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SCALE-DEPENDENT HABITAT SELECTION BY MOUNTAIN CARIBOU, COLUMBIA MOUNTAINS, BRITISH COLUMBIA

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Abstract: Mountain caribou, an endangered ecotype of woodland caribou (*Rangifer tarandus caribou*) are associated with late-successional forests, and protecting their habitat conflicts with timber extraction. Our objectives were to describe seasonal, scale-dependent caribou-habitat relationships and to provide a means for their integration with forest planning. Between 1992 and 1999, 60 caribou were radiolocated 3,775 times in the north Columbia Mountains of British Columbia. We analyzed caribou selection for multiple forest overstory and terrain attributes across 4 nested spatial scales, comparing successively smaller and closer paired landscapes (used and random). Seasonal habitat selection varied with scale for most attributes. During early winter, caribou preferred broad landscapes of low elevation, gentle terrain, high productivity, high canopy cover, and old and young forests of species indicative of a relatively mild, dry climate. Finer-scale preferences were for old western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) stands, high canopy closure, high productivity, and southern aspects. During late winter, caribou preferred broad landscapes of high elevation, northern aspects, and old Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) stands. Overstory preferences were similar at fine scales, coupled with low canopy closure and productivity, high elevations, and gentle terrain. During spring, caribou preferred broad landscapes of young and old closed canopy cedar, hemlock, and spruce forests of high productivity at low elevations. Preferences were similar at finer scales but included gentle slopes. Summer preferences included closed canopy, old spruce and subalpine fir forests of high productivity across scales, north and east aspects at broad scales, and gentle terrain at fine scales. Of the variables considered, linear combinations of subsets could explain and predict seasonal habitat selection across scales ($P < 0.001$). Our results confirm the close association of mountain caribou with old-growth forests, and describe relationships that can be accounted for in spatially explicit habitat—timber supply forecast models.

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Key words: British Columbia, caribou, Columbia Mountains, fragmentation, habitat selection, landscape, predictive modeling, *Rangifer tarandus*.

Woodland caribou inhabiting wet coniferous forests in the high-snowfall region of southeastern British Columbia and northern Idaho are known as mountain caribou (Heard and Vagt 1998). This corresponds to the mountain—arboreal ecotype of Edmonds (1991). Mountain caribou are strongly associated with late-successional forests (Rominger and Oldemeyer 1989, Stevenson et al. 1994, Simpson et al. 1997) where their primary winter food, arboreal hair lichens (*Bryoria* spp. and *Alectoria sarmentosa*), are abundant (Freddy 1974, Antifeau 1987, Simpson and Woods 1987, Rominger and Oldemeyer 1989, Seip 1992, Rominger et al. 1996). Many of these old forests are valuable for timber harvesting.

The north Columbia Mountains support about 400 (Flaa and McLellan 2000) of an estimated 2,400 mountain caribou (Simpson et al. 1997). Due to the small population size and conflicts with forest management, these caribou are provincially listed as endangered, and recent forest-practices legislation stipulates that special measures must be taken to manage for caribou habitat when planning forestry activities (Forest Practices Code of British Columbia Act 1993). This legislation requires the development of guidelines for integrating caribou habitat values at strategic and operational planning levels. The conservation efficacy of this approach depends on our ability to describe and predict caribou habitat relationships at the appropriate spatial scales.

Spatially explicit habitat models derived from empirical data provide an objective means to account for future caribou habitat supply in forestry planning. However, their applicability as management tools may be limited by a priori research design and analysis decisions. Apparent patterns of habitat selection are sensitive to the scale of comparison and distribution of available habitat, with studies conducted at different spatial scales potentially yielding different results (Porter and Church 1987, McLean et al. 1998, Garshelis 2000). Such decisions of scale have typically been arbitrary, based on convenience or justified based on the size of the species' home range (Morrison et al. 1998:141–146). Because habitat relationships may change along a continuum of spatial scale, several authors (Johnson 1980, Orians and Wittenberger 1991, Aebischer et al. 1993, Manly et al. 1993, Anderson and Gutzwiller 1996) have espoused that habitat relationship studies reflect the hierarchical nature by which animals select resources. Moreover, explicit consideration of habitat pattern is relevant only within the context of spatial scale (O'Neil et al. 1988, Kotliar and Wiens 1990, Lord and Norton 1990). Yet, perhaps due to technological and analytical limitations, there are few examples of multi-scale analyses of habitat selection by wide-ranging species. This in turn limits our ability to confidently integrate species-habitat associations

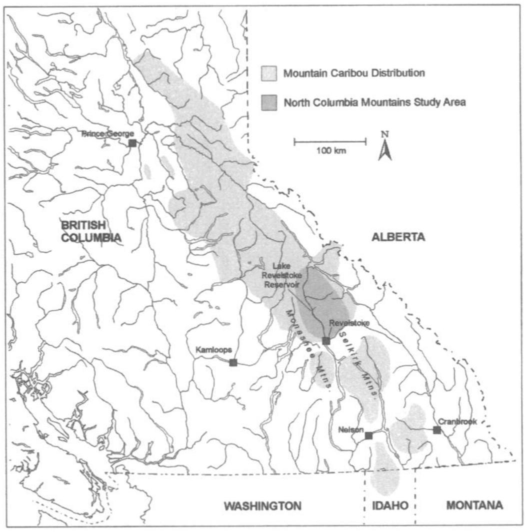

Fig. 1. Current general mountain caribou distribution and the north Columbia Mountains study area in southeast British Columbia.

with land management at ecologically relevant scales.

Ungulates are expected to respond to spatial variation in habitat conditions by making hierarchical foraging decisions ranging from broad landscapes or watersheds to specific portions of plants (Senft et al. 1987). We describe scale-dependent analyses of biotic and abiotic factors that are correlated with the seasonal selection of landscapes and forest stands by mountain caribou in the north Columbia Mountains of southeast British Columbia. We also derive and evaluate predictive multivariate models that integrate habitat selection across spatial scales.

STUDY AREA

The study area encompassed about 9,000 km^2 near the southern extent of contiguous occupied caribou habitat in southeast British Columbia (51°N, 118°W) and was bisected by the Lake Revelstoke Reservoir (Fig. 1). The Selkirk Mountains to the east of the reservoir and the Monashee Mountains to the west are rugged and dissected by deep, narrow valleys. Elevations range from 610 m to >3,000 m, with treeline at about 1,980 m.

The lower slopes of the study area are in the wet-cool Interior-Cedar-Hemlock (ICHwk) biogeoclimatic subzone (Meidinger and Pojar 1991). These forests form a closed canopy with climax stands dominated by western hemlock and western redcedar although other conifers

Table 1. Distribution of mountain caribou radiolocation and animal samples by year and season in the north Columbia Mountains, British Columbia, 1992–99. Mean seasonal end dates (i.e., end) when the greatest elevation shift occurred among animals are given for each year.

	Early winter			Late winter			Spring			Summer		
Yr	End	n_L[a]	n_A[b]	End	n_L	n_A	End	n_L	n_A	End	n_L	n_A
1992				23 Apr	62	16	02 Jun	55	18	30 Oct	119	15
1993	30 Jan	112	16	25 Apr	148	30	26 May	64	26	25 Oct	191	25
1994	26 Dec[c]	156	26	21 Apr	165	26	25 May	80	25	21 Oct	162	24
1995	02 Jan	133	24	25 Apr	138	27	28 May	106	32	13 Oct	183	30
1996	09 Jan	109	25	25 Apr	139	30	06 Jun	67	24	20 Oct	168	28
1997	15 Jan	139	23	20 Apr	145	32	25 May	89	34	29 Oct	173	33
1998	13 Jan	160	25	15 Apr	202	28	21 May	86	29	09 Oct	193	26
1999	16 Jan	84	24		147	22						
Multi-yr	11 Jan	893	53	22 Apr	1146	58	28 May	547	56	21 Oct	1189	57

[a] Radiolocation sample size.
[b] Animal sample size.
[c] 1993.

are locally abundant. Dominant shrubs include falsebox (*Pachistima myrsinites*), black huckleberry (*Vaccinium membranaceum*) and western yew (*Taxus brevifolia;* Ketcheson et al. 1991).

Midslopes of the Columbia Mountains are in the very wet cold Engelmann Spruce-Subalpine Fir subzone (ESSFvc), and forests are dominated by Engelmann spruce and subalpine fir. At higher elevations, subalpine fir grows in clumps forming mostly open subalpine parkland. Alpine, rock, and glaciers are dominant features at higher elevations, and avalanche paths are common at all elevations except the lowest valleys.

The study area is wet with most precipitation falling as snow during winter. The maximum annual snowpack at 2,000 m elevation averaged 350 ± 63 cm (1 SD) between 1965 and 1998 (Glacier National Park, unpublished data). Typical mean daily temperatures at 443 m and 1,875 m are −12°C and −11°C during January, and 26°C and 16°C during July (Anonymous 1982).

METHODS

Because >85% of the population is readily observed in late winter and available to be captured using a net-gun from a helicopter (Seip 1990, Flaa and McLellan 2000) we could ensure that the sample of radiocollared caribou had a geographic distribution representative of the population. In 1992 and 1993 we radiocollared 37 caribou, and between 1994 and 1999 we added 23 more to our sample to replace individuals that died. The total sample consisted of 50 females and 10 males, of which 52 were adults and 8 were juveniles. Between late October and January, all radiocollared caribou were located approximately once each week from a fixed-wing Cessna 337 aircraft. Tracking flights occurred every 2 weeks at other times of the year. Caribou locations were recorded on aerial photographs during the flight and transcribed to 1:20,000 forest-cover maps after each flight, and Universal Transverse Mercator coordinates were recorded to the nearest 100 m. Radiolocations were distributed over 8 years and all seasons (Table 1).

We tested the accuracy of radiolocating and plotting locations by dropping 10 collars from a helicopter and placing an additional 16 from the ground in typical caribou habitat. Because 60% of the telemetry locations included sightings of animals (39%) or their tracks (21%), we also estimated the accuracy of plotting 17 simulated observed animals. The locations of the simulated observed animals were determined using a non-differentially corrected global positioning system (GPS) receiver in the helicopter. The dropped collars and those placed from the ground were located using a real time, differentially correcting GPS receiver.

For analysis, we stratified radiolocation data by 4 seasons that typify mountain caribou foraging strategies and are characterized by distinct patterns of elevation use (Stevenson et al. 1994): Early Winter, Late Winter, Spring, and Summer. However, the specific dates of elevation shift may vary greatly among regions, years, and animals. Because using a set date to stratify data into seasons might fail to clearly define seasonal foraging strategies, we stratified data according to seasonal elevation shifts made by each individual during each year. We defined

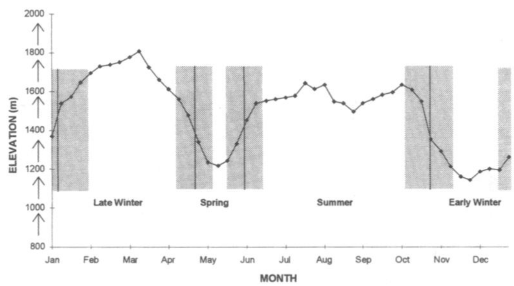

Fig. 2. Running 3-week mean elevations used by radiocollared mountain caribou in the north Columbia Mountains, British Columbia, 1992—99. Grey areas indicate multi-year seasonal transition periods used to define seasonal cut dates.

seasonal breaks separately for each animal as that date when the greatest elevation shift occurred, within a transition period defined for the entire population (Fig. 2).

We assembled habitat data in a geographic information system (GIS) for a zone that encompassed a radius of ≥17 km around all radiolocations, totaling about 11,000 km^2. Data were compiled from 1:20,000 digital forest inventory planning files (Resources Inventory Branch 1995) and Terrain Resource Information Management files (Surveys and Resource Mapping Branch 1992) and were rasterized to 100-m resolution, smaller than the 2-ha minimum mapping unit of forest inventory planning data. From these data sources we derived habitat variables associated with forest stand overstory and terrain attributes (Table 2). Forest overstory data were current to 1997. From the onset of the study to this date, natural and human disturbance affected 0.9% of forest land within a 17-km radius of all radiolocations. We expected that this, and any disturbance that occurred in the 2 years after the forest inventory was updated, would have a negligible effect on our results.

We selected stand variables under the assumption that the ecology and habitat associations of mountain caribou are largely influenced by forest structure (Stevenson et al. 1994). 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 distinct 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. Canopy closure depicted the ocular cover of the stand

Table 2. Independent variables considered for analyses of habitat selection by mountain caribou within the north Columbia Mountains, British Columbia, 1992–99.

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 productivity index
SPP-B	Subalpine fir composition (%)
SPP-S	Spruce composition (%)
SPP-C	Western redcedar composition (%)
SPP-H	Western hemlock composition (%)
SPP-FD	Douglas-fir composition (%)
SPP-DEC	Deciduous species composition (%)
SPP-P	Lodgepole (*Pinus contorta*) and white (*P. monticola*) pine composition (%)
ALPINE	Alpine tundra composition (%)
ELEV	Elevation (m)
SLOPE	Slope (%)
SOUTH	North → south aspect (0 → 1)
WEST	East → west aspect (0 → 1)
TERRAIN	Terrain ruggedness index
SEEPAGE	Potential seepage sites (%)

overstory. Site index reflected site productivity and is calculated with species-specific equations that incorporate stand age and height (Thrower et al. 1991). We considered overstory species composition for analysis because it may relate to seasonal forage availability and indicate climatic variability. Individual or grouped species were included if their spatial composition was >3% of the total analysis area. Matching our raster resolution and the maximum accuracy of radiolocations, we defined a 100-m edge around all lakes as potential seepage sites, which we expected to influence stand structure and composition. Non-forested alpine tundra encompassed all habitats above treeline, excluding extensive areas of rock and ice. Terrain variables included elevation and slope, and aspect was represented by 2 continuous (0 to 1) variables depicting north to south and east to west aspects. A terrain ruggedness index was derived by adapting a technique (Beasom et al. 1983) for GIS using elevation contours to yield a continuous (0 to 1) variable that is relative to the scale of contour data and pixel size. All GIS applications employed the raster-based software Idrisi for Windows 2.01 (Clark Labs 1997).

Our analysis design conformed to Thomas

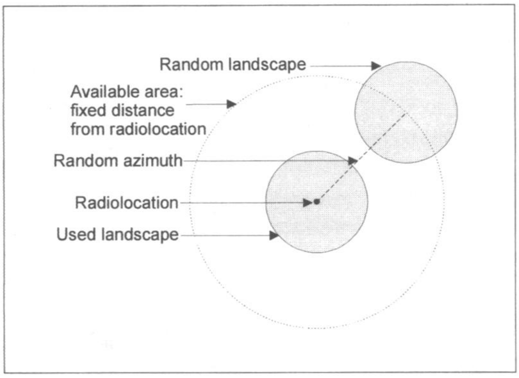

Fig. 3. Scale-dependent design for analyzing mountain caribou habitat selection in the north Columbia Mountains, British Columbia.

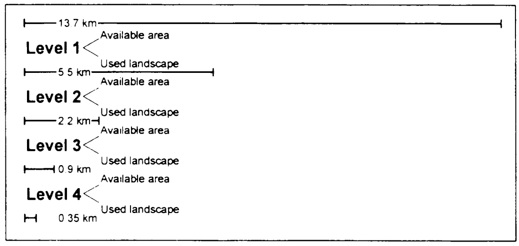

Fig. 4. Hierarchical scales considered in analyzing mountain caribou habitat selection in the north Columbia Mountains, British Columbia, 1992—99. Scales were defined by radii of available areas and landscape composition. The radius of available area was the distance from caribou radiolocations at which landscapes were randomly sampled. The landscape radius was that within which habitat composition was defined.

and Taylor's (1990) study design 2, with inferences relevant at the population level. We considered our study animals a representative sample of the population, each of which was located with similar frequency (radiolocations per animal: maximum = 184, $\bar{x}$ = 63 ± 49; 1 SD). We therefore pooled radiolocation data among caribou, as is appropriate where few locations are obtained from many animals (Manly et al. 1993).

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 the mean value of each variable 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 (Fig. 3). For some ungulates, radiolocation independence may be difficult to achieve for traditional space-use analyses (McNay et al. 1994). However, our scale-dependent design, based on caribou movement rates, defined areas for each radiolocation, within which we assumed that independent habitat choices had been made. At level 1, the broadest scale of analysis, caribou and paired random locations were separated by 13.7 km. We consider this the radius of the largest area potentially available to individual caribou, within our temporal sampling interval, because 95% of 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 measured (Fig. 4). At levels 2 to 4, random locations were generated at distances equivalent to the landscape radius at the previous level, and habitat composition was again measured in a circle of radius 0.4 times this distance. Although this multiplier is arbitrary, it ensured that the radius used to scale habitat composition at level 4, the finest scale of analysis, approximated our estimated 95% radiotelemetry error (see Results; Fig. 4). Moreover, the proportion of used landscape to available area was equal at all levels, and used landscapes did not overlap with respective random landscapes. Lands for which forest cover data were not available, and water bodies that do not freeze during winter, 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.

For each of the 20 variables (Table 2), we assessed univariate differences between landscapes caribou used and random landscapes, at each season and scale, using *t*-tests. Due to the number of variables (20) and levels (4) considered, all univariate tests were appropriately conservative ($\alpha = 0.05/(20 \times 4) = 0.000625$). For multivariate analyses, we employed multiple logistic regression to derive probabilistic resource selection functions (Trexler and Travis 1993, Manly et al. 1993) across all 4 spatial scales and for each caribou season. Model output was the probability (p) that the variable attribute combination at any given site defines caribou habitat. Caribou-used landscapes 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 to 13.7 km, spanning the 4 spatial scales.

We employed forward stepwise selection using the likelihood-ratio test (Hosmer and Lemeshow 1989) 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) log likelihood ratios, and we evaluated the significance of variable coefficients using chi-square tests of Wald statistics (Hosmer and Lemeshow 1989). Variables included in best-fit models were examined for multicollinearity using linear regression tolerance statistics (Menard 1995). Where collinearity occurred (tolerance <0.2; Menard 1995), 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.

RESULTS

Comparing our plotted collar locations to differentially corrected GPS locations showed 95% to be within 364 m ($\bar{x}$ = 148 ± 98; 1 SD). Comparing errors associated with locating and plotting dropped collars, as measured by non-differentially corrected GPS in the helicopter ($\bar{x}$ = 225 ± 106 m), to errors of plotting locations of simulated observed animals ($\bar{x}$ = 287 ± 175 m) suggested that most of the radiolocation error was due to the inaccuracy of plotting locations in extensive and often homogeneous forest types.

Mountain caribou univariate habitat selection varied across scale and by season for most variables (Table 3). However, overstory stands of >140 years were consistently selected over ≥3 scales during all seasons. During early winter, broad-scale preferences were for low elevation landscapes of gentle slope and terrain. Forests were of very young and old ages, high canopy cover and productivity, and primarily cedar, hemlock, and Douglas-fir (*Pseudotsuga menziesii*) composition. At level 3, caribou still preferred old cedar and hemlock forests of relatively high canopy closure and productivity, but also preferred southerly aspects. At the finest scale, caribou preferred high canopy closure and avoided youngest stands. During late winter, broadest-scale preferences were also for gentle terrain and old forests of higher canopy cover and site productivity than random. However, at level 2, caribou preferred landscapes of high elevation, low site productivity, and low canopy closure. Alpine was avoided at the broadest scale but was preferred at level 2. Northerly aspects were preferred at levels 1 and 2. Old, high elevation forests of subalpine fir and spruce composition were preferred across most scales, while subalpine fir stands associated with high elevations of gentle slope and terrain were preferred at the finest scale. During spring, caribou preferred, across most scales, low elevation landscapes of high site productivity, high canopy cover, high seepage, and very old forests of primarily spruce, cedar, and hemlock composition. Preferred landscapes were associated with very young forests only at levels 1 and 2. We noted little selection at level 4, with the exception of low elevations and gentle slopes. During summer, caribou preferred old subalpine fir and spruce forests of high canopy closure and site productivity across most or all scales. North and east aspects were preferred at broad scales, and gentle slopes were preferred at fine scales.

All best-fit seasonal multiple logistic regression models were significant (χ^2 > 245.6, df ≥ 7, P < 0.001). Overall classification success of used and random locations (habitat probability cutpoint p = 0.5) was 66.5% for early winter, 69.3% for late winter, 67.5% for spring, and 67.8% for summer (Table 4). The predictive subset of variables that best described caribou habitat selection represented all scales for each seasonal model except summer, within which level 1 was not represented (Table 4). Model performance across cutpoint habitat probability values suggested that optimal discrimination occured at p = 0.4–0.5 for early winter and late winter, p = 0.4 for spring, and p = 0.5 for summer (Fig. 5).

DISCUSSION

Our early winter results contrasted sharply with those from more northern areas within mountain caribou range. There, caribou preferred higher elevation forests dominated by

Table 3. Univariate analysis results[a] of scale-dependent habitat selection by mountain caribou in the north Columbia Mountains, British Columbia, 1992–99.

Variable[b]	Early winter				Late winter				Spring				Summer			
	1[c]	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	−	o	o	−−−	o	o
AGE-6–7	o	+	+	o	o	−	o	o	o	+	o	o	o	+	o	o
AGE-8–9	+++	+++	+++	++	+++	+++	+++	++	+++	+++	+++	o	+++	+++	+++	+++
SPP-S	+++	+	o	−	+++	+++	+++	o	+++	+++	++	o	+++	+++	+++	++
SPP-B	o	−−−	−−−	−−	+++	+++	+++	+++	o	o	−−−	−−	+++	+++	+++	+++
SPP-C	+++	+++	+++	o	o	−−−	−−−	−−−	+++	+++	+++	o	o	−−−	−−−	o
SPP-H	+++	+++	+++	++	o	−−−	−−−	o	+++	+++	+++	o	o	+++	+++	o
SPP-P	+++	++	+	+	−−−	−−−	−	o	+	+	o	o	−−−	−−−	o	o
SPP-DEC	+++	o	o	o	−−−	−−−	−	o	o	o	o	o	−	−−−	−−	o
SPP-FD	+++	+++	++	o	−−−	−−−	−−−	−	+++	o	−	o	−−−	−−−	−−−	−−
ALPINE	−−−	−−−	−−−	−	−−−	+++	o	o	−−−	−−−	−−−	o	−−−	−−−	−−−	−−
CANOPY	+++	+++	+++	+++	+++	−−−	−−	o	+++	+++	+++	o	+++	+++	+++	+++
SITE	+++	+++	+++	o	+++	−−−	−−−	o	+++	+++	+++	+	+++	+++	+++	++
SEEPAGE	+++	+++	o	o	o	−−−	+	++	+++	+++	o	o	o	−−−	−−	o
ELEV	−−−	−−−	−−−	o	o	+++	+++	+++	−−−	−−−	−−−	−−−	o	o	o	o
SLOPE	−−−	−−−	o	o	−−−	−−	−−−	−−−	−−	−−	−−−	−−−	o	−	−−−	−−−
SOUTH	+	o	+++	+	−−−	−−−	o	o	o	−−−	o	o	−−−	−−−	−−	o
WEST	−−	−−−	−	o	−−	o	+	o	−	−−	o	o	o	−−−	o	o
TERRAIN	−−−	−−−	o	o	−−−	−−	−−−	−−−	−	o	−	o	o	−−−	−−−	−−

[a] Preference or avoidance (*t*-tests) is indicated by +++/−−− ($P < 0.000625$), ++/−− ($P < 0.00625$), +/− ($P < 0.0625$), or "o" ($P \geq 0.0625$).
[b] See Table 1.
[c] Analysis level: broad (1) to fine (4) spatial scales.

Table 4. Variables and parameters ($P \leq 0.05$ unless indicated otherwise) associated with best-fit multiple logistic regression models ($P < 0.001$) of seasonal mountain caribou habitat selection in the north Columbia Mountains, British Columbia, 1992–99.

Season	Variable[a]	Level[b]	β	SE
Early winter	ELEV	2	−0.001	0.000
	AGE-8–9	4	0.008	0.002
	SPP-B	3	−0.022	0.006
	AGE-8–9	2	0.014	0.004
	AGE-6–7	3	0.019	0.006
	CANOPY	3	0.015	0.005
	AGE-3–5	1	0.020	0.007
	SOUTH	3	0.008	0.003
	Constant[c]		−0.145	0.365
Late winter	SPP-B	4	0.016	0.003
	SLOPE	4	−0.034	0.003
	SPP-C	4	−0.041	0.007
	CANOPY	1	0.044	0.008
	SITE	3	−0.067	0.010
	SLOPE	1	0.032	0.008
	SPP-P	1	−0.207	0.053
	AGE-8–9	4	0.007	0.002
	AGE-8–9	2	0.008	0.003
	WEST	3	0.005	0.002
	Constant		−1.337	0.451
Spring	ELEV	4	−0.002	0.000
	AGE-8–9	2	0.017	0.004
	CANOPY	1	−0.048	0.011
	SPP-FD	3	−0.053	0.012
	SITE	3	0.056	0.015
	AGE-6–7	2	0.055	0.017
	AGE-6–7	4	−0.019	0.009
	Constant		2.509	0.389
Summer	SLOPE	4	−0.029	0.004
	SLOPE	2	0.027	0.006
	SPP-C	3	−0.043	0.006
	SPP-FD	2	−0.126	0.024
	AGE-8–9	4	0.008	0.002
	SPP-B	4	0.013	0.003
	ELEV	2	−0.001	0.000
	CANOPY	3	0.012	0.004
	WEST	2	−0.010	0.004
	SPP-H	4	0.007	0.003
	SOUTH	2	−0.009	0.004
	Constant		1.477	0.551

[a] See Table 1.
[b] Indicates spatial scale of variable, from broadest (1) to finest (4).
[c] $P = 0.690$.

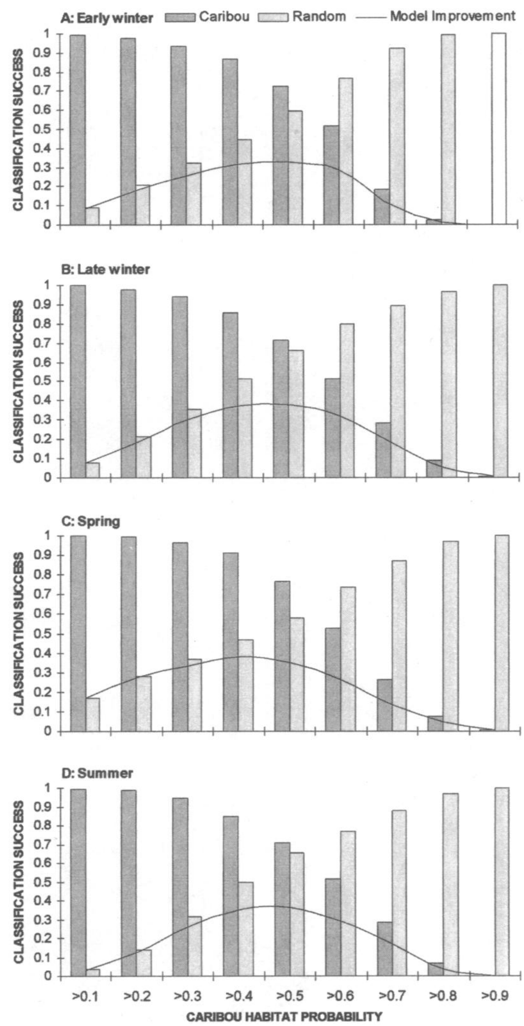

Fig. 5. Predictive efficiency of seasonal mountain caribou habitat models across cutpoint probability levels in the north Columbia Mountains, British Columbia. The model improvement curve indicates the proportion of correctly classified caribou locations minus incorrectly classified random locations, and defines each model's optimum cutpoint in discriminating caribou habitat from non-habitat.

subalpine fir and spruce during this season (Seip 1990, Terry et al. 2000), whereas north Columbia caribou avoided landscapes of high subalpine fir composition at all but the broadest scales and avoided high elevations at all but the finest scale. Even at the southern extreme of their distribution, mountain caribou used higher elevation forests of subalpine fir and spruce during early winter (Servheen and Lyon 1989, Rominger and Oldemeyer 1989) more than did caribou in our study area. Heavier snowfall in the Columbia Mountains (Demarchi 1996) may explain caribou preference for low elevation forests in 2 ways. First, higher costs of locomotion in unconsolidated, early winter snow may preclude the use of high elevations with typically deeper snow (Antifeau 1987). Second, because arboreal lichen only occurs above the height of the deepest winter snowpack (Goward 1998), this important food will be less available during early winter at all elevations where total snow accumulation is greater. This lack of available lichen on standing trees may force caribou to forage for lichen as litter fall and on fallen trees, or for shrubs such as falsebox, in closed canopy forests at low elevations where ground accumulation of snow is minimized. Moreover, predators may be fewer and less efficient in high snowfall regions, permitting greater use of low elevations by caribou (Terry et al. 1996).

As winter typically progresses, snow accumulation at low elevations prevents cratering for low-growing forage, while the high elevation snowpack deepens and settles, providing a supportive base for caribou to access arboreal lichen on standing trees (Stevenson et al. 1994). At broad scales, late winter associations with terrain, old forests, canopy cover, and site productivity were similar to early winter, but preferences for high elevations, spruce, subalpine fir, and northerly aspects was consistent with the expected change in foraging strategy. The discordant selection for alpine between levels 1 and 2 during late winter indicated that seasonal ranges were closely associated with relatively open, high elevation stands within the alpine-forest ecotone. Across all or most scales, preferences for gentle slopes at high elevations, and old, open subalpine fir stands of low productivity was consistent with mountain caribou across their distribution (Servheen and Lyon 1989, Seip 1990, Terry et al. 2000).

During spring, caribou preferred broad landscapes similar to those preferred during early winter in that they were associated with low elevations, high productivity, and old and young forests of spruce, cedar, hemlock, and Douglas-fir, with high canopy closure. However, the broad landscapes preferred during spring were associated with more rugged and steeper terrain than those preferred during early winter. This may explain finest-scale preferences for low elevations and gentle slopes during spring. Unlike early winter, spring results suggested that caribou used old forests and young plantations where emerging vegetation was first available, as reported in the Southern Selkirk Mountains (Servheen and Lyon 1989).

Mountain caribou foraging behavior generally is not limited by snow during summer. During this season, elevation was not a significant factor at any of the 4 scales, but old spruce and subalpine fir forests of high canopy closure on productive sites were preferred across scales. Northerly aspects were preferred at all but the finest scale, while gentle terrain was preferred at all but the broadest scale. These habitat selection patterns suggested that caribou may be responding to heat stress during summer. Although there was no clear association with elevation, caribou appeared to prefer landscapes and stands that would normally be associated with cooler conditions.

Across seasons, habitat selection at the finest scale (level 4) was detected among fewer variables than at broader scales. For the variables we have considered, selection should be detectable at this scale because the fixed distance of random locations was well beyond the radius of the minimum mapping unit, and used landscapes did not overlap with paired random landscapes. However, we expect that the scales at which specific attributes are selected will largely relate to their pattern of distribution in a given study area. Fine-scale selection may not be apparent if caribou are using broader landscapes within which attribute presence or absence is evenly dispersed. However, given that the energetic cost of access is typically lower for proximal versus distant habitats, foraging theory (Stephens and Krebs 1986) would suggest that caribou habitat use is more likely to vary at finer versus broader scales.

Results of our broad-scale analyses must be interpreted with caution as they are subject to the same limitations as traditional Type 1 (Thomas and Taylor 1990) analysis designs that define availability at the scale of some greater study area, often arbitrarily defined. In particular, mountain caribou habitat use may be largely influenced by traditional or historic factors, resulting in a lagged response to short-term habitat change. However, we expect that as our scales of investigation became finer, our results reflected habitat choices made by caribou over shorter time frames. This illustrates how a scale-dependent design may better discern actual preferences of species that are long-lived and wide ranging, or where habitat use is also influenced by conspecific-social or human factors.

Our best-fit multiple logistic regression models suggested that a linear combination of variables can efficiently discriminate caribou use from random locations across scales, and therefore resulting models are useful predictors of habitat quality for mountain caribou. During each season, the scales at which the best predictive variable subsets were represented indicated that models explained broad and fine-scale variation in the data. However, they have

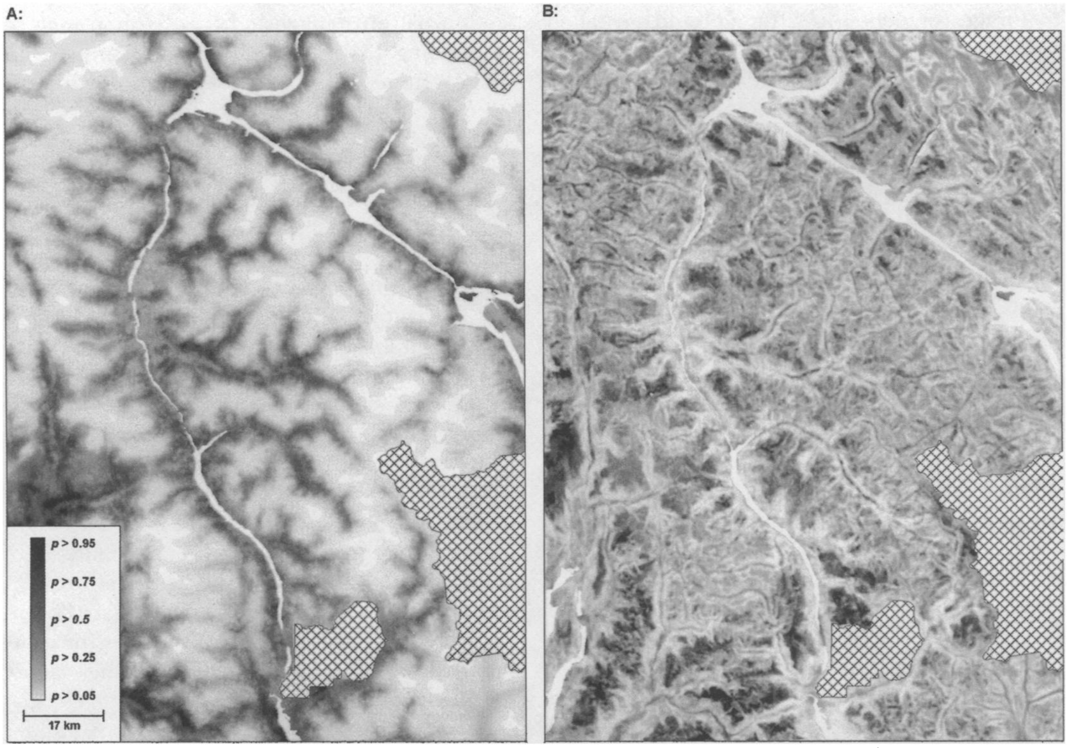

Fig. 6. Multiple logistic regression models of predicted caribou habitat selection during early winter (A) and late winter (B) within the north Columbia Mountains study area, British Columbia, 1992—99. Images depict a continuum of values reflecting caribou habitat selection probability.

not yet been validated with independent data. Meaningful validation requires data from different animals over several different years, which was not possible to obtain from our current dataset. Although verification with additional data is planned, we are confident in the predictive veracity of our interim seasonal models, a reflection of our spatial and temporal sampling extent which we assume has captured the expected variation in mountain caribou habitat selection within our study area. 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 north Columbia Mountains (Fig. 6).

MANAGEMENT IMPLICATIONS

Our results were consistent with seasonal foraging strategies expected for mountain caribou in an area with rugged mountains and a deep snowpack. However, the scale-dependent nature of certain relationships offers additional insight into their ecology and probable requirements in the Columbia Mountains. During all seasons, our results confirm the close association of this caribou ecotype with old forests. There is considerable demand for such stands by the forest industry, particularly those associated with low elevation, early winter caribou habitats. Although the conflict between caribou habitat and forestry is less during late winter, some stands associated with late winter habitats are also of high timber value. With increasingly efficient, cost-effective extraction technologies and reduced timber supply at lower elevations, a heightened management conflict can be expected during this season. Because suitable late winter foraging habitats are naturally disjunct, additional fragmentation may quickly negate landscape value to caribou, with long-term consequences given the lengthy rotations associated with high elevation forest management. In addition, landscape attributes associated with late winter habitats of caribou often coincide with those associated with recreational snowmobile activity, which may displace caribou from otherwise suitable habitat (Simpson 1987). Increased snowmobile access to late winter habitats may be facilitated by road building for high elevation timber extraction.

The landscape distribution of suitable stands may influence caribou energetic requirements during foraging (Parker et al. 1984) and predation risk (Seip and Cichowski 1996). That landscapes of greater old-growth forest composition were invariably preferred at levels 1 to 3 suggests that old-growth forest dispersion should be managed at several scales up to ≥100 km^2. However, despite the fundamental importance of this variable, managers must account for the entire combination of attributes associated with the preferred landscape matrix, which vary by scale and season.

Our results have been incorporated into the land-use plan for the Columbia Mountains (Province of British Columbia 1997). For strategic planning we defined 2 levels of habitat quality from the seasonal habitat models (i.e., $p > 0.4$ and $p > 0.6$). Although arbitrary, these probability cutpoints provide a somewhat liberal and conservative allocation of caribou habitat respectively, and all models performed relatively well at each. This provided a basis for delineating the location of early- and late-winter habitats at a 1:250,000 scale, within which old and mature forest retention guidelines were applied. At operational scales of 1:20,000, managers must ensure that the old and mature forest retention is consistent with fine-scale caribou habitat preferences, requiring that old forest types are not fragmented by young stands.

When incorporated in a spatially explicit timber supply model, our predictive multiple logistic regression models should assist managers by projecting potential impacts of alternative management scenarios through space and time. Yet, because our analyses were exploratory, prescriptive management from our results requires discretion. As with traditional habitat selection analysis designs, our results are dependent on the range and distribution of each variable at each scale (Porter and Church 1987), and the applicability of our models beyond the north Columbia Mountains is uncertain. Ultimately, a better understanding of the functional mechanisms behind the relationships we describe, and the range of tolerance of mountain caribou to the spatial dispersion of various attributes requires comparison among subpopulations subject to different types and levels of natural and human conditions. Only through comparison and replication of results across time and space can behaviors that are of adaptive significance and of probable requirement be inferred (Ruggiero et al. 1988).

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HABITAT USE BY FEMALE CARIBOU: TRADEOFFS ASSOCIATED WITH PARTURITION

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Abstract: We compared habitat use, forage characteristics, and group size among preparturient, parturient, and nonparturient female caribou (*Rangifer tarandus*) during and after the birthing season to test hypotheses involving acquisition of forage and risk of predation. We monitored 39 radiocollared females from the Mentasta caribou herd, Alaska, in 1994 and 40 animals in 1995. Group size of females giving birth at higher elevations was smaller ($P < 0.01$) than females without young that occurred at lower elevations at peak parturition; that difference did not persist into post parturition ($P > 0.5$). During peak parturition, females with young used sites with fewer predators ($P < 0.05$), a lower abundance of forage ($P < 0.05$), but with variable forage quality compared with those sites used by females without young. We hypothesized that parturient females used birth sites that lowered risk of predation, and traded-off forage abundance for increased safety. Nonetheless, few differences existed between parturient and nonparturient females in composition of diet or in indices of diet quality; we could not demonstrate a nutritional cost to maternal females from our analyses. We suggest that increasing population density might intensify intraspecific competition among females for birth sites, and thereby increase nutritional costs of using high-elevation areas with less forage but fewer predators.

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Key words: Alaska, caribou, diet, forage abundance, forage quality, group size, habitat use, parturition, predation risk, *Rangifer tarandus*, tradeoffs.

Acquiring resources necessary to survive and reproduce is a major component of fitness and constrains the types of habitats used by mammals (Fryxell and Sinclair 1988, White et al. 1997, Bowyer et al. 1998*a*). Among large herbivores, habitat selection often is related to availability and quality of forage (Klein 1970, Skogland 1980, Bowyer 1986, Albon and Langvatn 1992, Cameron et al. 1993), but also can depend upon other factors, such as mineral re-

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