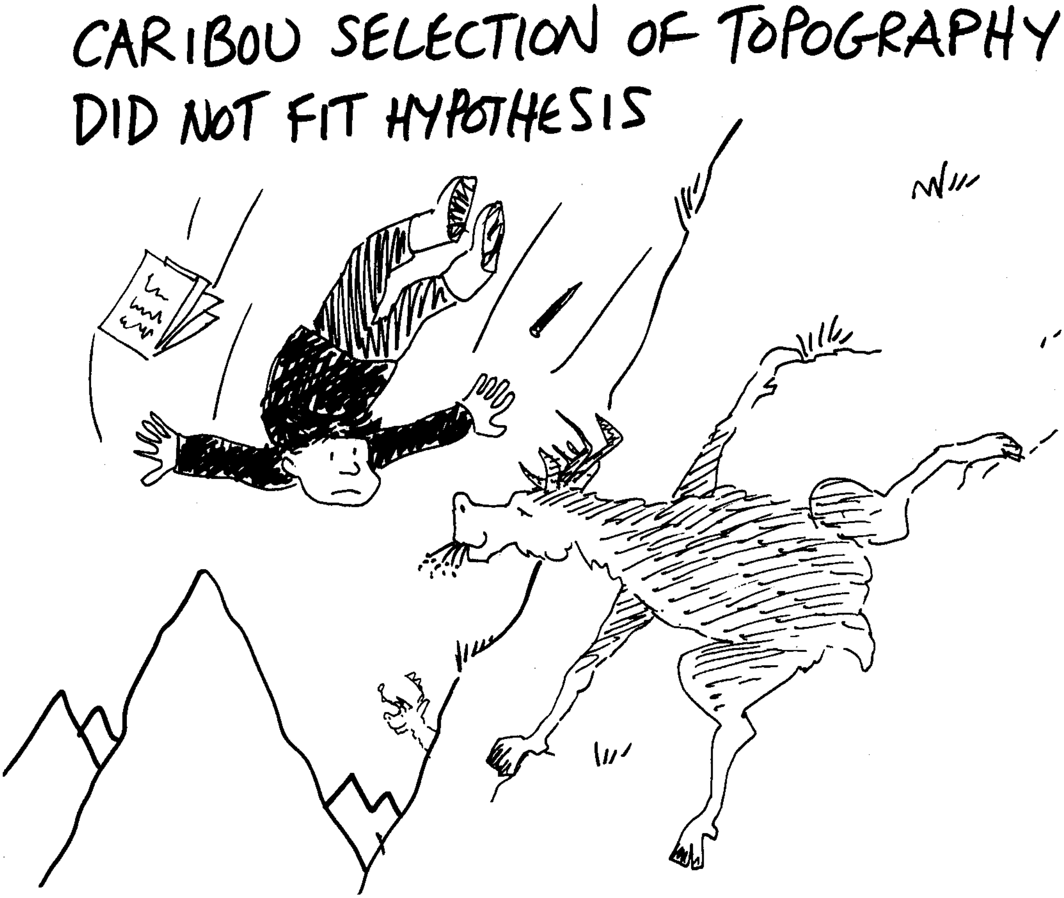

CARIBOU SELECTION OF TOPOGRAPHY DID NOT FIT HYPOTHESIS

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Feeding site selection by woodland caribou in north-central British Columbia

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Abstract: We examined the foraging habits of the northern woodland caribou ecotype (*Rangifer tarandus caribou*) at the scale of the individual feeding site. Field data were collected in north-central British Columbia over two winters (Dec 1996-Apr 1998). We trailed caribou and measured vegetation characteristics (species composition and percent cover), snow conditions (depth, density, and hardness), and canopy closure at terrestrial and arboreal feeding sites, and at random sites where feeding had not occurred. Logistic regression was used to determine the attributes of feeding sites that were important to predicting fine scale habitat selection in forested and alpine areas. In the forest, caribou selected feeding sites that had a greater percent cover of *Cladina mitis* and *Cladonia* spp, lower snow depths, and a lower percentage of debris and moss. Biomass of *Bryoria* spp. at the 1-2 m stratum above the snow significantly contributed to predicting what trees caribou chose as arboreal feeding sites. In the alpine, caribou selected feeding sites with a greater percent cover of *Cladina mitis, Cladina rangiferina, Cetraria cucullata, Cetraria nivalis, Thamnolia* spp., and *Stereocaulon alpinum* as well as lower snow depths.

Key words: arboreal, crater, foraging, lichen, *Rangifer*, snow.

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Introduction

The habitat requirements of the northern woodland caribou ecotype of British Columbia are largely unknown (Harrison & Surgenor, 1996). This ecotype has been the subject of few studies, but is known to inhabit areas of low to moderate snow depths in low elevation forests, and to forage primarily on terrestrial lichens during winter (Hatler, 1986; Cichowski, 1993; Lance & Mills, 1996; Wood, 1996). Most caribou research in British Columbia has focused on the mountain caribou ecotype which spends little time in low elevation areas during the winter, but forages instead on arboreal lichens at high elevations (Servheen & Lyon, 1989; Terry, 1994).

Further understanding of the life history strategies of the northern woodland caribou ecotype is important in view of increasing demands for timber in the province. Wintering populations of this ecotype use low elevation forests that are valued for commercial wood products (Cichowski, 1993; Wood, 1996). Consequently, they are likely to be negatively affected by habitat alteration, fragmentation, and increased road access.

As part of a larger research project to define the processes that affect the movements and distribution of northern woodland caribou across the landscape, we investigated the influence of forage species, abundance, and accessibility on the selection of individual feeding sites during winter. Specifically, we examined:

1. the influence of snow depth, density, and hardness as well as vegetation composition and abundance on the selection of terrestrial feeding sites at small spatial scales in forested and alpine habitats; and
2. the influence of lichen biomass on the selection of arboreal feeding sites.

Study Area

The group of caribou chosen for this study is known as the Wolverine herd (Heard & Vagt, 1998), and ranges throughout a 5100-km^2 area, approximately 250 km northwest of Prince George, British Columbia (Fig. 1). Terrain varies, from valley bottoms at approximately 900 m to alpine summits at 2050 m, and is characterised by numerous vegetation associations resulting from diverse topography,

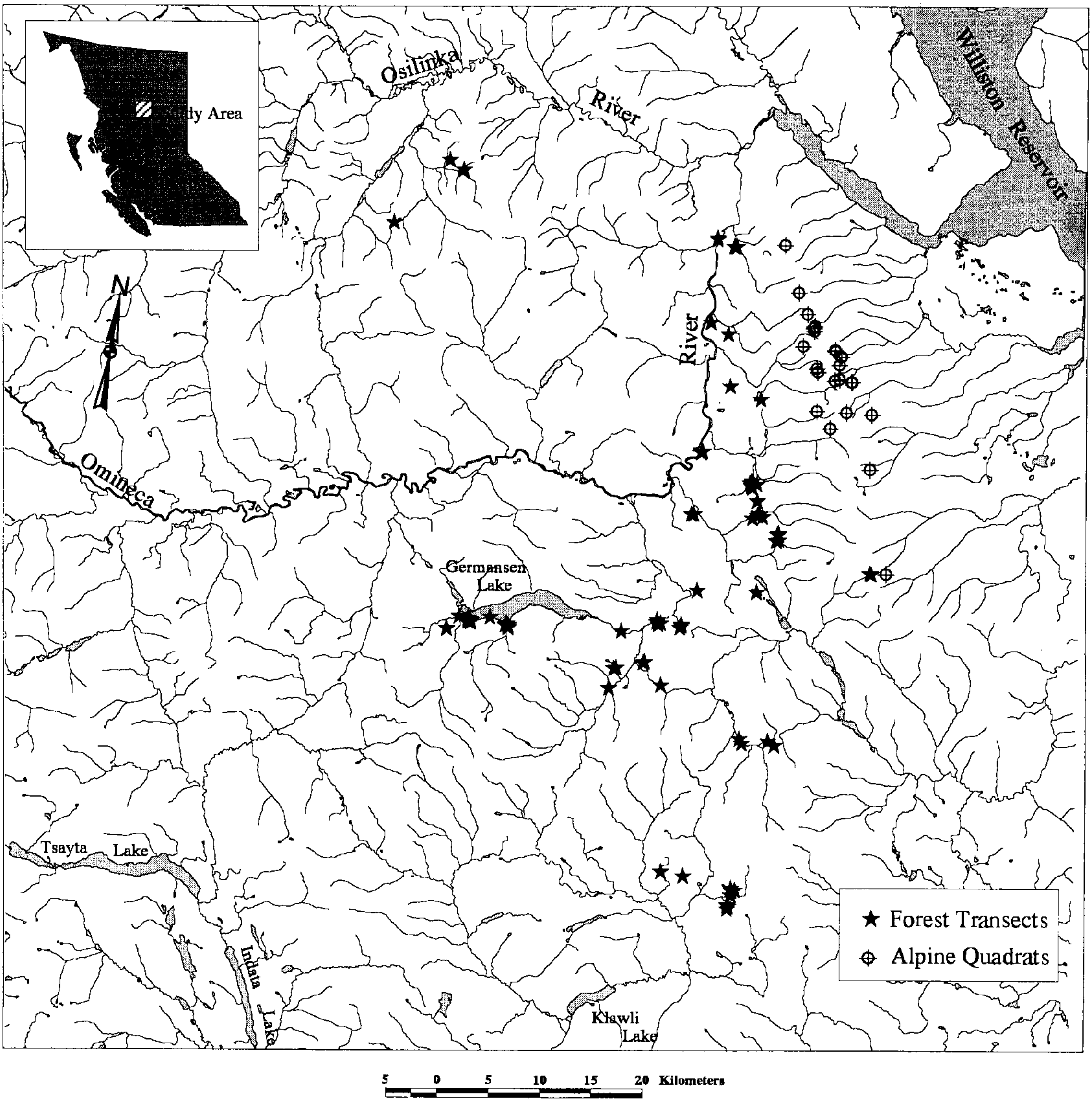

Fig. 1. Forest transects and alpine quadrats located across the winter range of the Wolverine herd (Dec 1996-Apr 1998).

soils, and succession. Forest types below 1100 m have been influenced extensively by wildfires and are dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), hybrid white spruce (*P. glauca* x *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*). Between 1100 and 1600 m, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (*P. engelmannii*) and subalpine fir (*A. lasiocarpa*). Elevations greater than 1600 m are alpine tundra and are distinguished by gentle to steep windswept slopes vegetated by shrubs, herbs, bryophytes, and lichens with occasional trees in krummholz form (MacKinnon *et al.*, 1990; DeLong *et al.*, 1993).

Materials and methods

Field investigations occurred at two to three week intervals between December and April, 1996-1997 and 1997-1998. After locating recent tracks of GPS-collared caribou or groups of non-collared caribou in the forest by air or ground survey, we assessed the immediate area for signs of foraging behaviour. Terrestrial feeding sites were characterised by meandering tracks, craters, and/or sniffing holes. Arboreal feeding sites were characterised by trampling, broken twigs, and fallen arboreal lichen at the base of trees. If some sign of foraging behaviour was present, we selected a random starting point in the snow along the caribou tracks greater than or equal to 20 paces from any ecotone border. Following this, we placed a measuring tape along a section of track that traversed a relatively homogenous stand or vegetation type, and all terrestrial (craters) and arboreal feeding sites found on a 100-m segment of track (transect) were counted. Using a random number table, a maximum of 12 sites were randomly selected on the transect for measurement: 3 sites where there had not been terrestrial feeding, 3 trees where there were no signs of arboreal feeding, and, if present, 3 cratering sites and 3 arboreal feeding sites (Fig. 2).

For statistical analyses, measures at feeding and non-feeding sites were pooled across transects. To minimise the likelihood of recording the behaviour of the same animal more than once (i.e., pseudoreplication; Hurlbert, 1984), we limited the number of samples to not exceed the observed or, where animals were not sighted, the average number of caribou typically occurring within a group during the winter (n=9; Wood, 1996; C. J. Johnson, unpubl.). Furthermore, because we wanted to sample all collared animals and visit as many geographically unique locations as possible, we restricted the maximum number of 100-m transects sampled at one location to 3, regardless of the number of animals observed. To further reduce the effects of spatial autocorrelation and allow an opportunity for changes in behaviour across space, and presumably time, successive transects were separated by a distance of 100 m. Therefore, at a location, we sampled a maximum of 9 terrestrial and 9 arboreal feeding sites and the 18 associated random sites across 3 transects.

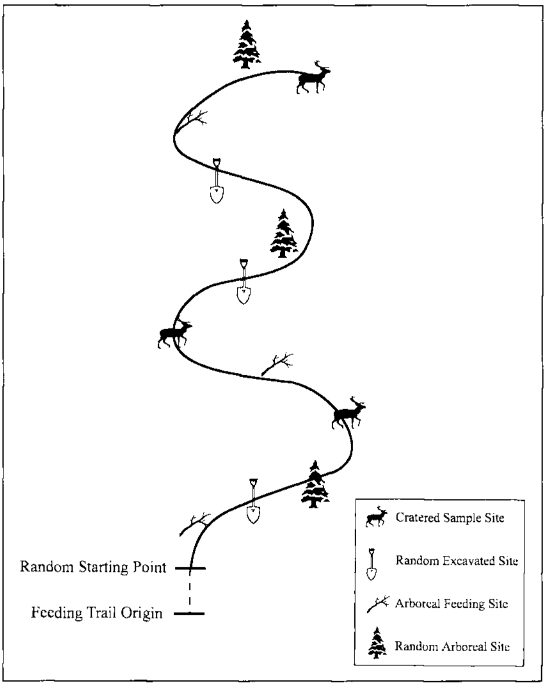

Fig. 2. Schematic representation of the sampling design used along a 100-m segment of recent caribou tracks in the snow.

In the alpine, safety concerns and the aggregated distribution of the feeding sites required us to use a 50 X 50-m quadrat rather than a 100-m segment of track. All craters in the quadrat were counted, and we randomly selected 3 to 6 craters for measurements, depending on time and weather constraints. The corresponding non-feeding sites were located at a random compass bearing and random number of paces (1-20 paces) from the sampled craters, regardless of the quadrat boundaries. For statistical analyses, measures at feeding and non-feeding sites were pooled across quadrats.

At all terrestrial feeding and random sites, snow depth was measured to the nearest 0.5 cm, and the penetrability (i.e., hardness) of the upper layer was estimated with an instrument of our own design which was similar to the Rammsonde penetrometer. A British Columbia Ministry of Environment, Lands, and Parks (1981) Snow Survey Sampling Kit was used to measure snow density by inserting a cylinder of known volume vertically into the snow, recording the depth minus the soil plug, and weighing the contents. Because the scale used to measure the mass of the cored snow is insensitive at low snow depths, density could not be reliably calculated for alpine sites. For cratered sites, the least disturbed edges were used for sampling. Following snow measurements, the snow was cleared and the percent cover of ground vegetation was assessed with a 0.5 m X 0.5-m point frame consisting of 16 vertical pins (Bookhout, 1994). Lichen and moss were identified to species, genus or morphological group, depending on ease and reliability of field classification. Species that occurred at fewer than 10 sample sites were pooled with the next most similar species or genus group, or were excluded. Percent cover of evergreen dwarf shrubs, grasses (Poaceae), and sedges were also recorded. However, with the exception of grass at alpine sites, there was no evidence of grazing on those plant types, so they were excluded from the analysis. At forested terrestrial sites, a moosehorn coverscope (Moosehorn Coverscopes, Medford, Oregon, USA) was used to assess percent canopy closure by taking one measure directly above each sampled site.

At each arboreal feeding and associated random site, a lichen clump (*Bryoria* spp.) with a predetermined oven-dried weight was used as a Standard Lichen Unit to visually estimate arboreal lichen biomass (Antifeau, 1987; Stevenson & Enns, 1993). The number of similar Units that occurred within the reach of a typical caribou (1-2 m above the snow) was counted and multiplied by the mass of the Standard Lichen Unit to obtain total biomass within the 1-2-m stratum. Tree species and diameter at breast height were also recorded.

We used multiple logistic regression analyses to estimate the influence of percent cover of vegetation, snow conditions, and canopy closure on the selection of terrestrial feeding sites by caribou in forested and alpine areas. To assess the selection of arboreal feeding sites, we tested a simple logistic regression model, consisting of foraged versus random trees as the dependent variable and grams of arboreal lichen in the 1-2 m stratum as the independent variable.

For the multiple logistic regression models (terrestrial forest and alpine), the Wald backward elimination procedure (SPSS Version 8.0) was used to identify the most parsimonious model for describing site selection of cratering locations (Menard, 1995). As recommended by Bendel & Afifi (1977), the α of 0.05 was relaxed to 0.15 during the backward elimination procedures to reduce the likelihood of excluding important variables. We used Pearson correlation values and tolerance scores with a collinearity threshold of 0.20 (Menard, 1995) to diagnose the presence of multicollinearity amongst the independent variables. Collinearity is the product of two or more highly correlated variables. It is an indication of redundancy within the statistical model and can lead to inflated error terms and in extreme cases render matrix inversion unstable (Tabachnick & Fidell, 1996). Although logistic regression is robust to most multivariate assumptions, data and model screening procedures were employed as recommended by Menard (1995) and Tabachnick & Fidell (1996); procedures were reported only if model validity was threatened.

For both terrestrial and arboreal feeding sites, we used the proportional reduction in the χ^2 statistic (R^2_L) to indicate how much the inclusion of each significant explanatory variable improved model fit; the higher the value, the better the measured variables explain the differences between selected and random sites (i.e., analogous to the linear regression R^2) (Hosmer & Lemeshow, 1989). Odds ratios were used to interpret the effect of each explanatory variable on the response variable and are more intuitive than the regression coefficient when discussing the relative strength of each explanatory variable. Univariate logistic function plots were used to graphically present the relationships between statistically significant vegetation, debris, and snow variables and the predicted probability of a caribou selecting a feeding site (Tabachnick & Fidell, 1996).

To provide a relative measure of the availability of forage species, we used Bonferroni corrected 95% confidence intervals to test differences in mean percent cover of lichen, mosses, grass, and debris between feeding and random sites, and among species (Neter *et al.*, 1990). The relationship between tree diameter at breast height and amount of arboreal lichen was investigated with a simple linear regression equation. An α of 0.05 was used for all tests of statistical significance.

Results

Over the two winters we examined caribou feeding sites along 85 forest transects and 23 alpine quadrats (Fig. 1). We sampled 461 terrestrial (206 feeding, 255 random) and 356 arboreal (102 feed-

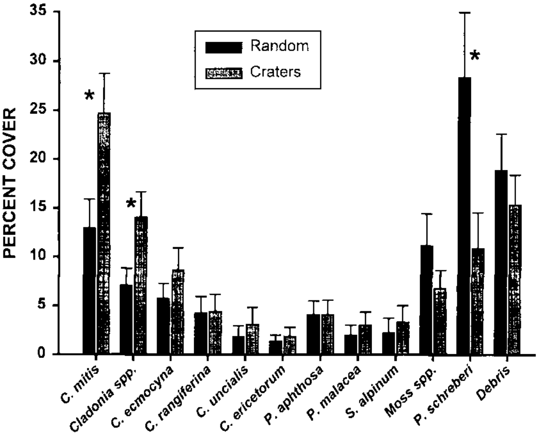

Fig. 3. Percent ground cover of lichens at random (n=255) and cratered (n=206) sites in forested locations. Vertical lines represent a half width of a Bonferroni-corrected 95% confidence interval and asterisks designate statistically significant differences between corresponding sites.

Table 1. Lichen and moss species and groups identified at terrestrial feeding and random sites; classification is based on ease and reliability of field identification, and frequency of occurrence in north-central British Columbia (Dec 1996-Apr 1998).

Ground Cover	Description	Location
Cladina mitis	Distinct lichen class.	Forest/Alpine
Cladina rangiferina	Distinct lichen class.	Forest/Alpine
Cetraria islandica	Distinct lichen class.	Alpine
Cetraria ericetorum	Distinct lichen class.	Forest
Cetraria nivalis	Distinct lichen class.	Alpine
Cetraria cucullata	Distinct lichen class.	Alpine
Peltigera aphthosa	Distinct lichen class.	Forest
Peltigera malacea	Distinct lichen class.	Forest
Cladonia uncialis	Distinct lichen class.	Forest
Cladonia spp.	Composite class consisting of rarely found and unidentified *Cladonia* species; composite of *C. uncialis, C. ecmocyna, C. gracilis, C. cenotea, C. chlorophaea, C. cornuta, C. crispata, C. deformis, C. fimbriata, C. multiformis, C. pyxidata,* and *C. sulphurina.*	Forest/Alpine
Cladonia ecmocyna	Composite class consisting of *C. ecmocyna* with a lesser component of *Cladonia gracilis* (J. Marsh, pers. comm.).	Forest
Stereocaulon alpinum	Composite class consisting primarily of *S. alpinum* with a small component of *S. glareosum, S. tomentosum,* and *S. paschale* (J. Marsh, pers. comm.).	Forest/Alpine
Thamnolia spp.	Composite class consisting of *T. vermicularis* and *T. subuliformis.*	Alpine
Lichen spp.	Composite class consisting of unidentified lichen species.	Alpine
Peltigera spp.	Composite class consisting of *P. aphthosa* and *P. malacea.*	Alpine
Cladina stellaris	Rare and omitted from analysis.	Forest
Nephroma arcticum	Rare and omitted from analysis.	Forest
Solorina crocea	Rare and omitted from analysis.	Forest
Dactylina arctica	Rare and omitted from analysis.	Alpine
Pleurozium schreberi	Composite class consisting primarily of *P. schreberi* with a lesser component of *Hylocomium splendens* and *Ptilium crista-castrensis.*	Forest
Moss spp.	Composite class consisting of unidentifiable or rare moss species and liverworts.	Forest/Alpine

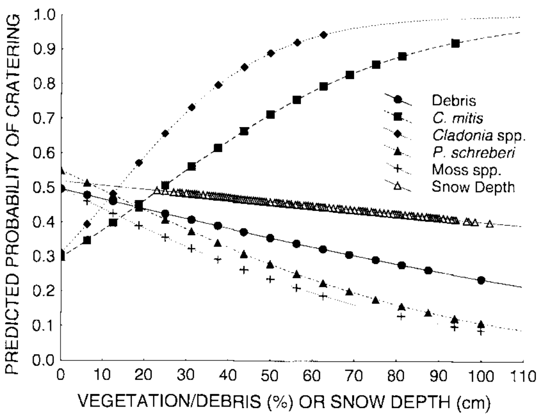

Fig. 4. Predicted probability of caribou cratering at terrestrial forest sites relative to the percent cover of vegetation or debris (measured in units of 6.25% cover) and snow depth (cm). Symbols illustrate the range of data collected in this study.

ing, 251 random) sites in the forest and 136 sites (70 feeding, 66 random) in the alpine. Nine distinct species of *Cladina, Cladonia, Cetraria,* and *Peltigera* lichens and 8 composite groupings of lichen and moss types were regularly observed at alpine and forested terrestrial feeding sites (Table 1). *Cladina stellaris, Nephroma arcticum, Solorina crocea,* and *Dactylina arctica* were also noted, but because they occurred at <10 feeding sites and could not be easily grouped with another lichen species, they were excluded from the analysis. *Bryoria* spp. were the dominant arboreal lichens.

Feeding Sites in Forest Locations

Average snow depths at cratered sites ranged from 23-97 cm and at random sites from 27-102 cm. Average snow hardness at cratered and random sites ranged from 0.27-3.19 g/cm^2 and 0.25-4.2 g/cm^2

Table 2. Summary of multiple logistic regression model derived using the Wald backward elimination procedure for terrestrial and arboreal feeding sites in forested locations in north-central British Columbia (Dec 1996-Apr 1998).

TERRESTRIAL FEEDING SITES (n=460; model χ^2=128.576, df=6, P<0.001)

Variables Retained in Model	B	SE	P	Odds Ratio
Moss spp.	-0.030	0.011	0.007	-3.0%
Debris	-0.026	0.008	0.002	-2.5%
Pleurozium schreberi	-0.023	0.006	<0.001	-2.3%
Snow Depth	-0.021	0.007	0.002	-2.0%
Cladina mitis	0.024	0.008	0.003	+2.4%
Cladonia spp.	0.042	0.011	<0.001	+4.3%
Constant	1.173	0.565	0.040	
Variables Excluded From Model				
Canopy Closure			0.289	
Snow Hardness			0.174	
Snow Density			0.325	
Cladina rangiferina			0.165	
Cladonia ecmocyna			0.155	
Cladonia uncialis			0.961	
Cetraria ericetorum			0.996	
Stereocaulon alpinum			0.862	
Peltigera aphthosa			0.456	
Peltigera malacea			0.642	

ARBOREAL FEEDING SITES (n=356; model χ^2=17.009, df=1, P<0.001)

Variable	B	SE	P	Odds Ratio
Bryoria spp. (g/1-2 m)	0.095	0.026	<0.001	+9.9%
Constant	-1.183	0.145	<0.001	

and snow density from 5-46.97 g/cm^3 and 6.25 - 40 g/cm^3, respectively.

Percent cover of all of the lichen species was greater at cratered sites, but non-overlapping confidence intervals revealed differences only for *Cladina mitis* and *Cladonia* spp. (Fig. 3). At cratered sites *C. mitis* and *Cladonia* spp. averaged 24.7% (standard error of the mean ±1.40) and 14.0% (±0.90), respectively, relative to 12.9% (±1.04) and 7.1% (±0.60) at random sites. In contrast, random sites had a greater percent cover of mosses and debris than crater sites. *Pleurozium schreberi* was the only non-lichen variable to differ significantly, having an average percent cover of 10.6% (±1.25) and 26.2% (±2.19) for cratered and random sites, respectively. Canopy closure ranged from an average of 27.1% (±1.85) at cratered sites to 28.8% (±1.61) at random sites.

The multiple logistic regression model used to describe site selection of terrestrial feeding sites in the forest, correctly classified 71.2% of the cases as crarered or random sires and explained 20.2% (R^2_L=0.202) of the between feeding site variation (Table 2). Snow depth, percent cover of debris, *C. mitis, Cladonia* spp., and the two moss classes significantly contributed to the statistical differentiation of cratered and random sites (Fig. 4). *Cladonia* spp. had the highest odds ratio at +4.3% and the greatest influence on the selection of cratering sites by caribou (Table 2, Fig. 4). Snow depth had the least influence on selection of a feeding site; in this case, the odds ratio implies that a 1 cm increase in snow depth will reduce the likelihood that a caribou will crater by 2% (Table 2, Fig. 4).

Although tolerance scores for each variable in the model were greater than 0.20, several of the variables were significantly bivariate correlated. *Cladina*

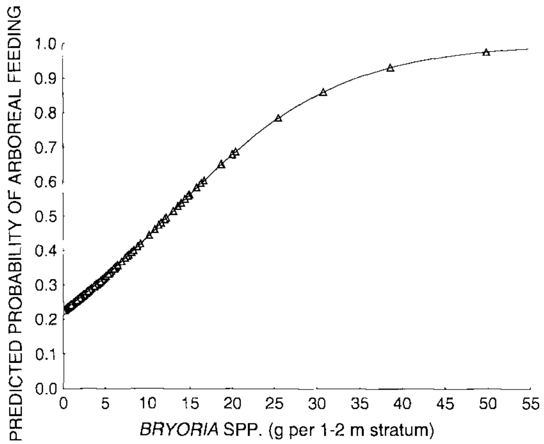

Fig. 5. Predicted probability of caribou choosing an arboreal feeding site relative to the grams of *Bryoria* spp. within the 1-2 m stratum above the snow. Symbols illustrate the range of data collected in this study.

mitis was negatively correlated with debris (r=-0.227), *P. schreberi* (r=- 0.403), and moss spp. (r=-0.155), and *Cladonia* spp. was correlated with *P schreberi* (r=- 0.370). This indicates that there may not be a direct relationship between site selection and the presence or absence of these moss and lichen species.

When choosing to browse arboreal lichen, caribou selected those trees with a greater biomass of *Bryoria* spp. than found in randomly available trees. On average, selected trees had 4.9 g (±0.74) in the 1-2 m stratum versus 2.3 g (±0.24) for random trees. *Pinus contorta* was the dominant tree species at both selected (81%) and random sites (90%). The simple logistic regression model indicated that the amount of *Bryoria* spp. was a meaningful predictor of what trees caribou chose to browse (Table 2, Fig. 5). The model accounted for only a small amount of the variation between feeding and random sites (R^2_L=0.039); however, 72.2% of the cases were correctly classified as feeding or random sites. The odds ratio indicated that a 1 g increase in the amount of *Bryoria* spp. would increase the likelihood of a caribou foraging by 9.9%. There was a significant, but weak linear relationship between tree diameter and arboreal lichen abundance (F=17.495, df=250, P<0.001, R^2=0.066).

Feeding Sites in Alpine Locations

Average snow depth per quadrat ranged from 3-37 and 0-69 cm, and snow hardness between 0.54-28.89 and 0-30.38 g/cm^2 for cratered and random sites, respectively. Percent cover of lichen classes was typically greater at cratered sites, but not sig-

Table 3. Summary of multiple logistic regression model derived using the Wald backward elimination procedure for terrestrial feeding sites in alpine locations in north-central British Columbia (Dec 1996-Apr 1998).

TERRESTRIAL FEEDING SITES (n=136; model χ^2=58.748, df=9, P<0.001)

Variables Retained in Model	B	SE	P	Odds Ratio
Cetraria islandica	-0.106	0.062	0.085	-10.1%
Snow Depth	-0.071	0.023	0.002	-6.8%
Stereocaulon alpinum	0.036	0.015	0.014	+3.7%
Cetraria nivalis	0.060	0.026	0.022	+6.2%
Snow Hardness	0.064	0.040	0.112	+6.6%
Cladina mitis	0.087	0.023	<0.001	+9.1%
Cetraria cucullata	0.095	0.033	0.004	+10.0%
Cladina rangiferina	0.159	0.052	0.002	+17.2%
Thamnolia spp.	0.240	0.119	0.044	+27.1%
Constant	-1.888	0.699	0.007	
Variables Excluded From Model				
Debris			0.626	
Cladonia spp.			0.146	
Peltigera spp.			0.900	
Lichen spp.			0.464	
Moss spp.			0.700	
Poaceae			0.216	

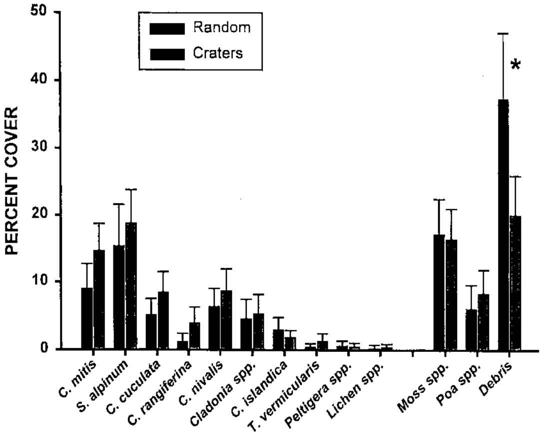

Fig. 6. Percent ground cover of lichens at random (n=66) and cratered (n=70) sites in alpine locations. Vertical lines represent a half width of a Bonferroni-corrected 95% confidence interval and asterisks designate statistically significant differences between corresponding sites.

nificantly so, with *C. mitis, Stereocaulon alpinum,* and *Cladina rangiferina* demonstrating the largest differences (Fig. 6). Debris was the only variable to illustrate a significant difference in percent cover, being more prominent at random (mean=37.3%±3.30) than cratered sites (mean=20.0%±1.99).

The multiple logistic regression model used to describe site selection of terrestrial feeding sites in the alpine accounted for 31% of the between site variation, and correctly classified 76.5% of the cratered and random sites (Table 3). Statistically significant variables were snow depth, percent cover of *C. mitis, C. rangiferina, Cetraria cucullata, Cetraria nivalis, Thamnolia* spp., and *S. alpinum* (Fig. 7). *Thamnolia* spp. had the highest odds ratio at +27.1% and the greatest influence on the selection of feeding sites followed by *C. rangiferina,* and *C. cucullata* at +17.2 and + 10%, respectively (Table 3, Fig. 7). *Cladina mitis* and *C. rangiferina* (r= + 0.171) and *C. rangiferina* and *C. nivalis* (r=- 0.239) were the only significant bivariate correlations for variables identified as important by the logistic regression model. Most cover types were highly correlated with debris, with the highest correlation occurring with *S. alpinum* (r=- 0.453).

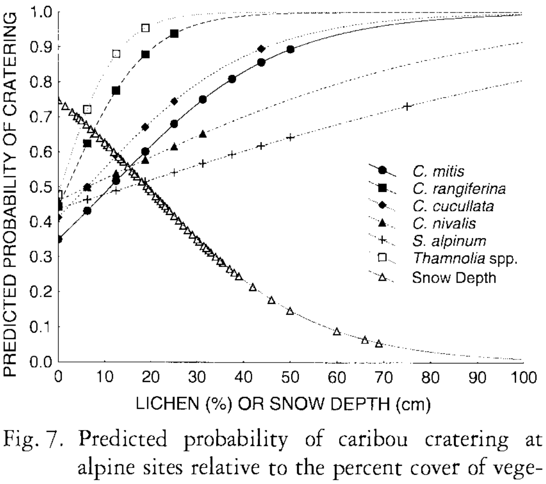

Fig. 7. Predicted probability of caribou cratering at alpine sites relative to the percent cover of vegetation or debris (measured in units of 6.25% cover) and snow depth (cm). Symbols illustrate the range of data collected in this study.

Discussion

Past studies have found that most continental populations of caribou and reindeer (*R. t. tarandus*) forage primarily on fruticose lichens throughout the winter (Pegau, 1968; Helle & Saastamoinen, 1979; White & Trudell, 1980; Klein, 1982; Boertje, 1984; Skogland, 1984; Cichowski, 1993; Terry, 1994), and that snow conditions may restrict access to this food source (Laperriere & Lent, 1977; Skogland, 1978; Duquette, 1988; Brown & Theberge, 1990). However, with few exceptions (e.g., Bergerud, 1974; Thing, 1984; Frid, 1998), most investigators failed to classify forage beyond food type or genus or to consider the interaction between snow conditions and forage selection. Furthermore, the lack of comparison control sites has frequently resulted in the analysis of forage availability as opposed to selection by the animals. We attempted to improve upon these studies by investigating the influence of lichen species in combination with the limiting effects of snow on the fine scale selection of feeding sites in forested and alpine areas.

Selection of Feeding Sites by Caribou

Using data collected over two years across a broad geographic area, we developed statistically significant models to predict the selection by woodland caribou of terrestrial and arboreal feeding sites in forested locations, and terrestrial feeding sites in alpine areas. All three of the models had relatively low explanatory power (R^2_L) indicating that the independent variables (i.e., ground cover and snow condition) captured only a small proportion of the differences between selected and random sites. We believe that this is a consequence of four sources of error in our sampling design and analysis. First, it is likely that we did not recognise, measure, or include all of the variables that are important to the cognitive processes that caribou use when choosing where to feed. For instance, we allowed the backward elimination procedure to determine the most parsimonious model. This excluded certain variables that contributed relatively little new statistical information, but which may have been of some importance to explaining overall differences between the selected and random sites. It is also possible that model aptness was affected by aggregate variables, such as *Cladonia* spp., which may have masked or confounded individual lichen species that were highly selected or avoided by caribou. Frid (1998) identified a similar limitation within his study of crater site selection by woodland caribou.

Second, although we are confident in our ability to identify feeding sites, it is possible that some sites were incorrectly classified. Caribou may have cratered but not fed at certain terrestrial sites, or trees may have been incorrectly classified as browsed when they were not. Sampling error also may have been introduced by classifying our random sites as non-selected sites when in actuality caribou did not make a choice, but passed by that location for reasons not directly related to a foraging decision (e.g., satiation, minor disturbance). Furthermore, because caribou remain in an area for some period of time, our random samples may contain a proportion of sites that would have been cratered at a later date. To reduce this source of error, we should have chosen random sites where it could be confirmed that a caribou had made a decision not to crater, such as unexcavated sniffing holes (e.g., Helle, 1984). Because snow conditions often made the identification of sniffing sites difficult, this approach was abandoned in favour of sampling random locations along the tracks.

Third, we assumed that the lichens remaining at a sampled feeding site were representative of the pre-cratering lichen cover, although the foraging and digging actions of caribou may have resulted in our underestimating the percent cover of lichen at feeding sites. To minimise this bias, we chose percent cover, as opposed to biomass, as our measure of relative lichen availability. Caribou rarely cropped the entire lichen thalus, thus using a point frame with 6.25% increments we were able to accurately and precisely measure percent cover by species at feeding sites.

Fourth, selection strategies of the caribou may have changed during or between winters, confounding the importance of individual variables. For example, nutritional requirements may vary over time or abundance of lichen species may vary spatially, resulting in temporally variable selection patterns. This, and the sources of error listed above did not invalidate our results, but rather forced us to test a more conservative model (which may have decreased the likelihood of obtaining significant differences).

Influence of Vegetation on Feeding Site Selection

Numerous conclusions, in some cases contradictory, have been reported by researchers using field studies or cafeteria-type experiments to investigate preference and selection of lichen species by caribou and reindeer (see DesMeules & Heyland, 1969). Bergerud & Nolan (1970) concluded that comparing food lists between areas or populations is of little value because caribou are adapted to eat most species of plants and, therefore, localised studies reflect only what is available rather than universal selection criteria by *Rangifer.* We also recognise that there may be inter-population variability, but feel that our results placed in the context of other works add to the understanding of the similarities and plasticity in foraging habits of these animals.

Our data indicate that northern woodland caribou select cratering sites based on the percent cover of several lichen species. In most cases our results agree with other studies. For example, *C. mitis* is commonly reported as being preferred or selected by caribou and reindeer (Helle & Saastamoinen, 1979; Helle, 1984; Lance & Mills, 1996). Cafeteria-type experiments have concluded that caribou (*R. t. caribou*) preferred a mixture of *C. stellaris, C. mitis,* and *Cladonia uncialis,* followed by *C. rangiferina, Cetraria islandica,* and *Stereocaulon* spp. (DesMeules & Heyland, 1969); and that reindeer exhibited a preference for *C. stellaris, C. rangiferina, Stereocaulon paschale, Cetraria richardsonii,* and *Peltigera aphthosa,* in that order (Holleman & Luick, 1977). Analysis of faecal samples from the Porcupine caribou herd (*R. t. granti*) indicated that their winter diet consisted predominantly of *Cladonia* and *Cladina* spp., followed by *Stereocaulon, Cetraria* and *Peltigera* spp.; the proportions of these species, however, may have been more related to availability than to selection (Russell *et al*, 1993). Danell *et al.* (1994) assigned high preference rankings to *Cladina arbuscula,* which is morphologically indistinguishable from *C.*

mitis, C. rangiferina, and *S. 'paschale* and a low ranking to *P. schreberi.* Research by Frid (1998) in the southern Yukon is the most comparable to ours in method and species designation. He reported that the probability of a woodland caribou digging a crater increased as the percent cover of *Cladonia* spp., *C. mitis, C. cucullata,* and *C. islandica* increased, but the amount of *C. rangiferina, C. nivalis, P.eltigera* spp., and *Stereocaulon* spp. had no effect. With a few exceptions, mostly being the lichens selected in the alpine, those results are in accordance with the findings of our study.

Through our conclusions we do not infer causal relationships between feeding site selection and the importance of individual lichen and moss species. We emphasise this *caveat* because of the high correlations between several of the significant lichen and moss species. For example, where the model shows a strong effect for lichen and mosses at forested sites, caribou may be selecting for lichens or may be avoiding mosses; the statistical importance of one may be the product of the presence or absence of the other. *P.leurozium schreberi* may be an important discriminating variable only because it occurs where *C. mitis* and *Cladonia* spp. are not found, not because caribou avoid sites where it is found. High negative correlations likely occur because these species of moss and lichen have distinct light and moisture requirements and, therefore, grow in different locations (Robinson *et al,* 1989; Ahti & Oksanen, 1990).

Interpretation of our results is complicated by the inconsistencies in selected lichen species across forested and alpine sites. Most notably, *C. rangiferina* and *S. alpinum,* which were important discriminating variables at alpine sites, were not selected, even though available, by caribou at forested sites. Our results from the forested sites agree with most of the above cited studies that have shown that these species, especially *Stereocaulon* spp., are relatively less palatable. This discrepancy suggests that depending on location, forest or alpine, animals may have differenr foraging strategies.

We observed that the majority of the lichens found in forested areas appeared more vigorous and occurred in greater abundance than those in the alpine (Figs. 3 & 6; C. J. Johnson, unpubl.). Furthermore, at alpine sites clumps of lichen were more unevenly distributed, being separared by bare areas of rock or debris, as reflecred by the high negative correlation between debris and *S. alpinum.* Caribou in the less productive alpine areas may be less selective, taking advantage of those sites with the greatest amount of lichen regardless of palatability. The use of a larger number of species and less palatable yet more prevalent lichens, such as *S. alpinum,* may be an adaptation to a less productive environment where foraging decisions are based largely on availability. This is consistent with the hypothesis of Bergerud & Nolan (1970) that caribou are adaptive and flexible in the forage species they select.

In our study area, woodland caribou in the forest fed on both terrestrial and arboreal lichens; although, based on feeding site frequency, it appeared that cratering is the predominant activity (C. J. Johnson, unpubl.). Comparable findings were reported for our study animals by Wood (1996) and for other woodland caribou populations (Cichowski, 1993). Selection of arboreal lichen may increase following some threshold in accessibility or availability of terrestrial lichen (Bergerud, 1974; Sulkava & Helle, 1975; Helle & Saastamoinen, 1979; Helle, 1984; Vandal & Barrette, 1985).

Our study animals selected trees, principally *P. contorta,* that supported the greatest biomass of arboreal lichen. Across the transects we sampled, which occurred mainly in *P. contorta* or mixed *P. contorta - P. glauca* x *P. engelmannii* stands, the predominant epiphyte was *Bryoria* spp. with only trace amounts of *Alectoria sarmentosa. Bryoria* spp. has been reported as a highly palatable food type (Danell *et al,* 1994) and studies of the mountain caribou ecotype have revealed preference for this lichen group over other alectorioid species (Rominger & Robbins, 1996). The lack of a strong linear relationship between amount of lichen within the 1-2 m stratum and tree diameter suggests that lichen growth and the selection of arboreal feeding sites is related to factors orher than tree size.

Influence of Snow Conditions and Canopy Closure on Site Selection

Although caribou are well adapted to deep snow environments (Telfer & Kelsall, 1984), snow can hinder both the accessibility and detection of forage. Previous studies identified the threshold depth for cratering by caribou and reindeer to range from 50-80 cm (Formozov, 1946; Pruitt, 1959; Stardom, 1975; LaPerriere & Lent, 1977; Helle & Saastamoinen, 1979; Darby & Pruitt, 1984), although craters as deep as 123 cm have been reported (Brown & Theberge, 1990). The ability to crater is also influenced by other snow conditions including hardness and ice layers (Formozov, 1946; Skogland, 1978; Helle & Tarvainen, 1984; Adamczewski *et al.,* 1988; Brown & Theberge, 1990). Bergerud & Nolan (1970) concluded that Newfoundland caribou could not smell terrestrial lichens under snow exceeding 25 cm in depth, but Helle (1984) reported that reindeer in Finland detected lichens through a snow thickness of 91 cm. Over our two-year study period, the maximum crater depths we observed were 97 and 50 cm for forested and alpine sites, respectively.

Canopy closure increases snow interception and correspondingly reduces snow depth and the effort necessary to expose lichens (Schaefer, 1996). Across the range of the Wolverine herd, canopy closure did not affect the selection of cratering sites. In contrast, Cichowski (1993) and Lance & Mills (1996) found that cratering occurred most often in forested areas with more open canopies. In both cases, however, there was an interaction with the presence of terrestrial lichen suggesting that open canopy stands were more productive. Our analysis used a moosehorn coverscope as opposed to a visual estimate of canopy closure (Cichowski, 1993; Lance & Mills, 1996). The latter estimates closure of a much larger portion of the canopy (i.e., scale of the stand) than the coverscope (i.e., scale of the feeding site). This likely accounts for rhe differences between our results and other studies.

If a caribou attempted to forage optimally by expending as little energy as possible when cratering, then selection of sites with shallower, softer, and less dense snow would be expected as long as the additional search time did not exceed the cost of finding more accessible lichens (Fancy & White, 1985). In agreement with this premise, LaPerriere & Lent (1977) found snow depths and hardness to be less in feeding areas relative to adjacent uncratered areas. At the individual feeding sites we surveyed, caribou appeared to partially meet these criteria by selecting locations to crater where snow depths were shallower than random sites. The greatest effect, as indicated by the odds ratio and univariate logistic plots (Fig. 4, 7), was in the alpine where because of uneven topography and drifting snow, we observed snow depths to be much more variable. Neither snow hardness nor density appeared to influence crater site selection. In other studies, Frid (1998) found no effect of snow depth or penetrability on crater site selection, but attributed this to the relatively low snow depths of his study area (mean=31.5 cm, standard deviation=5.8). Cichowski (1993) found that crater sites had greater snow depths, but reduced penetrability when compared to random sites. Duquette (1988) studying the Porcupine herd, reported that snow depths were deeper along migration trails than within adjacent feeding areas, and snow hardness did not differ between the two areas.

Management Implications

Our research suggests that particular scale-specific habitat characteristics may be important to manage for, or consider during an assessment of the winter range of the northern woodland caribou of British Columbia. Forested areas should be managed to contain terrestrial lichen mats with a high percent cover of *C. mitis, Cladonia* spp., and a high biomass of arboreal lichen (*Bryoria* spp.). *Cladina mitis, C. rangiferina, C. cucullata, C. nivalis, S. alpinum,* and *Thamnolia* spp. are important species that should be considered when assessing and managing alpine areas. Because snow may limit access to forage, and restrict use to specific areas of the range, snow depths should be considered in conjunction with the availability of lichens when assessing the suitability and availability of caribou winter range.

Our results describe selection of foraging sites by caribou at one explicitly defined scale, the individual feeding site. However, the relationship between an organism and its environment is often complicated by multiscale influences. Factors from both finer and broader scales may act in unison to elicit responses that may not be detected by measurements designed to record responses at one particular scale. To accommodate the recording and understanding of these interactions, a multiscale hierarchical approach should be pursued (Senft *et al.,* 1987; Kotliar & Wiens, 1990; Wiens *et al.,* 1993). This study was designed to measure just one of many scales that may be televant to how caribou perceive and respond to their environment (Johnson, 1980). The results and conclusions must, therefore, be viewed within the context of other scale-sensitive influences on movement and distribution across the landscape (e.g., large scale distribution of snow, habitat patch configuration, predation risk) which are necessary considerations when managing the winter range of woodland caribou (Cumming, 1992). We are currently investigating the affects of those influences on the foraging behaviour, movements, and distribution of woodland caribou at stand and landscape scales.

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