Winter habitat ecology of mountain caribou in relation to forest management

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Summary

1. During winter, mountain caribou *Rangifer tarandus caribou* live in late successional and old-growth coniferous forests, where they feed almost exclusively on arboreal lichens. Because some of these forests are also valuable to the forest industry, caribou ecology and forest management remains a central conservation issue in British Columbia. To improve our understanding of caribou habitat use in relation to forest management, we investigated the winter habitat selection patterns of mountain caribou at a range of spatial scales between 1988 and 1993 in the northern Cariboo Mountains, British Columbia.

2. Within winter ranges, caribou selected forest stands dominated by subalpine fir ($> 80\%$ *Abies lasiocarpa*) and with moderate slopes (16–30%) during early winter (November–December). Although stands with moderately high timber volumes (201–300 m^3 ha^{-1}) were used the most during early winter, caribou used these stands in proportion to their availability. Caribou primarily used open-canopy subalpine fir stands (i.e. parkland) later in the winter (January–March), where low stocking and inoperable timber volumes (< 100 m^3 ha^{-1}) reduced direct conflicts with forest harvesting.

3. Characteristics of subalpine forests at early winter caribou foraging areas did not differ significantly from random sites for most variables measured. However, a multivariate analysis indicated that sites used by caribou had slightly less total basal area, more moderate slopes and slightly heavier lichen loads than unused sites.

4. Within early winter foraging areas, caribou chose foraging paths with more trees and greater accessible lichen biomass per standing tree compared with random paths. Although windthrown trees and lichen litterfall were encountered infrequently, caribou rarely rejected these sources of lichen when encountered.

5. The relatively low basal area (27 m^2 ha^{-1}) and minor component of economically valuable Engelmann spruce *Picea engelmannii* ($< 20\%$) at early winter caribou foraging areas suggests less conflicts with forestry compared with other caribou populations in southern British Columbia and Idaho.

6. Selection silvicultural systems may provide solutions to caribou–forestry conflicts, particularly in mid-elevation subalpine fir stands (1325–1525 m) that may have both operable timber volumes and high caribou numbers.

Key-words: foraging strategies, forestry, habitat selection, *Rangifer tarandus*, ungulate winter range.

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Introduction

Woodland caribou *Rangifer tarandus caribou* (Gmelin) that live in deep snowpack ecosystems of British Columbia, Canada, are typically referred to as 'mountain caribou' (Stevenson & Hatler 1985; Seip & Cichowski 1996). There are approximately 2366 of these caribou and all are found in British Columbia or Idaho, USA (Simpson, Kelsall & Leung 1994). In Idaho, the estimated 45 mountain caribou (Wakkinen *et al.* 1996) are currently listed as endangered in the US. In British Columbia, mountain caribou are listed as vulnerable. The Yellowhead caribou herd that lives in the northern Cariboo Mountains accounts for approximately 40% (*c.*1000) of the entire mountain caribou population (Simpson, Kelsall & Leung 1994).

During winter, mountain caribou live in old-growth forests, where they feed almost exclusively on arboreal lichens (*Bryoria* spp., *Alectoria sarmentosa*) (Stevenson & Hatler 1985; Antifeau 1987; Rominger, Robbins & Evans 1996). Some forests that caribou use during winter are valuable to the forest industry and therefore integrating caribou and forestry has been a major conservation issue for many years (Stevenson & Hatler 1985; MacKinnon 1996). Specifically, silvicultural systems such as clear-cutting conflict with maintaining mountain caribou habitat, primarily because of the long rotation periods (at least 150 years) required to re-establish sufficient arboreal lichen biomass (Armleder & Stevenson 1996). Because economic and social costs of conserving old-growth forests can be high, it is critical to know the types of forests and old-growth attributes caribou prefer during winter to ensure forests with these characteristics receive adequate consideration during land management planning.

Because large herbivores interact with their environment at a variety of spatial and temporal scales (Jarman 1974; Belovsky 1978; Owen-Smith & Novellie 1982; Senft *et al.* 1987; Sæther & Anderson 1990; Stuth 1991), recent investigations have stressed the importance of recognizing habitat selection as a scale-dependent process and have recommended that field studies incorporate more than one spatial scale (Morris 1987; Senft *et al.* 1987; Bell 1991; Danell, Edenius & Lundberg 1991; Orians & Wittenberger 1991; Turner *et al.* 1993). Studies conducted at several scales improve the resolution of factors that determine ecological patterns and their interrelationships among scales (Wiens 1989).

To gain a better understanding of how mountain caribou exploit their winter environment, we examined winter habitat selection by mountain caribou at several spatial scales. The first scale involved selection of broad forest types within early and late winter home ranges. Within these selected forest types, we measured the selection of early winter foraging areas. Within the foraging areas, we determined factors influencing the foraging paths taken by the caribou. Finally, we estimated variables influencing the selection of individual trees from which caribou fed along foraging paths. We did not specifically address the selection of food because caribou consume an almost monophagous diet of arboreal lichen during winter and lichen genera selection has been determined in cafeteria trials using captive animals (Rominger, Robbins & Evans 1996).

Study area

The study area was located east of Prince George, British Columbia (centre 53°N, 121°W), and covered 15 000 km² of the Fraser River watershed. This extensive study area included the plateaux of the northern Cariboo Mountains as well as portions of the McGregor Plateau and Rocky Mountains (Fig. 1). This area is primarily mountainous, with elevations rising from 650 m in the valleys to rugged peaks at 2200 m. The valley bottoms and lower slopes (650–1220 m) of the study area occur in the sub-boreal spruce (SBS) and interior cedar–hemlock (ICH) biogeoclimatic zones (Coupé, Stewart & Wikeem 1991). These forests are dominated by interior spruce *Picea engelmannii* Parry ex Engelm. *x glauca* (Moench) Voss, western red cedar *Thuja plicata* Donn ex D. Donn and western hemlock *Tsuga heterophylla* (Raf.) Sarg. Mid- and upper elevations (1220–1677 m) occur in the Engelmann spruce–subalpine fir (ESSF) biogeoclimatic zone and are dominated by subalpine fir *Abies lasiocarpa* (Hook.) Nutt. and Engelmann spruce *Picea engelmannii* Parry ex Engelm. At higher elevations (1677–1800 m) subalpine fir grows in clumps forming an open parkland. Alpine tundra (treeless) exists above 1800 m (Coupé, Stewart & Wikeem 1991).

Two permanent high elevation snow stations (1740 and 1650 m elevation) were located in the study area. Combining 19 years of data from these stations resulted in average 1 March snowpacks of 197 cm (125–323) (BC Snow Survey 1988–93). During our study period (1988–93), these data indicated an average 1 March snowpack of 228 cm (137–323). Annual measurements indicated that the 1992/93 winter received below average snowfall (165 cm), but all remaining winters received normal to above average snowfalls. Specifically, the 1989/90, 1990/91 and 1992/92 winters received above average snowfalls (323, 283 and 248 cm, respectively) whereas the 1988/89 winter was near average (218 cm).

Mean snowpack depths between November–January were obtained during our early winter snow trailing investigation. During this period, snow depths ranged from 68 to 178 cm during the 1991/92 winter to 42–119 cm during the 1992/93 winter.

The dominant land-use activity was timber harvesting. Clear-cut blocks of 70–1300 ha were common and were distributed predominantly in valley
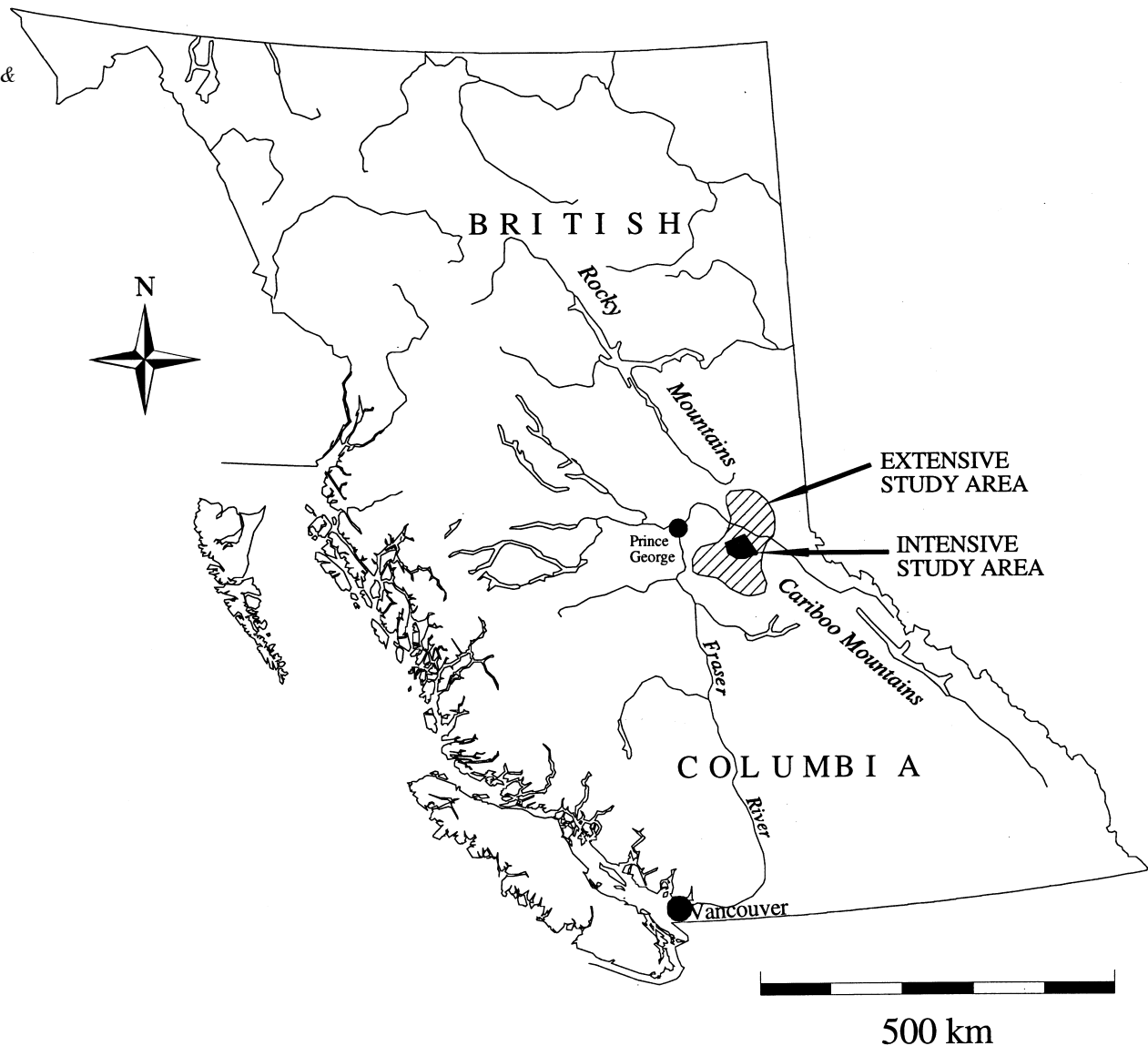
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Fig. 1. Location of extensive and intensive (snow trailing) study areas, northern Cariboo Mountains, British Columbia.

bottoms. Higher elevation (1200–1650 m) cut blocks were present but dispersed.

Within the larger study area, we selected a 250-km^2 wintering area (Sugarbowl-Raven Lake) used by an estimated 146 (1 SD = 21) caribou to conduct a more intensive investigation of habitat selection patterns including early winter foraging strategies. This intensive study area (Fig. 1) was typical of other portions of the larger study area.

Methods

Our objective was to investigate habitat-use patterns by measuring relative use and availability at each scale of resource selection using samples of data gathered via radio-collared caribou. Although samples of used and available resource units were deter-

mined for individual animals, the telemetry data were pooled over individuals and years to increase cell frequencies. Habitat variables at caribou foraging areas (snow trailing data) did not differ between years ($\chi^2 < 2.8$, 1 d.f., $P > 0.05$), so data were also pooled.

RADIO-TELEMETRY

Thirty adult caribou (24 females, six males) were captured by net-gun from a helicopter in March 1988 and fitted with radio-collars in the extensive study area. An additional five female and one male caribou were collared between 1989 and 1990 to replace those that died. Caribou were located approximately once a month during the winters of 1988/89, 1989/90 and 1990/91 using a fixed wing air-

craft. For each caribou location, elevation, aspect and Universal Transverse Mercator (UTM) co-ordinates were recorded. Aspects were grouped into two categories: warm (136–270°) and cool (271–135°). Percentage slope was grouped as: < 15%, 16–30%, 31–45% and > 45%. Based on stand characteristics recorded from the aircraft, 1 : 15 000 forest cover maps, and 1 : 15 000 aerial photographs, locations were placed in one of six habitat categories (Table 1). Average forest stand volumes were estimated using species composition, forest age class, height and stocking descriptions for each stand (BC Ministry of Forests 1991) and grouped into four volume categories: (i) inoperable ($< 100 \, m^3 \, ha^{-1}$); (ii) 100–200 $m^3 \, ha^{-1}$; (iii) 201–300 $m^3 \, ha^{-1}$; and (iv) > 300 $m^3 \, ha^{-1}$.

During the winters of 1991/92 and 1992/93 we concentrated the telemetry effort in the intensive study area (Fig. 1) to permit more frequent monitoring during early winter when caribou were suspected to use more valuable low elevation forests. In March 1992, five additional adult female caribou were collared to add to the previous sample of six animals in this area. These 11 caribou were located once a week from a helicopter.

Season descriptions followed Rominger & Oldemeyer (1989) and Servheen & Lyon (1989) and were defined by caribou elevational movements. Early winter commenced when caribou moved from high elevation fall ranges to lower elevations and usually coincided with the first persistent snowfall. Late winter began when most radio-collared caribou moved to alpine and subalpine habitats. The early winter period was usually November and December, however, slow snow accumulation in 1992/93 extended the early winter period to mid-January.

SNOW TRAILING

We visited locations of radio-collared caribou between fresh snowfalls when tracks could be followed easily. Caribou tracks were followed until we encountered evidence of foraging (e.g. trampling around base of tree). The foraging decision process

was investigated by collecting data along three transect types. (i) 'Foraging path transects' (FPT) were completed first and were centred along the caribou track. FPTs were sampled where the focal animal walked and were used to identify the types of trees or lichen litterfall that the caribou foraged upon or walked past. Foraging was identified by trampling around the base of trees or by a step towards a tree indicating a standing posture. Depending on daily time constraints, we completed three to five consecutive 2 × 50-m long transects centred on the caribou tracks. 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. (ii) 'Foraging area transects' (FAT) sampled the immediate area the animal was using including alternative paths the caribou could have taken. These transects were straight 2 × 50-m transects and were completed every 50 m along the FPT at a random direction from the FPT. (iii) 'Available forest transects' (AFT) sampled the broader ESSF forest stand types available to caribou within their early winter home range but not used by the focal animal at that time. These transects were also 2 × 50 m and were located at random compass bearings and distances from the caribou foraging area. AFTs were completed at random directions from the caribou location; however, when daylight was limited, transects were completed systematically at approximately 100-m elevation bands and their direction was constrained by a safe travel route down the mountain.

Along each transect type, we recorded the following tree characteristics: (i) tree species; (ii) diameter at breast height (d.b.h.); (ii) tree vigour, modified from Thomas's (1979) snag classification, which included (a) live, (b) tight-bark snag, (c) loose-bark snag, (d) no-bark snag and (e) windthrow; (iv) activity, foraged or walked past; (v) cumulative distance between each tree; (vi) lichen abundance visually estimated using a standard c.10-g clump and divided into two strata, (a) number of lichen clumps within approximate reach of caribou (0–1·6 m) from the snow surface, which reflected the average sinking

Table 1. Habitat categories available to the Yellowhead caribou herd, northern Cariboo Mountains, British Columbia

Habitat category	Ecological description
Alpine	Mostly treeless except for krummholz/mountain top ridges
Subalpine parkland	Upper elevation ESSF/mosaic of open areas (subalpine meadows) and clumps of small subalpine fir trees dominated by *Bryoria* spp. lichens
Subalpine fir (spruce)	Mid-upper elevation ESSF forests/ > 80% subalpine fir (minor component of spruce < 20%)
Subalpine fir–spruce	Low-middle elevation ESSF forests/60–80% subalpine fir (major component of spruce 20–40%)
Cedar–hemlock–spruce	Valley bottom forests/mixed coniferous/cedar, hemlock, and/or spruce
Other	Immature forests (clear cuts/plantations < 100 years old) non-forested land including non-commercial brush, swamps, and meadows

depth of 35 cm ($\pm$ 8 cm SD; Terry 1994) and an approximate total foraging height of *c.* 195 cm, and (b) number of lichen clumps not within reach of caribou under present snowpack depths (1·6–3·2 m); and (vii) lichen genera composition estimated visually (percentage *Alectoria sarmentosa*/*Bryoria* spp.) using 10% intervals. Three to five fixed area plots (0·01 ha) and variable plots (i.e. prism swings; Basal Area Factor (BAF) = 4) were used to determine tree density and basal area, respectively, at each foraging area and random site. Both live and dead trees (> 10 cm d.b.h.) were included in both plot types. Although we recorded the incidence of windthrown trees, we did not include windthrown tree density in the analysis because data from 0·01-ha plots were insufficient to provide reliable estimates on a stem ha^{-1} basis. To ensure snow characteristics were similar for all transect types, data were collected on the same day. Sampling began when snow depths at caribou-use sites had reached 40–60 cm.

STATISTICAL ANALYSIS

Radio-telemetry

Nine wintering areas were delineated using the 95% isopleth of the harmonic mean (Dixon & Chapman 1980) estimator generated from the computer program HOME RANGE (Ackerman *et al.* 1990). Each wintering area contained between two and nine radio-collared caribou. Winter range isopleths were used to delineate early and late winter range boundaries on 1 : 50 000 forest cover type maps, and from these the availability of habitats was estimated using random point locations (Marcum & Loftsgaarden 1980). These nine winter ranges were pooled and represented the multi-annual composite winter range of the caribou population. Radio-locations were pooled over years and individuals to provide a total of 275 early winter and 344 late winter locations. The same forest cover variables recorded for caribou radio-locations were recorded for each random point ($n = 1000$).

Independence of radio-locations was assumed because of the long interval between locations (7–27 days) and because only one location was used when two or more collared animals were together. Nonforested land and immature stands were grouped to minimize the number of habitat types (Alldredge & Ratti 1986). We used selection ratios to compare habitat use to availability using the methods of Manly, MacDonald & Thomas (1993). If elevation, forest cover type, aspect, slope and operability classes were significantly different from random, Bonferroni confidence intervals were constructed around selection ratios to determine which categories differed. All statistical tests were considered significant at $\alpha = 0.05$.

Snow trailing

Selection of foraging areas from available forests. Both univariate and multivariate techniques were used to compare foraging areas (FATs) to available forests (AFTs). Foraging areas were considered the experimental unit and transect types considered the sampling unit. Foraging areas visited were assumed to be independent because of the relocation frequency. The 3–5 FATs completed at each foraging area were averaged to provide one independent observation. Similarly, AFTs were averaged each sampling day to provide one independent observation. A total of 49 caribou foraging areas and 30 random sites were used in the analysis. Independent *t*-tests were used to compare foraging areas and random sites as well as to select variables for inclusion in a multivariate model. We used a direct discriminant analysis to compare the effects of multiple variables considered simultaneously on group separation (SYSTAT; Wilkinson 1996). We used an approximated *F*-statistic (Wilks' Lambda) to test the overall relationship between caribou foraging areas and unused sites. Prior probabilities were adjusted to reflect different sample sizes between caribou foraging areas and unused sites. We used the jackknife method to reduce potential bias associated with misclassification rates. Percentage variables were arcsine transformed, square root plus 1 transformations were applied to tight-bark snag and loose-bark snag tree densities, and lichen abundance estimates were log transformed to stabilize variances (Zar 1984). With one exception (multivariate model, see below), all statistical tests were considered significant at $P < 0.05$.

Selection of foraging paths. The three to five foraging path transects completed at each foraging area were averaged to provide one independent observation. Mean number of trees per 50-m transect, and all tree attribute variables found along foraging path (FPT) and matched random transects (FAT), were compared using paired *t*-tests.

Because univariate comparisons could not account for the multivariate structure of the data, a log–linear analysis was also used for this level of selection. A log–linear model was used to identify interrelationships among tree characteristics and to compare foraging paths with random paths. Transect type (i.e. FPT vs. FAT) was considered as the dichotomous dependent variable and d.b.h. class (10–20 cm, 25–35 cm, 40–50 cm, > 50 cm), tree vigour (live standing tree, tight-bark snag, loose-bark snag) and lichen abundance within reach (nil, < 1 clump, 1–2 clumps and > 2 clumps) were used as explanatory variables. Because we considered transect type as a category or response variable, the log–linear analysis was similar to a logit model (Colgan & Smith 1978; Tabachnick & Fidell 1989; Manly,

MacDonald & Thomas 1993). The result was a four-way ($2 \times 4 \times 3 \times 4$) contingency table ($n = 4357$ trees) designed 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 G). A more stringent alpha level was used ($P = 0.01$) to assess significant effects to account, in part, for non-independence of trees that were encountered successively and because more than one model was generated from the same data set (see below). 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.

Selection of trees along foraging paths. To determine 'acceptability' of each lichen source (i.e. whether caribou stopped to forage or walked past), the total number of foraged cases recorded along the foraging pathway was compared with the total frequency of occurrence of each lichen source (e.g. standing tree, windthrow, etc.) along the foraging path.

Standardized selection ratios (Manly, McDonald & Thomas 1993) were used to rank arboreal lichen sources from most to least preferred. These have the advantage of being robust to errors associated with inclusion of large but seldom used resources.

A log–linear model was also used to investigate proximate cues (tree attributes) that caribou use to make foraging choices among trees they encounter along their foraging pathway. Because successive trees encountered may not be statistically independent and appropriate statistical techniques remain controversial (Owen-Smith & Cooper 1987; Noon & Block 1990), this analysis is also considered exploratory. Activity (i.e. foraged or walk passed) was considered the binary response variable, and tree vigour and lichen abundance (within reach) were used as explanatory variables. Because caribou usually consumed almost all arboreal lichen on windthrown trees, this analysis was confined to standing trees. The result was a $2 \times 3 \times 4$ contingency table ($n = 2838$ trees). The model was fitted using log–linear methods as described previously (Fienberg 1977; Dixon 1990).

We used the simple deletion method to determine the simplest and best fit models. Because count and proportion data are vulnerable to overdispersion, which can result in erroneous significance levels during model fitting (Crawley 1993), we examined all models for significant overdispersion. Significant overdispersion was indicated if the residual deviance or G statistic divided by the degrees of freedom was significantly greater than 1 (Crawley 1993).

Results

HABITAT SELECTION WITHIN WINTER RANGES (TELEMETRY)

Early winter

Habitat use differed significantly from random during early winter for most habitat components ($P < 0.001$). Caribou selected mid-elevation forests between 1525 and 1677 m that were dominated (> 80%) by subalpine fir and on 16–30% slopes (Table 2). In contrast, low elevation forests, stands with high timber volumes (> 300 m³ ha⁻¹) and steep slopes were used significantly less than their occurrence. Caribou used forests with moderate (201–300 m³ ha⁻¹) timber volumes the most (45% locations), but used these stands in proportion to their availability. Similarly, inoperable (< 100 m³ ha⁻¹) and low timber volume (100–200 m³ ha⁻¹) stands were used in proportion to their availability. Caribou used warm and cool aspects equal to their availability ($P = 0.200$; Table 2).

Late winter

Caribou habitat use also differed significantly during late winter ($P < 0.001$). During this period, subalpine parkland forests above 1677 m elevation and forest stands that had inoperable (< 100 m³ ha⁻¹) timber volumes were strongly selected for by caribou (Table 2). Lower elevation forests, including those that had a large component (> 40%) of Engelmann spruce (i.e. subalpine fir–spruce) as well those dominated by western red cedar or western hemlock (cedar–hemlock–spruce), were used significantly less than their occurrence (Table 2). Similar to early winter, caribou used moderate slopes significantly more than their availability during late winter ($P < 0.001$) but warm and cool aspects were used in proportion to their availability ($P = 0.50$; Table 2).

SNOW TRAILING

Selection of early winter foraging areas

The univariate analysis (*t*-test) revealed that one variable, total tree basal area, was significantly different ($P = 0.013$; Table 3) between foraging areas and unused sites. Caribou foraging areas had a total (i.e. live and dead stems) tree basal area of 27 m² ha⁻¹, while unused sites had 34 m² ha⁻¹. We chose a less rigorous standard of $P < 0.10$ for inclusion into a multivariate model to ensure that variables that might be important in discriminating between foraging areas and unused sites were included. Three variables approached this significance level, includ-

Table 2. Estimated percentages of different habitat components available to mountain caribou and their relative selection during early and late winter, northern Cariboo Mountains, British Columbia

Habitat component % available	Early winter		Late winter	
	% use	% available	% use	
Elevation (m)				
> 1677	10·3	10·6	10·3	27·8 +
1526–1677	20·1	45·3 +	20·1	45·6 +
1376–1525	21·8	28·8	21·8	20·5
1220–1375	24·6	8·8 –	24·6	3·5 –
< 1220	23·3	6·6 –	23·3	2·6 –
Forest cover				
Alpine	5·5	1·8 –	6·0	11·1
Subalpine parkland	9·6	9·8	9·0	31·9 +
Subalpine fir (spruce)	30·8	49·5 +	32·0	41·8
Subalpine fir–spruce	20·5	19·6	19·0	9·1 –
Cedar–hemlock–spruce	22·9	14·2 –	23·0	4·7 –
Other	10·7	5·1 –	11·0	1·5 –
Aspect				
Cool	46·9	41·9	53·5	51·0
Warm	53·1	58·1	46·5	49·0
Slope (%)				
< 15	20·1	20·2	17·7	22·2
16–30	39·8	52·5 +	42·7	52·7 +
31–45	36·1	26·4 –	35·5	20·0 –
> 45	4·0	0·8 –	4·1	5·1
Timber volume (m³ ha⁻¹)				
< 100	22·0	26·9	26·5	56·6 +
100–200	31·5	24·0	36·4	20·8 –
201–300	37·4	44·7	30·8	22·6 –
> 300	9·1	4·4 –	6·3	0·0

Early winter: caribou use $n = 275$, random $= 1000$ points; late winter: caribou use $n = 342$; random $= 1000$ points. Plus sign (+) indicates use > availability (lower confidence interval for selection ratio above 1); minus sign (–) use < availability (upper confidence limit for selection ration below 1); no sign indicates use $=$ availability (Bonferroni confidence intervals for selection ratio includes 1).

ing total basal area, lichen abundance above reach of caribou and slope (Table 3). None of the variables entered into the multivariate model was autocorrelated (all pairwise comparisons; $r < 0.10$). A test of the equality of group means revealed only a moderately significant separation of caribou foraging areas and unused sites ($F = 3.41$, $P = 0.023$). A single discriminant function consisting of these three variables correctly classified 70% of all caribou foraging areas and 64% of random sites.

Selection of foraging paths: early winter

Caribou foraging paths had significantly more trees per 50 m (13 trees) than occurred along random paths (eight trees) ($P = 0.001$; Table 4). Caribou foraging paths had similar proportions of subalpine fir and Engelmann spruce compared with paired random transects. Similarly, caribou foraging paths (FPT) contained similar proportions of live, dead and windthrown trees as random transects (FATs; Table 4). Although caribou foraging paths had simi-

lar proportions of *A. sarmentosa* and *Bryoria* spp. as FATs, caribou foraging paths had slightly more arboreal lichen per tree compared with random paths ($P = 0.021$; Table 4).

Log–linear model: transect (T) × tree diameter (D) × tree vigour (V) × lichen abundance (L)

The best model to fit the foraging path selection data included the TL interaction and the DVL three-way interaction ($G = 41.4$, 44 d.f., $P = 0.585$). The significant TL interaction ($P < 0.001$) indicated that caribou chose foraging paths that contained trees with greater lichen abundance compared with random paths. Lambda parameters indicated that caribou paths had significantly more trees that supported > 2 clumps of lichen and significantly fewer trees with no lichen than random paths (Table 5). This result is similar and consistent with the previous paired *t*-test comparisons.

The TDL and TVL three-way interactions were not significant, indicating that caribou chose fora-

Table 3. Early winter habitat characteristics measured at caribou foraging areas and unused sites in the Engelmann spruce–subalpine fir (ESSF) biogeoclimatic zone. Sugarbowl-Raven Lake, northern Cariboo Mountains, British Columbia

Attribute	Foraging area	Unused sites	P
Total tree density (stems ha^{-1})*	689 ± 40	759 ± 50	0·387
Live tree density (stems ha^{-1})	513 ± 31	601 ± 43	0·104
Tight-bark snag density (stems ha^{-1})	98 ± 13	86 ± 12	0·813
Loose-bark snag density (stems ha^{-1})	81 ± 12	70 ± 11	0·823
Total basal area (m^2 ha^{-1})*	27 ± 1·8	34 ± 1·7	0·013
d.b.h. (cm)	29 ± 1	28 ± 1	0·444
% subalpine–fir†	84 ± 2	82 ± 3	0·545
% Engelmann spruce†	16 ± 2	18 ± 3	0·580
% slope	14 ± 2	18 ± 2	0·087
Mean no. lichen clumps (within caribou reach)‡	0·7 ± 0·07	0·8 ± 0·14	0·961
% *Alectoria sarmentosa* (within caribou reach)‡	39 ± 4	46 ± 5	0·295
Mean no. lichen clumps (above caribou reach)§	3·1 ± 0·21	2·5 ± 0·26	0·074
% *Alectoria sarmentosa* (above caribou reach)§	48 ± 4	57 ± 4	0·198
Total no. lichen clumps	3·8 ± 0·25	3·3 ± 0·33	0·212

Numbers are means ± 1 SE.
*Estimates include live and dead stems > 10 cm d.b.h.
‡Percentage of basal area.
‡Lichen abundance numbers represent the mean number of *c*. 10 g clumps estimated to be in reach of a foraging caribou (≤ 1·6 m from snow surface); % *Bryoria* spp. can be determined as 100 minus % *Alectoria*.
§Lichen abundance numbers represent the mean number of *c*. 10 g clumps not within reach of a foraging caribou (1·6–3·2 m from snow surface).

Table 4. Univariate comparisons (paired *t*-test) of tree characteristics between caribou foraging path transects (FPT) and paired foraging area transects (FAT). Sugarbowl-Raven Lake, northern Cariboo Mountains, British Columbia

| Tree attribute	Foraging path	Random	P
Number of trees/50 m	13 ± 4	8 ± 3	0·001
% subalpine fir	86 ± 2·0	86 ± 2·0	0·884
% Engelmann spruce	13 ± 1·7	13 ± 1·6	0·944
% live stems	75 ± 1·5	70 ± 3·0	0·125
% tight-bark snags	8·8 ± 1·1	8·4 ± 1·3	0·703
% loose-bark snags	14·0 ± 1·1	14·5 ± 1·6	0·761
% windthrow	2·8 ± 0·6	2·9 ± 0·01	0·867
Lichen abundance (within reach)	0·671 ± 0·06	0·595 ± 0·053	0·021
% *Alectoria sarmentosa*	43 ± 4	42 ± 4	0·566

Numbers are means ± 1 SE. Lichen abundance represents the mean number of *c*. 10-g clumps estimated to be in reach of a foraging caribou (≤1·6 m from snow surface); % *Bryoria* spp. can be determined as 100 minus % *Alectoria*.

Table 5. Log–linear results of significant tree characteristics identified between caribou foraging path transects (FPT) and paired foraging area transects (FAT) as indicated by the ratio of the log–linear parameter estimates (lambda) to their standard errors

Lichen abundance (within reach)	Foraging path (FPT)		Random path (FAT)	
	λ/SE	Marginal %	λ/SE	Marginal %
Nil	−4·425*	14·5	4·425	19·4
< 1 clump	2·187	32·6	−2·187	29·3
1–2 clumps	−0·988	34·0	0·988	36·0
> 2 clumps	3·322*	18·9	−3·332	15·3

*P < 0·01 (λ/SE > 2·58 significantly different from zero).
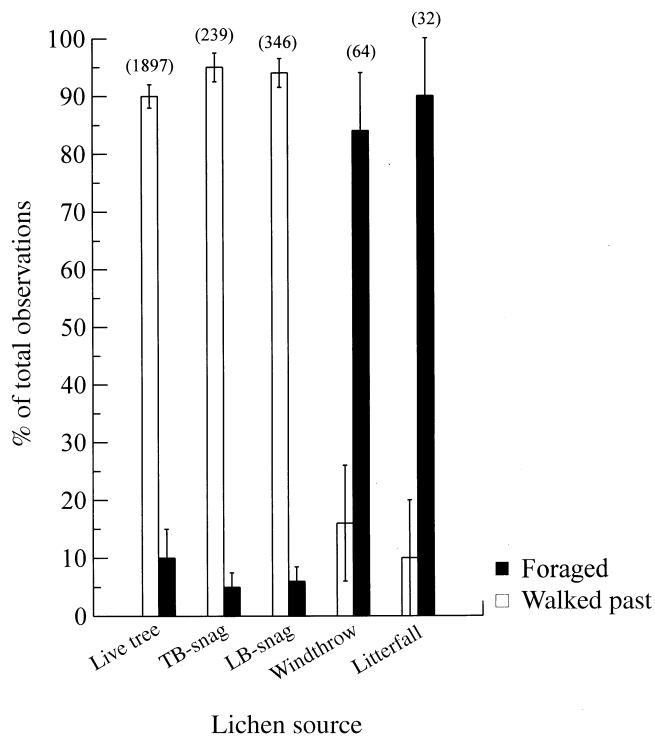
Fig. 2. Comparison of arboreal lichen sources encountered along caribou foraging paths and their relative use (foraged vs. walk past). TB snags = tight-bark snags; LB snags = loose-bark snags. Bars are 95% binomial confidence intervals. Sample sizes are given above bars in parentheses.

ging paths based neither on an association between tree diameter and lichen abundance ($P = 0.393$), nor tree vigour and lichen abundance ($P = 0.524$). Similarly, caribou did not choose foraging paths based on tree diameter ($P = 0.569$) or vigour ($P = 0.186$) considered alone.

Selection of trees along foraging paths: early winter

Caribou rarely walked past windthrown trees or lichen litterfall when they encountered these forage sources. In contrast, most standing trees appeared to be passed by (Fig. 2). When the proportions of foraged cases for each lichen source were compared with their relative availability, a similar pattern of

foraging decisions was evident. Although standing trees were encountered more frequently and comprised the majority of foraged cases (59%), windthrown trees and lichen litterfall were 10 and 15 times (respectively) more likely to be foraged than standing trees (Table 6).

Of the log–linear model, *activity* (A) × *vigour* (V) × *lichen abundance* (L), the best fit of the foraging path data included three two-way interactions: AL, AV and VL ($G = 9.69$, 6 d.f., $P = 0.139$). The significant AL interaction ($P < 0.001$) indicated a difference in lichen abundance between foraged trees and those passed by. The pattern of parameter estimates suggested that caribou walked past more trees with no lichen and foraged upon significantly more trees

Table 6. Estimated probabilities of selection and relative preference rankings for different arboreal lichen sources encountered along caribou foraging paths

Arboreal lichen source	Occurrence (%)	Foraged (%)	SSR	Rank
Litterfall	0·01	0·12	0·539	1 b
Windthrown tree	0·02	0·17	0·382	2 b
Standing live trees	0·73	0·59	0·036	3 a
Tight-bark snags	0·18	0·11	0·027	4 a
Loose-bark snags	0·06	0·02	0·015	5 a

SSR = standardized selection ratio. Rankings from top to bottom represent decreasing likelihood of selection. Rank orders with similar letters indicate selection ratios are not significantly different from each other ($P > 0.05$).

Table 7. Log–linear results of tree selection along caribou foraging paths as shown by parameter estimates (lambda) divided by their standard errors

	Activity			
	Foraged		Walk past	
Lichen abundance (within reach)	λ/SE	Marginal %	λ/SE	Marginal %
Nil	−4·068*	4·2	4·068	15·5
< 1 clump	3·708*	37·7	−3·708	32·2
1–2 clumps	3·622*	40·8	−3·622	33·2
> 2 clumps	0·622	17·4	−0·622	19·0
Tree vigour				
Live standing	3·605*	86·8	3·605	75·3
Tight-bark snag	−1·329	5·3	1·329	9·2
Loose-bark snag	−1·108	7·9	1·108	15·5

*$P < 0.01$ (λ/SE > 2·58 significantly different from zero).

supporting < 1 clump or 1–2 clumps (Table 7). Although there was a positive association between foraging activity and trees supporting > 2 clumps of lichen, the parameter estimate was not significantly different from random. The significant AV interaction ($P < 0.001$) suggested that caribou foraged at trees with different tree vigour. The parameter estimates indicated a positive and significant association between foraged trees and live stems. Although there was a negative association between foraged trees and snags (tight-bark and loose-bark), neither parameter estimate was significantly different from random (Table 7). The AVL three-way interaction was not significant ($P = 0.138$), indicating that caribou did not stop to forage at trees based on an association between tree vigour and lichen abundance.

Discussion

The hierarchical framework used to investigate habitat selection by mountain caribou suggests that decisions are made at both larger (forest cover type) and smaller (individual trees) spatial scales. The magnitude of differences between use and availability of habitat variables, however, varied among scales. The telemetry data clearly indicated that caribou select mid-elevation forests dominated by subalpine fir and moderate slopes during early winter. This habitat selection pattern is consistent with caribou that winter in similar plateau terrain in the Quesnel Highlands of British Columbia (Seip 1992). In contrast, caribou in more rugged regions of British Columbia make greater use of valley bottom forests dominated by western red cedar and western hemlock during early winter (Antifeau 1987; Simpson & Woods 1987; Servheen & Lyon 1989; Seip 1990). Lower snow depths, wolf *Canis lupus* densities and/ or availability of alternative food sources such as falsebox *Paxistima myrsinites* have been suggested as possible explanations to explain greater use of

lower elevations in more mountainous regions (Terry *et al.* 1996).

Similar to the findings of Rominger & Oldemeyer (1989) at the southern extreme of mountain caribou distribution, we found mountain caribou to forage in areas with less tree basal area and more moderate slopes than unused sites. Less tree basal area reflects more open stand conditions that may provide better conditions for arboreal lichen growth (e.g. increased air flow, air-born nutrients, light) as well as improved predator detection. Caribou did not appear to choose foraging areas based on the amount of lichen on standing trees within their reach. The slightly higher lichen abundance above their reach, however, suggests that caribou may be using areas with an overall higher lichen abundance, which may provide greater availability of arboreal lichen either as litterfall or on windthrown trees.

Within early winter foraging areas, caribou chose foraging paths with similar tree attributes (i.e. tree species and vigour) as those found on other available but unused paths (Table 4). However, caribou did choose foraging paths with more trees per unit distance and slightly more arboreal lichen per tree than unused paths, which suggests tree spatial distribution and lichen abundance are proximate cues caribou use to move through their foraging environment.

Similarly, along their selected foraging path, caribou stopped more frequently to feed on standing trees with higher lichen loads than other trees available along the path. Interestingly, caribou did not necessarily choose to forage on trees with the highest lichen abundance as these trees were sometimes passed by without any evidence of being utilized. Instead, caribou selected trees with intermediate levels of arboreal lichen biomass. Although selected trees must have had more lichen before the animal removed some, we believe caribou spend a relatively short amount of time foraging at each tree, which

results in minimal amounts being utilized. Therefore, we contend that our estimates of post-foraging lichen abundance are not significantly biased and are partly supported by short residences times reported elsewhere (Rominger, Robbins & Evans 1996).

Although ours is the first study to investigate early winter selection of foraging paths and trees by wild caribou, Rominger, Robbins & Evans (1996) found that bottle-raised caribou foraged primarily on standing subalpine fir and dead trees that also supported greater than average lichen biomass during late winter field trials. They report that caribou in their study spent much less time foraging at each tree than theoretical foraging models predicted. However, they also found that residence time at trees increased with increasing lichen abundance, further suggesting that lichen abundance is a relatively strong proximate cue influencing caribou winter foraging decisions.

In this study, caribou rarely rejected lichen litter-fall or lichen accessible on windthrown trees when these lichen sources were encountered (Fig. 2). We observed heavy trampling at windthrown trees, indicating that caribou fed intensely on the high lichen biomass accessible on them compared with that available on standing trees. Simpson, Hebert & Woods (1987) and Rominger & Oldemeyer (1989) also reported heavy foraging on recently windthrown trees during early winter when arboreal lichen on standing trees is scarce. Rominger & Oldemeyer (1989) found subalpine fir to be the most common windthrown species and suggested that caribou may use stands dominated by subalpine fir to increase the probability of encountering these sources of abundant lichen. Similarly, in our study area, 90% of the windthrown trees encountered by caribou were subalpine fir (Terry 1994). Other studies on subalpine forest ecology have also documented a greater likelihood of subalpine fir windfall compared with Engelmann spruce in subalpine forests (Veblen 1986).

Overall, it appears that caribou make foraging choices at a broad spatial scale by selecting forests dominated by subalpine fir (> 80%) during early winter and at a finer scale where they clearly select windthrown trees. Although at intermediate spatial scales (i.e. selection of foraging areas) caribou showed selection for some of the variables that we measured, differences between habitat characteristics used and available were relatively small (Table 3). The relatively similar tree characteristics distributed throughout these subalpine forests may have constrained opportunities for selection at that scale.

During early winter, it appears that caribou forage on the relatively sparse amount of lichen available on standing trees, but because ingestion rates are probably very low, tree residence times are also likely to be short. We suggest that a short residence

time at each tree results in increased movement during early winter and thus greater encounter rates with windthrown trees that have abundant and accessible arboreal lichen. The initial abundance of available lichen on most windthrown trees results in longer residence times, indicated by the heavy trampling. Therefore, despite the stochastic nature of windstorms and fallen trees which provides an uncertain environment for caribou to exploit efficiently, the relatively high mobility of mountain caribou during early winter (Simpson & Woods 1987) appears to be part of a foraging strategy caribou use to find scarce available lichen sources. Although high mobility during winter has energetic costs (Parker, Robbins & Hanley 1984), the morphological adaptations of mountain caribou (Telfer & Kelsall 1984) enable efficient locomotion in deep snow areas, where they rarely sink to depths considered excessive (> 50% brisket height) (Terry 1994). Finally, we suggest that the relatively high *in vitro* digestibility (82%) of arboreal lichen (Rominger, Robbins & Evans 1996) may minimize digestive constraints and permit caribou to forage more extensively by reducing rumination time.

Although we were unable to account for interannual variation in caribou habitat selection patterns, our study period did cover a range of winter conditions including a record high and low snow winter. Despite this range in winter conditions, we did not observe large differences in habitat use among years. Instead, we noticed that snow accumulation rate affected the lengths of both early and late winter seasons. During years when snow accumulation was relatively rapid, caribou made elevational shifts from mid-elevation forests dominated by subalpine fir stands to subalpine parkland areas earlier compared with the year when snow accumulated more slowly.

Management implications

Caribou use of subalpine fir forests on moderate slopes conflicts with clear-cut timber harvesting systems. However, the relatively low basal area, moderate timber volumes, and lower percentage of Engelmann spruce found at early winter foraging areas, suggests less conflict between forestry and caribou habitat compared with other areas in British Columbia (Simpson, Terry & Hamilton 1997). The relatively high snag component (25–30% of stem density) found in these subalpine fir forests also indicates less merchantable timber in early winter ranges. Lower elevation stands (1220–1375 m) with a larger component of Engelmann spruce received little use by caribou during both early and late winter, and suggests that timber harvesting could occur in these more economical forest types with little direct impact on caribou foraging habitat. However, access management (e.g. permanent road deactiva-

tion, gates, restricted snowmobile use) is required to reduce potential impacts (e.g. snowmobile harassment) of increased road access into subalpine forests. Although valley bottom forests did not appear to be used as foraging areas during early winter, caribou moved across them, indicating that some valley bottom forests should be managed as travel corridors to help maintain landscape-level connectivity between seasonal ranges and subpopulations.

To minimize habitat fragmentation and potential increased predation on caribou (Seip 1991), maintaining large contiguous tracts of mature and old forests is preferable to maintaining fragmented patches of mature forest interspersed with clear-cuts (Seip 1998). Forestry planning at the landscape-level should attempt to provide large contiguous areas that contain primarily mid- and upper elevation (> 1376 m) forests that contain > 80% subalpine fir.

Caribou–forestry conflicts may be most severe in mid-elevation subalpine fir stands with operable timber volumes (201–300 m^3 ha^{-1}). Because over 40% of the early winter caribou locations occurred in these forests, alternative forest management practices are needed to ensure arboreal lichens are maintained over the long-term. Although some even-aged management of subalpine fir–spruce stands may be tolerable, selection silvicultural systems that mimic natural disturbance patterns of upper elevation subalpine forests are recommended within early winter habitats (Stevenson *et al.* 1994; Seip 1998). Alexander (1986) and Stevenson *et al.* (1994) recommended residual basal areas of 20 m^2 ha^{-1} in spruce–fir forests after selective cutting. However, the low initial basal area of subalpine fir stands identified as early winter habitat in this study (27 m^2 ha^{-1}) suggests little basal area can be removed and long cutting cycles may be required to allow residual stocking to recover.

Forests must be managed not only to maintain an abundance of lichen, but also managed so that lichen becomes available to caribou. During early winter, the available biomass of arboreal lichen to caribou on windthrow equals or exceeds that available on standing trees (Rominger & Oldemeyer 1991). Therefore, managed stands must also produce windthrow and litterfall. However, preliminary studies of heavy (*c.* 50%) timber volume removal using single tree selection indicated that trees are vulnerable to wind scouring and catastrophic windthrow which would not provide caribou foraging habitat over the long term (Terry 1994). Therefore, lighter volume removals (20–30%) and group selection silvicultural systems have been recommended to retain arboreal lichen biomass and limit excessive windthrow (Armleder & Stevenson 1996).

Silvicultural systems that alter the spatial and temporal availability of arboreal lichens may influence foraging energetics by affecting both energy intake and costs. To ensure forest stands remain as viable winter foraging areas (i.e. provide adequate lichens to maintain energy/nutrient intake) for caribou over the long-term, stand management prescriptions should attempt to maintain adequate tree densities of lichen bearing trees. The results from this study indicated that early winter caribou foraging areas contained an average total tree density of *c.* 700 stems ha^{-1}. As a preliminary recommendation we suggest that at least 400–500 stems ha^{-1} of lichen-bearing trees should be maintained in managed forests, which corresponds to typical late winter range tree densities found in subalpine parkland habitats (Terry 1994; Rominger, Robbins & Evans 1996). Our results further suggest that live subalpine fir trees that support > 50% *Bryoria* spp. lichens should be the priority tree species maintained during harvesting operations.

References

Ackerman, B., Leban, F., Samuel, M. & Garton, E. (1990) *User's Manual for Program home range*. Technical Report 15. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho.

Alexander, R.R. (1986) *Silvicultural Systems and Cutting Methods for Old Growth Spruce-Fir Forest in the Central and Southern Rocky Mountains*. General Technical Report RM-126. USDA Forest and Range Experimental Station, Fort Collins, Colorado.

Alldredge, J.R. & Ratti, J.T. (1986) Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management*, **50**, 157–165.

Antifeau, T.D. (1987) Significance of snow and arboreal lichen in the winter ecology of mountain caribou (*Rangifer tarandus caribou*) in the north Thompson watershed of British Columbia. MSc Thesis. University of British Columbia, Vancouver, BC.

Armleder, H.M. & Stevenson, S.K. (1996) Using alternative silviculture systems to integrate mountain caribou

and timber management in British Columbia. Proceedings of the sixth North American Caribou workshop, Prince George, British Columbia, 14 March 1994. *Rangifer*, **9** (Special Issue), 141–148.

BC Ministry of Forests (1991) *Average Piece Size and Volume per Hectare by Inventory Stratum*. Timber Supply Analysis Support. BC Ministry of Forests, Prince George Forest Region, Prince George, BC.

BC Snow Survey (1988–93) *Snow Survey Bulletins*. BC Ministry of Environment, Lands and Parks, Hydrology Section, Water Management Division, Victoria, BC.

Bell, W.J. (1991) *Searching Behaviour. The Behavioural Ecology of Finding Resources*. Chapman & Hall, London, UK.

Belovsky, G.E. (1978) Diet optimization in a generalist herbivore, the moose. *Journal of Theoretical Population Biology*, **14**, 76–104.

Colgan, P.W. & Smith, J.T. (1978) Multidimensional contingency table analysis. *Quantitative Ethology* (ed. P. Colgan), pp. 145–175. John Wiley & Sons, New York, NY, USA.

Coupé, R., Stewart, A.C. & Wikeem, B. (1991) Engelmann spruce-subalpine fir zone. *Ecosystems of British Columbia* (eds D. Meidinger & J. Pojar), pp. 223–237. Special Report Series No. 6. BC Ministry of Forests, Victoria, BC.

Crawley, M.J. (1993) *Methods in Ecology: GLIM for Ecologists* (eds J.H. Lawton & G.E. Likens), pp. 226–264. Blackwell Scientific Publications, Oxford, UK.

Danell, K., Edenius, L. & Lundberg, P. (1991) Herbivory and tree stand composition: moose patch use in winter. *Ecology*, **72**, 1350–1357.

Dixon, W.J. (1990) *BMDP Statistical Software. Vol. 1. Part 3. Analysis of Multi-Way Tables: Log-Linear Models*. University of California Press, Berkeley, CA.

Dixon, K.R. & Chapman, J.A. (1980) Harmonic mean measure of animal activity areas. *Ecology*, **61**, 1040–1044.

Fienberg, S.E. (1977) *The Analysis of Cross-Classified Categorical Data*. The MIT Press, Cambridge, MA.

Jarman, P.J. (1974) The social organization of antelope in relation to their ecology. *Behaviour*, **48**, 215–267.

MacKinnon, G.A. (1996) A mountain caribou strategy for British Columbia. *Rangifer*, **9** (Special Issue), 149–152.

Manly, F.J., McDonald, L.L. & Thomas, D.L. (1993) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Chapman & Hall, London, UK.

Marcum, C.L. & Loftsgaarden, D.O. (1980) A nonmapping technique for studying habitat preferences. *Journal of Wildlife Management*, **44**, 963–968.

Morris, D.W. (1987) Ecological scale and habitat use. *Ecology*, **68**, 362–369.

Noon, B.R. & Block, W.M. (1990) Foraging behaviour: analytical considerations for study design. *Studies in Avian Biology*, **13**, 126–133.

Orians, G.H. & Wittenberger, J.F. (1991) Spatial and temporal scales in habitat selection. *American Naturalist*, **137** (Supplement), 29–49.

Owen-Smith, R.N. & Cooper, S. (1987) Assessing food preferences of ungulates by acceptability indices. *Journal of Wildlife Management*, **51**, 372–378.

Owen-Smith, R.N. & Novellie, P. (1982) What should a clever ungulate eat? *American Naturalist*, **119**, 151–178.

Parker, K.L., Robbins, C.T. & Hanley, T.A. (1984) Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management*, **48**, 474–488.

Rominger, E.M. & Oldemeyer, J.L. (1989) Early-winter habitat of woodland caribou, Selkirk Mountains, British Columbia. *Journal of Wildlife Management*, **53**, 238–243.

Rominger, E.M. & Oldemeyer, J.L. (1991) Arboreal lichen on windthrown trees: a seasonal forage resource for woodland caribou, Selkirk Mountains, British Columbia. *Rangifer*, **6** (Special Issue), 475–480.

Rominger, E.M., Robbins, C.T. & Evans, M.A. (1996) Winter foraging ecology of woodland caribou in northeastern Washington. *Journal of Wildlife Management*, **60**, 719–728.

Sæther, B.-E. & Anderson, R. (1990) Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. *Canadian Journal of Zoology*, **68**, 993–999.

Seip, D.R. (1990) *Ecology of Woodland Caribou in Wells Gray Provincial Park*. Wildlife Bulletin No. B-68. BC Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria, BC.

Seip, D.R. (1991) Predation and caribou populations. *Rangifer*, **7** (Special Issue), 46–52.

Seip, D.R. (1992) *Habitat Use and Population Status of Woodland Caribou in the Quesnel Highlands, British Columbia*. Wildlife Bulletin No. B-71. BC Ministry of Environment, Lands and Parks, Victoria, BC.

Seip, D.R. (1998) Ecosystem management and the conservation of caribou habitat in British Columbia. *Rangifer*, **10** (Special Issue), 203–211.

Seip, D.R. & Cichowski, D. (1996) Population ecology of caribou in British Columbia. *Rangifer*, **9** (Special Issue), 73–80.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience*, **37**, 789–799.

Servheen, G. & Lyon, J.L. (1989) Habitat use by woodland caribou in the Selkirk Mountains. *Journal of Wildlife Management*, **53**, 230–237.

Simpson, K. & Woods, G.P. (1987) *Movements and Habitats of Caribou in the Mountains of Southern British Columbia*. Wildlife Bulletin No. B-57. BC Ministry of Environment, Lands and Parks, Victoria, BC.

Simpson, K., Hebert, K. & Woods, G.P. (1987) *Critical Habitats of Caribou in the Mountains of Southern British Columbia*. Wildlife Working Report WR-23. BC Ministry of Environment, Lands and Parks, Victoria, BC.

Simpson, K., Kelsall, J.P. & Leung, M. (1994) *Integrating Management of Mountain Caribou and Forestry in Southern British Columbia*. BC Ministry of Environment, Victoria, BC.

Simpson, K., Terry, E. & Hamilton, D. (1997) *Toward a Mountain Caribou Management Strategy for British Columbia – Habitat Requirements and Sub-population Status*. Wildlife Working Report WR-90. BC Ministry of Environment, Lands and Parks, Victoria, BC.

Stevenson, S.K. & Hatler, D.F. (1985) *Woodland Caribou and their Habitat in Southern and Central British Columbia*. Report 23. BC Ministry of Forests, Victoria, BC.

Stevenson, S., Armleder, H., Jull, M., King, D., Terry, E., Watts, G., McLellan, B. & Child, K. (1994) *Mountain Caribou in Managed Forests: Preliminary Recommendations for Managers*. BC Ministry of Forests, Research Branch, Victoria, BC.

Stuth, J.W. (1991) Foraging behaviour. *Grazing Management – An Ecological Perspective* (eds R. Heitschimdt & J.R. Stuth), pp. 65–83. Timber Press, Portland, Oregon, USA.

Tabachnick, B.G. & Fidell, L.S. (1989) Multiway frequency analysis. *Using Multivariate Statistics*, 2nd edn

(ed. J. Rothman), pp. 236–315. Harper Collins Publications, New York, NY.

Telfer, E.S. & Kelsall, J.P. (1984) Adaptation of some large North American mammals for survival in snow. *Ecology*, **65**, 1828–1834.

Terry, E. (1994) Winter habitat selection and foraging patterns of mountain caribou. MSc Thesis. University of British Columbia, Vancouver, BC.

Terry, E., McLellan, B., Watts, G. & Flaa, J. (1996) Early winter habitat use by mountain caribou in the North Cariboo and Columbia Mountains, British Columbia. Proceedings of the Sixth North American Caribou Workshop, Prince George, BC, March 1–4, 1994. *Rangifer*, **9** (Special Issue), 133–140.

Thomas, J.W. (1979) *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington*. Agricultural Handbook No. 553. USDA Forest Service, Washington, DC.

Turner, M.G., Yeyang, W.u., Romme, W.H. & Wallace, L.L. (1993) A landscape simulation model of winter foraging by large ungulates. *Ecological Modelling*, **69**, 163–184.

Veblen, T.T. (1986) Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology*, **67**, 644–649.

Wakkinen, W., Compton, B.B., Zager, P. & Skalski, J.R. (1996) *A Census Technique for Monitoring Woodland Caribou*. Idaho Department of Fish and Game, Bonners Ferry, ID.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Wilkinson, L. (1996) *Multivariate Models*. Systat Inc., Chicago, Illinois.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs, NJ.