WINTER HABITAT SELECTION AND FORAGING PATTERNS OF MOUNTAIN CARIBOU

by

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ABSTRACT

Winter habitat use and foraging patterns of mountain caribou (Rangifer tarandus caribou) were studied in the North Cariboo Mountains near Prince George, British Columbia. Radiotelemetry data indicated caribou used balsam-spruce stands (1373-1677 m) extensively during the early winter (Nov-Dec) period. During late winter (Jan-Apr) caribou shifted to higher elevation subalpine parkland habitats, however, mid-elevation balsam-spruce stands continued to be used extensively in 1992-93 when snow accumulation was below normal. A hierarchical analysis of caribou foraging decisions (following caribou tracks in snow) during the early winter suggested caribou are using balsam-spruce forests in a random manner as they search for recently windthrown trees. Caribou appeared to make coarse-grained (i.e., non-random) decisions at relatively large spatial scales including home range selection (Engelmann Spruce-Subalpine Fir biogeoclimatic zone) and habitats (balsam-spruce) within home ranges. These findings suggest that macro-habitat characteristics (elevation, forest cover type and slope) may be better predictors overall of caribou use than are micro-habitat characteristics. Forest managers should attempt to provide large contiguous stands of ESSF forests during landscape-level planning, as well as travel corridors to facilitate seasonal movements. Maintaining large contiguous stands of ESSF forests should allow caribou to forage extensively as they search for sparsely distributed windthrown trees. Alternative silvicultural systems (i.e., selection cutting) may maintain caribou foraging habitat if the prescription is conservative with respect to residual basal area and tree density. Maintaining pre-harvest species composition, live to snag ratios and a range of diameter classes with abundant arboreal lichens is recommended.

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PART 1. MACRO-HABITAT SELECTION

Introduction

Woodland caribou (*Rangifer tarandus caribou*) that feed on arboreal lichens in winter ("mountain caribou" ecotype) have been identified as an old growth dependent species and remain a provincial research and management priority as conflicts related to forest harvesting increase (B.C. Environment 1989, McKinnon 1994, Stevenson et al. 1994).

Clearcut harvesting of forests has been perceived to be incompatible with maintaining winter habitat and caribou populations primarily because mountain caribou depend almost exclusively on mature lichen-bearing trees for winter forage (Stevenson and Hatler 1985, Child et al. 1991). In response to conflicts associated with clearcut harvesting, numerous radio-telemetry studies have been conducted to determine habitat use and seasonal movement patterns (Antifeau 1987, Simpson and Woods 1987, Rominger and Oldemeyer 1989, Servheen and Lyon 1989, Seip 1990, 1992a). These studies have reported the early winter period (Nov-Jan) as a critical time for caribou as they descend from high elevation subalpine habitats to lower elevations seeking accessible forage and better snow conditions. As a result, the early winter period is also where the majority of caribou-forestry conflicts occur. During these months caribou use commercial forests dominated by balsam-spruce and/or low elevation hemlock-cedar stands.

In an effort to obtain more region-specific information, the Ministry of Environment Lands and Parks (Prince George Region) initiated the Mountain Caribou in Managed Forest Program (MCMF) in 1988. The MCMF's main goal was to seek integrated solutions to the caribou-forestry conflict. As a component of the program, a radio-telemetry study was undertaken east of Prince George to determine seasonal movements and habitat selection patterns. This section reports the results of the radio telemetry study and focuses on winter habitat use. Use-availability analyses were used to investigate 2 levels of selection: (i) selection of the winter home range, and (ii) selection of habitats within the home range *(sensu* Johnson 1980).

The null hypotheses under investigation were caribou use habitats, aspects, and slopes in a random manner (i.e., in proportion to availability). The alternative hypotheses were caribou use at least one habitat, aspect or slope more or less than its occurrence.

Study Area

The study area was located 80 km east of Prince George, B.C. (51°N, 120°W) and covered a large geographic area (15,000 km²) encompassing portions of the Fraser River watershed. This area included the more subdued plateaus of the northern part of the Cariboo Mountains south of the Yellowhead Highway 16 and parts of the McGregor Plateau and Rocky Mountains to the north (Fig.1). Elevations in the Fraser Plateau, McGregor Plateau and the Cariboo Mountains range from 650 - 2200 meters. The landscape is dominated by four biogeoclimatic zones: Sub-Boreal Spruce (SBS) in the valley bottoms; Interior Cedar Hemlock (ICH) located above the SBS to approximately 1150 m; Engelmann Spruce-Subalpine Fir (ESSF) between 1150-1800 m, and the Alpine Tundra (AT) above 1800 m (Meidinger et al. 1984, Coupé et al. 1991). North of Highway 16 the McGregor range, Bearpaw ridge and Mt. Severeid contain SBS, ICH, ESSF and AT biogeoclimatic zones, whereas the Captain Otter and Dezaiko Ranges are occupied by SBS, ESSF and AT.



Figure 1. Map of the study area and composite caribou winter ranges (1-9).

1 = Captain-Otter; 2 = Dezaiko-Herrick; 3 = Mt.Severeid; 4 = Bearpaw ridge;

5 = Sugarbowl-Raven Lake; 6 = George Mtn; 7 = Narrow Lake; 8 = North Haggen; 9 = South Haggen. Boundaries are 95% harmonic mean isopleths for composite winter ranges. Stipled areas represent winter ranges or portions of winter ranges that contain an ICH zone.

South of Highway 16, the Sugarbowl and North Haggen ranges contain all four biogeoclimatic zones, whereas, Narrow Lake, George Mtn. and the South Haggen ranges do not contain an ICH zone. The ESSF zone supports predominately mature (>140 years old) forests (age classes 7,8,9; MoF forest stand map classification) and is dominated by subalpine fir (Abies lasiocarpa) and Engelmann spruce (Picea engelmanni). ESSF forests form a relatively closed canopy at low and mid elevations, and open canopy stands at higher elevations where trees tend to grow in clumps forming parkland conditions. Characteristic shrub species found in the ESSF include white-flowered rhododendron (Rhododendron albiflorum), oval-leaved blueberry (Vaccinium ovalifolium), and black huckleberry (Vaccinium membranaceum). Mean annual precipitation in the ESSF is approximately 1327 mm (889-1878 mm) most of which falls as snow. Snowpacks of 1.0 - 3.5 m are common at high (≥ 1500 m) elevations. The dominant land use activity is timber harvesting. Clearcut blocks (70-1300 ha) are common and distributed throughout the study area, predominately in low elevation valley bottoms. High elevation (1200-1650 m) cutblocks are present but dispersed. In the south por2tion of the study area (Bowron Valley) extensive salvage timber harvesting (50,000 ha) took place between 1980-1985 to eradicate a spruce-beetle (Dendroctonus spp.) infestation. This area is currently supporting immature plantation forests (<20 years old) dominated by interior spruce (*Picea* spp.) and lodgepole pine (*Pinus Contorta*).

Moose (Alces alces) are common in the study area, but are found primarily in lower elevation habitats (SBS and ICH). Wolves (Canis lupus), wolverine (Gulo gulo), black bears (Ursus americanus) and grizzly bears (Ursus arctos) are present in the study area, but densities are unknown.

Methods

Radio-Telemetry

Thirty adult caribou (24 female, 6 male) were captured by net-gun from a helicopter in March 1988 and fitted with radio transmitters (Telonics freq 151. MHz). Six additional adult caribou (5 female, 1 male) were collared throughout the study period to replace those that died. Collared caribou were assumed to be a representative sample of the approximately 700-1,000 caribou that make up the Yellowhead population.

Caribou were located approximately once each month between March 1988 and December 1991 from a Cessna 172 fixed wing aircraft. However, during the 1992-93 field season (Oct-Feb), I confined the monitoring to one winter range (Sugarbowl-Raven Lake) and relocated 11 collared adult female caribou once a week using a Bell Jet Ranger Helicopter. Monitoring was conducted in this intensive study area to facilitate sample points for ground trailing (see Part 2) and assess the use of lower elevation habitats. Ninety-one early and 54 late winter locations were obtained.

During the early and late winter periods, 28% and 49% of the relocations respectively, included a visual sighting of the collared animal. Topographic attributes including elevation, aspect, and slope were recorded and each location marked on a 1:250,000 topographic map.

Habitat Analysis

I separated the winter months (15 October - 15 April) into early winter and late winter based on caribou movements. Early winter (15 October - 15 December) commenced when caribou moved from high elevation summer ranges to lower elevations and usually coincided with the first persistent snowfall. The late winter period (16 December - 15 April)

commenced when radio-collared caribou had made altitudinal shifts from mid-elevation early winter habitats to higher elevation subalpine parkland habitats.

The commencement and duration of each winter period varied with snow accumulation rates and years, but the core early winter period usually occurred between November and December. The exception was 1992-93 when snow accumulation was slow and below normal which extended the early winter period to approximately 18 January. Late winter usually ended in late March or April.

Caribou Use

To determine habitats caribou used, caribou locations (UTM co-ordinates) were plotted on 1:15,000 forest cover type maps and forest stand descriptions recorded. Locations were checked against 1:15,000 black and white photographs and placed in one of the following 8 habitat categories: (1) alpine; (2) subalpine parkland; (3) balsam; (4) balsam-spruce; (5) spruce-balsam; (6) cedar-hemlock-spruce; (7) immature forests [recent clearcuts, Not-Sufficiently Restocked (NSR) land (i.e., plantations <20 years old, burns, stands < 120 years)]; (8) non-forest (i.e., brush, swamps, meadows). Low elevation forest stands leading in cedar, hemlock or spruce were grouped together to represent the ICH forest communities and to minimize the number of habitats used in the analysis (Alldredge and Ratti 1986) *Habitat A vailability*

Small sample sizes of relocations during 1988-91 necessitated pooling data across years and individuals for each winter period which produced composite winter ranges. Each composite winter range (n = 9) contained 2-9 collared caribou and 20-50 locations per range. Winter ranges were delineated using the harmonic mean (Dixon and Chapman 1980) estimator

generated from the computer program HOME RANGE (Ackermann et al. 1990). Although all home range estimators are subject to sample size bias and lack of precision (Boulanger and White 1990), the harmonic mean estimator was used in this study because it assumed no underlying distribution, and caribou locations were clustered which indicated core areas of habitat use. The 95% isopleth was used as the delineation boundary for overlay on 1:50,000 forest cover type maps to determine the availability of habitat types within the winter ranges. The 95% contour was adequate for seven of the ranges, however, two ranges with small sample sizes (n = 20) resulted in extensive range boundaries that included large areas of low elevation habitat (SBS) with no caribou locations. To improve the delineation of these two wintering areas, I used the 65% harmonic mean isopleth. I estimated the availability of habitats by plotting random points (Marcum and Loftsgaarden 1980); 100-150 random points per winter range stabilized proportions $\pm 1\%$ and were pooled. Topographic attributes (aspect, slope) were estimated in the same manner using 1:50,000 topographic maps. Percent slope was grouped into the following categories: $\leq 15\%$, 16-30%, 31-45%, >45%.

Selection of Winter Ranges

To determine selection of winter ranges, the proportion of biogeoclimatic zones present within the home range boundaries were compared to the availability of biogeoclimatic zones throughout the study area using the chi-square test of homogeneity (Marcum and Loftsgaarden 1980). Estimates of availability throughout the study area were determined by plotting random points (n = 1200) on 1:250,000 biogeoclimatic maps (Ministry of Forests, B.C.). Habitat composition within winter home ranges was determined by overlaying each composite winter home range boundary (n = 9) on 1:250,000 biogeoclimatic zone maps using

approximately 50 random points. These were pooled (n = 437) and compared to availability throughout the study area.

Statistical Analysis

Habitat selection patterns during the early winter period were similar for both extensive (1988-91) and intensive (1992-93) monitoring periods (P > 0.05) so locations were pooled across years (1988-92) and individuals.

Because not all of the ranges contained the same habitat types, pooling all ranges would have violated one of the assumptions of the chi-square test (i.e., habitat availability is the same for all animals). To meet this assumption, composite winter ranges were stratified into two groups according to the availability of forest cover types: (1) Cedar-Hemlock stands present (CHP) within winter range; (2) Cedar-Hemlock stands absent (CHA) within winter range (see Fig.1). If more than one collared caribou were relocated together, then only one of the locations was included in the analysis to meet the independent sample assumption of the chi-square test (Alldredge and Ratti 1986, 1992). Because relocation intervals were relatively long, (monthly 1988-91, weekly 1992-93), samples were considered statistically independent. Contingency tables were used to determine interactions of variables. Chi-square tests of homogeneity were used to compare resource use to estimated availability (Thomas and Taylor 1990). If resource use differed significantly from availability, Bonferroni confidence intervals were constructed to determine which forest cover types, aspects, and slope classes were used to a greater or lesser extent than availability (Marcum and Loftsgaarden 1980). The null hypotheses under investigation were: H_0 : caribou use forest cover types, aspects and slopes in proportions equal to their availability while the alternative hypotheses using the chi-square

test is: H_a : at least one forest cover type, aspect, slope class is used more or less than availability. All statistical tests were considered significant at $\underline{P} \le 0.05$.

Because the inclusion of habitats that comprise a large proportion of a home range but are infrequently used can lead to inflated chi-square estimates of preference (Johnson 1980, Aebischer et al. 1993, Manly et al. 1993), I also used Manly's standardized selection ratio to compare conclusions to the chi-square analysis. Conclusions regarding preference or avoidance using standardized selection ratios have the advantage of being robust to errors from inclusion of infrequently used habitats..

Manly et al. (1993) standardized selection ratio (SSR):

 $SSR = \hat{w}_i / (\sum_{j=1}^{I} \hat{w}_j)$

where,

$\hat{w}_i = \frac{proportion(use)}{proportion(available)}$

in habitat_i. This standardized form of selection ratios add to 1 and therefore can be interpreted as the estimated probability that a habitat would be selected if all habitats were equally available (see Manly et al. 1993 pp. 40-52).

RESULTS

Seasonal Movements

Elevation shifts occurred twice annually with caribou descending to lower elevations in November and again in May as they migrated between summer and winter ranges. During the early winter period caribou used ESSF forests almost exclusively, particularly forest stands between 1373-1677 m elevation. By late winter (Jan-Mar), caribou were located most often in stands above 1526 m elevation (Fig. 2).

Although the relatively long interval between relocations precludes any definitive statements regarding daily or weekly movements, some general movement patterns were evident on a seasonal basis. Most of the radio-collared caribou (19 of 36) were very unpredictable in their movement patterns. Although they made seasonal migrations (10-40 km), summer and winter ranges were interchangeable and varied between years. About one-third (11 of 36) of the collared caribou also made seasonal migrations (10-40 km) between summer and winter ranges, however, winter and summer ranges did not overlap indicating a more distinct migration pattern. Multi-annual home ranges averaged 438 km² (range = 164-745 km²). Only 6 radio-collared caribou did not migrate but used the same area for both summer and winter range. Consequently, these caribou had annual home ranges that were relatively small compared to migrators (mean = 110 km²; range 83-133 km²).

Selection of Winter Ranges

This level of analysis confirms the importance of the ESSF relative to other forest communities available throughout the study area. Although ESSF forests comprised about 46% of the study area, a minium of 80% of early and late winter caribou ranges included AT-ESSF and ESSF forests - predominantly mature (>140 years old) balsam and balsam-spruce stands. The ICH and SBS biogeoclimatic zones represented a very small proportion (<7%) of caribou winter ranges (Fig. 3).



Figure 2. Percent of caribou locations showing monthly elevational use for the Yellowhead population, Prince George, British Columbia 1988-93. Number of locations given above bars.



Figure 3. Composition of caribou winter ranges within the study area. Yellowhead population, Prince George, British Columbia. "+" indicates caribou winter ranges included a significantly greater proportion of a biogeoclimatic zone compared to the availability throughout study area; "-" indicates caribou winter ranges comprised a significantly smaller proportion. winter home ranges n = 437; study area n = 1200.

Selection of Habitats within Winter Ranges

Forest Cover Types

Habitat use differed significantly between early and late winter for both CHP ($\underline{X}^2 =$ 74.0, 7 df, P < 0.001) and CHA ($\underline{X}^2 = 25.8$, 6 df, P < 0.001) winter ranges. Balsam-spruce was the most frequently (>50% locations) used habitat during the early winter whereas subalpine parkland and alpine habitats were used to a greater extent in late winter.

Caribou used balsam-spruce stands significantly more than their availability and immature stands significantly less in both winter range types (CHP: $\underline{X}^2 = 30.9$, 7 df, $\underline{P} < 0.001$; CHA: $\underline{X}^2 = 42.3$, 6 df, $\underline{P} < 0.001$). Spruce-balsam stands were used significantly less than their abundance in CHA ranges, but in proportion to their abundance in CHP ranges. Although lower elevation cedar-hemlock stands were used in proportion to availability, they were used infrequently (12/162 locations) (Fig. 4).

Late winter habitats were also used disproportionately (CHP: $\underline{X}^2 = 88.4$, 7 df, $\underline{P} < 0.001$; CHA: $\underline{X}^2 = 78.1$, 6 df, $\underline{P} < 0.001$). Although caribou continued to frequently use stands leading in balsam and balsam-spruce, only subalpine parkland habitats were used significantly more than their availability (Fig. 5).

In contrast, caribou used habitats in similar proportions between early and late winter during the low-snow winter ($\underline{X}^2 = 11.3$, 7 df, $\underline{P} = 0.127$). Although caribou increased their use of subalpine and alpine habitats during the late winter, they continued to use midelevation, balsam-spruce stands extensively (56% of 54 locations).



CHA

CHP

Figure 4. Percent of early winter (Nov-Dec) caribou locations in each forest cover type for CHP and CHA ranges. Prince George, B.C 1988-92. CHP: use = 162 random = 1032); CHA use = 112, random = 500. "+" indicates use is significantly greater than random; "-" indicates use is significantly less than random; no sign indicates no significant difference.



CHA

CHP

Figure 5. Percent of caribou locations in each forest cover type during late winter (Jan-Apr) for CHP and CHA winter ranges. Prince George, B.C. 1988-91. Cedar-hemlock present (CHP) ranges: use = 122; random = 428); Cedar-hemlock absent (CHA): use = 165; random = 526). "+" indicates use is significantly greater than random; "-" indicates use is significantly less than random; no sign indicates no significant difference.

Standardized Selection Ratios (SSR)

Selection ratios revealed habitat selection patterns consistent with the chi-square analyses for both winter periods (Table 1). Balsam and balsam-spruce forest types were identified as the most likely habitats to be used during the early winter, whereas subalpine parkland stands were the most likely habitat to be used during the late winter (1988-92). In late winter subalpine parkland habitats were 3 times (SSR_{parkland} = 0.497) as likely to be selected compared to the next most likely habitat (SSR_{balsam} = 0.153). In contrast, the probability of subalpine parkland being selected in the low-snow winter (1992-93) was about equal to balsam and balsam-spruce stands. Balsam-spruce stands were about 2.5 times (SSR_{balsam-spruce} = 0.261) as likely to be selected during the low-snow winter compared to previous late winters (SSR_{balsam-spruce} = 0.096).

A spect and Slope

Use of slopes and aspects did not differ between CHP and CHA ranges ($\underline{P} > 0.05$), so data were pooled for these analyses.

Caribou use of aspects were significantly different between early winter and late winter ($\underline{X}^2 = 19.55$, 7 df, $\underline{P} = 0.007$). Although caribou used north (27%) and south (25%) aspects the most during both winter periods, southwest aspects received greater use (14% of 271) during the early winter compared to late winter (6% of 341). Caribou used northeast aspects rarely during early winter (3% of 271), but increased their use (8% of 341) in late winter. In addition to seasonal variation, caribou did not use aspects in proportions equal to their availability during early winter ($\underline{X}^2 = 50.4$, 7 df, $\underline{P} < 0.001$) or late

	Early Winter (Nov-Dec) 1988-92	• • • • • • • • • • • • • • • • • • •
Habitat	SSR	
Balsam-spruce	0.232	
Balsam	0.231	
Subalpine Parkland	0.147	
Cedar-Hemlock-Spruce	0.127	
Spruce-Balsam	0.098	
Non-forest	0.095	• •

Table 1. Caribou use of forest cover types during winter using standardized selection ratios (SSR). Habitats are ranked according to their likelihood of use.

Late Winter (Jan-Apr)

0.035

0.032

	<u>1988-92</u>	1993 (low-snow winter)	
Habitat	SSR		SSR
Subalpine Parkland	0.497	Balsam-Spruce	0.261
Balsam	0.153	Balsam	0.234
Alpine	0.132	Subalpine Parkland	0.224
Balsam-Spruce	0.096	Alpine	0.206
Spruce-Balsam	0.024	Spruce-Balsam	0.075
Cedar-Hemlock-Spruce	0.007	Cedar-Hemlock-Spruce	0.000
Immature	0.000	Immature	0.000
Non-forest	0.091	Non-forest	0.000

SSR calculated as

Alpine

Immature

 $B_i = \hat{w}_i / (\sum_{i=1}^l \hat{w}_i)$

where \hat{w}_i = proportion use/proportion available.

winter ($\underline{X}^2 = 19.6$, 7 df, $\underline{P} = 0.007$). In early winter, caribou used southwest aspects in greater proportion than their abundance, whereas northeast, and east aspects were used significantly less than their abundance. Most aspects were used in proportion to their availability, during late winter, except for east aspects which were used significantly less than their availability (Fig. 6).

Caribou did not use slopes in significantly different proportions between early winter and late winter ($\underline{X}^2 = 7.9$, 3 df, P = 0.05). However, slope categories were used non-randomly ($\underline{X}^2 = 26.4$, 3 df, P < 0.001). Moderate slopes (16-30%) were used in greater proportions and moderately steep slopes (31-45%) were used less than their occurrence, other slope classes were used in proportion to their occurrence (Fig. 7).

Forest Productivity - Site Class (Good, Medium, Poor)

During the early winter, seventy-five percent of the radio-collared caribou were located in forest cover types rated as good, medium or poor for forest productivity. Within these, the majority of locations (85%) occurred on poor productivity sites and the remaining 15% on medium productivity sites. Caribou used all forest productivity classes in proportion to their abundance ($\underline{X}^2 = 3.37$, 2 df, $\underline{P} = 0.185$).



Late Winter

Early Winter

Fig. 6. Percent of caribou locations for each aspect category during the early (Nov-Dec) and late winter (Jan-Apr) periods. Prince George, B.C. early winter: use = 271, random = 525; late winter: use = 341, random = 525. "+" indicates significantly greater than random. "-" indicates significantly less than random.



Fig. 7. Percent of caribou locations for each slope class during winter (Nov-Apr). Prince George, B.C. use = 533, random = 750; "+" indicates significantly greater than random. "-" indicates significantly less than random.

DISCUSSION

Caribou clearly did not use habitats in proportion to their availability. Not only did their habitat use suggest selection was occurring for certain forest types and topographic features, but it was also evident that winter conditions influenced which habitats were used. Caribou used mid-elevation (1300-1600 m) balsam-spruce stands extensively during the early winter which is consistent with habitat selection patterns reported in the Quesnel Highlands of B.C. (Seip 1992a). In contrast, caribou use of forest cover types differed from more mountainous regions where caribou make extensive use of cedar-hemlock stands during the early winter (Simpson and Woods 1987; Servheen and Lyon 1989; Seip 1990; McLellan and Flaa 1993). In this study, caribou used these habitats infrequently. Only 6 collared caribou were located a total of 12 times between 1988-1993. These results are contrary to those of Bloomfield (1979), who studied mountain caribou (without telemetry) east of Prince George, and reported cedar-hemlock forests were a "major constituent of caribou range in the early winter". Admittedly, caribou travelled through cedar-hemlock forests as they migrated between winter and summer ranges, but the extent to which they used these stands as winter foraging areas appeared minimal. Reasons why caribou infrequently used low elevation cedarhemlock stands are not clear, but may be related to predator avoidance or lack of forage (Terry et al. 1994).

By mid-December or January caribou had moved to high elevation subalpine parkland stands. The elevational shift to subalpine parkland stands is consistent with all previous mountain caribou studies in British Columbia (Edwards et al. 1960; Bloomfield 1979; Antifeau 1987; Simpson and Woods 1987; Rominger and Oldemeyer 1989; Servheen and

Lyon 1989; Seip 1990, 1992*a*) and is likely related to the deep snowpacks (2-3 m) that enable caribou to reach lichen-bearing branches and forage exclusively on arboreal lichens. Although the sample was small, caribou in this study did not use subalpine parkland stands during the low-snow winter (1992-93) (13% of 54 locations) as much as they did in previous late winters (36% of 122). Instead, they continued to use balsam-spruce stands extensively. This difference between years may be attributed to the relatively shallow snowpack that occurred during the 1992-93 winter. Snow accumulation at this time was slow and high elevation snowpacks were 66% of normal (148 cm April 1, MOELP, Snow Survey 1993). Because relatively deep snowpacks are required before caribou are able to forage on arboreal lichens at these elevations, the low snowpack probably reduced arboreal lichen accessibility thus creating relatively poor foraging conditions in subalpine parkland stands. An apparent greater occurrence of windthrow and lichen litterfall in mid-elevation balsam-spruce stands (*pers. obs*) may also have kept caribou in these habitats during 1992-93.

The variable snow conditions between years suggests that the relative importance of mid-elevation balsam-spruce stands may increase in years when snow accumulation is slow and below that required to reach lichen-bearing branches. In years when snow accumulation is relatively rapid and firm enough to support arboreal foraging, high elevation subalpine parkland stands appears to be the preferred late winter range.

Because the majority of caribou used high elevation habitats with commercially marginal volumes, conflicts with timber harvesting should be minimal in late winter. Instead, snowmobilers and heli-ski operations probably pose a greater source of disturbance to caribou during the late winter (Simpson 1987).

Although there was a slight indication that caribou preferred southwest aspects during early winter and used east aspects infrequently, all aspects were used during both winter periods. Because aspects are likely intercorrelated with other habitat characteristics interpretations are difficult. Nonetheless, these results are similar to other studies that reported caribou use all aspects during winter, but that some aspects are used more than others depending on the geographic region (Scott and Servheen 1985; Simpson and Woods 1987; Seip 1990). Regional variation in caribou use of aspects probably reflects mountain orientation, physiographic relief and local weather patterns.

Caribou preferred moderate slopes (16-30%) in this study, which is consistent with other caribou habitat studies (Scott and Servheen 1985; Simpson and Woods 1987, Rominger and Oldemeyer 1989). Again, why moderate slopes are used extensively is not clear, but is probably correlated with mid-elevation forests and subalpine basins caribou use during the winter.

Management Implications

Caribou use of balsam-spruce forests on moderate slopes during the early winter conflict with conventional timber harvesting practices. In this region, the majority of radiocollared caribou were frequently located above 1525 m elevation, but only occasionally below 1372 m, which suggests caribou-forestry conflicts may be most severe between 1373-1525 m. Although some even-aged management (e.g., clear cutting) of mid-elevation balsam stands may be tolerable, selection silvicultural systems are recommended where appropriate within this elevation band. Managers should also attempt to provide forested habitats that extend from valley bottoms to subalpine areas to function as travel corridors between winter and summer ranges.

PART 2. MICRO-HABITAT SELECTION IN EARLY WINTER

Following Tracks in Snow

Introduction

Large herbivores interact with their environment at a variety of spatial and temporal scales (Jarman 1974; Belovsky 1978; Owen-Smith and Novellie 1982; Sæther and Anderson 1990; Senft et al. 1987; Senft 1989; Stuth 1991). To gain a better understanding of how animals perceive their environment, recent investigations have stressed the importance of recognizing habitat selection as a scale-dependent process and have recommended that field studies and experiments incorporate more than one spatial scale (Morris 1987; Senft et al. 1987, Bell 1991; Danell et al. 1991; Orians and Wittenberger 1991). Studies conducted at several scales provide a better resolution of factors that determine ecological patterns and their interrelationships among scales (Wiens 1989).

Resource managers also require knowledge of habitat use patterns at both larger (watershed, landscape) and smaller (micro-site) spatial scales to integrate wildlife habitat requirements into land management decisions (Noss and Harris 1986; Hunter 1990; Salwasser 1990). To complement the macro-habitat use patterns reported above, I used ground trailing (following tracks in snow) techniques to investigate micro-habitat selection by mountain caribou. Following tracks of large herbivores as a means of "thinking like the animal" has only been applied in a limited number of foraging studies (Wetzel et al. 1975; Belovsky 1978, Owen-Smith and Cooper 1987; Renecker and Hudson 1986; Sæther and Anderson 1990; Ward and Saltz 1994). Following the path herbivores choose allows the investigator to record resource items encountered by the animal and reduces the potential bias of estimating resource availability solely by what the investigator deems available. Because mountain caribou consume an almost monophagous diet of arboreal lichen during winter, diet selection is not as important compared to other wintering cervids. Instead, lichen abundance or some correlate of lichen abundance, such as tree size or species, may be proximate cues influencing foraging decisions. During the early winter, I followed caribou tracks in snow to identify proximate cues caribou may be using in their foraging decision process. Identifying tree characteristics important to caribou may help resource managers develop silvicultural prescriptions to mitigate the effects of forest harvesting and maintain caribou winter habitat. To determine how caribou were using the ESSF forests, a nested hierarchy of decisions was investigated: (1) selection of foraging areas within the ESSF; (2) selection of foraging paths within foraging areas; and (3) selection of foraged trees along the chosen path. The null hypothesis for each level of selection was caribou use habitat and tree characteristics in proportions to their occurrence. The alternative hypothesis was caribou use ESSF forests in a non-random manner.

Study Area

The ground trailing was carried out in the Sugarbowl-Raven Lake area 80 km east of Prince George, British Columbia (53°N, 121°W). The area covered approximately 250 km² and contained four (SBS, ICH, ESSF, AT) biogeoclimatic zones. Two high elevation (1220-1500 m) cutblocks (70-100 ha) were clearcut during the study. Eleven radio-collared adult female caribou were available as focal animals for ground trailing and were assumed to be a representative sample of the estimated 146 \pm 21 (MOELP unpubl. data) caribou using the Sugarbowl-Raven Lake winter range.

Methods

Transect sampling

The foraging decision process was investigated by collecting data along three transect types. The first transect type completed were *foraging path transects*. These transects were designed to sample where the focal animal walked and to identify its feeding behaviour for each tree or forage item encountered (i.e., foraged or walkpassed). Three to five consecutive 2 m x 50 m long transects centred on the caribou track were completed. The transect width (2 m) was chosen to reflect the "search path" of a foraging caribou that may take a small step to reach lichen-bearing branches. Foraging areas were loosely defined as those areas where straight tracks, characteristic of travelling, began to fan out or criss-cross suggesting a searching/foraging bout had begun. Foraged trees were identified by trampling around the base of trees, or by a step towards a tree indicating a standing posture. Intensity of feeding was indexed qualitatively by the degree of trampling (light, moderate, heavy).

The second type of transect was *foraging area transects*. These transects were completed after foraging path transects and were designed to sample the area the animal was using. These were straight 2 m x 50 m transects and completed in a random direction every 50 m along the caribou foraging path (Fig. 8). Finally, *forest type transects* (2 m x 50 m) were conducted. This third transect type sampled the ESSF forest types where the focal animal was not located at that particular time. In addition, fixed area plots (0.01 ha) and prism swings were completed at the end of the foraging area and forest type transects to determine tree density and basal area. Both live and dead trees were included in all transect and plot types.



Figure 8. Schematic diagram of caribou use and random transects used to assess foraging decisions within a foraging area. Circles are fixed area plots (0.01 ha) used to determine tree density.

To ensure snow characteristics were similar for all transect types, data were collected on the same day. This limited the distribution of forest type transects to within a few km of the foraging path and foraging area transects. Typically, after data were collected along foraging path and foraging area transects, forest types were sampled at random compass bearings and distances away from the caribou foraging area, or at 150 m elevation bands across the forest type.

Variables

Along each transect type the following tree characteristics were recorded: (1) tree species; (2) DBH (cm); (3) tree vigour modified from Thomas's (1979) snag classification which included (i) live, (ii) tight-bark snag, (iii) loose-bark snag, (iv) no-bark snag, and (v) windthrow. (4) activity - foraged or walked passed; (5) cumulative distance between each tree; (6) lichen abundance visually estimated using a standard 10 g clump and divided into two strata: (a) number of lichen clumps within reach of caribou (0 - 1.6 m) from snow surface; (b) number of lichen clumps not within reach of caribou under present snowpack depths (1.6 m -3.2 m). (7) lichen genera composition estimated visually (% *Alectoria samentosa/Bryoria* spp.) using 10 percent intervals. Eighty-three matched pairs of foraging path and foraging area transects were completed in 1991-92 and 104 in 1992-93.

Snow conditions

To obtain independent estimates of caribou sinking depths, a spring scale attached to a ski-pole was pressed to maximum tension (tension = 22 kg) and used as an index of caribou sinking depth. Measurements were taken at 10 m intervals along each 50 m transect of the caribou foraging path adjacent to the measured caribou sinking depths. Five subsamples were averaged to provide one observation per 50 m transect and a simple regression equation was
generated to provide estimates of caribou sinking depths along random paths: CSD = 10.65 + .631PP ($r^2 = 0.77$, $S_{y.x} = 5.1$, n = 289). Where CSD = predicted caribou sinking depth (cm) and PP (pole penetration cm). I used the predicted values to test the hypothesis that caribou select foraging paths to minimize sinking (paired t-test). Unfortunately, too few random samples were taken in elevations above caribou foraging areas to determine if caribou use areas that minimize sinking depths; thus, only selection data within the foraging area are presented. Snow conditions were described qualitatively following Luttmerding et al. (1990).

The majority of ground trailing was carried out during the early winter periods (Nov-Jan) 1991-93; however, three caribou use sites surveyed in 1990 were included in some analyses. Sampling began when snow depths at caribou use sites had reached 30-60 cm. Caribou were monitored weekly using a helicopter and ground trailing conducted after fresh snowfalls.

Because snow conditions could potentially influence foraging strategies, I conducted the analyses by year to reflect the different winter conditions. In relative terms, 1991-92 was a short winter with high elevation snowpacks within normal limits. Snow accumulated relatively quickly in November and December but tapered off considerably by the end of January. In 1992-93, however, the winter was relatively dry and snow packs well below normal (66% of normal, B.C. Environment Snow Survey 1993). Snowpacks during this year were also low relative to 1991-92. Specifically, at a bench mark of 1525 m elevation, snow depths were similar by the end of November (60 cm versus and 51 cm). By the end of December, snow depths had accumulated to 130 cm in 1991 compared to only 57 cm in 1992. By the end of January snow depths were about 160 cm in 1991-92 and 100 cm in 1992-93. Therefore, I considered 1992-93 as a "low-snow" winter.

Statistical Analysis

Both univariate and multivariate techniques were used to compare differences between caribou use and random transects. Analyses were conducted separately for each level of selection to identify potential effects of spatial scale.

A total of 52 caribou foraging areas (1372-1677 m) were sampled during Nov-Jan 1991-93 (1991-92 n = 15); 1992-93 n = 37). Telemetry locations of individual animals provided ground trailing sample points. Because these were at least 7 days apart, foraging areas visited were assumed to be independent and were considered the experimental unit. Three subsample plots of tree density and basal area were averaged to provide one independent observation for each foraging area. Independent *t*-tests were used to compare basal area and tree density of caribou foraging areas and random sites. These variables were log-transformed to stabilize variances.

Selection of foraging areas

Small sample sizes of random forest type transects precluded a log-linear analysis (see below) for foraging area selection, so this level of selection was analyzed using univariate chi-square comparisons for each tree characteristic.

Lichen abundance was a complicating factor for foraging area selection. Availability of arboreal lichen on standing trees generally increases with increasing snow depths (Edwards et al. 1960; Antifeau 1987; E. Terry, this study) and thus availability of lichen varied monthly, weekly and occasionally daily. Due to severe time constraints (i.e., it was difficult to sample both caribou use areas and random sites on the same day), sufficient replicate samples of caribou forage areas and random transects for each day or week were not obtained. As a less than perfect alternative, the analyses were stratified by month which

grouped sampling days into relatively "homogeneous" blocks. Separate univariate comparisons were made between lichen abundance in caribou foraging areas and in random sites.

Selection of foraging paths

Mean number of trees/50 m transect, lichen abundance and lichen genera composition along foraging paths and matched random transects were compared using paired *t*-tests. Lichen abundance was log transformed and genera composition arcsine transformed before analysis. Wilcoxons' Signed-Ranks was used to compare species composition and tree vigour of foraging paths with matched random transects.

Log-linear analysis

Because univariate comparisons could not account for the multi-variate structure of the data set, a log-linear analysis was used for this level of selection to explore more complex hypotheses. Log-linear models were used to identify interrelationships among tree characteristics (excluding lichen abundance) and compare foraging paths with random paths. Transect type (i.e., foraging path vs random) was considered as the dichotomous dependent variable and tree species (balsam, spruce), vigour (live, tight-bark snag, loose-bark snag, windthrow) and DBH class (10-20 cm, 25-35 cm, 40-50 cm, > 50 cm) used as explanatory variables. Because I considered transect type as a response variable the log-linear analyses are similar to logit models (Tabachnick and Fidell 1989; Colgan and Smith 1978). The result was a 4-way multidimensional contingency table. The primary goal of the multi-dimensional analyses was to test hypotheses of tree selection by investigating higher order interactions that included transect type. Interactions were screened for significant effects using partial and marginal associations (log-likelihood ratio \underline{G}^2). I was interested primarily in interactions that included transect type, but other significant interactions were included to obtain models that

fit the data although they are not discussed in detail. Each model can be written similar to ANOVA models. For example, a significant transect (T) x DBH (D) interaction (TD) in a contingency analysis is analogous to a DBH main effect in an ANOVA and would indicate dbh classes occur in different proportions in the two transect types, likewise, a three-way association such as transect x DBH x vigour (TDV) would be comparable to a DBH x vigour interaction in ANOVA and can be interpreted such that tree vigour varies with tree diameter but depends on transect type. A more stringent alpha level was used (P = 0.01) to assess significant effects to account, in part, for non-independence of trees (trees are really pseudoreplicates) and because more than one model was generated from the same data set. A model "fits" the data if the cell frequencies it predicts are close to the observed frequencies, that is, if the value of \underline{G}^2 is small and <u>P</u> values large (<u>P</u> > 0.05, Fienberg 1977). Relationships among categorical variables were examined using marginal percentages and parameter estimates (lambda) divided by their standard error. These estimates can be interpreted as approximate standard normal deviates (Fienberg 1977, Dixon 1990). The magnitude of the estimates can be used to assess relative importance and the sign indicates the direction of the effect. Because the marginal totals were not fixed (i.e., counts were the result of sampling effort and not chosen in advance) and transects were not independent, parameter estimates are considered disputable, and inferences drawn from them are exploratory (McCullagh and Nelder 1987; M. Lesperence, pers comm.). None of the tables had < 20% of the expected frequencies less than 5 and thus the analyses were assumed to have adequate power. All analyses were run using BMDP (Dixon 1990).

Selection of trees along foraging paths.

To determine "acceptability" (i.e., whether caribou foraged or walked past) of each lichen source, the total number of foraged cases were compared to the total frequency of occurrence within each category. Log-linear models were also used to investigate proximate cues (tree attributes) caribou use to make forage choices among trees they encounter. Because successive trees encountered may not be statistically independent and appropriate statistical techniques remain controversial (Owen-Smith and Cooper 1987; Noon and Block 1990), this analysis is also considered exploratory. Nonetheless, the binary response variable was activity (foraged or walk past) and DBH class, tree vigour and lichen abundance were used as explanatory variables. Because caribou usually consumed all arboreal lichen on windthrown trees, this analysis was confined to standing trees. Only transects sampled at snow depths > 70 cm were included to reduce potential bias associated with lichen accessability. Because some of the trees had obviously been foraged, the higher lichen strata was used as an index of lichen abundance recognizing its potential short-comings as a proximate cue. Using the lower strata of lichen abundance may have resulted in erroneous conclusions (i.e., caribou feed on trees with no lichen). Here, I was most interested in describing the characteristics of foraged trees (interactions that included activity) and exploring a general tenet of foraging theory -"take the largest" (Stephens and Krebs 1986). That is, do caribou forage on trees with the most lichen ? Trees along the caribou path were classified according to: activity (foraged, walk past); lichen abundance (nil, < 2 clumps, 2-6 clumps, > 6 clumps); and, DBH (10-20 cm, 25-35 cm, 40-50 cm, >50 cm). The result was a 2 x 4 x 4 contingency table. A similar log-linear analysis was done replacing tree size (DBH) with tree vigour (live, tight-bark snag, loose-bark snag). All models were fit using log-linear methods (Fienberg 1977; BMDP4F,

Dixon 1990).

Analyses for each level of selection were confined to the elevation band (1372-1677 m) where the majority of caribou spend the early winter (i.e., closed canopy ESSF, see Part 1) and where potential caribou-forestry conflicts are most severe. Because some habitat characteristics varied with elevation (e.g., tree species composition and lichen genera composition), the ESSF was further stratified into homogeneous blocks for some analyses: lower ESSF (1372-1524 m), upper ESSF (1525-1677 m), and subalpine parkland (>1677 m). Relative preference (selection) or avoidance was inferred for all levels of resource use if characteristics occurred in significantly different proportions than estimated availability.

RESULTS

Within Habitat Decisions: Selection of Foraging Areas

Tree density and basal area

Average tree densities of caribou foraging areas (641 stems/ha) were not significantly different from random sites (690 stems/ha; $\underline{P} = 0.389$) (Table 2), however, total (live and dead stems) basal area of caribou use sites were slightly lower (29 m²/ha) compared to random sites (33 m²/ha; $\underline{P} = 0.032$)(Table 3).

Table 2. Total tree density^{*} (stems/ha) at caribou foraging areas and random sites in the Engelmann Spruce-Subalpine Fir Zone (ESSF), Prince George, B.C. 1990-93

Elevation (m)	Caribou Use	n ,	Random Sites	n
1373-1677	641 ± 68	51	690 ± 64	135
>1677	366 ± 186	9	no data	

numbers are means \pm 95% CI

* estimates include live and dead stems ≥ 10 cm dbh.

> 1677 m typical of late winter subalpine parkland habitat

Table 3. Mean basal areas (m²/ha) at caribou foraging areas and random sites in the Engelmann Spruce-Subalpine Fir Zone (ESSF), Prince George, B.C. 1990-93

	<u>Elevation 1373-1677 m</u>				
	Caribou Use $(n = 58)$	Random Sites (n	= 181)		
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Live	21 ± 8	23 ± 12			
Snag	8 ± 4	10 ± 8			
Total	29 ± 10	33 ± 15			
	· · · · · · · · · · · · · · · · · · ·				

numbers are means ± 1 SD

Tree characteristics (species, dbh, vigour)

Caribou forage areas had similar proportions of subalpine fir (85%) and spruce (15%) compared to random sites in both years (1991-92 $\underline{X}^2 = 6.4$, 1 df, $\underline{P} = 0.05$; 1992-93 $\underline{X}^2 = 1.22$, 1 df, $\underline{P} = 0.269$). Stratifying the ESSF into lower (1372-1525 m) and upper (1526-1677 m) elevation bands also revealed no significant difference in tree species composition between caribou use and random sites ($\underline{P} > 0.05$). However, the proportions changed: lower ESSF (1372-1525 m) foraging areas were comprised of 75% subalpine fir and 25% spruce, whereas upper ESSF foraging areas (1526-1677 m) contained 90% subalpine fir and 10% spruce.

Diameter (DBH) distributions of caribou foraging areas were significantly different from random sites in 1991-92 ($\underline{X}^2 = 22.7, 3 \text{ df}, \underline{P} < 0.001$) but not to those in 1992-93 ($\underline{X}^2 = 0.213, 3 \text{ df}, \underline{P} = 0.978$). Caribou foraging areas had fewer (29%) 25-35 cm stems compared to random sites (41%) and slightly more (18%) 40-50 cm trees compared to random (11%).

Caribou foraging areas had similar proportions of live, dead and windthrown trees as random sites in 1991-92 ($\underline{X}^2 = 1.92$, 3 df, $\underline{P} = 0.389$), but not in 1992-93 ($\underline{X}^2 = 12.4$, 3 df, $\underline{P} = 0.006$). During this low-snow year, caribou foraging areas had similar proportions of live stems (70%), new snags (6%) and old snags (18%) compared to random sites (70%, 7%, 21% respectively); but had 3 times more windthrown trees (6%) than random sites (2%).

Arboreal lichen abundance and genera composition

The number of lichen clumps per standing tree were significantly different between caribou foraging areas and random sites only during December 1991 ($\underline{X}^2 = 31.8$, 3 df, $\underline{P} < 0.001$). In this month, caribou foraging areas contained trees with less lichen (within reach of caribou) than trees at random sites (Fig.9). However, this was not the case when the number

of lichen clumps above the reach of caribou was compared to random sites ($\underline{P} < 0.05$). This comparison revealed foraging areas had more trees with heavier lichen loads than did random sites, and significantly fewer trees with no lichen (Fig.10). Foraging areas and random sites had similar amounts of lichen per standing tree compared to random sites in January 1992. Caribou did not select foraging areas with significantly different lichen clumps per standing tree compared to random sites in any month during the low-snow winter (1992-93) ($\underline{P} > 0.05$).

Caribou used foraging areas with significantly different lichen genera compositions than random sites in both years (1991-92: $\underline{X}^2 = 53.8$, 4 df, $\underline{P} < 0.001$; 1992-93 $\underline{X}^2 = 22.5$, 4 df, $\underline{P} < 0.001$). In 1991-92, foraging areas had significantly more trees (30%) dominated by *Alectoria sarmentosa* compared to those at random sites (17%). By contrast, during the lowsnow winter, twice as many trees (26%) supporting *Bryoria* spp. occurred at foraging areas compared to random sites (11%) (Fig.11). These patterns were similar when data were stratified into 1372-1525 m and 1526-1677 m elevation bands ($\underline{P} < 0.001$).

Within Foraging Area Decisions - Selection of the Foraging Path

Number of trees in search path width (per 50 m transect)

Caribou used paths with significantly more trees (13 trees/50 m) per unit distance than occurred along random paths (8 trees/50 m; paired- \underline{t} , $\underline{P} < 0.001$ years pooled).



Figure 9. Proportion of standard lichen clumps within reach of caribou at caribou forage areas and random sites for December, 1991. Prince George, B.C. "+" indicates significantly greater than random; "-" indicates significantly less than random. Bonferroni <u>Z</u>-test P = 0.05.



Figure 10. Proportion of standard lichen clumps (10 g) above reach of caribou at caribou forage areas and random sites for December, 1991. Prince George, B.C. "+" indicates significantly greater than random; "-" indicates significantly less than random. Bonferroni Z-test P = 0.05.



1992-93

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1991-92

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Figure 11. Lichen genera composition at caribou foraging areas and random sites (1372-1677 m) elevation. Prince George, B.C. 1991-92 and 1992-93.Bryoria = < 5% Alectoria; Bry-dom = 5-35% Alectoria; Mixed = 35-65% Alectoria; Alec-dom = 66-95% Alectoria; Alectoria = >95% Alectoria. "+" indicates significantly greater than random (Bonferroni Z-test P = 0.05).

Composition of search paths

Caribou paths had similar proportions of live balsam (Wilcoxon, $\underline{P} = 0.301$); dead balsam (Wilcoxon, $\underline{P} = 0.210$); live spruce (Wilcoxon $\underline{P} = 0.885$) and dead spruce (Wilcoxon $\underline{P} = 0.581$) compared to random paths. However, significantly more windthrown trees were found along paths caribou chose (1990-91:Wilcoxon $\underline{P} = 0.001$; 1992-93: Wilcoxon $\underline{P} =$ 0.010) than random paths. Caribou paths had approximately 5 times (mean = 0.200) the number of windthrown trees compared to random paths in 1990-91 (mean = 0.042) and twice the number (mean = 0.776) compared to random paths (mean = 0.336) during the low-snow winter. No significant difference was apparent in 1991-92 (Wilcoxon $\underline{P} = 0.345$).

Lichen abundance and genera composition

Caribou chose foraging paths with similar amounts of lichen available on standing trees compared to random paths in all years (paired-t: 1990-91: 2 df, $\underline{P} = 0.13$; 1991-92: 17 df, $\underline{P} = 0.203$; 1992-93, 35 df, $\underline{P} = 0.06$). This pattern was consistent for the upper lichen strata for all years ($\underline{P} > 0.05$). Caribou foraging paths also had similar proportions of *Bryoria* and *A lectoria* as random paths (1991-92: $\underline{P} = 0.771$; 1992-93: $\underline{P} = 0.521$). On average, trees on caribou paths consisted of 39% *A lectoria* compared to 38% found on random paths in 1991-92. Similarly, in 1992-93, trees along caribou paths supported lichen clumps consisting of 45% *A lectoria* compared to 43% for random paths. This pattern was the same for measures of lichen above the reach of caribou (1991-92 $\underline{P} = 0.480$; 1992-93 $\underline{P} = 0.263$).

Snow conditions

Caribou sank on average only 2 cm less along their chosen path compared to random paths over most snow types. Although this was statistically significant for some snow types, the biological relevance suggests caribou do not need to choose foraging paths to minimize sinking, at least at these snow depths (Table 4).

Log-linear model

transect (T) x species (S) x diameter (D) x vigour (V)

The model that best fit the 1991-92 data included the TS, SD, SV and DV interactions ($\underline{G}^2 = 23.6, 21$ df, $\underline{P} = 0.313$). TD and TV interactions were not significant, indicating caribou chose foraging paths with both similar tree sizes ($\underline{G} = 0.68, 3$ df, $\underline{P} =$ 0.878) and vigour ($\underline{G} = 5.3 \underline{df}=2 \underline{P} = 0.07$) compared to trees along random paths. The significant TS interaction ($\underline{G} = 9.3, 1$ df, $\underline{P} = 0.002$) suggested caribou chose foraging paths with slightly more subalpine fir (90%) compared to random paths (85%) (Table 5). All third and fourth order interactions were not significant. The best model that fit the 1992-93 data included the TD, SD, SV and DV interactions ($\underline{G}^2 = 39.2, 37$ df, $\underline{P} = 0.373$). TS and TV interactions were not significant ($\underline{G} = 0.04, 1$ df, $\underline{P} = 0.84; \underline{G} = 2.1, 3$ df, $\underline{P} = 0.551$ respectively) suggesting caribou chose paths with similar proportions of balsam, spruce, live stems, snags, and windthrow compared to random paths. Lambda parameters suggested caribou paths had significantly fewer 10-20 cm trees than random paths. Positive associations were indicated between large diameter trees and paths caribou chose but estimates were not significant (P > 0.01) (Table 6). All third and fourth order interactions were not significant.

Table 4. Caribou sinking depths and predicted sinking depths of random paths in different snow conditions. Prince George, B.C. 1990-93.

Snow Type	Caribou Path	Random Path ¹	Proportion of Brisket ²	Р
dry powder $(n = 45)$	40 ± 8	42 ± 6	57	0.01
heavy powder $(n = 58)$	42 ± 6	40 ± 2	60	0.001
subsurface crust (n = 69)	28 ± 11	30 ± 9	40	0.962
surface crust $(n = 25)$	24 ± 6	27 ± 4	34	0.391
wet-heavy $(n = 49)$	23 ± 11	25 ± 3	33	0.009

numbers are means ± 1 SD. n = number of matched pair transects

1 Predicted sinking depth from regression equation.

2 Caribou sinking depths as a proportion of brisket height (70 cm).

Table 5. Log-linear results of significant tree characteristics identified between caribou foraging paths and random paths as indicated by the ratio of the log-linear parameter estimates to their standard errors. 1991-92.

Parameter estimates			Marginal Percents		
Tree Species	Caribou Path	Random Path	Caribou Path	Random Path	
Subalpine Fir	2:76**	2.76	90	85	
Spruce	-2.76**	2.76	10	15	

** P < 0.01 (>2.58 significantly different from zero) number of trees used in analysis: caribou path (n = 910); random (n = 591) Table 6. Log-linear results of significant tree characteristics identified between caribou foraging paths and random paths as indicated by the ratio of the log-linear parameter estimates to their standard errors. 1992-93.

	Parame	eter estimates	Margina	l Percents
Tree size (dbh)	Caribou Use	Random	Caribou Path	Random Path
10-20 cm	-4.54**	4.54	39	49
25-35 cm	-1.69	1.69	29	29
40-50 cm	1.87	-1.87	23	16
>50 cm	2.20*	-2.20	9	6

* P < 0.05 (>1.96 significantly different from zero)

** P < 0.01 (>2.58 significantly different from zero)

number of trees used in analysis: caribou path (n = 1050); random (n = 601)

Within Foraging Path Decisions: Selection of Trees Along the Foraging Path.

Foraged vs walked past ("acceptability")

Caribou rarely rejected windthrown trees or lichen litterfall when they encountered these forage sources. In contrast, most standing trees were passed (Fig. 12). When the proportions of foraged cases for each lichen source were compared to their relative availabilities, a similar pattern of foraging decisions was evident. Although windthrown trees and lichen litterfall were rarely encountered, they were 10 times and 15 times (respectively), more likely to be foraged as were the more frequently encountered standing trees (Table 7).

Log-linear models

No significant differences ($\underline{P} > 0.05$) were detected between years for selection of trees along the foraging path so data were pooled.

activity (A) x vigour (V) x lichen abundance (L)

The best model that fit the data included three two-way interactions: AL, AV, and VL $(\underline{G}^2 = 7.24, 6 \text{ df}, \underline{P} = 0.299)$. The significant AL interaction suggested a difference in lichen abundance between foraged trees and those passed by. The pattern of parameter estimates suggested caribou foraged fewer trees with low lichen loads. In contrast, a positive association was indicated between foraged trees and trees supporting 2-6 clumps and trees with > 6 clumps of lichen (Table 8). Although there was a negative association between foraged trees and snags, and a positive association between foraged trees and live stems, neither parameter estimates were significantly different from random.



LICHEN SOURCE

Figure 12. Caribou "acceptability" of arboreal lichen sources. Prince George, B.C. 1990-93. Bars are disputable 95% binomial CI's. Sample sizes given above bars.

Table 7.	Estimated	probabilities	of selection	for different	sources	of lichen	caribou
encounter	red along the	heir foraging	paths using	standardized	selection	n ratios.	

Foraging Decision							
Lichen source	% Foraged $(n = 247)$	% Encountered $(n = 2552)$	SR	SSR	RANK		
Live trees	0.59	0.73	0.808	0.036	(3)		
Tight-bark snags	0.11	0.18	0.611	0.027	(4)		
Loose-bark snags	0.02	0.06	0.333	0.015	(5)		
Windthrown trees	0.17	0.02	8.50	0.382	(2)		
Litterfall	0.12	0.01	12.0	0.539	(1)		

SR (selection ratio) = proportion foraged/proportion encountered along foraging path SSR (standardized selection ratio) see Manly et al. 1993 for details. pp.49-52. Ranks represent decreasing probabilities of selection The VL interaction considered all trees along the foraging path (i.e., no selection) and indicated a positive and significant association between live stems and lichen abundance, a positive association between new snags and lichen abundance; and a negative association between old snags and lichen abundance. The three way interaction (saturated model) was not significant.

activity (A) x dbh (D) x lichen abundance (L)

Two second order interactions (AL and DL) were significant and provided a best fit model ($\underline{G}^2 = 13.61$, 9 df, $\underline{P} = 0.327$). The AL association was consistent with the preceding model. The DL interaction suggested there was a negative association between small diameter stems (10-20 cm) and greater lichen loads (2-6 and >6 clumps); a positive trend between the middle diameter classes (25-50 cm) and lichen abundance, and trees > 50 cm indicating a decline in lichen abundance (Table 9). The AD interaction was not significant which suggests caribou do not discriminate between trees based on size alone or size combined with lichen (3 way interaction not significant) along their foraging path.

Lichen genera composition

Caribou foraged trees with similar lichen genera composition (higher strata) to those trees available along the foraging path ($\underline{X}^2 = 8.58$ 4 df, $\underline{P} = 0.07$).

Table 8. Log-linear results of tree selection by mountain caribou as shown by parameter estimates (lambda) divided by their standard error. Prince George, B.C. 1990-1993.

Activity			Tree Vigour		
Lichen Abundance (above reach of caribou)	Foraged	Walk Past	Live	New Snag	Old Snag
no lichen	-2.78*	2.78	-3.00*	-1.71	4.93**
< 2 clumps	-2.69*	2.69	-6.59**	1.28	3.86**
2-6 clumps	3.37**	-3.37	3.50**	1.45	-4.30**
>6 clumps	6.64**	-6.64	6.11**	0.15	-4.56**
Vigour			÷ ·		
Live	2.19	-2.19			
New Snag	-1.17	1 17			
Old Snag	-0.277	0.277	· .		

* P < 0.01 (> 2.58 significantly different from zero) ** P < 0.001

Table 9. Log-linear results of tree selection by mountain caribou as shown by parameter estimates (lambda) divided by their standard error. Prince George, B.C. 1990-1993.

	Activi	ty .	Tr	ee diameter (d	cm) .	· ·
Lichen Abundance	Foraged	Walk Past	10-20 cm	25-35 cm	40-50 cm	>50 cm
no lichen	-2.53	2.53	6.28***	-2.31	-2.57	0.828
<2 clumps	-2.42	2.42	3.91*	-1.52	-0.94	-0.279
2-6clumps	2.58	-2.58	-0.61	2.78	2.50	-3.55**
>6 clumps	6.49***	-6.49	-11.91***	3.51**	3.96**	2.21

** P < 0.01 (> 2.58 significantly different from zero) *** P < 0.001

DISCUSSION

Selection of foraging areas

Theoretical considerations of optimal foraging theory suggest foraging ungulates should choose patches or habitats where food biomass or bite sizes are greatest (Owen-Smith and Novellie 1982; Bunnel and Gillingham 1985; Senft et al. 1987). If resource patches or habitats differ in quality across larger areas, then individuals should exhibit some degree of selection among patches or habitats (Wiens 1976; Stephens and Krebs 1986).

Therefore, if areas within balsam-spruce forests differed in quantity of accessible lichen then caribou should have shown some degree of selection for foraging areas. That is, lichen abundance or some correlate of lichen abundance (tree characteristic) should have been found in greater proportions in areas caribou use than in the surrounding forest. My results provided weak support for this level of selection. Although there was an indication caribou chose foraging areas with more lichen clumps, this was only evident during Decemeber 1991. This was weak evidence, however, given the higher lichen strata (above a caribou's foraging reach) was used. In fact, there was a greater proportion of trees supporting less lichen (<1 clump) accessible to caribou (lower strata) in foraging areas than at random sites during this month. That no significant differences were found during January of the same year, or during the low-snow winter (1992-93), further weakens the idea that caribou select for lichen abundance on standing trees at this scale. On a larger scale, however, it is likely caribou have selected the ESSF biogeoclimatic zone because it has relatively more arboreal lichen available than the SBS or ICH biogeoclimatic zones.

During the low-snow winter (1992-93), there were significantly more windthrown trees

at caribou foraging areas than at random sites. The incidence of windthrown trees at caribou foraging areas is consistent with previous studies (Edwards et al. 1960; Antifeau 1987; Simpson et al. 1987; Rominger and Oldemeyer 1989). For example, Rominger and Oldemeyer (1989) found caribou foraging areas had 3 times as many windthrown trees than did random sites. They suggested caribou may be using higher elevations stands that contain a subalpine fir component because windthrown trees were predominantly (84%) subalpine fir. In this study, the majority of windthrown trees were also subalpine fir (balsam) (90%). This provides further evidence that windthrow may be partly responsible for the caribou's extensive use of high elevation stands dominated by balsam.

Caribou foraging areas had similar proportions of balsam-spruce and vigour of standing trees compared to those at random sites suggesting they did not select feeding areas based on these characteristics. Although the narrow range of available tree species and tree vigour classes may have constrained opportunites for selection, it is also possible that these characteristics are poor correlates of accessible lichen. Although some researchers have demonstrated a positive correlation between lichen biomass and subalpine fir trees (Van Daele and Johnson 1983; Detrick 1984), others have found more lichen on recently dead snags (Stevenson 1979). Nonetheless, in this study, recently dead snags and tree species did not appear to influence caribou foraging patterns. There was, however, an indication that lichen abundance was generally correlated with diameter which may have resulted in the greater number of large diameter (40-50 cm) trees found in caribou foraging areas during 1991-92. This winter had fewer occurrences of windthrow, but deeper snowpacks than the low-snow winter which may have have provided more foraging opportunities on standing trees. Overall,

it appears that caribou were not selecting for foraging areas or groups of standing trees with any particular attribute other than occurrence of windthrow.

Selection of foraging paths

With few exceptions, caribou appeared to forage in a random manner within foraging areas. Caribou chose paths independent of trees species, vigour of standing trees, lichen abundance and lichen genera. However, caribou did chose paths with more windthrown trees than random paths in two of the three years. This further suggests a windthrown tree is an important proximate cue in directing caribou foraging movements.

Even though caribou appeared to show no selection within a foraging area, caribou paths had more trees /50 m than did random paths and suggests they may be "sampling" their environment concurrently. Repeated sampling of the environment has been suggested as a means by which animals "track" the spatial and temporal variance of food availability (Stephens and Krebs 1986). I suggest that the apparent random movement patterns with respect to trees other than windthrow may serve a "sampling" function for caribou.

Selection along foraging paths

Recent studies of winter foraging by large herbivores (Vivås and Sæther 1987; Astrom et al. 1990; Lundberg and Danell 1990; Danell at al. 1991) suggest that individual trees and shrubs are treated as "patches" and are generally exploited according to optimal patch use models (Charnov 1976). Most patch use models are extensions of Charnov's marginal value theorem, which predicts animals will move to a new patch when intake rates decline below the average intake available in other patches. It has also been suggested that because high quality patches are often sparsely distributed, selective use of these forages are also commonly associated with increased search times (Jarman 1974).

In this study, I suggest that patterns of tree selection by caribou during early winter are in qualitative agreement with these predictions. Unlike standing trees, caribou rarely rejected windthrown trees once they were encountered and appeared to feed intensively on them. The relatively high feeding intensity was probably related to the high biomass readily accessible on windthrown trees compared to biomass available on standing trees.

The advantage of feeding on windthrown trees is clear when the number of accessible bites and the potential energy gained per tree are considered. A windthrown tree may provide over 200 times more accessible lichen clumps than on standing trees (n = 2 visual estimates only; unpubl. data) and suggests caribou prefer to concentrate their feeding activity where the number of bites are highest. Compared to standing tress, the relatively long "giving-up-time" (indicated by heavy trampling), further suggests windthrown trees were treated as "high quality patches". That the majority of standing trees were passed by, provides further evidence that caribou were spending much more effort searching than stopping to feed at every tree.

Whether caribou actively search for windthrown trees or simply concentrate their feeding activity when they encountered one, is not clear from my data. Although the stochastic nature of windstorms and tree falls provide an uncertain environment to exploit (*sensu* Caraco 1980), windthrown trees that occur along cutblock edges are also used frequently by caribou (Simpson et al. 1987; B. McLellan, *pers comm.*; E. Terry unpubl. data).

These observations suggest that caribou have some capacity to learn and remember where high quality patches occur.

Unlike other temperate ungulates that tend to reduce activity and ruminate longer during winter in response to seasonal declines in forage quantity or quality (Moen 1976, Robbins 1983), the relatively high digestibility (82%) of arboreal lichen (Rominger and Robbins 1994) may minimize digestive constraints. This would allow caribou to forage extensively by reducing rumination time while increasing time and energy available to search for highly preferred trees such as windthrow. Although the cost of locomotion increases with snow sinking depth (Parker et al. 1984, Fancy and White 1987), those reported here suggest caribou rarely sink to depths considered excessive (>50% brisket height). Thus, the energetic cost associated with searching and travelling may be partly offset by their relatively superior. locomotion abilities in snow (Telfer and Kelsall 1984), and the obvious energetic gains when this concentrated energy patch is encountered. The relatively small amount of accessible lichen on standing trees during early winter, probably encourages movement (search effort) by caribou to seek high quality patches such as windthrown trees.

High mobility during early winter is consistent with a similar trailing study of caribou (Simpson and Woods 1987). They followed caribou trails in the Selkirk Mountains, B.C. and found caribou moved three times as far between feeding stations during early winter as they did in late winter. However, the fact that caribou appear to be mobile foragers during periods of food scarcity is not unique. Other ungulates also exhibit high mobility during seasons when food quality or quantity is low (Renecker and Hudson 1986; Risenhoover 1986;

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McCorquodale 1993; Ward and Saltz 1994).

Although exploratory, the log-linear analyses indicated that given sufficient snow depths to reach lichen-bearing branches, caribou chose standing trees with higher lichen loads and suggests that caribou will forage on standing trees selectively. However, because the amount of lichen on a standing tree probably declines quite quickly as a caribou feeds on it, the need to move to less depleted trees likely influences search patterns and provides the motivation to look elsewhere. The best strategy to follow will likely vary with snowpack depth, lichen accessibility, alternate food sources, (e.g. shrubs) as well as with the physiological state of the forager (McFarland 1977; Caraco 1980; Mangel and Clark 1986.).

The high degree of acceptability of lichen litterfall suggests caribou did not pass by a "free bite" and is also consistent with pre2dictions for an animal foraging in a low productive and stochastic environment (*sensu* Caraco 1980). Other ungulates such as black-tailed deer (*Odocoileus hemionus columbianus*) and mule deer (*O. h. hemionus*) also take advantage of this opportunistic energy source when encountered in winter (Stevenson and Rochelle 1984; Waterhouse et al. 1991).

Conclusions

The foraging patterns reported here suggest that once selected, caribou are using balsam-spruce forests in a random manner as they search for recently windthrown trees. Although there was an indication that trees with high lichen loads were foraged more often, the consistent use of windthrown trees suggests caribou concentrated their feeding activity where accessible lichen biomass was highest. Standing trees are likely to be of greater relative importance in years with relatively rapid snow accumulation and few occurrences of windthrow and lichen litterfall.

Logistical difficulties and daily time constraints limited the length of caribou track (search/foraging bout) that could be assessed. Trailing over longer distances than I used (> 500 m) may reveal a clearer sequence of decisions and provide additional information about how caribou exploit their foraging environment. Recent developments in foraging theory related to large herbivores also suggests research efforts should be directed towards direct observation of caribou foraging behaviour. Although this study included *a posteriori* interpretations of caribou foraging behaviour, general foraging patterns have been described and can provide a basis for further hypothesis testing and experimental research. Decisions associated with searching for a "good tree", bite size, bite rate, and how long to stay at each tree (giving-up-time), are the realm of optimal foraging models (Charnov 1976; Chesson 1983; Edenius 1991; Rominger *in prep*). Direct observations of caribou foraging behaviour and attempts to define the functional response (Holling 1959; Crawley 1983; Gross et al. 1993) may provide further insights into caribou foraging decisions and patch selection strategies.

PART 3. CARIBOU HABITAT CHARACTERISTICS AND SILVICULTURAL SYSTEMS: A PRELIMINARY COMPARISON

Introduction

Alternate silvicultural systems (selection cutting) have been proposed to integrate mountain caribou habitat and timber harvesting (Stevenson 1979; Stevenson and Hatler 1985; Armleder and Waterhouse 1990; Stevenson et al. 1994). Selection cutting methods such as group or single tree selection have been proposed because they may provide a sustained yield of timber as well as maintain lichen-bearing trees. In this section, I provide a preliminary comparison of habitat characteristics between areas caribou used and three high elevation ESSF partial-cuts.

Methods

Silvicultural Prescriptions.

Two partial-cuts (CP32, CP37 George Mountain, ca. 100 ha) were harvested at 50% volume removal using a 35 cm diameter-limit cut. Both blocks were harvested using fellerbunchers and the majority of snags were retained. A third partial-cut (CP376, Pinkerton Mountain, 66 ha) was harvested at a lower target volume of 30% using single tree selection. Unlike the two George Mountain blocks, this stand had a higher pre-harvest spruce component and the majority of snags were harvested. Two harvesting methods were used in this block for comparative purposes: one portion of the block was hand-felled while the other portion was harvested using a feller-buncher. Both treatment areas were marked-to-cut using a q value of 1.3 (B. Harding *pers comm*).

Partial-cut blocks were visited once or twice during the winter to monitor caribou use

and sample stand characteristics. Blocks were sampled using 0.01 ha fixed area plots and prism (BAF 4) plots spaced at 100 m intervals along striplines 200 m apart.

Habitat and tree characteristics used for comparisons were confined to caribou use areas sampled within the elevational range of the partial-cut blocks (1372-1677 m). Comparisons of lichen abundance were confined to caribou foraging areas sampled at similar snow-pack depths as the partial-cut blocks (\pm 20 cm of mean partial-cut snowpack). Both foraging area and caribou path transects were used for comparisons. All comparisons were made relative to the most recent assessment of the partial-cut blocks (1992-93).

RESULTS

Tree density and basal area

Post-harvesting tree densities including live and dead stems were approximately 33-50% less than caribou foraging areas. CP37 (George Mt. #2) had the highest residual tree density (567 stems/ha), while CP376 (Pinkerton Mt.) had the lowest (336 stems/ha). CP32 (George Mt #1) provided an intermediate tree density (429 stems/ha) compared to these 2 blocks (Appendix 1). Residual tree densities of all partial-cuts were more similar to caribou late winter forage areas than early winter (Fig.13). On the other hand, residual basal areas were intermediate between caribou early winter and late winter foraging areas (Table 10). The low residual tree density and basal area of the Pinkerton block (CP376) indicated the actual volume removed was higher (50%) than the planned 30% volume removal.



Figure 13. Frequency distribution of total tree densities at caribou use areas and three high elevation partial-cut blocks. Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone - Prince George, B.C. Estimates include live and dead stems ≥ 10 cm dbh. EW = early winter; LW = late winter

Table 10. Mean basal areas (m^2/ha) at three high elevation partial-cut blocks and caribou use sites - Engelmann Spruce-Subalpine Fir Zone (ESSF), Prince George, B.C.

5	Live	Snag	Total
CP32 (George Mt)	13	9	22
CP37 (George Mt)	15	13	28
CP367 (Pinkerton)	16	6	22
Caribou Use (EW)	21 ± 1	8 ± 1	29 ± 1
Caribou Use (LW)	10 ± 2	4 ± 2	14 ± 3

Basal area of caribou use sites are means \pm 1SE EW = Early Winter (n = 58) LW = Late Winter (n = 10)

Spatial distribution of trees

Although sample sizes were small, nearest-neighbour distances suggested CP32 and CP367 were relatively more "clumped" compared to early winter caribou use areas. CP37 tree distances suggested a similar spatial distribution to early winter caribou use areas. A higher degree of aggregation (clumpiness) was more typical of open-canopied subalpine parkland stands. Mean tree-to-tree distances found along caribou foraging paths were about 2 m with trees slightly farther apart (3 m) in more general foraging areas. Maximum distance between trees in the lower ESSF was 25 m (Appendix 2).

Tree species composition

Post-harvesting tree species composition of all blocks were similar to caribou foraging areas (Table 11).

Tree diameter distribution

Diameter distributions were significantly different from caribou foraging areas in all three partial-cut blocks (CP32: $\underline{X}^2 = 14.75$, 3 df, $\underline{P} = 0.002$; CP37: $\underline{X}^2 = 12.11$, 3 df, $\underline{P} = 0.007$; CP376: $\underline{X}^2 = 9.78$, 3 df, $\underline{P} = 0.02$). CP32 differed the most by having relatively few larger trees greater than 35 cm. Both CP37 and CP376 had similar diameter distributions compared to caribou foraging areas, except both blocks had fewer large diameter trees (>50 cm) (Fig.14).

Table 11. Tree species composition as a proportion of basal area for three partial-cut blocks and caribou forage areas, Prince George, B.C.

Subalpine Fir %			Engelmann	Spruce %
Elevation (m)	Partial-Cut	Caribou Use	Partial-Cut	Caribou Use
CP32 (1372-1677)	88	85 ± 2 (n=61 pooled)	12	15 ± 1
CP37 (1525-1677)	94	$94 \pm 2 \ (n = 29)$	6	6 ± 2
CP367 (1360-1500)	70	$76 \pm 2 \ (n = 32)$	30	24 ± 2
> 1677		100 (n = 10)		0`

species composition of caribou use sites are means $\pm 1SE$.



Figure 14. Proportion of diameter classes at caribou use areas and three high elevation partial-cut blocks. Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone. Prince George, B.C. Percent of trees is proportion of total stems tallied using fixed area (0.01 ha) plots.

Tree vigour

The proportions of live and dead trees in all three partial-cut blocks were significantly different compared to caribou use areas (CP32: $\underline{X}^2 = 95.4$, 4 df, $\underline{P} < 0.001$; CP37: $\underline{X}^2 = 86.4$, 4 df, $\underline{P} < 0.001$; CP367: $\underline{X}^2 = 36.8$, 4 df, $\underline{P} < 0.001$). CP32 differed the most from caribou forage areas by having more no-bark snags, windthrown trees and fewer live stems (Fig.15). CP37 also had fewer live stems compared to caribou use sites, but had more loose-bark and no-bark snags. CP367 had similar proportions of live stems and windthrown trees as caribou foraging areas, but had significantly fewer tight-bark and loose-bark snags.

Lichen abundance

Lichen abundance within reach of caribou was significantly different in the first George Creek block (CP32) compared to both caribou forage areas and caribou foraging paths $(\underline{X}^2 = 66.8, 3 \text{ df}, \underline{P} < 0.001; \underline{X}^2 = 135.5, 3 \text{ df}, \underline{P} < 0.001; \text{ snowpack} = 100 \text{ cm})$. The difference was mostly due to the very high percentage of trees in the partial-cut supporting no lichen within reach of caribou (81% of 104) (Fig.16). In contrast, trees in the second George Creek block (CP37) supported similar lichen loads compared to caribou forage areas and caribou paths (\underline{X}^2 =5.99, 3 df, $\underline{P} = 0.112; \underline{X}^2 = 6.71, 3 \text{ df}, \underline{P} = 0.082;$ snowpack = 90 cm) (Fig.17).

Lichen availability in the Pinkerton block also differed significantly compared to caribou forage areas and caribou foraging paths ($\underline{X}^2=19.17$, 3 df, $\underline{P} < 0.001$; $\underline{X}^2 = 24.06$, 3 df, $\underline{P} < 0.001$). The difference was mainly due to the higher percentage of trees in the partial-cut supporting less than 1 clump of lichen (Fig.18).



Figure 15. Proportion of tree vigour classes at caribou use areas and three high elevation partial-cut blocks. Engelmann Spruce Subalpine-Fir (ESSF) biogeoclimatic zone. Prince George, B.C. CP32 (n = 147 trees); CP37 (n = 872 trees); CP367 (n = 523); Caribou use (n = 80 forage area plots (subsample 1429 trees).



Figure 16. Proportion of lichen clumps within reach of caribou. George Mountain CP32. mean snowpack 100 cm. partial-cut (n = 104) trees; caribou use (n = 206) trees. range of snow depths used 80-120 cm.



Figure 17. Proportion of lichen clumps within reach of caribou. George Mountain CP37. mean snowpack 90 cm. partial-cut (n = 187) trees; caribou use (n = 448) trees. range of snow depths used 70-110 cm.



Figure 18. Proportion of lichen clumps within reach of caribou. Pinkerton Mountain CP376. mean snowpack 84 cm. partial-cut (n = 240) trees; caribou use (n = 448). range of snow depths used 70-110 cm.

DISCUSSION

Habitat characteristics and tree attributes of the partial-cut blocks varied in their ability to provide similar caribou habitat characteristics.

Post-harvest tree densities of partial-cuts were approximately 200-300 stems/ha lower than tree densities found in early winter foraging areas, suggesting the stands were more similar to late winter habitats (i.e., high elevation balsam or subalpine stands). Likewise, residual basal areas (live stems) were 25-30% below basal areas of early winter caribou use sites. The mean basal area of early winter foraging areas (21 m²/ha live stems) indicates that maintaining stand basal areas to approximately 20 m²/ha per silvicultural entry (Stevenson et al. 1994) may provide caribou foraging habitat, assuming trees support adequate lichen loads. The 3 partial-cut trials, however, were already below (13-16 m²/ha) this recommended residual basal area (Alexander 1986, Stevenson et al. 1994) and suggests 50% volume removal was probably too high to meet silvicultural objectives and possibly for caribou habitat objectives as well. The relatively low initial basal area of many high elevation balsam-spruce stands, also suggests there may be feasibility constraints in attempting to apply selection methods over portions of caribou winter range. Furthermore, if 20 m²/ha were maintained on the first entry, subsequent entries will require relatively long cutting cycles to allow basal area stocking to recover (Stevenson et al. 1994).

Tree species composition in all blocks were similar to caribou foraging areas at comparable elevations and suggests prescriptions were adequate in maintaining proportions of subalpine fir and spruce. In contrast, diameter distributions of all partial-cuts were significantly different from caribou forage areas. The relatively few large diameter stems

found in the George Mountain blocks simply reflected the 35 cm diameter-limit prescription. Likewise, too many trees in the > 50 cm dbh class may have been marked-to-cut in the Pinkerton block. Although, the number of trees in each dbh class per ha would be more informative, the percentages presented here suggests that retaining a greater proportion of large diameter trees (> 50 cm) would bring diameter distributions closer to those found in caribou use sites. Even though data from caribou use areas indicated live stems and new snags between 25-50 cm dbh provided the most accessible lichen of standing trees, large diameter trees (> 50 cm) are important sources of lichen litterfall and possibly windthrow. Maintaining a range of diameter classes seems appropriate to meet both caribou habitat and silvicultural objectives.

The proportions of live stems and snag classes in the partial-cuts also differed from caribou use sites. CP32 and CP37 (George Mountain) had more loose-bark and no-bark snags than caribou use sites, while CP367 (Pinkerton) had fewer. Older snags, especially those that have lost most of their branches and bark, provided the least amount of lichen and were used infrequently by caribou (see Part 2). Although this may suggest older snags may not be necessary to maintain adequate caribou habitat, other species considerations (e.g., cavity nesting birds) may warrant their retention.

CP32 and CP367 had significantly more trees with lower lichen loads compared to caribou use sites and caribou paths. Higher lichen loads from unlogged adjacent plots (unpubl. data) suggested the lower lichen loads may be a result of the open canopy and increased wind exposure. Although lichen that is lost from the branches of trees (litterfall) as well as blowdown, would be temporarily available (assuming a caribou encounters it), these lichen
sources will only be of benefit to caribou for a relatively short period. In summary, the low tree densities taken together with the low lichen loads (especially CP32) indicates early winter caribou habitat has not been maintained and suggests the long term utility of these partial-cuts as potential caribou foraging areas have been compromised. Although CP37 trees supported similar lichen loads to areas caribou used, reducing the amount of basal area or volume removed per entry is recommended to retain a greater standing total crop of arboreal lichen and possibly the number of lichen clumps per tree.

Opening up the canopy will also affect snow depths as well as snow characteristics. Because lichen availability is a function of snowpack depth, the dynamic relationship between snow and forage will change according to the degree of canopy removal, site specific wind patterns as well as the characteristics of residual trees. The effects of silvicultural prescriptions on snow conditions and caribou use requires further study.

Conclusions

Comparisons of habitat characteristics between partial-cut blocks and caribou use areas should be viewed carefully. Whether other silvicultural prescriptions can provide caribou habitat attributes *over the long term* is unknown. Although the data presented here represented a "snapshot" of the stands, the residual tree densities and lower lichen loads suggests these stands have marginal long term value as foraging areas. Because caribou appeared to do more searching for windthrown trees than foraging standing trees (see Part 2), further complicates an attempt to provide recommendations that would help in developing silvicultural prescriptions. Of course, the ultimate criteria to determine if alternate silvicultural

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systems can provide caribou habitat will be whether caribou perceive these blocks as potential foraging habitat and *use them*. Although caribou used the partial-cuts infrequently (caribou tracks were found once (CP32) over a total of 10 ground and aerial surveys) the partial-cuts were dispersed and comprised a very small portion of their winter range. Partial-cut trials should be concentrated in caribou home ranges and monitored on a regular basis to determine caribou use. To provide detailed pre-harvest silvicultural prescriptions, relationships between lichen abundance and tree characteristics should be further verified in a snow-free period using methods similar to Armleder et al.(1992).

Management practices that alter the spatial and temporal availability of lichens may influence foraging energetics by affecting both energy intake and costs. Research efforts should be directed towards monitoring stands for caribou use and silvicultural response as well as quantifying the energetic relationship between foraging efficiency and various harvesting prescriptions.

GENERAL CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Forest management strategies designed to integrate the habitat requirements of mountain caribou will require considerations at both landscape and stand level spatial scales. The telemetry data suggested caribou made coarse-grained decisions (non-random) at relatively large spatial scales including home range selection (ESSF) and habitats (balsamspruce, subalpine parkland) within home ranges and suggests macro-habitat characteristics (elevation, forest cover type and slope) may be better predictors overall of caribou use. Thus, it is recommended forest managers attempt to provide large contiguous stands of ESSF forests

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during landscape level planning as well as travel corridors to facilitate seasonal movements. During early winter, standing trees provided few accessible bites of lichen to caribou which appeared to encourage search effort for more profitable trees (i.e., windthrow). Although there are probably many variables that interact to affect windthrow rates, the majority of windfall was balsam which suggested caribou may be using mid-elevtion stands with a large balsam component to optimize the probability of encountering these abundant sources of lichen. Maintaining large contiguous stands of ESSF forests should allow caribou to forage extensively as they search for these "high quality patches" as well as use their summer strategy of spacing out to reduce the risk of predation (Bergerud et al. 1983, Bergerud and Page 1987, Seip 1992*b*).

Alternate silvicultural systems (i.e., selection cutting) may maintain caribou foraging habitat, over the long term, if the prescription is conservative with respect to residual basal area and tree density. Although the hierarchical analyses of foraging decisions suggested windthrown trees were a key component of a caribou's foraging environment, maintaining preharvest species composition, live to snag ratios and a range of diameter classes with abundant arboreal lichens are recommended.

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APPENDICES

Location	Elevation (m) mean range	Tree Density * (stems/ha)	
CP32 (George Ck)	1560 (1372-1677)	429	
CP37 (George Ck)	1600 (1525-1677)	527	
CP367 (Pinkerton)	1430 (1360-1500)	332	
Blocks pooled	1530 (1360-1677)	$429 \pm 113 \ (n = 3)$	
Caribou Use (EW)	1525 (1372-1677)	$641 \pm 68 (n = 51)$	
Caribou Use (LW)	> 1677	$366 \pm 186 \ (n = 9)$	

Appendix 1. Total tree densities of three high elevation partial-cut blocks: ESSF, Prince George, British Columbia.

* numbers are means \pm 95% CI. Estimates include both live and dead stems \geq 10 cm. CP32 (George Mountain #1); CP37 (George Mountain #2): CP367 (Pinkerton Mountain). EW = early winter closed canopy ESSF; LW = late winter subalpine parkland.

Appendix 2. Preliminary comparison of nearest-neighbour distances (m) at caribou use areas and 3 high elevation partial-cut blocks. Prince George, B.C.

	caribou path	foraging area EW LW	CP32	CP37	CP367 (hand)	CP367 (bunch)
NN1	2.1	2.8 3.0	3.4	2.3	3.2	3.6
NN2	1.9	2.1 1.2	2.1	2.1	2.2	1.6
***	2.3 (0.1-16.5)	3.1 (1-25)			, ,	•

NN1 = mean point to nearest tree (m).

NN2 = mean tree-to-nearest tree distance (m).

*** mean distance to nearest tree using 2 x 50 m transect data (n = 4 forage areas; subsample 165 trees). Range of distances are given in brackets. EW = Early winter closed canopy ESSF; LW = Late winter subalpine parkland.