	++	++	o	o	+++	o	o	o
	M - t	o	o	o	o	- - -	o	o	o	o	o	o	o	- - -	- -	- - -	-
SPP_C	H - M	- - -	o	o	o	- - -	+++	+++	o	o	o	o	o	- - -	o	o	o
	H - t	- - -	- - -	+	o	- -	++	+++	++	o	- - -	o	o	- - -	o	o	+++
	M - t	o	-	+	o	+	o	o	+	o	o	o	o	- - -	o	o	+
SPP_H	H - M	- - -	o	o	o	- - -	+++	+++	o	o	o	o	o	o	++	+	o
	H - t	- - -	o	o	o	o	+	o	o	o	o	o	o	- -	o	+	o
	M - t	o	o	+	o	+	- - -	- - -	o	o	o	o	o	o	o	o	o
SPP_P	H - M	o	- -	-	-	- - -	- - -	- - -	o	- - -	- - -	- -	o	- - -	- - -	- - -	- -
	H - t	o	o	o	- -	- - -	- - -	- - -	o	- - -	- -	-	o	- - -	- - -	- - -	-
	M - t	o	o	o	o	o	o	o	o	o	o	o	o	+++	+++	o	o
SPP_FD	H - M	- - -	-	o	o	- - -	o	o	o	- - -	o	o	o	- - -	- -	o	o
	H - t	- - -	o	-	o	-	o	o	o	-	-	o	o	o	+++	o	o
	M - t	-	o	o	o	+++	o	o	o	o	o	o	o	+++	+++	o	o

Table 3. Continued.

		Early Winter [b]				Late Winter				Spring				Summer			
Variable	Comparison [c]	1[d]	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
SPP_DEC	H - M	-	- -	o	o	- - -	- - -	- - -	o	- - -	o	o	o	- - -	- - -	- -	o
	H - t	-	-	o	o	- -	o	- - -	o	- -	o	o	o	o	o	-	o
	M - t	o	o	o	o	o	o	o	o	o	o	o	o	+++	o	o	o
ALPINE	H - M	+++	+++	+++	+	+	o	o	o	o	++	+++	o	o	o	o	o
	H - t	+++	+++	o	+	o	+	o	o	o	++	o	o	o	+	+	o
	M - t	o	o	-	o	o	+	o	o	o	o	o	o	o	o	+	o
CANOPY	H - M	- - -	-	-	o	- - -	+	+	o	o	o	- -	-	o	o	+	o
	H - t	- - -	-	o	-	o	o	o	o	o	- -	o	o	- - -	o	o	o
	M - t	- -	o	o	o	+	o	o	-	o	o	o	o	- - -	-	- - -	-
SITE	H - M	- - -	- - -	- - -	o	- - -	o	o	o	- - -	- - -	- -	-	- - -	-	o	o
	H - t	- - -	- - -	o	-	- - -	-	o	o	-	- - -	o	o	- - -	-	o	o
	M - t	o	o	o	o	+	o	o	o	o	o	o	o	o	o	o	o
SEEPAGE	H - M	- - -	- - -	- -	o	+++	o	o	o	o	- - -	o	o	o	- -	o	o
	H - t	o	- -	o	o	o	-	o	o	o	-	o	o	o	- -	o	o
	M - t	+	o	o	o	- -	- -	o	o	o	o	o	o	o	o	o	o
ELEV	H - M	+++	+++	+++	o	+++	o	o	o	++	+++	++	o	+++	++	o	o
	H - t	+++	+++	o	o	+++	+	o	o	o	+++	++	o	+++	o	o	o
	M - t	o	o	- -	o	- - -	o	o	o	o	o	o	o	o	o	o	o
SLOPE	H - M	o	o	o	o	o	o	o	o	o	o	o	o	-	o	o	+
	H - t	o	+	o	o	o	+	+	o	o	o	+	o	-	o	o	o
	M - t	o	o	o	o	o	++	o	o	o	o	o	o	o	o	o	o
SOUTH	H - M	o	o	o	o	o	o	o	o	o	+	o	o	o	+++	o	o
	H - t	o	o	o	o	o	+	o	o	+++	++	o	+	+++	+++	o	o
	M - t	o	o	o	o	o	o	o	o	+	o	o	o	+++	+++	o	o
WEST	H - M	o	o	o	o	- -	o	o	o	- - -	o	o	o	- - -	- - -	o	o
	H - t	o	o	o	o	o	o	o	o	- - -	o	o	+	- - -	o	o	o
	M - t	o	o	o	o	+	o	o	o	o	o	+	o	- - -	o	o	o
TERRAIN	H - M	o	o	o	o	o	o	o	o	o	o	o	o	o	+	o	o
	H - t	+	o	o	o	o	+	+	o	o	+	o	o	-	o	o	o
	M - t	o	o	o	o	o	o	o	o	o	o	o	o	- -	-	o	o
CURVA	H - M	o	+	o	o	o	+	o	o	o	o	o	o	o	o	o	o
	H - t	o	o	o	o	o	o	o	+	o	-	+	o	o	o	o	o
	M - t	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o

[a] Bonferroni pairwise multiple comparison test significance is indicated by +++/ - - - (*P* < 0.0005), ++/ - - (*P* < 0.005), +/ - (*P* < 0.05).

[b] Seasons defined by Simpson et al. (1997): early winter ends 15 Jan; late winter ends 15 Apr.; spring ends 31 May; summer ends 31 Oct.

[c] H: Highland ecoregion zone; M: Mountain ecoregion zone; t: transitional zone

[d] Analysis level: broad (1) to fine (4) spatial scales.

Table 4. Univariate analysis results of scale-dependent habitat selection by caribou within the HIGHLAND zone of the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 – 2000. Caribou location sample sizes are in parentheses in season headings. Results are based on univariate *t* tests.[a] Variables are as defined in Table 2.

	Early Winter (697)				Late Winter (921)				Spring (409)				Summer (980)			
Variable	1[b]	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
AGE_1-2	---	---	---	o	---	---	---	o	---	---	o	o	---	---	---	O
AGE_3-5	---	---	o	o	---	---	--	o	---	---	o	o	---	---	-	o
AGE_6-7	o	o	o	o	---	o	o	o	---	o	o	o	---	---	-	o
AGE_8-9	+++	+++	+	o	+++	++	o	o	+++	+	o	-	+++	+++	+++	o
SPP_S	+	o	o	-	o	---	---	--	o	o	o	--	o	+	o	o
SPP_B	+++	+++	+++	+	+++	+++	+++	++	+++	+++	o	o	+++	+++	+++	+
SPP_C	o	o	o	o	---	---	-	o	o	---	o	o	---	---	-	o
SPP_H	+	o	o	o	---	---	-	o	o	--	o	o	---	---	-	o
SPP_P	-	---	-	-	---	---	---	o	---	---	-	o	---	---	---	-
SPP_FD	---	---	--	o	---	---	-	o	---	---	-	o	---	---	o	o
SPP_DEC	---	---	o	o	---	---	---	-	---	-	o	o	---	---	---	-
ALPINE	o	o	o	o	+++	+++	+	o	+++	o	o	o	+++	o	-	o
CANOPY	o	+	o	-	---	---	---	o	---	-	o	--	---	o	o	o
SITE	---	---	---	--	---	---	---	o	---	---	-	--	---	---	o	o
SEEPAGE	-	---	---	o	o	---	--	o	o	---	--	o	o	---	---	o
ELEV	+++	+++	+++	++	+++	+++	+++	+++	+++	+++	+	o	+++	+++	+++	++
SLOPE	o	+++	o	o	+++	+++	o	-	++	+++	o	o	+++	+	---	o
SOUTH	o	--	o	++	o	o	o	+	+	o	++	o	---	+	--	o
WEST	+++	o	o	o	o	o	--	o	---	o	o	o	---	o	o	o
TERRAIN	+	++	o	o	+++	+++	o	o	+++	+++	o	o	+++	++	-	o
CURVA	o	o	o	+	---	--	o	o	--	o	o	o	---	o	o	o

[a] Preference/avoidance (*t*-tests) is indicated by +++/--- ($P < 0.0005$), ++/-- ($P < 0.005$), +/- ($P < 0.05$), or “o” ($P \geq 0.05$).

[b] Analysis level: broad (1) to fine (4) spatial scales.

Table 5. Univariate analysis results of scale-dependent habitat selection by caribou within the MOUNTAIN zone of the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 – 2000. Caribou location sample sizes are in parentheses in season headings. Results are based on univariate *t* tests.[a] Variables are as defined in Table 2.

	Early Winter (621)				Late Winter (770)				Spring (493)				Summer (1576)			
Variable	1[b]	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
AGE_1-2	o	- - -	o	o	- - -	- - -	- - -	o	- - -	-	o	o	- - -	- - -	- -	o
AGE_3-5	-	o	o	o	- - -	- -	o	o	- - -	o	o	o	- - -	- - -	o	o
AGE_6-7	o	- -	o	o	- - -	o	o	o	- - -	o	-	o	- - -	-	o	o
AGE_8-9	+++	+++	+++	o	+++	o	o	o	+++	+++	++	o	o	++	+	o
SPP_S	o	+++	+	o	o	o	-	o	o	++	+	o	-	+++	o	o
SPP_B	o	+++	+++	+	+++	+++	+++	+	o	+	+	o	+	+++	+++	+
SPP_C	+++	++	o	o	o	- - -	- - -	-	o	o	o	o	o	- - -	- - -	- -
SPP_H	+++	+	o	o	o	- - -	- - -	o	o	o	o	o	-	- - -	- - -	-
SPP_P	- -	- - -	o	o	- - -	- - -	o	o	- - -	-	o	o	- - -	- - -	- -	o
SPP_FD	+	o	o	o	- - -	- - -	-	o	- -	o	o	o	- - -	- - -	-	o
SPP_DEC	-	-	o	o	- - -	- - -	o	o	- - -	-	o	o	- - -	- - -	-	o
ALPINE	- - -	- - -	- - -	-	++	++	o	o	o	- -	- - -	o	++	- -	-	o
CANOPY	+++	+++	+	o	-	- - -	- - -	o	o	+	o	o	-	o	o	o
SITE	+++	+++	o	o	- - -	- - -	- - -	o	-	o	o	o	- - -	-	-	o
SEEPAGE	+	o	o	o	o	- -	o	o	o	o	o	- -	-	o	- - -	-
ELEV	- - -	- -	o	o	+++	+++	+++	++	o	-	-	o	+++	+++	+++	+++
SLOPE	o	o	o	o	+++	+++	o	- - -	+++	++	o	o	+++	+++	-	- - -
SOUTH	- -	- - -	o	o	o	-	o	o	-	- - -	o	o	- - -	- - -	- - -	o
WEST	+++	o	o	o	o	o	o	o	+++	o	o	o	+++	+++	o	o
TERRAIN	o	o	o	o	+++	++	o	- -	+++	o	o	o	+++	o	-	-
CURVA	o	-	o	o	-	- - -	o	-	- -	o	o	o	- - -	o	-	o

[a] Preference/avoidance (*t*-tests) is indicated by +++/--- ($P < 0.0005$), ++/-- ($P < 0.005$), +/- ($P < 0.05$), or "o" ($P \geq 0.05$).

[b] Analysis level: broad (1) to fine (4) spatial scales.

Table 6. Differential seasonal and scale-dependent caribou selection for forest overstory and terrain variables among 2 ecoregion zones and the "Revelstoke study area" in the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 - 2000. A positive sign[a] indicates that higher values of that variable were preferred more or avoided less in the first of the 2 compared zones. A negative sign indicates that higher values of that variable were preferred less or avoided more in the first of the 2 compared zones.

		Early Winter [b]				Late Winter				Spring				Summer			
Variable	Comparison [c]	1[d]	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
AGE_1-2	H - M	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
	H - R	- - -	- -	o	o	- - -	- - -	o	o	- - -	-	o	o	- - -	- - -	o	o
	M - R	+++	++	o	o	+++	+++	o	o	+++	+	o	o	+++	+++	o	o
AGE_3-5	H - M	+++	+++	o	-	+++	o	o	-	+++	+++	o	o	+++	o	-	o
	H - R	- -	- -	o	o	- - -	- - -	o	o	- - -	-	o	o	- -	- - -	o	-
	M - R	++	++	o	o	+++	+++	o	o	+++	+	o	o	++	+++	o	+
AGE_6-7	H - M	+++	o	o	o	+++	o	o	o	++	o	o	o	+++	o	o	o
	H - R	o	+++	o	o	-	o	o	o	- -	o	o	o	- - -	- - -	o	o
	M - R	o	- - -	o	o	+	o	o	o	++	o	o	o	+++	+++	o	o
AGE_8-9	H - M	o	++	+	o	o	o	o	o	o	o	o	o	o	+	o	o
	H - R	o	o	- -	o	+++	++	o	o	+++	o	-	- -	+++	+++	+	o
	M - R	o	o	++	o	- - -	- -	o	o	- - -	o	+	++	- - -	- - -	-	o
SPP_S	H - M	o	- - -	- -	o	+	- - -	- -	o	o	-	o	- -	++	o	o	o
	H - R	-	-	o	o	-	- - -	- - -	- - -	- -	- - -	-	- - -	-	- -	- - -	- - -
	M - R	- - -	o	o	o	- - -	- - -	- - -	- -	- -	o	o	o	- - -	- -	- - -	- -
SPP_B	H - M	- - -	o	o	o	- - -	o	o	o	- - -	- - -	o	o	- - -	- - -	- - -	- -
	H - R	+++	+++	o	o	+++	+	o	o	+++	++	o	o	+++	+++	o	o
	M - R	- - -	- - -	o	o	- - -	-	o	o	- - -	- -	o	o	- - -	- - -	o	o
SPP_C	H - M	o	- - -	- - -	- - -	o	-	o	o	o	o	-	o	o	o	o	o
	H - R	- - -	-	o	o	- - -	+++	+++	o	o	- -	o	o	- - -	o	o	+
	M - R	+++	+	o	o	+++	- - -	- - -	o	o	++	o	o	+++	o	o	-
SPP_H	H - M	- - -	o	o	o	- - -	+++	+++	o	o	o	o	o	-	+	+	o
	H - R	- - -	- - -	- - -	- - -	- - -	+	+	o	-	- - -	-	o	- - -	- - -	- - -	- - -
	M - R	o	- - -	- - -	- - -	-	-	o	-	o	- - -	o	o	-	- - -	- - -	- - -
SPP_P	H - M	o	- - -	- -	- - -	- - -	- - -	- - -	o	- - -	- - -	- - -	o	- - -	- - -	- - -	- - -
	H - R	- - -	- - -	- - -	- - -	- - -	- - -	- - -	o	- - -	- - -	- - -	-	- - -	- - -	- - -	- - -
	M - R	- -	-	o	o	- -	o	o	o	o	o	o	o	- - -	o	o	o
SPP_FD	H - M	- - -	-	-	o	- - -	o	o	o	- - -	-	o	o	- - -	o	o	o
	H - R	- - -	- - -	- - -	o	- - -	o	o	o	- - -	-	o	o	- - -	o	o	o
	M - R	-	- - -	o	o	- - -	o	o	o	- -	o	+	o	- -	o	+	o

Table 6. Continued.

		Early Winter[b]				Late Winter				Spring				Summer			
Variable	Comparison[c]	1[d]	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
SPP_DEC	H - M	o	o	+	+	+++	+++	++	+	o	o	o	o	+++	+++	+++	+++
	H - R	- - -	- - -	o	o	- - -	- - -	- - -	o	- - -	o	o	o	- - -	- -	- - -	-
	M - R	+++	+++	o	o	+++	+++	+++	o	+++	o	o	o	+++	++	+++	+
ALPINE	H - M	- -	-	o	o	+	+++	++	+	o	o	o	o	++	+++	+++	+++
	H - R	+++	+++	+++	++	o	o	o	o	o	+++	++	o	o	+	o	o
	M - R	- - -	- - -	- - -	- -	o	o	o	o	o	- - -	- -	o	o	-	o	o
CANOPY	H - M	o	+++	+++	o	o	+++	++	o	+++	+++	+++	+	o	++	o	+
	H - R	- - -	- - -	o	-	- - -	++	o	o	-	- - -	- -	-	o	o	o	o
	M - R	+++	+++	o	+	+++	- -	o	o	+	+++	++	+	o	o	o	o
SITE	H - M	- - -	- - -	- -	o	- - -	o	o	o	- - -	- - -	-	o	- - -	-	o	o
	H - R	- - -	- - -	- - -	-	- - -	- -	o	o	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
	M - R	- - -	- - -	-	o	- - -	o	o	o	- - -	- - -	-	o	- - -	- - -	- - -	- - -
SEEPAGE	H - M	- - -	- - -	- - -	o	+	o	o	o	o	- - -	o	o	o	- - -	o	o
	H - R	- - -	- - -	- - -	o	o	-	- - -	o	o	- - -	- - -	o	o	-	o	o
	M - R	- - -	- - -	o	o	o	o	-	o	-	o	o	- -	o	o	o	o
ELEV	H - M	o	o	o	o	+	o	o	o	o	o	o	o	+++	o	o	o
	H - R	+++	+++	+++	++	+++	+++	o	o	+++	+++	+++	+++	+++	+++	+++	o
	M - R	+++	+++	+++	o	+++	+	o	o	+++	+++	+++	+++	+++	+++	+++	+++
SLOPE	H - M	o	+	o	o	o	o	o	o	o	o	o	o	-	o	o	+
	H - R	+++	+++	o	o	+++	+++	+++	+++	+++	+++	+++	+++	+++	++	+	+
	M - R	+++	+++	o	o	+++	+++	+++	+	+++	+++	+	+++	+++	+++	+++	o
SOUTH	H - M	o	+	o	o	o	o	o	o	++	++	o	o	+	+++	o	o
	H - R	o	o	o	o	++	o	o	o	++	o	+	o	o	+++	o	o
	M - R	-	- - -	-	o	++	o	o	o	o	o	o	o	-	o	o	o
WEST	H - M	o	o	o	o	o	o	o	o	- - -	o	o	o	- - -	- -	o	o
	H - R	+++	+++	o	o	o	o	- - -	o	o	o	o	o	- - -	+	o	o
	M - R	+++	+++	o	o	++	o	-	o	+++	o	o	o	+++	+++	o	o
TERRAIN	H - M	o	+	o	o	o	o	+	o	o	+	o	o	o	o	o	o
	H - R	+++	+++	o	o	+++	+++	+++	+	+++	+++	o	o	+++	+++	+	o
	M - R	+++	+	o	o	+++	+++	++	o	+++	++	o	o	+++	++	++	o

[a] Bonferroni pairwise multiple comparison test significance is indicated by +++/ - - - (*P* < 0.0005), ++/ - - (*P* < 0.005), +/ - (*P* < 0.05).

[b] Seasons defined by Simpson et al. (1997): early winter ends 15 Jan; late winter ends 15 Apr.; spring ends 31 May; summer ends 31 Oct.

[c] H: Highland ecoregion zone; M: Mountain ecoregion zone; R: Revelstoke study area within the North Columbia Mountains

[d] Analysis level: broad (1) to fine (4) spatial scales.

Table 7. Variables and parameters associated with best-fit multiple logistic regression models of seasonal caribou habitat selection in the "Highland" zone of the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 - 2000.

Season	Variable	Level[a]	β	SE	P^{*}	Model CS[b]	Model P^{**}
Early Winter	CANOPY	1	-0.031	0.014	0.0324	64.1	<0.0001
	ELEV	1	-0.003	0.001	<0.0001		
	AGE_1-2	2	-0.012	0.006	0.0327		
	CURVA	2	1408.6	525.83	0.0074		
	CANOPY	2	0.038	0.011	0.0007		
	SPP_FD	2	-0.028	0.015	0.0538		
	SPP_H	2	0.029	0.008	0.0001		
	ALPINE	3	-0.012	0.004	0.0059		
	CURVA	4	55.562	25.958	0.0323		
	ELEV	4	0.003	0.000	<0.0001		
	SITE	4	-0.050	0.018	0.0047		
	SLOPE	4	-0.016	0.005	0.0019		
	Constant		-1.066	0.924	0.2483		
Late Winter	ELEV	1	-0.002	0.001	<0.0001	68.6	<0.0001
	SPP_FD	1	-0.056	0.027	0.0351		
	AGE_6-7	2	0.024	0.008	0.0044		
	SPP_P	2	-0.031	0.008	0.0001		
	AGE_1-2	3	-0.009	0.006	0.1008		
	TERRAIN	3	0.041	0.013	0.0018		
	ALPINE	4	-0.010	0.002	<0.0001		
	CURVA	4	82.422	25.152	0.0010		
	SPP_DEC	4	-0.192	0.075	0.0107		
	ELEV	4	0.004	0.000	<0.0001		
	SPP_S	4	-0.006	0.003	0.0225		
	SLOPE	4	-0.026	0.006	<0.0001		
	Constant		-2.982	0.745	0.0001		

Table 7. Continued.

Season	Variable	Level[a]	β	SE	P^*	Model CS[b]	Model P^{**}
Spring	SEEPAGE	1	0.090	0.050	0.0688	60.7	<0.0001
	AGE_8-9	2	0.016	0.004	0.0002		
	SEEPAGE	2	-0.130	0.033	0.0001		
	AGE_8-9	4	-0.007	0.003	0.0182		
	SPP_FD	4	-0.026	0.013	0.0496		
	SPP_P	4	-0.021	0.009	0.0253		
	SITE	4	-0.047	0.017	0.0071		
	Constant		0.055	0.343	0.8725		
Summer	WEST	1	-0.040	0.010	0.0001	63.7	<0.0001
	AGE_1-2	2	-0.050	0.010	<0.0001		
	SEEPAGE	2	-0.052	0.018	0.0046		
	SITE	2	0.095	0.024	0.0001		
	AGE_8-9	3	0.008	0.002	<0.0001		
	SOUTH	3	-0.006	0.003	0.0431		
	CURVA	4	50.411	21.093	0.0169		
	ELEV	4	0.003	0.000	<0.0001		
	SPP_P	4	-0.019	0.007	0.0077		
	SLOPE	4	-0.016	0.005	0.0005		
	Constant		-2.475	0.745	0.0009		

[a] Indicates spatial scale of variable, from broadest (1) to finest (4).

[b] Classification success (%) at cutpoint $P = 0.5$

* Wald chi-square statistics

** Reduced (–2)loglikelihood ratio chi-square statistic

Table 8. Variables and parameters associated with best-fit multiple logistic regression models of seasonal caribou habitat selection in the "Mountain" zone of the Columbia Highlands and Northern Columbia Mountains, British Columbia, 1984 - 2000.

						Model	
Season	Variable	Level[a]	β	SE	P^*	CS[b]	P^{**}
Early Winter	ELEV	2	-0.004	0.001	<0.0001	63.8	<0.0001
	SITE	2	-0.082	0.027	0.0028		
	SLOPE	2	0.028	0.009	0.0024		
	AGE_8-9	3	0.013	0.002	<0.0001		
	ALPINE	3	-0.019	0.004	<0.0001		
	ELEV	4	0.003	0.000	<0.0001		
	SLOPE	4	-0.011	0.005	0.0179		
	Constant		0.037	0.732	0.9599		
Late Winter	AGE_1-2	1	0.035	0.013	0.0066	66.5	<0.0001
	SPP_H	1	0.030	0.009	0.0008		
	CURVA	2	-969.1	481.81	0.0443		
	SPP_P	2	-0.087	0.032	0.0068		
	SLOPE	2	0.024	0.008	0.0015		
	AGE_1-2	3	-0.031	0.010	0.0030		
	ALPINE	3	-0.012	0.003	0.0001		
	SPP_B	4	0.011	0.003	<0.0001		
	ELEV	4	0.002	0.000	<0.0001		
	SPP_FD	4	0.030	0.010	0.0029		
	SITE	4	-0.061	0.019	0.0016		
	SLOPE	4	-0.018	0.004	<0.0001		
	Constant		-2.956	0.652	<0.0001		

Table 8. Continued.

Season	Variable	Level[a]	β	SE	P^*	Model CS[b]	Model P^{**}
Spring	SPP_DEC	2	-0.230	0.114	0.0425	62.3	<0.0001
	SPP_P	2	-0.130	0.049	0.0082		
	SLOPE	2	0.049	0.010	<0.0001		
	SOUTH	2	-0.012	0.006	0.0401		
	AGE_6-7	3	-0.038	0.017	0.0268		
	ALPINE	3	-0.012	0.002	<0.0001		
	SPP_FD	4	0.032	0.011	0.0050		
	SEEPAGE	4	-0.034	0.009	0.0001		
	SLOPE	4	-0.020	0.005	0.0001		
	Constant		-0.068	0.418	0.8716		
Summer	CURVA	1	-2837.2	790.35	0.0003	61.8	<0.0001
	SPP_P	1	-0.129	0.035	0.0002		
	SLOPE	1	0.049	0.010	<0.0001		
	TERRAIN	1	-0.036	0.018	0.0458		
	WEST	1	0.030	0.008	0.0003		
	CURVA	2	-691.0	269.99	0.0105		
	SPP_DEC	2	-0.267	0.091	0.0032		
	ELEV	2	-0.002	0.000	<0.0001		
	SOUTH	2	-0.019	0.004	<0.0001		
	AGE_8-9	3	0.007	0.003	0.0075		
	ALPINE	3	-0.008	0.002	<0.0001		
	SPP_B	3	0.008	0.003	0.0039		
	SITE	3	-0.081	0.019	<0.0001		
	ELEV	4	0.002	0.000	<0.0001		
	SLOPE	4	-0.018	0.003	<0.0001		
	Constant		-0.995	0.487	0.0410		

[a] Indicates spatial scale of variable, from broadest (1) to finest (4).

[b] Classification success (%) at cutpoint $P = 0.5$

* Wald chi-square statistics

** Reduced (–2)loglikelihood ratio chi-square statistic

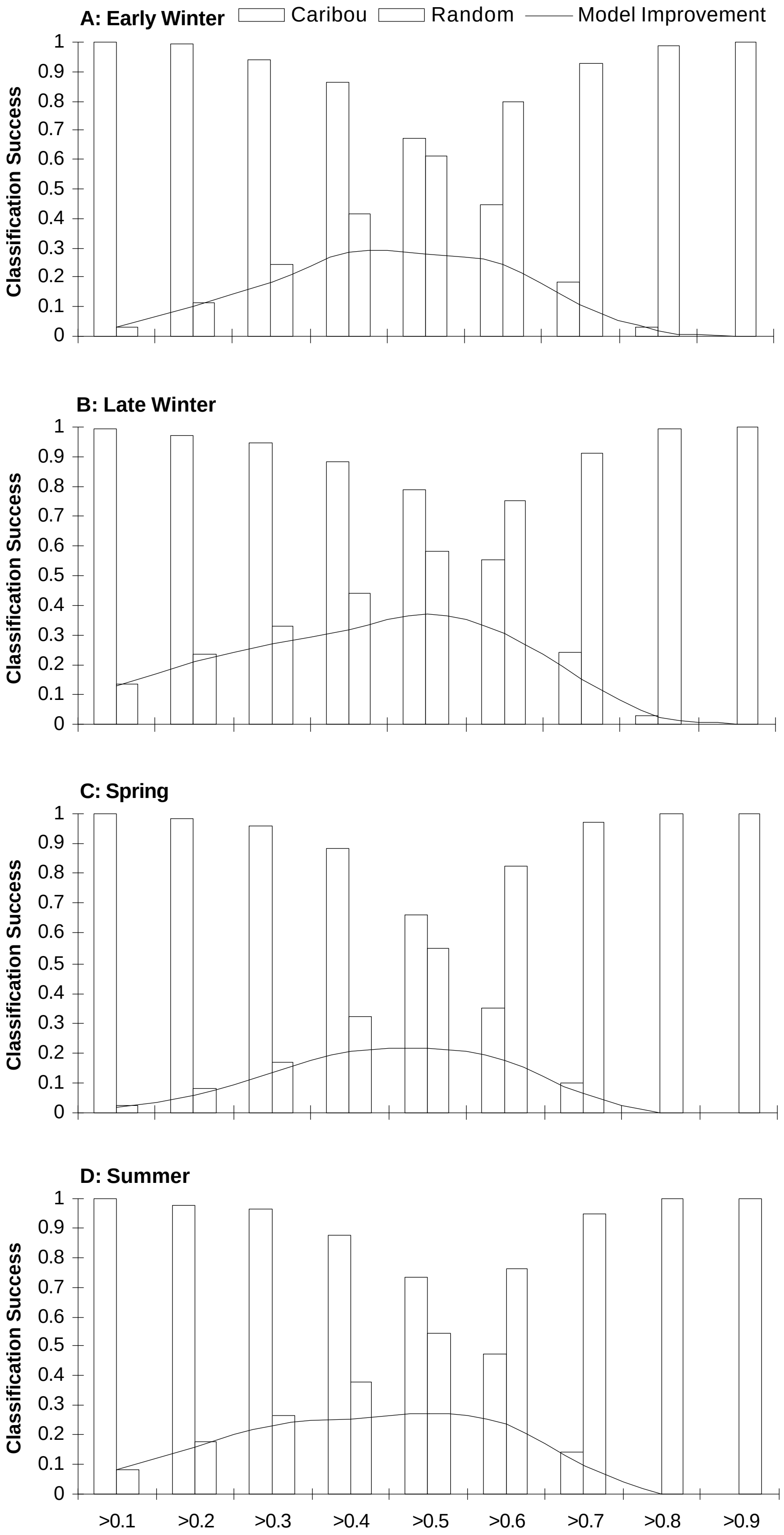

Figure 4. Predictive efficiency of HIGHLAND zone seasonal caribou habitat models across cutpoint probability levels in the Columbia Highlands and North Columbia Mountains, British Columbia, 1984 - 2000. Model improvement (correctly classified caribou minus incorrectly classified random) indicates the optimal classification cutpoint in discriminating caribou from random locations.

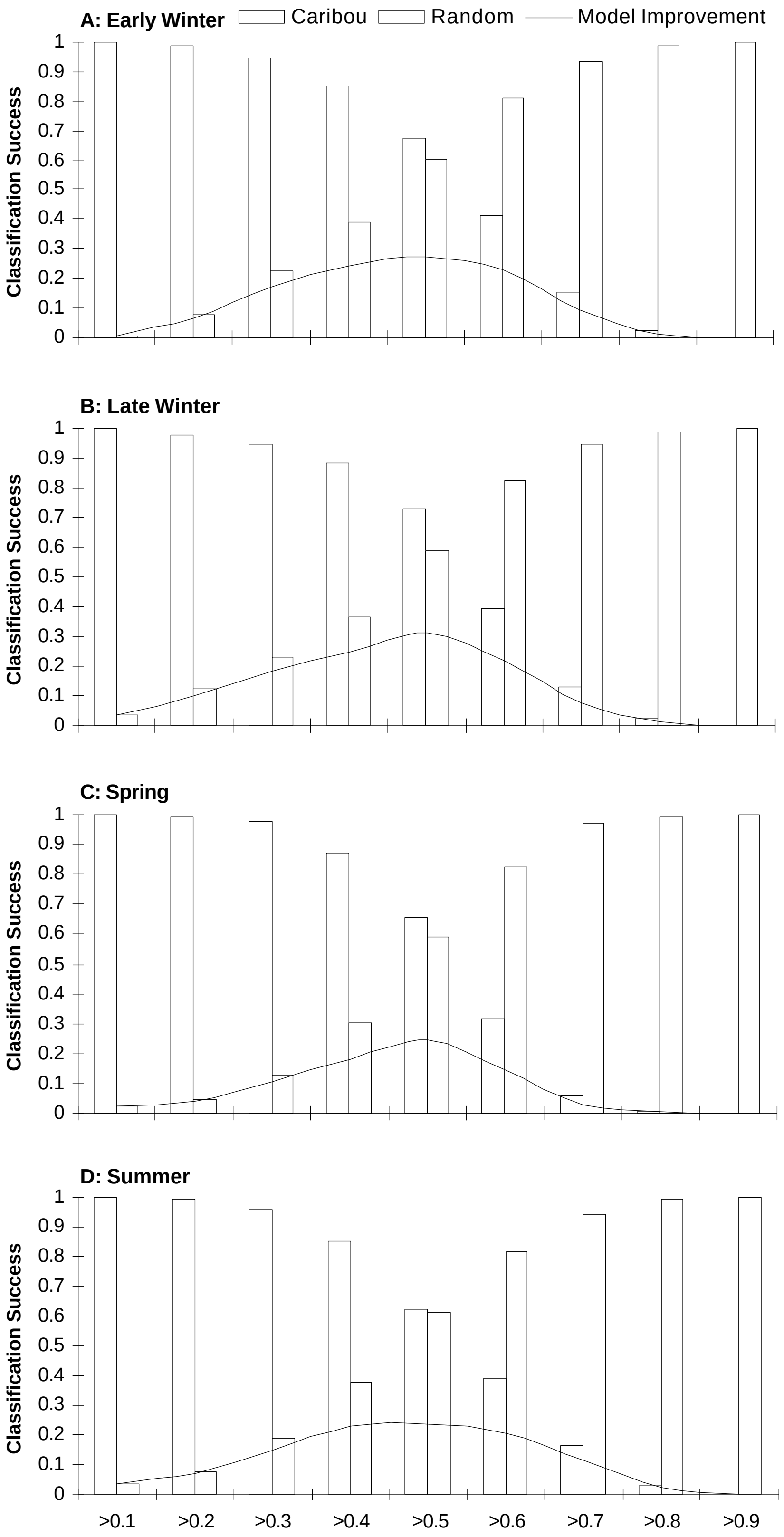

Figure 5. Predictive efficiency of MOUNTAIN zone seasonal caribou habitat models across cutpoint probability levels in the Columbia Highlands and North Columbia Mountains, British Columbia, 1984 - 2000. Model improvement (correctly classified caribou minus incorrectly classified random) indicates the optimal classification cutpoint in discriminating caribou from random locations.

DISCUSSION

Habitat selection varied with scale in both the Highland and Mountain zones, suggesting that spatial scale is an important parameter in understanding and describing caribou habitat relationships in the Columbia Highlands and North Columbia Mountains. As was also found from similar scale-dependent analyses for the Revelstoke study area (Apps et al. 2000) and the southern Purcell Mountains (Apps and Kinley 2000), either the strength of selection changed across scales, or in some cases, the direction of habitat selection changed between broad and fine scales. For example, in both the Highland and Mountain zones, selection for slope and terrain ruggedness was generally positive at broader scales and negative at finer scales. This suggests that caribou were associated with broad landscapes of steep and rugged terrain, but in fact preferred gentle sites within those landscapes. In both zones, selection for oldgrowth forest (age classes 8 and 9) during each season was generally positive at broader scales but neutral at finer scales. This broad-scale preference may have reflected the distribution of such stands within the analysis area. Fine-scale preferences may not be apparent if caribou are using broad landscapes where preferred attributes are of relatively contiguous distribution. In fact, the little selection evident for most variables at the finest scale (level 4) in both the Mountain and Highland zones is somewhat expected. Where caribou occur, there has historically been very little natural disturbance, much of the area has been in long-term protected status, and outside parks there has been a moratorium on logging above 1500 m within the Cariboo Region to protect caribou habitat (J. Young, MELP, pers. comm.). Moreover, forest cover mapping was more generalized within Wells Gray Provincial Park, potentially limiting our ability to detect fine-scale selection.

Seasonal differences in habitat selection were also apparent from our results. However, seasonal differences were more pronounced in the Mountain zone than in the Highland zone. For example, during all seasons within the Highland zone, caribou preferred landscapes of higher elevation and alpine composition, and either avoided or did not prefer landscapes of higher cedar composition. In contrast, during early winter, caribou in the Mountain zone preferred landscapes of higher cedar composition and avoided landscapes of higher elevation and alpine composition. This pattern was also apparent during spring, though to a lesser extent, and is consistent with observations that mountain caribou inhabiting more rugged terrain tend to show stronger seasonal variation in habitat selection than do those associated with more subdued topography (Simpson and Woods 1987, Servheen and Lyon 1989, Seip 1990, 1992, Terry et al. in press).

In both zones, caribou generally appeared to be less selective for habitat during spring than during other seasons. Caribou may in fact have been highly selective during spring, but our results may have been influenced by the occurrence of multiple habitat selection strategies within the dates used to define that season. For example, many caribou may have retained late winter behaviours into the early part of the “spring” season, or switched to summer behaviours in the latter part of spring. Such variation is expected among all seasons because the Simpson et al.

(1997) seasonal cut dates are general and cannot account for the fact that shifts in seasonal foraging strategies will occur at different times among years, areas, and animals. However, it is more likely to influence results during spring because this season is considerably shorter, sample sizes are typically lower, and the persistence of snow is highly variable among years and locations.

Expected differences that relate to topography and climate were also apparent in comparing habitat selection within the Highland and Mountain zones to that of the Revelstoke study area. The Revelstoke study area occurs within the North Kootenay Mountains ecosection and was associated with the most rugged and wettest portion of the North Columbia Mountains ecoregion. For terrain variables as well as site index and alpine, comparisons among areas indicate that Revelstoke caribou were much more selective for gentle terrain and productive, forested sites. Moreover, although caribou made distinct elevation shifts among seasons near Revelstoke, they were not as selective for higher elevations as caribou within the Highland or Mountain zones. We surmise that this is because the highest elevations near Revelstoke are mostly of rock and ice or excessively steep terrain, and are inherently unsuitable habitat. In comparison, terrain associated with highest elevations in the Highland and Mountain zones is more subdued and more likely to represent useable habitat. This pattern is also somewhat apparent in comparing the Highland to the more rugged Mountain zone, but the contrast is not as extreme as when compared to the Revelstoke area. Comparisons among the three areas also indicate that Highland caribou showed a much stronger avoidance of landscapes composed of youngest stands and pine stands across scales and seasons. This may reflect a greater distribution of these less suitable stand types, which may also be concentrated at the lowest elevations avoided by these caribou across seasons. In contrast to the more rugged areas where low elevation landscapes of cedar and hemlock are preferred during early winter, Highland caribou were never positively associated with these species and continued to prefer high elevations during seasons when caribou in the Mountain zone and Revelstoke study area preferred lower elevations. Subalpine fir was generally selected by Highland caribou across seasons.

Differences among zones or study areas are due to both actual preferences or requirements of study animals and the distribution and availability of habitat attributes. Among regions, both will vary with physiography, climate, predation risk, and both natural and human disturbance history. Variation within zones is also expected among animals, years, and to some degree, geographically. Variation must be meaningfully compartmentalized in order to understand and model mountain caribou-habitat relationships. Although Demarchi's (1996) 1:250,000 ecosections are logical strata for splitting among broad differences in physiography and climate, they do not necessarily provide an ideal division for analyses and modeling. This was demonstrated by the fact that habitat selection within a "transition" zone, encompassed entirely within the Columbia Highlands ecoregion, was in fact more characteristic of the Mountain zone than the Highland zone.

The inference of ecologically meaningful relationships from multivariate models must be tempered with caution (Rextad et al. 1988). However, our best-fit MLR models suggest that a linear combination of variables we considered can efficiently discriminate caribou use from random locations across scales and therefore are useful predictors of habitat quality within the study area. During each season, the scales at which the best predictive variable subsets were represented indicate that models explained both broad- and fine-scale variation in the data. Although the overall classification success of season- and zone-specific models was slightly lower than reported for other subpopulations (Apps and Kinley 2000, Apps et al. 2000), this is expected given the extensive areas and time frame from which caribou data were collected. Models reflect patterns that are consistent among data sources and are unlikely to be “overfit” to any particular area or dataset. Applied within a GIS (resource selection probability equation 8.5: Manly et al. 1993), seasonal models represent decision-support tools useful for strategic and operational forestry planning and spatially explicit timber and habitat supply analyses within the Columbia Highlands and North Columbia Mountains (Appendix 2).

MANAGEMENT IMPLICATIONS

The caribou habitat selection patterns that we report from this analysis are consistent with our current understanding of mountain caribou ecology and how it differs between regions of subdued and rugged terrain. Therefore, we suggest that previously recommended guidelines for mountain caribou habitat management (Stevenson et al. 1994, Simpson et al. 1997) are appropriate within our analysis area:

- Identify and reserve core habitat areas. Cores can be identified by combining telemetry data, showing use intensity, with model output predicting landscapes of high habitat quality.
- Create special management zones peripheral to core habitat areas. These would require greater old forest retention and modified silvicultural practices as compared to integrated land-use zones.
- Maintain movement habitat to link population centers across fracture zones. This may be guided by movement vector mapping or movement intensity analyses, in conjunction with model output predicting landscapes of relatively higher habitat quality.
- Employ uneven-aged forest management outside of reserves. Ongoing forestry trials designed to minimize the loss of caribou habitat while producing timber are now beginning to provide guidance for appropriate methods.

- Conduct ongoing habitat modeling and model testing. The current models, while based on a relatively large dataset, should be considered testable hypotheses. Data gained through future telemetry monitoring can be used to test their predictive efficacy.
- Reduce access. This should reduce habitat fragmentation, displacement due to motorized disturbance, and the risk of poaching and predation. Because of their preference at all scales for higher elevations and the presence of less rugged mountain tops, caribou in this study area may be even more vulnerable to disturbance from recreation based in open areas, such as heli-tourism and snowmobiling, than are caribou in the Revelstoke study area.
- Minimize the creation of habitat for other ungulates to decrease caribou predation risk. Clearcutting and other forms of fragmentation may improve habitat quality for other ungulates, attracting predators into caribou landscapes that would not normally support an abundant prey base (Kinley and Apps in press). Preliminary results of harvesting trials suggest that openings of 1 to 2 tree lengths may be so small that they are essentially part of the forest, rather than creating edge or patches of early-seral habitat (H. Armleder, MOF, pers. comm.). Therefore, very small patch harvesting may not create the edge/early seral habitat favored by moose, elk and deer, thereby reducing caribou predation risk.

The fact that caribou habitat selection in the transition zone of the Highlands ecoregion appears to bear greater resemblance to that of the Mountains has important implications. Within the transition zone, the greater elevational shifts exhibited during early winter, similar to the Mountain zone and in contrast to the Highland zone, indicate a need to manage for oldgrowth habitat in the ICH and lower ESSF here, rather than simply within the mid to upper ESSF. This should be reflected in guidelines, planning and practices of ministries and licensees responsible for forest management.

Our results support the presumption that stands representing suitable mountain caribou habitat are oldgrowth. The landscape distribution of suitable stands may influence both caribou energetic requirements during foraging and predation risk. Considering the consistency with which broad landscapes of higher oldgrowth composition were preferred across seasons and zones, we suggest that the disperson of such stands be managed at scales of at least 100 km^2. However, despite the fundamental importance of this variable, managers must account for the entire combination of overstory and terrain attributes associated with preferred habitat, which vary by season, region and scale. The predictive habitat models we describe may assist by projecting the potential impacts of alternate management scenarios through space and time.

As a final caveat, we recommend that our results be applied with some discretion in prescriptive management. We have described and modeled patterns over extensive areas and time, and results are influenced by spatial, temporal, and seasonal variation in both habitat selection strategies and habitat availability that cannot practically be accounted for. Moreover, our results must be considered in the context of accuracy and scale of both the caribou location and habitat data on which analyses were based. Therefore, our results are applicable for decision-support in broad, strategic-level planning, but may be less applicable at the operational or stand level. For site-specific decisions requiring field inspection, such as cutblock layout and harvest prescription, models are best derived through field sampling of habitat attributes.

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APPENDIX 1.

Differences, by zone, in the mean composition of caribou used and random landscapes across scales for each variable.

Notes:

- Scale of the Y axis may differ among variables, seasons and zones
- Significant differences are indicated in Tables 4 and 5.

APPENDIX 2.

Map 1. Ecoregions and ecosections associated with the caribou habitat modeling area and environs.

Map 2. Distribution of caribou location data, by source, used for habitat selection analyses described in this report.

Maps 3 – 6. Predicted seasonal habitat quality for mountain caribou in the Columbia Highlands and North Columbia Mountains. *P* values indicate the probability cutpoint used to classify caribou habitat, equating to habitat “suitability”.