# Scale-dependent microhabitat selection by threatened mountain caribou (*Rangifer tarandus caribou*) in cedar–hemlock forests during winter

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**Abstract:** Mountain caribou, an endangered ecotype of woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788), live in late-successional coniferous forests where they depend largely on arboreal lichens as winter forage. While radio-telemetry has been used to understand caribou habitat selection patterns at broad scales among and within populations, here we use snow-trailing in old cedar–hemlock forests between 1992 and 2003 to study three finer scales of habitat selection: (1) forest stands used for foraging from available forest stands (among-stand selection), (2) foraging paths within selected stands relative to random paths within those same stands (within-stand selection), and (3) feeding items along foraging paths. Relative to stands that were available on the landscape, caribou selected stands with more windthrown trees and standing snags. Within stands, caribou selected paths that had more live trees, snags with branches and bark, and trees with larger diameters. All of these habitat attributes facilitate access to arboreal lichen. Of the potential forage items encountered along foraging paths, caribou preferred to feed on windthrown trees, lichen litterfall and falsebox (*Paxistima myrsinites* (Pursh.) Raf.). Our results go beyond telemetry studies by revealing that not all old forests are of equal value to mountain caribou. Prioritization among old stands will help refine conservation measures, as will silvicultural systems that incorporate key habitat attributes to maintain winter habitat in low-elevation cedar–hemlock ecosystems.

**Résumé :** Le caribou de montagne, un écotype menacé du caribou des bois (*Rangifer tarandus caribou* Gmelin, 1788), vit dans des forêts de conifères aux derniers stades de succession où il dépend largement des lichens arboricoles comme fourrage d'hiver. Alors qu'à grande échelle la radiotélémétrie a été employée pour comprendre les divers choix d'habitat par le caribou parmi et dans des populations, nous nous sommes servis ici des pistes laissées par le caribou sur la neige dans de vieilles forêts de cèdres et de pruches enter 1992 et 2003 pour étudier le choix d'habitat à trois échelles plus fines : (1) les peuplements forestiers utilisés pour se nourrir parmi les peuplements disponibles (choix entre peuplements); (2) le trajet emprunté par le caribou pour se nourrir à l'intérieur de ces peuplements comparativement à des trajets aléatoires dans ces mêmes peuplements (choix à l'intérieur des peuplements) et (3) les items qui ont servi de nourriture le long des trajets empruntés pour se nourrir. Parmi les peuplements disponibles dans le paysage, le caribou a choisi ceux où il y avait plus d'arbres reversés par le vent et de chicots. A l'intérieur des peuplements, le caribou a choisi les traject le long desquels on trouvait plus d'arbres vivants, plus de chicots avec des branches et de l'écorce et les arbres avec les plus forts diamètres. Tous ces attributs d'habitat facilitent l'accès aux lichens arboricoles. Parmi les items potentiellement comestibles rencontrés le long des trajets empruntés pour se nourrir, le caribou a préféré les arbres renversés par le vent, les lichens tombés au sol et *Paxistima myrsinites* (Pursh.) Raf. Nos résultats vont au-delà de ceux obtenus par radiotélémétrie car ils révèlent que toutes les vieilles forêts n'ont pas la même valeur égale pour le caribou de montagne. La priorisation parmi les vieux peuplements devrait améliorer les mesures de conservation, de même que les systèmes sylvicoles qui incorporent des attributs clés d'habitat susceptibles de maintenir un habitat hivernal dans les écosystèmes de cèdre et de pruche à basse altitude.

## Introduction

In the interior wet belt of British Columbia, low-elevation forests form part of the Interior Cedar–Hemlock (ICH) biogeoclimatic zone (Meidinger and Pojar 1991), which is characterized by climax stands of western redcedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees. Because of the abundant precipitation (100–215 cm/year; Environment Canada 2005), these forests are highly productive and infrequently burned by wildfires,

and therefore commonly consist of large, old trees. As well, the ICH ecosystem contains the greatest diversity of tree species (18) relative to the 14 other biogeoclimatic zones in British Columbia (Ketcheson et al. 1991). Consequently, these forests have high biological value because they support a great variety of organisms (Bunnell et al. 1999; Herbers et al. 2004), but are also highly valuable to the forest industry (Meidinger and Pojar 1991).

The mammal species of greatest concern in the interior wet belt is woodland caribou (*Rangifer tarandus caribou*

Gmelin, 1788), where an endangered ecotype, called mountain caribou (Heard and Vagt 1998), are found. This ecotype differs from other woodland caribou in that they are almost entirely dependent on arboreal lichens (*Bryoria* spp. and *Alectoria sarmentosa* Ach.), particularly late in winter when deep snow (1 to 5 m; Glacier National Park, unpublished data) covers terrestrial foods (Rominger and Oldemeyer 1989; Seip 1992; Rominger et al. 1996). In these deep snowfall areas, mountain caribou generally descend to lower elevations early in winter when snow begins to accumulate higher in the mountains, and are often found in the ICH forests. The caribou return to higher elevation, sub-alpine forests later in winter when snow depth and consolidation provides the lift needed for the animals to access arboreal lichen in the forest canopy (Apps et al. 2001; Kinley et al. 2003). Because arboreal lichens are most abundant in old coniferous forests, integrating timber harvesting with mountain caribou habitat requirements is a major resource management challenge requiring a hierarchy of decisions across a variety of spatial scales (Stevenson et al. 2001).

Resource selection by animals is also a hierarchical process occurring across spatial scales (Johnson 1980; Wiens et al. 1986). Recent advances in Geographic Information Systems (GIS) have enabled spatial analyses and mapping of animal habitat across a variety of these scales (Apps et al. 2001; Johnson et al. 2004). These spatially explicit products have led to a greater understanding of animal distribution and habitat requirements, and have proved useful to land-use planners (Minister's Advisory Committee 1999). However, these products are limited to scales that can be mapped and therefore exclude finer scales of resource selection. These currently unmapped, finer scales often reveal some of the mechanisms underlying resource selection such as thermal and security cover requirements and in particular, selection of foods and feeding sites. Thus, quantifying finer scales of resource selection is needed not only to help understand some of the mechanisms underlying broader scales of habitat selection by the animals, but also to develop management prescriptions to maintain critical habitat attributes.

Our study focuses on mountain caribou and continues the investigation of resource selection initiated at broader scales by Apps et al. (2001) and Apps and McLellan (2006). Across the largest scales that comprise most of the distribution of mountain caribou, Apps and McLellan (2006) determined that the extent of wet and very wet climatic conditions, the distribution of old (>140 years) forests, and remoteness from human development were among the most important factors differentiating where mountain caribou persisted from where they had been extirpated. At four finer scales (0.38 km² to 590 km²), radio-telemetry locations and a variety of mapped variables were used to describe and delineate caribou habitat relationships across the landscape (Apps et al. 2001). In these analyses, old forests were consistently selected by mountain caribou across all four scales. However, to determine whether variation in caribou habitat selection could be explained beyond the level of digital maps, in this study we explored the habitat selection process of mountain caribou at three finer scales using field data within old ICH forests by examining: (1) selection among stands, by comparing forests used for foraging to available stands, (2) selection within stands, by comparing paths where caribou foraged paired with randomly directed potential paths, and (3) items that were chosen for feeding at varying intensities along the caribou path compared to items that were ignored. It is hoped that increasing our knowledge of features that influence habitat selection at fine scales within these old forests will help managers implement prescriptions that will maintain and recruit forest stand attributes important to caribou.

## Study area

The 12 000 km² study area is located in the northern Columbia Mountains (51°N, 118°W; Fig. 1), centered on two major drainages and associated tributaries: the North Thompson River and the Revelstoke Reservoir portion of the Columbia River. From west to east, major landscape features are the Cariboo Mountains, the North Thompson River, the Monashee Mountains, the Revelstoke Reservoir, and the Selkirk Mountains. The area is steep and rugged with elevations ranging from 610 m to >3000 m and is also wet with most precipitation falling as snow. The maximum annual snowpack at 2000 m elevation averaged 350 ± 63 cm (1 SD) between 1965 and 1998 (Glacier National Park, unpublished data).

The lower slopes (<1400 m) of the study area are in the "wet cool" and "very wet cool" ICH (ICHwk and ICHvk, respectively) biogeoclimatic subzone (Meidinger and Pojar 1991), and are dominated by climax stands of western hemlock and western redcedar. Stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western white pine (*Pinus monticola* Dougl.), and white birch (*Betula papyrifera* Marsh.) are present on drier sites in the ICH, but less common in the ICHvk. Mid- and upper slopes (1400–1900 m) are in the "very wet cold" Engelmann Spruce – Subalpine Fir subzone (ESSFvc) and the "wet cold" subzone (ESSFwc). These forests are usually dominated by Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), but mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) is common in some stands (Coupé et al. 1991). Interspersed throughout both the ICH and ESSF are <30-year-old regenerating clear-cut forests. Owing to high snowfall and steep terrain, avalanche paths are common at all but the lowest elevations.

## Methods

Radio-collared caribou were used to locate foraging sites. These animals were captured using a net-gun fired from a helicopter during late winter when >85% of the population is in subalpine forests where they are readily observed and easily caught (Wittmer et al. 2005*a*). Between late October and January, all radio-collared caribou were located approximately once each week from a Cessna 337 aircraft. Because fresh snow obliterates caribou tracks and foraging sign, we investigated caribou use sites shortly after they were located and before fresh snow accumulated. To ensure that we maintained a representative sample of locations, we visited sites of individual caribou sequentially. Sampling began in early November when snow depths in ICH forests reached ~5–20 cm, and ended in mid-January when snow depths were 30–100 cm.

**Fig. 1.** Map of study area (black-outline polygon) in southern British Columbia, Canada.
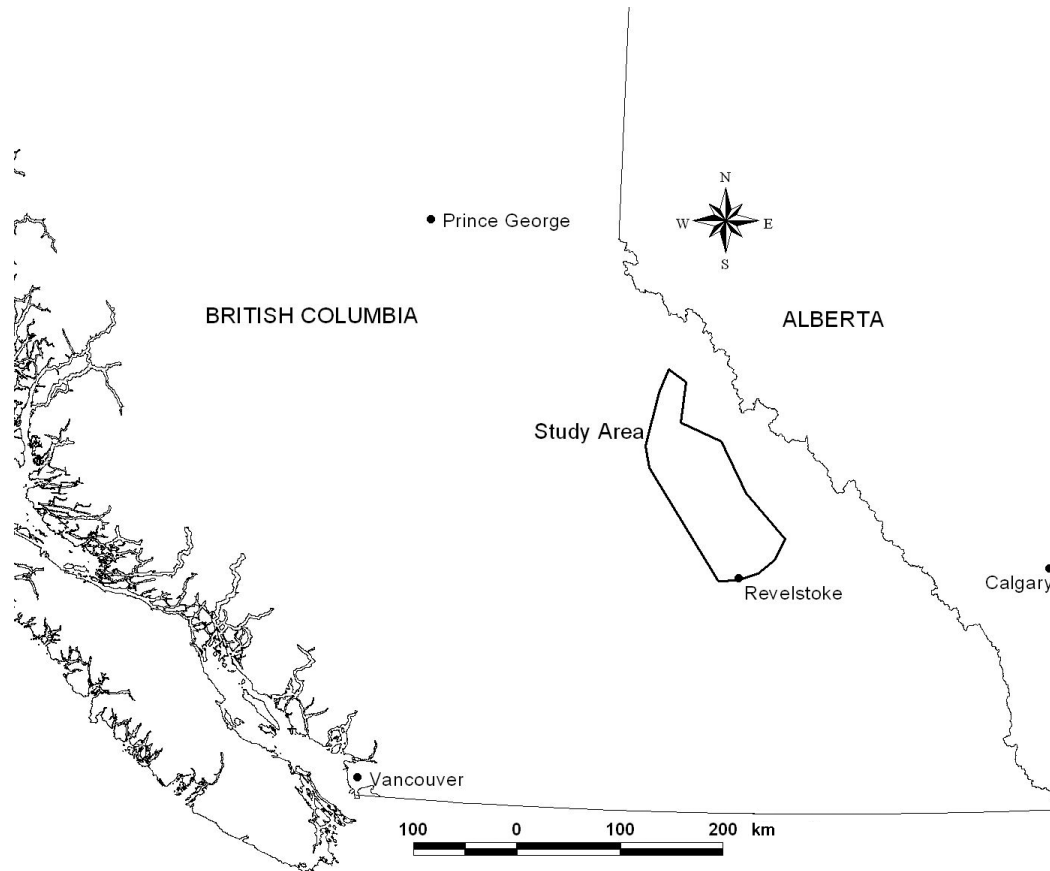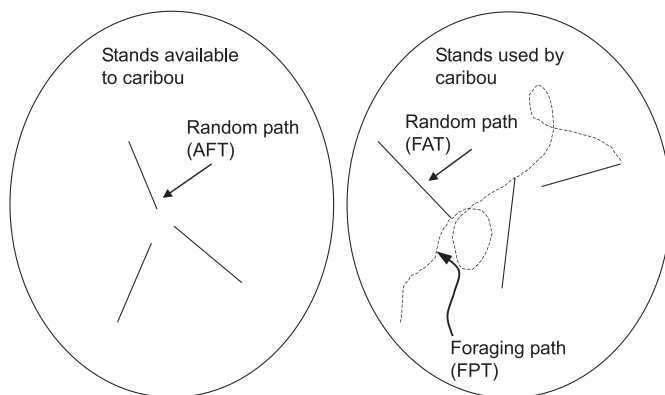


**Fig. 2.** Diagram of study design showing caribou foraging path transects (FPTs; dashed line), matched with random foraging area transects (FATs; solid line), in stands where caribou were found to forage. Also sampled were a pool of available stands with corresponding available forest transects (AFTs). Each of the three random transects was 50 m long. FPTs were 150 m long.



Our field sampling methods were similar to those used by Terry et al. (2000). Once the tracks of the target group of caribou were located, they were followed until evidence of foraging (e.g., trampling around base of tree) was encountered to ensure sites sampled had not been used only for traveling or searching for suitable foraging habitat. Microhabitat selection and the foraging decision process was investigated by collecting data along three linear transect types (Fig. 2). First, foraging path transects (FPT) were centered along the caribou track. FPTs were used to identify the stand characteristics along the path chosen by the animal and also the features of trees that caribou did or did not forage on. FPTs were 150 m in length and 2 m wide to reflect the "search path" of a foraging caribou that may take a small step to reach shrubs or lichen-bearing branches (Terry et al. 2000). Secondly, foraging area transects (FAT) sampled the immediate area of forests that the animal was using (Fig. 2). FATs were also 2 m × 150 m, but were subdivided into three 50 m straight segments starting every 50 m along the FPT, and went along a random bearing. Comparing FATs with FPTs enabled us to identify factors that influence caribou movements while foraging within a stand. Next, available forest transects (AFT) sampled the forest stands available to caribou within their winter composite home range (Fig. 2). AFTs were the same as FATs and consisted of three straight 2 m × 50 m segments. Thus, comparing AFTs to FATs enabled us to identify attributes among forested stands that caribou chose to forage in, compared with stands available in the ICH. To efficiently sample the winter composite home range using AFTs, we placed a grid over the area and within each of the 23 11 km × 14 km cells, randomly located one transect that went from far above tree line to valley bottom with the constraint that very hazardous avalanche terrain was avoided. Sampling was often conducted after a fresh, deep snowfall and on clear days so the field crew could be safely dropped off with their skis in the high mountains. Sites sampled were located in ICH

forests at random elevations along these transect lines. No AFTs or FATs were located in regenerating cutblocks because caribou rarely use these sites during winter foraging (Apps et al. 2001).

Along each transect we recorded the following variables: (1) tree or shrub species; (2) tree diameter at breast height (DBH); (3) tree vigor modified from (Thomas 1979) snag classification, which included (*i*) live, (*ii*) tight-bark snag, (*iii*) loose-bark snag, (*iv*) no-bark snag, and (*v*) recent windthrow (fallen during the current winter); (4) lichen abundance on trees or snags visually estimated using a standard ~10 g clump (Terry et al. 2000) and divided into two strata: (*i*) number of lichen clumps within approximate reach of caribou (0–1.8 m) from the snow surface; (*ii*) number of lichen clumps not within reach of caribou (1.8–3.6 m) under present snowpack depths; (5) lichen genera composition estimated visually (% *A. sarmentosa* and (or) *Bryoria* spp.) using 10% intervals; and (6) feeding intensity. Feeding intensity was estimated by the amount of trampling in the snow around the tree or shrub and categorized as (*i*) "walk past" where there was no evidence that caribou made a movement towards the forage item, (*ii*) "stepped towards", where the tracks indicated that the caribou took at least one step towards the forage item, (*iii*) "light trample", where the caribou spent some time at the item, but individual hoof prints could be seen and <25% of area around tree was tracked, (*iv*) "medium trample", where 25%–50% of area around a forage item was tracked, and (*v*) "heavy trample", where >50% of the area around the forage item was trampled.

Sampling long, thin (2 m wide) transects provides an index of stem abundance, but stem density estimates would be unreliable because of the high degree of edge. To provide forest managers with estimates of stem densities and basal area of available vs. used stands, a 5.64 m radius (100 m²) circular plot was located at the end of each 50 m segment for FATs and AFTs. Both live and dead trees (≥10 cm DBH) were recorded. Although we recorded the incidence of windthrown trees, we did not include windthrown tree biomass in the analysis because data from 100 m² plots were insufficient to provide reliable estimates.

## Statistical analysis

We conducted univariate and multivariate analyses at each of the three scales of habitat selection. Small sample sizes required pooling data within and among years; therefore our analysis does not account for potential changes in habitat and foraging selection patterns as snow accumulated.

Our univariate analyses focused on how well parameters were estimated and the magnitude of the difference between comparisons, rather than null hypothesis tests (Johnson 1999). Thus, we present means and 95% confidence limits (CL), and percent differences calculated as (used – available) / available × 100, when appropriate. CLs were derived from bootstrapping and using the percentile method (Efron and Tibshirani 1993), which avoids the need for transformations of non-normal or proportional data.
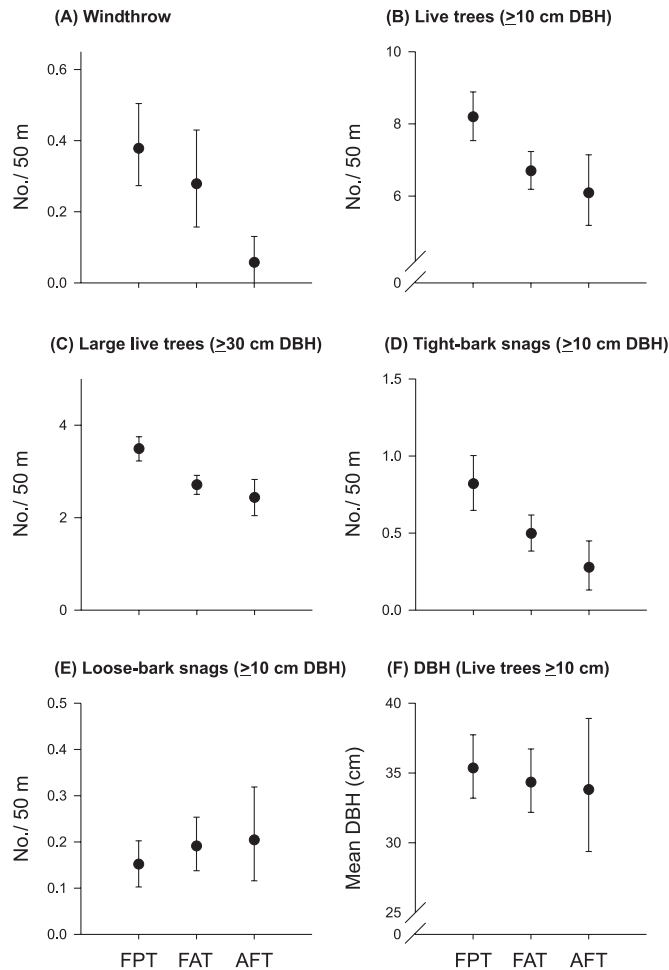
Univariate summaries were used to make comparisons among FPTs, FATs, and AFTs. Total (for trees) or mean (for lichen or DBH) values from the three 50 m segments of the FATs and AFTs were averaged across each stand, to provide one independent observation per stand, which was the sampling unit. Similarly, stem density values from the three 100 m² circular plots were averaged to provide one independent value per stand.

Some comparisons were excluded because of potential biases. For example, shrub abundance was not compared between FPTs and FATs because caribou often dug for some shrub species, but we would have been unable to measure the abundance of those shrubs along FATs because they would have been buried by snow. Similarly, litterfall was only evaluated along FPTs, because of the difficulty quantifying litter in an unbiased manner owing to temporal changes in litter abundance depending on wind and snow events. For our finest scale of analysis (selection of items to forage upon from those encountered along FPTs), our univariate summary involved comparing the proportion of forage items encountered along the FPT that were ignored (walk past), to the proportion of items that were foraged at varying levels of intensity (step towards, light, medium, or heavy trample).

Owing to the differing nature of the data, each of the three scales of habitat selection required different multivariate analytical procedures; however, all multivariate analyses used Akaike's Information Criteria (AIC) to distinguish among competing models and particularly among variables (Burnham and Anderson 1998: p. 140). AIC is an index of model parsimony, which is a compromise between including too few (i.e., bias) or too many (i.e., variance) parameters. To index how well the models represent the data, we present measures of goodness-of-fit for the most parameterized (global) and best model in each model family, as suggested by Anderson and Burnham (2002). We evaluated variables for collinearity at each scale and eliminated variables that were highly correlated ($r > 0.5$) with variable(s) that we presumed were more biologically relevant. When comparing stands used by caribou for foraging to stands available across the study area (FATs vs. AFTs), we used binary logistic regression to determine the relative influence of eight variables. Five variables were based on abundance per 50 metres, including the number of live trees (LIVE), windthrow (WINDT), tight-bark snags (SNAGTIGHT), and live hemlock (LIVETSHE). We also included DBH as a covariate, and created a variable to index biomass for each genera of lichen, which was simply the product of the number of lichen clumps within reach of caribou per standing tree and the percent composition of each lichen genera (*A. sarmentosa*, ALE_L, or *Bryoria* spp., BRY_L. Using combinations of these variables we created 27 candidate models that were based, a priori, on earlier observations of caribou foraging ecology (Terry et al. 2000; Kinley et al. 2003). Identical models were used to compare foraging path selection within stands (FPTs vs. FATs), so that we could test if caribou select their resources hierarchically by determining how the relative importance of individual variables shifted across scales. Within stands, FPTs and FATs were paired, so we used conditional logistic regression fit to a cox-proportional hazards model, which is well suited to matched designs (Hosmer and Lemeshow 2000). Models were evaluated for overdispersion, and if necessary quasi-AIC methods were used. Given that the ratio of parameters to independent samples was <40, we used a small-sample correction factor for

**Fig. 3.** Mean values for the abundance of (A) windthrow; (B) live trees (≥10 cm DBH); (C) large live trees (≥30 cm DBH); (D) tight-bark snags (≥10 cm DBH); (E) loose-bark snags (≥10 cm DBH); and (F) tree DBH along mountain caribou foraging trails (FPT) with matched random trails (FAT), and trails in random stands (AFT) in Interior Cedar Hemlock (ICH) ecosystems. Error bars are bootstrapped 95% CI. Sample sizes are 116, 121, and 23 for FPT, FAT, and AFT, respectively.

**Fig. 4.** Mean values of lichen biomass per tree (no. of 10 g clumps) (A) within the reach of caribou, (B) above the reach of caribou; percent composition of *Bryoria* spp. lichen (C) within the reach of caribou, (D) above the reach of caribou, along mountain caribou foraging trails (FPT) with matched random trails (FAT), and trails in random stands (AFT) in Interior Cedar Hemlock (ICH) ecosystems. Error bars are bootstrapped 95% CI. Sample sizes are 116, 121, and 23 for FPT, FAT, and AFT, respectively.
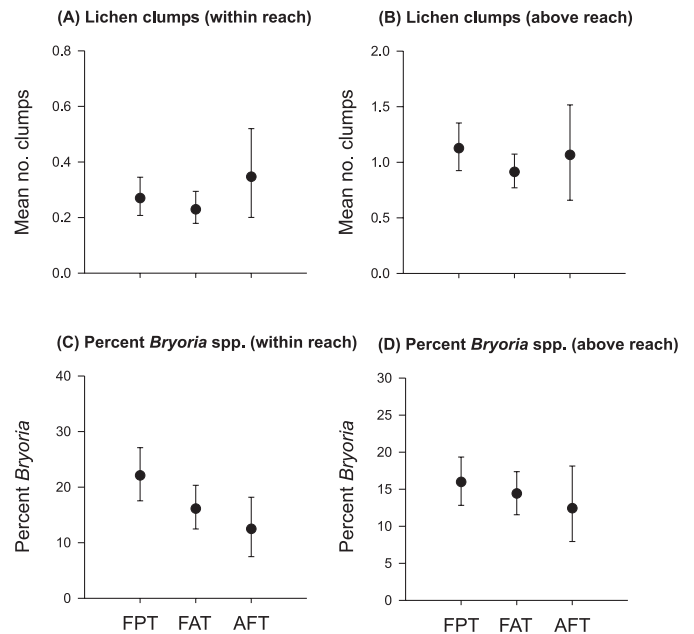




avoid overestimating AIC weights the AIC calculation was performed using a sample size equal to the number of stands sampled. Individual variables were again evaluated using AIC weights, and $r^2$ were presented as an indication of model fit for the best and global model.

## Results

We sampled 116 stands in which caribou foraged and recorded data along matched FPTs and FATs. We sampled five more FATs (totaling 121) but at these sites did not complete FPTs owing to insufficient snow for tracking under portions the forest canopy. We also collected data along 23 AFTs to characterize available stands in the ICH.

### Selection among stands: areas used for foraging (FATs) compared with available stands (AFTs)

Recently windthrown trees are rare. Although they were found only along 43% of the FATs, this was five times more frequent than along AFTs (Fig. 3A). Tight-bark snag abundances were also higher along FATs (Fig. 3D), as was the percent composition of Douglas-fir, which was found in 6.2% of the FATs but in <1% of the AFTs. No other attributes sampled along these linear transects showed pronounced differences among stands (Figs. 3 and 4). The circular plots revealed stem densities of tight-bark snags to be 116% more abundant in foraging areas compared with random stands, and live trees were 21% more abundant (Table 1). The higher live stem densities found in foraged stands did not translate into a difference in basal area between stand types. Douglas-fir was virtually absent from the

AIC units (AICc; Burnham and Anderson 1998: p. 51). To account for model selection uncertainty, we calculated unconditional parameter estimates and SEs from the top model set using model-averaging techniques (Burnham and Anderson 1998). Only models within four AIC units of the best model are presented and considered as the top model set.

Finally, along FPTs we used multivariate linear regression to determine the influence of individual forage items on feeding intensity. Feeding intensity was given an ordinal value of 0–4 corresponding to walk past, step towards, light, medium, and heavy trample, respectively. In addition to the variables described above, at this finest scale we were able to examine the influence of falsebox (PAMY) and litterfall (LTR) on feeding intensity. Variables were log transformed to better approximate normality for the distribution of residuals. We used the residual sum of squares (RSS) from regression models to derive AIC values so that we could again evaluate parsimony among models. Although the RSS was calculated using data for each potential forage item, to

**Table 1.** Forest attributes derived from 100 m$^2$ circular plots in stands that were used by caribou for foraging ($n = 121$) vs. a random sample of available stands ($n = 23$).

| Attribute | Random area | | | Foraging area | | | Difference (%)[a] |
|---|---|---|---|---|---|---|---|
| | LCL | Mean | UCL | LCL | Mean | UCL | |
| Live trees/ha[b] | 305.4 | 374.8 | 445.2 | 408.5 | 453.5 | 500.5 | 21.0 |
| Tight-bark snags/ha[b] | 8.6 | 20.7 | 35.5 | 33.6 | 44.8 | 58.7 | 116.4 |
| Loose-bark snags/ha[b] | 9.7 | 17.2 | 25.8 | 10.1 | 14.6 | 19.9 | –15.1 |
| Large live trees/ha[c] | 134.4 | 162.3 | 189.2 | 161.5 | 177.6 | 192.9 | 9.4 |
| Basal area live (m$^2$/ha) | 41.5 | 50.9 | 60.3 | 47.0 | 52.6 | 58.7 | 3.3 |
| Basal area dead (m$^2$/ha) | 4.0 | 8.9 | 15.9 | 8.7 | 11.7 | 14.8 | 31.5 |
| *Thuja plicata* (%) | 14.8 | 20.8 | 26.1 | 21.8 | 23.8 | 25.2 | 14.4 |
| *Tsuga heterophylla* (%) | 51.4 | 53.4 | 55.6 | 49.4 | 52.3 | 55.3 | –2.1 |
| *Pseudotsuga menziesii* (%) | 0.0 | 0.9 | 1.9 | 4.6 | 7.5 | 10.3 | 733.3 |

**Note:** Upper (UCL) and lower confidence limits (LCL; 95%) were obtained by bootstrapping samples.

[a](used – available) / available $\times$ 100.

[b]$\geq$10 cm DBH.

[c]$\geq$30 cm DBH.

**Table 2.** (*a*) Top models (0–4 $\Delta$AIC$_c$ units) using logistic regression to predict caribou habitat selection among stands (FAT [$n = 121$] vs. AFT [$n = 23$]) from snow transects, in Interior Cedar – Hemlock ecosystems; (*b*) AIC$_c\omega$ for individual variables are provided with unconditional parameter estimate and SEs from weighted averages of the top model set.

(*a*) Model structure.

| | AIC$_c$ | $k$ | –2 ln L | $\Delta$AIC$_c$ | AIC$_c\omega$ |
|---|---|---|---|---|---|
| SNAGTIGHT ALE_L WINDT | 353.3 | 4 | 345.0 | 0.0 | 0.48 |
| LIVE SNAGTIGHT ALE_L WINDT | 355.0 | 5 | 344.6 | 1.8 | 0.20 |
| LIVE SNAGTIGHT DBH ALE_L WINDT | 355.9 | 6 | 343.2 | 2.6 | 0.13 |

(*b*) Parameter estimates.

| Variable | Estimate[a] | SE[a] | AIC$_c\omega$ |
|---|---|---|---|
| Intercept | 161.31 | 34.11 | |
| SNAGTIGHT | 34.6 | 21.16 | 0.96 |
| ALE_L | –0.95 | 0.29 | 0.94 |
| WINDT | 82.24 | 48.27 | 0.93 |
| LIVE | 1.29 | 1.87 | 0.45 |
| DBH | 0.18 | 0.22 | 0.23 |
| LIVE $\times$ DBH | | | 0.09 |
| BRY_L | | | 0.08 |
| LIVETSHE | | | 0.02 |

**Note:** (*a*) AIC$_c$ are Akaike units corrected for small sample size, $k$ are the number of parameters, –2 ln L is the –2 log likelihood, $\Delta$AIC$_c$ is the difference in AIC$_c$ units between the top model and the *i*th model, and AIC$_c\omega$ are Akaike weights; (*b*) models and variables are sorted by decreasing AIC$_c\omega$.

[a]$\times 10^{-2}$. Blank cells mean variables were not included in top model set, but were part of the overall model family.

stands available but comprised 7.5% of stems in stands used for foraging (Table 1). Because fewer AFTs ($n = 23$) were sampled than FATs ($n = 121$), AFTs were estimated with less precision, as shown by the slightly larger CL (Figs. 3 and 4; Table 1).

Multivariate modeling results were generally consistent with univariate observations, with tight-bark snags and windthrow as the dominant attributes positively associated with stands used for foraging, and with *A. sarmentosa* biomass (per tree) negatively associated with foraging stands (Table 2*a*). More live trees and larger diameters were also positively associated with caribou foraging areas, but AIC$_c\omega$ indicated that they were only about half as important as snags, windthrow, and lichen abundance (Table 2*b*). Model

fit as indexed by the total area under the receiver operation curve (*c*-statistic) was 0.69 for the global model and 0.70 for the best model. The ratio of deviance to degrees of freedom ($\hat{c}$) was less than 1, so quasi-AIC methods were not used.

**Selection within stands: comparing foraging paths (FPTs) with matched random paths (FATs)**

The abundance of live trees, large live trees, and tight-bark snags was greater along caribou foraging trails (FPT) compared with the matched FATs (Fig. 3). Tree species composition was similar at this scale of selection.

Multivariate modeling revealed that windthrow was no longer as strong a predictor of caribou selection at this finer scale, because the AIC$_c\omega$ for windthrow was less than half
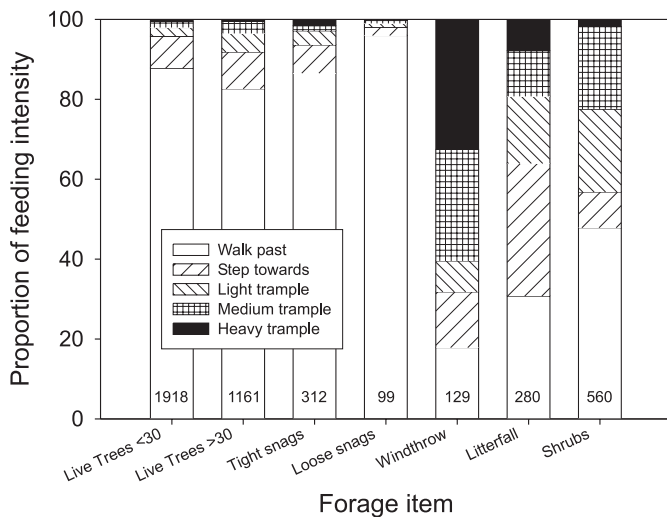
**Table 3.** (*a*) Top models (0–4 $\Delta AIC_c$ units) using conditional logistic regression to predict caribou habitat selection within stands (FPT vs. FAT [*n* = 116]) from snow transects in Interior Cedar – Hemlock ecosystems; (*b*) $AIC_c\omega$ for individual variables are provided with unconditional parameter estimate and SEs from weighted averages of the top model set.

(*a*) Model structure.

| | $AIC_c$ | *k* | –2 ln L | $\Delta AIC_c$ | $AIC_c\omega$ |
|---|---|---|---|---|---|
| LIVE SNAGTIGHT DBH LIVExDBH BRY_L | 609.0 | 5 | 598.8 | 0.0 | 0.41 |
| LIVE SNAGTIGHT DBH LIVExDBH BRY_L WINDT | 609.3 | 6 | 597.0 | 0.3 | 0.35 |
| LIVE SNAGTIGHT DBH LIVExDBH BRY_L ALE_L | 610.7 | 6 | 598.3 | 1.7 | 0.18 |

(*b*) Parameter estimates.

| Variable | Estimate[a] | SE[a] | $AIC_c\omega$ |
|---|---|---|---|
| LIVE × DBH | 0.48 | 0.21 | 1.00 |
| DBH | –0.57 | 1.18 | 1.00 |
| LIVE | 3.46 | 6.42 | 1.00 |
| SNAGTIGHT | 37.48 | 9.75 | 1.00 |
| BRY_L | 3.08 | 0.98 | 0.99 |
| WINDT | 5.09 | 5.01 | 0.41 |
| ALE_L | 0.04 | 0.07 | 0.24 |
| LIVETSHE | | | 0.06 |

**Note:** (*a*) $AIC_c$ are Akaike units corrected for small sample size, *k* are the number of parameters, –2 ln L is the –2 log likelihood, $\Delta AIC_c$ is the difference in $AIC_c$ units between the top model and the *i*th model, and $AIC_c\omega$ are Akaike weights; (*b*) models and variables are sorted by decreasing $AIC_c\omega$.
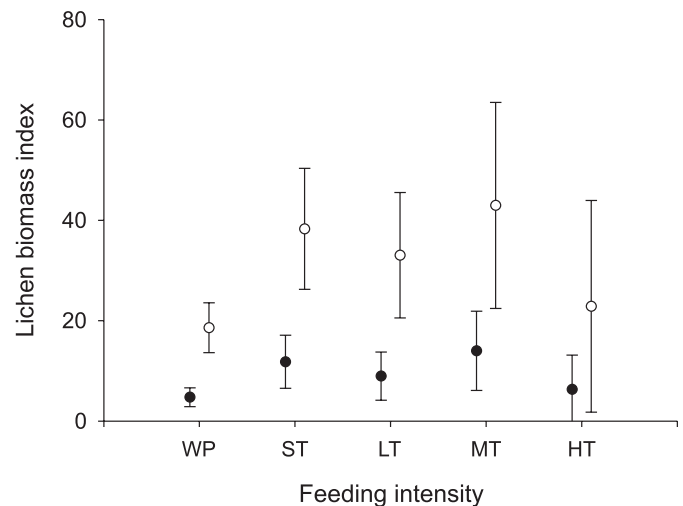
[a] $\times 10^{-2}$. Blank cells mean variable was not included in top model set, but was part of the overall model family.

**Fig. 5.** Proportion of feeding intensity classes for forage items available to mountain caribou. Feeding intensity classes were walk past, step towards, light trample, medium trample, and heavy trample (see text for details). Live trees <30 were <30 cm DBH and live trees >30 were ≥30 cm DBH. Number of each item is presented in the bar graph.



**Fig. 6.** Lichen biomass index (no. of 10 g clumps per tree within reach of mountain caribou × % composition) as a function of feeding intensity for *Alectoria sarmentosa* (open circles) and *Bryoria* spp. (solid circles) in Interior Cedar – Hemlock (ICH) ecosystems. Feeding intensity categories are walk past (WP), step towards (ST), light trample (LT), medium trample (MT), and heavy trample (HT). Error bars are bootstrapped 95% CI.



of the highest ranked variables (Table 3*b*). The number of tight-bark snags, live trees, and trees with larger diameters were key variables positively associated with caribou foraging path selection, each having AIC weights near 1. The interaction term revealed that as trees became more numerous, larger DBH became more important at explaining caribou selection. *Bryoria* spp. biomass was also an important variable positively associated with caribou selection, with an AIC weight of 0.99. The area under the ROC was 0.65 for both the global and best model.

## Feeding intensity on forage items along caribou trails (FPTs)

We observed 4459 potential forage items along caribou trails, of which 24% received at least some level of use (i.e., step towards or more). Trees and snags formed the dominant proportion (>75%) of potential forage items, but were foraged upon only 13.8% of the time (Fig. 5). In contrast, windthrown trees and litterfall were foraged upon 82.2% and 69.3% of the time, respectively (Fig. 5). Of the 241 shrubs that were foraged in the light, medium, and

**Table 4.** (*a*) Top models (0–4 $\Delta AIC_c$ units) using linear regression to predict caribou foraging intensity along FPTs (*n* = 116) from snow transects, in Interior Cedar – Hemlock ecosystems; (*b*) AIC$\omega$ for individual variables are provided with unconditional parameter estimate and SEs from weighted averages of the top model set.

(*a*) Model structure.[a]

| | AIC | *k* | RSS | $\Delta$AIC | AIC$\omega$ |
|---|---|---|---|---|---|
| WINDT ALE_L PAMY LTR | 214.6 | 121 | 91.6 | 0.0 | 0.33 |
| WINDT ALE_L PAMY BRY_L LTR | 216.0 | 122 | 91.2 | 1.4 | 0.16 |
| WINDT ALE_L PAMY LTR DBH | 216.1 | 122 | 91.2 | 1.4 | 0.16 |
| WINDT BRY_L PAMY LTR | 216.4 | 121 | 93.1 | 1.8 | 0.13 |
| WINDT ALE_L PAMY BRY_L LTR DBH | 217.5 | 123 | 90.7 | 2.9 | 0.08 |
| WINDT ALE_L PAMY BRY_L SNAGTIGHT LTR | 217.9 | 123 | 91.1 | 3.3 | 0.06 |

(*b*) Parameter estimates.

| Variable | Estimate[b] | SE[b] | AIC$\omega$ |
|---|---|---|---|
| Intercept | 41.63 | 21.09 | |
| WINDT | 343.85 | 14.60 | 1.00 |
| LTR | 242.60 | 9.72 | 1.00 |
| PAMY | 376.30 | 9.11 | 1.00 |
| ALE_L | 0.57 | 0.10 | 0.87 |
| BRY_L | 0.39 | 0.24 | 0.50 |
| DBH | 0.15 | 0.11 | 0.28 |
| SNAGTIGHT | –1.24 | 1.30 | 0.13 |
| LIVE | | | 0.03 |

**Note:** (*a*) AIC are Akaike units, *k* is the number of parameters, RSS is the residual sum of squares, $\Delta$AIC is the difference in AIC units between the top model and the *i*th model, and AIC$\omega$ are Akaike weights; (*b*) Models and variables are sorted by decreasing AIC$\omega$.

[a]All models include stand (sampling unit) as a covariate

[b]$\times 10^{-3}$. Blank cells mean variable was not included in top model set, but was part of the overall model family.

heavy trampled categories, 94% of those were falsebox. Trees that were foraged upon had higher lichen biomass relative to those available in the forest, but biomass dropped off in the heavy trampled category (Fig. 6).

Feeding intensity was best predicted by models that included windthrow, falsebox, litterfall, and to a lesser extent higher amounts of *A. sarmentosa* and *Bryoria* spp. biomass (Table 4). The abundance of live stems and tight-bark snags was not a good predictor of feeding intensity. The best and global model in ICH forests both had $r^2$ values of 0.52, and the distribution of residuals for the global model was improved with log-transformed feeding intensity, but remained slightly positively skewed with a longer right tail.

## Discussion

In early winter, when snow begins to accumulate at high elevations and buries terrestrial foods, mountain caribou generally descend in elevation. In portions of the interior wetbelt where snowfall is relatively moderate, caribou rarely descend far but remain in spruce and fir forests at mid- to high elevations (Rominger and Oldemeyer 1989; Terry et al. 2000; Kinley et al. 2003). In more extreme snowfall areas, such as the Columbia Mountains, all caribou monitored by radio telemetry descend to the ICH forests in the valleys (Apps et al. 2001). It is in these highly productive forested areas where conflicts between forestry and caribou habitat requirements are greatest and therefore an understanding of the foraging ecology of caribou is most needed.

In the Columbia Mountains, Apps et al. (2001) used radio telemetry and a variety of digital basemaps to estimate caribou habitat selection at four landscape scales. These analyses suggested that during early winter, caribou selected broad landscapes with low elevation, gentle terrain, high productivity, high canopy cover, and old and young forests. At finer landscape scales, they found preferences for old western hemlock and western redcedar stands. These results, when combined with census and telemetry locations, enabled the delineation of areas where forestry practices and caribou habitat requirements would be integrated (Minister's Advisory Committee 1999). How best to integrate forestry practices and caribou habitat requirements within these delineated areas in ICH forests was not as easily resolved and requires an understanding of how caribou select habitat at fine scales.

At both the broadest and finest of the three scales investigated in this study, windthrow was a strong predictor of caribou habitat selection. Although windthrow is relatively rare and was recorded in less than half the stands used by caribou, overall it was much more abundant in stands used by caribou for foraging than in those available. When caribou encountered windthrow along their foraging path, the snow adjacent to this substrate was far more likely to be heavily trampled, reflecting heavy feeding, compared with snow near any other foraging item. Often, the entire length of the fallen tree was stripped of lichen. However, at the within-stand level, windthrow was not an important predictor of caribou selection. This result does not mean that windthrow became unimportant to caribou at the mid-scale, but rather, windthrow levels were relatively invariant at this scale. The

implication is that once a caribou finds a stand with a high level of windthrow, it could be expected to encounter these horizontal stems simply by following a random search path.

The importance of windthrown trees to mountain caribou in winter is not limited to ICH forests, but appears to be a consistent pattern across their distribution, including populations that spend the early winter at higher elevations (Rominger and Oldemeyer 1989; Terry et al. 2000; Kinley et al. 2003). Of the 129 pieces of windthrow encountered in our study, only 23 (17%) were ignored. This foraging rate on pieces of windthrow is identical to that reported by Terry et al. (2000) in higher elevation, ESSF forests. The importance of windthrow is likely due to the large volume of easily accessible lichen that is found in the upper canopy that would otherwise be out of reach. In addition, a higher proportion of the lichen in the upper canopy consists of *Bryoria* spp., (Goward 1998; Campbell and Coxson 2001; Stevenson et al. 2001), which is the genera favoured by caribou (Terry 1994; Rominger et al. 1996).

In addition to windthrow, stands used by caribou for foraging had more tight-barked snags, and tended to have less *A. sarmentosa* per tree than stands available in the ICH. Although uncommon, stands with a higher abundance of Douglas-fir were also selected by caribou. Both Douglas-fir and tight-barked snags (all species combined) generally have more dead branch substrate for arboreal lichen attachment and growth than live trees of several other species, and thus have more lichen available to caribou (R. Serrouya and B.N. McLellan, unpublished data).

At the within-stand scale, larger trees, passing more live trees and tight-bark snags, and higher levels of *Bryoria* spp. biomass were the strongest factors that influenced caribou forage paths. Relative to *A. sarmentosa*, *Bryoria* spp. are rare in ICH forests, yet the occurrence of *Bryoria* spp. strongly influenced caribou foraging paths. Live trees and snags appeared to benefit caribou simply because of the increased opportunity for foraging on stems and encountering litterfall. Tight-barked snags that had not yet lost branches may provide the added benefit of high lichen biomass because of greater light penetration, ventilation, and dead substrate for optimal lichen attachment (Stevenson 1979). In addition, lichen growing on snags has less mixing of conifer needles and twigs than lichen growing on live trees and thus may be more palatable, and branches from snags are more likely to break off and provide lichen litterfall to caribou. Larger trees may be important because they tend to be older and contain more lichen biomass (R. Serrouya and B.N. McLellan, unpublished data), and they provide greater snow interception cover (D'Eon 2004), thereby facilitating movement and access to preferred forage items (Kirchhoff and Schoen 1987; Servheen and Lyon 1989) such as falsebox that may otherwise be buried. Interestingly, large trees were negatively correlated with tree abundance ($r = -0.47$), yet the interaction term from the regression indicated that caribou selected paths with the unusual conditions where larger and more abundant trees occurred (Table 3). However, at mean densities of 453.5 stems per hectare (Table 1), stands where caribou foraged are still far less dense than regenerating clearcuts, which are avoided by caribou (Apps et al. 2001).

Falsebox and litterfall were nearly as important as windthrow to predict caribou feeding intensity along FPTs. Falsebox is still available to caribou in ICH forests during early winter because snow levels have not accumulated to bury this shrub deeply enough to inhibit cratering. Although Rominger et al. (2000) suggested falsebox is less preferred than arboreal lichens on windthrown trees, our results indicate it is still used heavily as an alternative food source. Unlike the results from the two broader scales, live trees and snags were not important predictors of feeding intensity along FPTs. Although caribou foraged most frequently on live trees and snags, most feeding intensity on these items was light, and caribou walked past most of these without stopping to feed. Live trees and snags, however, produce the litterfall and may become windthrow that are highly selected at this finest scale.

Multi-scaled analyses of habitat selection highlight the need for caution when distinguishing between habitat use, selection, and importance, particularly when analyses cover only a few spatial scales. An apparent lack of selection for an attribute at one scale may be caused by an abundance of the attribute owing to selection at a broader scale (McLellan 1986; Garshelis 2000). Analyses conducted at multiple scales help clarify how the selection process may shift as the perspective changes. For example, selection of old trees was high at very broad scales where caribou remain in regions with a disproportionate amount of old forests (Apps and McLellan 2006). In our current study, which was restricted to old forests, selection for old trees was not evident at the among-stand scale because the opportunity for selection was more constrained. However, at the within-stand scale, foraging paths (FPT) had more trees than random paths (FAT), and finally at the scale of forage items, trees were again not selected. The lack of selection of old trees at the finest scale can be explained by the strong selection of individual forage items such as litterfall and windthrow, but these are nonetheless a product of the presence of older trees. The analyses across scales more clearly indicates the importance of habitat attributes and even suggests some of the mechanisms underlying the habitat selection process. In this case, caribou appear to seek an abundant source of arboreal lichen that is only available during early winter as litterfall and particularly on windthrown trees, and these occur unpredictably within older forests.

One fine-scale foraging decision that caribou make is when to leave a tree (patch) as they deplete the lichen and move to another tree. It appears that caribou foraged on standing or windthrown trees until they depleted the lichen biomass to levels found on trees that were not foraged upon (Fig. 6). The marginal value theorem (MVT; Charnov 1976) predicts that a forager should leave a patch when the benefit rate falls below the average of the surrounding patches. Although we did not set out to investigate this theorem, our results suggest that the foraging behaviour of mountain caribou approximates predictions of the MVT, because caribou depleted most patches to a similar degree before moving on to the next patch.

## Management implications

Mountain caribou rely on habitat attributes that are associated with old forests: windthrown trees, snags, litterfall, and high lichen biomass. This dependence places caribou in con-

flict with traditional multiple-pass clearcut logging because it typically takes longer than a commercial rotation for some attributes to develop, particularly windthrown trees. Furthermore, many old stands, particularly when diseased, are targeted for salvage logging to establish a young plantation. It is these stands, however, that provide an influx of lichen in the form of litterfall and windthrow where it is most accessible to caribou.

In the Columbia Mountains, recent measures have been enacted to ensure that a proportion of the landbase remains as old forests. In ICH ecosystems, 40% of the publicly owned landbase that caribou use during winter must be older than 140 years (Minister's Advisory Committee 1999). Many forest licensees are trying to achieve these targets using static retention areas; however, there is little guidance regarding how to spatially allocate retention areas in ICH forests (but see Terry et al. 2000 and Kinley et al. 2003 for ESSF forests). Our work has provided managers with information on the importance of retaining stands with higher levels of *Bryoria* biomass, greater potential for windthrow, and those that contain falsebox, which also contain a mature canopy that provides good snow interception cover. Given that all our sampling took place in old forests, we have shown that caribou discern among stands of old forest, and as such we have provided managers with a tool to prioritize old stands for conservation.

Of greater concern is how attributes important to mountain caribou will persist and develop over time. Static retention areas are unlikely to provide a continuous supply of caribou forage because some may burn, blow down, or be lost to epidemic disease or insects. To mitigate these concerns, larger areas could be retained, or a more economical approach would be to develop silvicultural practices that create and retain attributes sought by caribou. The partial-cut silviculture methods described by Stevenson et al. (2001) designed primarily for maintaining arboreal lichen for caribou in higher elevation spruce and fir forests may be adapted to lower elevation forests of hemlock and cedar. However, because of the long time scales involved with the development of key attributes and because operational trials have only just begun, we are uncertain whether these measures will maintain caribou forage in the long term. We recommend using forest stand models with simulated harvesting scenarios to help predict levels of key attributes into the future.

Although the fine-scale habitat selection process of caribou reflects their daily foraging requirements, it is "apparent competition" (Holt 1977, 1984) leading to high predation rates that appears to be the proximate cause of mountain caribou population declines (Seip 1992; Wittmer et al. 2005*a*, 2005*b*). Apparent competition is an indirect process whereby a predator species is maintained at a sufficient abundance by its primary prey species that it negatively affects the abundance of a secondary prey species. In the case where mountain caribou are the secondary prey, the primary prey are often moose (*Alces alces*) or deer (*Odocoileus* sp.) and the major predators are wolves (*Canis lupus*) and cougar (*Puma concolor*; Seip 1992; Wittmer et al. 2005*a*, 2005*b*). Therefore, in addition to maintaining foraging opportunities for caribou, silvicultural prescriptions must ensure that foraging opportunities are not enhanced for these other ungulates.

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