Chris J. Johnson · Katherine L. Parker
Douglas C. Heard

Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales

Abstract We examined the foraging behavior of woodland caribou (*Rangifer tarandus caribou*) relative to the spatial and temporal heterogeneity of their environment. We assessed (1) whether caribou altered their behavior over time while making trade-offs between forage abundance and accessibility; and (2) whether foraging decisions were consistent across spatial scales (i.e., as scale increased, similar decision criteria were used at each scale). We discuss whether caribou adjusted their behavior to take advantage of changing forage availability through time and space. At the scale of the feeding site (as revealed by discriminant function analyses), caribou in both forested and alpine (above tree-line) environments selected sites where the biomass of particular lichen species was greatest and snow the least deep. Caribou did not select those species with the highest nutritional value (i.e., digestible protein and energy) in either area. Where snow depth, density, and hardness limited access to terrestrial lichens in the forest, caribou foraged instead at those trees with the greatest amount of arboreal lichen. Selection of lichen species and the influence of snow differed across time, indicating that in this system the abundance or accessibility of forage temporally influenced foraging behavior. A path analysis of forest data and multiple regression analysis of alpine data were used to test the hypothesis that variables important at the scale of the feeding site explained foraging effort at the scale of the patch. For forest patches, our hypothesized model reliably explained foraging effort,

but not all variables that were statistically important at the scale of the feeding site were significant predictors at the scale of the patch. For alpine patches, our hypothesized model did not explain a statistically significant portion of the variation in the number of feeding sites within the patch, and none of the individual variables from the feeding site remained statistically significant at the patch scale. The incongruity between those variables important at the scale of the feeding site and those important at the patch showed that spatial scale affects the foraging decisions of woodland caribou. At the scale of the landscape, there was a trade-off between forage abundance and accessibility. Relative to the alpine environment, caribou in the forest foraged at feeding sites and patches with greater amounts of less variably distributed lichen, but deeper less variable snow depths. Considering the behavioral plasticity of woodland caribou, there may be no distinct advantage to foraging in one landscape over the other.

Introduction

Foraging behavior by animals is a series of consecutive decisions arising from choices such as what to eat, when to eat, and where to eat. Although simple from a reductionist perspective, those choices and resulting decisions are a complex function of interactions involving changes in the environment, and changes in the past, present, and future internal states of animals (Cheverton et al. 1985; Mangel and Clark 1986; Ludwig and Rowe 1990; Sinclair and Arcese 1995; Bowyer et al. 1998). Therefore, the decision-making process for free-ranging animals faced with variable and stochastic environments is not as simple as optimal foraging hypotheses developed for controlled experiments would suggest (Schluter 1981; Mangel and Clark 1986).

Predictions of optimality are difficult to test when observed behavior is the product of complex decisions

C.J. Johnson (✉) · K.L. Parker
Faculty of Natural Resources and Environmental Studies,
University of Northern British Columbia, 3333 University Way,
Prince George, B.C., Canada V2N 4Z9
e-mail: cjj1@ualberta.ca
Tel.: 780-492-6267

D.C. Heard
British Columbia Ministry of Environment, Lands and Parks,
1011 4th Ave., Prince George, B.C., Canada, V2L 3H9

Present address:
C.J. Johnson, Department of Biological Sciences,
University of Alberta Edmonton, Alberta, T6G2E9, Canada

made by animals responding to multiple variables. Describing the behavioral choices available to an animal is further complicated by the identification of the appropriate spatial and temporal scales. Turner et al. (1989) defined scale as the spatial or temporal dimensions of an object or process, characterized by both grain and extent. Allen and Hoekstra (1992) argue that it is necessary to consider several scales simultaneously: the one in question, one below for mechanisms, and one above for context.

During winter (December–April), northern woodland caribou (*Rangifer tarandus caribou*) in the boreal and sub-boreal forests of central and northern British Columbia, Canada, make foraging decisions that are likely complicated by trade-offs between abundance and accessibility of forage that occur at multiple spatial and temporal scales. Those decisions are dependent on locations on the landscape, daily nutritional state, seasonal energy and protein budgets, and scale-dependent spatial and temporal variation in the environment. Because woodland caribou can be tracked in the snow and their feeding sites identified reliably, these herbivores are an excellent model for investigating complex multi-scale foraging strategies that have evolved within heterogeneous, stochastic landscapes.

At a small spatial scale, caribou select a particular forage species to consume. Although the winter forage consists almost exclusively of lichens, caribou may choose from species differing in morphological structure, growing location, patch size, nutritional content, and abundance (e.g., Ahti 1964; Moser et al. 1979; Carroll and Bliss 1982; Robinson et al. 1989; Ahti and Oksanen 1990). At a somewhat larger scale, animals choose sites at which to forage. For woodland caribou during winter, this can be either a terrestrial site where the snow must be cratered (excavated) to access lichens growing on the ground, or an arboreal site where lichens growing on lower tree branches can be browsed directly (Bergerud 1974; Sulkava and Helle 1975; Helle and Saastamoinen 1979; Helle 1984; Vandal and Barrette 1985). Selection for feeding sites has been linked to availability and accessibility of forage, which is influenced by snow conditions and amount and type of both terrestrial and arboreal lichens (Formozov 1946; Skogland 1978; Helle and Saastamoinen 1979; Helle 1984; Helle and Tarvainen 1984; Adamczewski et al. 1988; Brown and Theberge 1990; Cichowski 1993; Frid 1998; Johnson et al., in press).

At the next level, caribou choose patches in which to concentrate their feeding sites. From a foraging perspective, this could be related to mean abundance of terrestrial or arboreal lichens by species, mean snow conditions relative to other patches, or a trade-off between abundance and accessibility. At an even greater spatial scale, caribou in north-central British Columbia choose between patches across forested or alpine landscapes. Those locations differ in plant composition and snow conditions, but are closely juxtaposed, allowing for choice with relatively little additional energetic cost of moving between the two landscapes. Few studies have been conducted at those latter two scales and none have focused on the integration of foraging behavior across all four scales.

The objectives of this study were to assess (1) whether caribou exhibited trade-off decisions in response to the temporal or spatial variability of forage and snow conditions, and (2) whether foraging decisions were consistent across scales (i.e., as spatial scale increases, similar decision criteria are used at each scale). We discuss the results of our two objectives in the context of whether caribou adjusted their decisions to maximize nutritional gain and minimize foraging costs through time and space.

We predicted that relative to the *forage* and *feeding site*, caribou should: (1) select terrestrial lichen species highest in digestible protein and energy; (2) choose feeding sites with less deep, less dense, and less hard snow; (3) choose sites with greater amounts of terrestrial lichens as snow depth, density, and hardness increase; and in the forest (4) begin foraging on arboreal lichens following a decrease in accessibility (snow conditions), choosing those trees with the greatest biomass of lichens.

Relative to the *patch*, caribou should: (5) forage in patches in proportion to the abundance of the lichen species that were selected at the scale of the feeding site; (6) forage on terrestrial lichens to a greater extent in more accessible patches with mean snow conditions that are relatively less deep, dense, and hard; and (7) browse on arboreal lichens in forested patches with unfavorable snow conditions for cratering or low biomass of terrestrial lichens. And, relative to two *landscapes* that differ in lichen abundance and snow conditions, caribou should: (8) choose to forage across the landscape that has the greatest mean biomass of lichens and least restrictive snow conditions (i.e., depth, density, and hardness).

Materials and methods

Study area

The group of caribou chosen for this study is known as the Wolverine herd (Heard and Vagt 1998), and ranges throughout a 5100-km^2 area, approximately 250 km northwest of Prince George, British Columbia. Terrain varies, from valley bottoms at approximately 900 m to alpine summits at 2050 m and is characterized by numerous vegetation associations resulting from diverse topography, 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×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. Elevations above 1600 m are alpine tundra and are distinguished by gentle to steep, windswept slopes vegetated with shrubs, herbs, bryophytes, and lichens with occasional trees in krummholz form (MacKinnon et al. 1990; DeLong et al. 1993). Snow depths ranged from 23 to 102 cm and 0 to 69 cm in forested and alpine habitats, respectively, during this study.

Sample design and data collection

Field investigations occurred at 2- to 3-week intervals between December and April 1996–1997 and 1997–1998 (Johnson 2000). We defined a *feeding site* as a discrete terrestrial (50×50 cm) or arboreal (1- to 2-m stratum) foraging location; a *patch* as a collection of feeding sites representing the composition and availability of lichens and snow conditions across a 100-m linear distance (forest) or 50×50-m (alpine) quadrat; and a *landscape* as a collection of patches with unique ecological factors (e.g., vegetation and animal communities, climate, topography).

After locating recent tracks in the snow of radio-collared or non-collared caribou in the forest, we assessed the immediate area for signs of foraging behavior: meandering tracks, craters and/or sniffing holes at terrestrial feeding sites, and trampling at the base of trees, broken twigs, and arboreal litter at arboreal feeding sites. If some sign of foraging behavior was present, we selected a starting point in the snow along the caribou tracks using a random number table of distances, defined our transect by placing a 100-m tape along the track, and counted all terrestrial (craters) and arboreal feeding sites. A maximum of 12 sites were randomly selected for measurement along the 100-m transect: 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.

In alpine areas, we used a 50×50-m quadrat as our sampling unit rather than a 100-m length of track because of the aggregated distribution of the feeding sites and safety concerns in precipitous terrain. All craters in the quadrat were counted, and we randomly selected three to six craters for measurements. The corresponding non-feeding sites were located at a random compass bearing and random number of paces (1–20 paces) from the sampled craters.

To minimize the risk of pseudoreplicating our sample unit, the feeding site, 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, unpublished work). Furthermore, because we wanted to sample all collared animals and visit as many geographically separate locations as possible, we restricted the maximum number of transects sampled at one location to three, for a maximum of nine terrestrial and nine arboreal feeding sites. To further reduce the effects of spatial autocorrelation and allow an opportunity for changes in behavior across space, and presumably time, successive transects were separated by a distance of 100 m. At alpine locations only one quadrat per group of animals was sampled, within which three to six craters and corresponding random sites were measured.

At each terrestrial feeding and random site, we measured snow depth to the nearest 0.5 cm, and the penetrability (i.e., hardness) of the upper snow layer with an instrument of our own design which was similar to the Rammsonde penetrometer (Mellor 1964; Skogland 1978). 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 the measurements of snow depth, density, and hardness, the snow was cleared and the percent cover of lichens, moss, and debris and standing height of lichens were assessed with a 16-pin, 0.5×0.5 m point frame (Bookhout 1994). Each pin was marked vertically at 1-cm intervals. Lichen and moss were identified to species, genus, or morphological group depending on ease and reliability of field classification (hereafter referred to as distinct or composite classes). The volume of lichens within each frame was calculated by multiplying the area covered by each identified lichen species by its corresponding mean height (Fleischman 1990).

At each arboreal feeding and 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 (g) (Antifeau 1987; Stevenson and Enns 1993). We counted the number of units that occurred within the reach of a typical caribou (1–2 m above the snow) and multiplied those units by the mass of the standard lichen unit to obtain total biomass within the 1- to 2-m stratum. Before field studies commenced, technicians were trained to standardize measurement techniques and were assessed for consistency in estimates of biomass of arboreal lichens.

Estimation of terrestrial lichen biomass

Because caribou remove lichens during foraging, there is the potential to consistently underestimate lichen volume at foraged craters and arboreal feeding sites. At arboreal feeding sites, caribou removed only small amounts of lichen from one or two branches (i.e., differences in the amounts of arboreal lichen between selected and random trees were difficult to distinguish visually). Assuming that caribou select trees with a greater biomass of lichen, this bias would lessen differences between random and foraged trees, but because it was our impression that only small amounts were removed, removal was unlikely to invalidate our results. At forested terrestrial sites, however, we observed that the lichen was often cropped close to the ground. To provide an estimate of pre-foraged volume, a correction factor was calculated for each lichen species that consistently had a large proportion of its volume removed. We regressed the volume against the corresponding area covered by each species for random and then for cratered sites; confidence intervals were used to test for differences between slopes and intercepts (Lewis-Beck 1980). Where significant, the difference between the slopes of the two equations was multiplied by the area of that particular lichen species for each crater. When added to the measured volume remaining at each crater, this provided an estimate of the volume of lichens that was present before a caribou fed at that site. Volume of terrestrial lichens was converted to biomass (g dry weight m^{-2}) with ratio estimates (Cochran 1977) calculated by Fleischman (1990) for percentage cover to biomass for *Peltigera* spp. and volume (dm^3 m^{-2}) to biomass for all other fruticose lichens.

Analyses of forage selection at feeding sites

Relative to the selection of forage and feeding sites, we used a discriminant function analysis (DFA) to describe the foraging decisions of caribou (Tabachnik and Fidell 1996). At forested sites, DFA was designed to statistically separate four potential foraging sites: (1) terrestrial lichen feeding or cratering; (2) random terrestrial sites; (3) arboreal feeding; and (4) random arboreal sites. Because trees were not present at alpine locations, that analysis involved only a comparison of two sites: (1) terrestrial lichen feeding; and (2) random terrestrial sites. We tested three models for both forested and alpine locations. The first model described feeding sites based on the biomass of lichen species, area of moss and debris, snow depth, density, and hardness. The second and third models were similar except that lichen biomass within each model was replaced by an interaction term [(lichen biomass×week, calculated from the sampling date) or (lichen biomass×Northing× Easting, universal transverse mercator, UTM, geographic locations)] to test whether the foraging behavior of caribou differed over time or space.

At arboreal feeding and random sites, only the biomass of arboreal lichens was estimated; there were no measurements made specifically beneath the trees for terrestrial lichens or snow conditions. Therefore, those sites could not be compared directly with terrestrial feeding or random sites because different variables were measured. To allow a comparison of terrestrial versus arboreal feeding choices, lichen biomass and snow conditions at all terrestrial sites move within the 100-m transect were averaged and those values were applied during our analysis to the arboreal feeding and random sites. Similarly, the average biomass of arboreal lichens was applied to the craters and terrestrial random sites on

the same transect. In effect, this recombination of measured variables allowed us to compare those sites chosen by caribou to random sites of the same behavior (terrestrial or arboreal) as well as to the alternative feeding behavior.

We used a χ^2-statistic to test the significance of the successive discriminant functions (canonical roots) generated by the four-group model. Model reliability was further assessed using the explained between-group variance, and non cross-validated classification results (Williams 1983; Williams et al. 1990; Tabachnik and Fidell 1996). Within each function, differences between feeding and random sites were interpreted from a visual examination of group centroid plots (Tabachnik and Fidell 1996). The importance of the individual variables (vegetation, snow) in differentiating the feeding and random sites was assessed with parallel discriminant ratio coefficients (DRCs, Thomas and Zumbo 1996). Variables of importance were ranked in ascending order; a variable was considered unimportant if its DRC was below $1/(2P)$, where P represents the number of variables in the model (Thomas and Zumbo 1996). To assess whether a relationship existed between the potential energetic cost of digging a crater and the biomass of excavated lichens, each statistically important snow measure was regressed against each important lichen species.

Analyses of patch selection

We examined two relationships at the scale of the patch. First, we investigated the importance of vegetation and snow on the foraging efforts and patch use by caribou. Second, we tested whether foraging relationships and selection strategies used by caribou at the scale of the feeding site were related to foraging strategies at the scale of the patch. For both questions we assumed a priori that there was a linear relationship between the importance of each variable at the scale of the feeding site and foraging effort, as determined by the number of feeding sites per transect or quadrat in the patch. Importance reflects the relative influence of each independent variable on the discrimination of groups (i.e., feeding locations) in the DFA. For example, if the lichen *Cladina mitis* was important at the feeding site, then as biomass of *C. mitis* increased, there should have been a correspondingly greater foraging effort (i.e., more craters) in patches with more *C. mitis*. We used a path analysis to determine whether there was a linear multi-scale relationship between feeding sites (terrestrial and arboreal) and patches in the forest, and to measure the importance of individual variables for patch selection (Mitchell 1992; Shipley 1997). Only one dependent variable (number of craters) was measured at alpine patches, and therefore we used a multiple regression analysis to address previous objectives. The results of the DFAs were used to select important vegetation or snow variables and specify relationships within the path analysis and multiple regression models. Because the number of animals at a particular location also may explain differences in feeding intensity, the number of animals at each patch during the time of sampling move was included as an independent variable. Where animals were not sighted, the average number of caribou typically occurring within a group during winter was used (Wood 1996; C.J. Johnson, unpublished work). To accommodate the constraint of time on foraging behavior and recognize that an animal can not feed at two places simultaneously, the number of craters was used as an explanatory determinant of the number of arboreal feeding sites.

For the path analysis of scale-sensitive selection, population parameters were estimated with the generalized least squares method (Ullman 1996). Model fit was evaluated using a χ^2-statistic with the desired outcome being a nonsignificant difference between the sample correlation matrix and the estimated population correlation matrix. Because this statistic is sensitive to sample size (Ullman 1996), the Joreskog adjusted goodness of fit index, McDonald's index of noncentrality, the Steiger-Lind RMSEA index, and the root mean square standardized residual were also used to assess model fit. Good fit is indicated by values >0.95 for the former two indices, and by values <0.05 for the latter two indices (StatSoft 1997). The standardized path coefficient (analogous to the β coefficient of multiple regression) represented the contribution to the model of each independent variable and was tested with the asymptotic normal statistic (T, StatSoft 1997).

Analyses of landscape selection

At the largest spatial scale, selection by caribou for feeding sites and patches was assessed between two distinct landscapes: alpine and forest. We tested whether animals that spent the winter in one of those two areas chose an environment with greater or less biomass and variability of important lichen species, and more or less extreme and variable snow conditions. Results of investigations performed at scales of the feeding site and patch were used to select the lichen species and snow conditions that were included in the landscape analyses. From the scale of the feeding site, differences were tested for all terrestrial feeding sites between landscapes. From the scale of the patch, average lichen and snow conditions of both feeding and random sites across all transects or quadrats were compared between landscapes. Independent *t*-tests calculated with separate group variances were used to test for differences in mean biomass of important lichen species (as defined by analyses at the scale of the forage species) and snow conditions (snow depth and hardness) between landscapes. The coefficient of variation (CV) served as a measure of lichen and snow variability across the two landscapes.

All statistical tests were performed with STATISTICA (Release 5.1; StatSoft 1997) and were considered significant at an α of 0.05. Where appropriate, effect sizes are reported as a measure of practical significance (Cohen 1992; Kirk 1996). Effect-size statistics eliminate the confounding effects of sample size when illustrating group differences or the strength of relationships between variables. Cohen (1992) defined a medium effect size as one that is visible to the naked eye of a careful observer, a small effect size as one that is noticeably smaller than medium, but not so small as to be trivial and a large effect size as the same distance above medium as small was below. We used the effect size index r (product-moment correlation) for the DFA and f^2 (multiple partial correlation) for the regression analyses, where 0.10, 0.30, and 0.50 and 0.02, 0.15, and 0.35 represent small, medium, and large effect sizes, respectively. Variables were transformed as necessary to improve normality and reduce the influence of outliers. Variables used in the path analysis, regression analyses, and confidence intervals were tested for independence with the Durbin-Watson d statistic, a residual correlation (P) threshold of 0.30, and through inspection of residuals (Savin and White 1977; Ostrom 1990). Where unacceptable levels of autocorrelation were detected, the Cochrane-Orcutt procedure was used to transform the offending dependent and independent variables (Neter et al. 1990).

Results

Over two winters, we examined caribou feeding sites along 85 forest transects and 23 alpine quadrats. We sampled 461 terrestrial (206 feeding, 255 random) and 353 arboreal (102 feeding, 251 random) sites in the forest and 136 sites (70 feeding, 66 random) in the alpine. On forested transects, the lichen volumes measured for four lichen species were consistently (all $P<0.05$) lower at crater sites than at random terrestrial sites. Regression coefficients (B) for the relationships between volume (cm^3) and cover (cm^2) varied for *C. mitis* (crater: $B=1.45\pm0.064$; random: $B=1.57\pm0.046$, SE), *C. rangiferina* (crater: $B=1.52\pm0.042$; random: $B=1.65\pm0.044$), *Cetraria ericetorum* (crater: $B=1.32\pm0.036$; random: $B=1.40\pm0.039$), and *Peltigera malacea* (crater: $B=1.15\pm0.043$; random: $B=1.247\pm0.034$). Pre-foraging volumes for those species were corrected accordingly. At

Fig. 1 Mean discriminant function scores (centroids±SE) for feeding sites used by caribou and random sites at forested locations in north-central British Columbia (December 1996–April 1998). Separation of terrestrial from random sites is illustrated at the *first function*, terrestrial feeding (*n*=202) from random terrestrial sites (*n*=252) at the *second function*, and arboreal feeding (*n*=99) from random arboreal sites (*n*=254) at the *third function*. Important variables are listed below each function with the direction of influence indicated by *arrows* (distinct moss or lichen classes: *Cetraria ericetorum, Cladina mitis, Cladina rangiferina, Cladonia uncialis, Peltigera aphthosa*; composite moss or lichen classes: *Cladonia ecmocyna, Pleurozium schreberi, Stereocaulon alpinum, Cladonia* spp., *Bryoria* spp.)
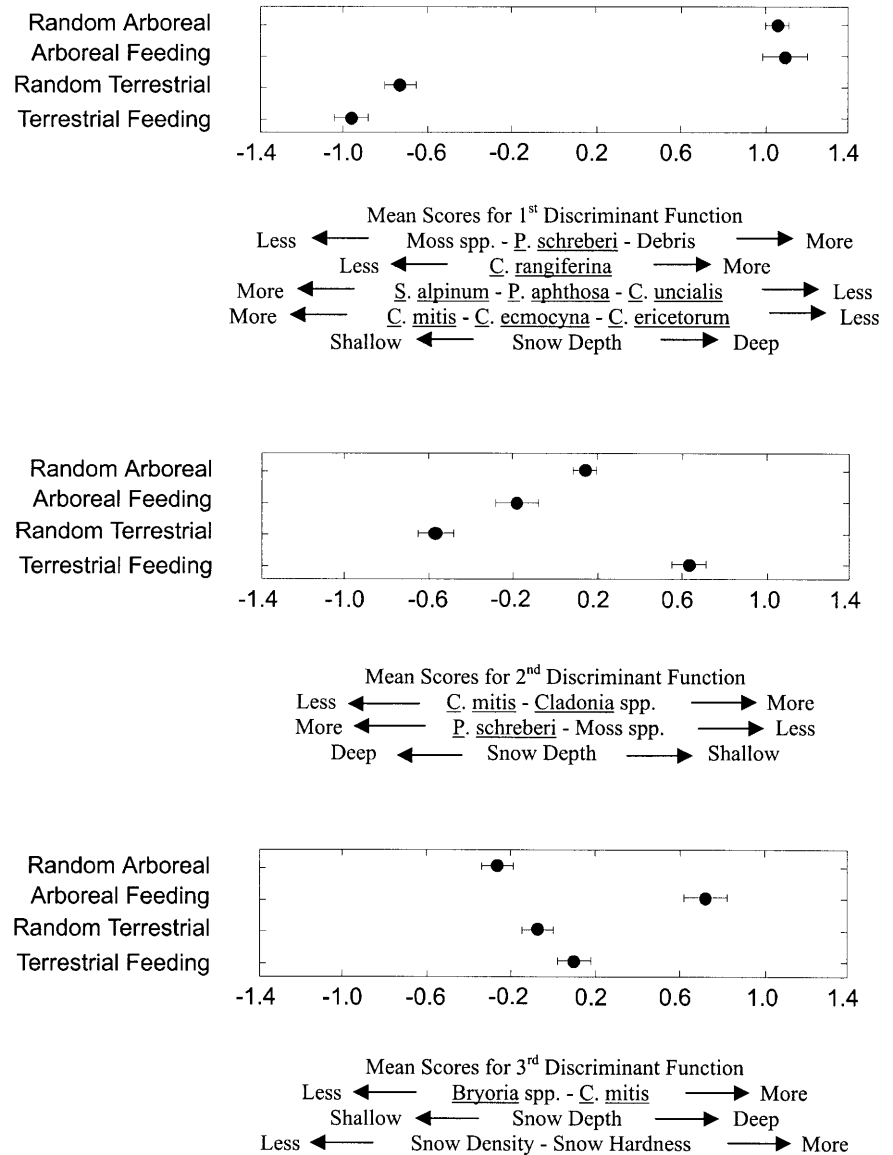
alpine locations, the volume of lichens did not consistently differ (all *P*>0.05) between foraged and random sites for any species of lichen. There were no significant differences (all *P*>0.05) in the regression intercepts between foraged and random sites for forested or alpine lichens.

Forage and feeding site selection

In forested locations, vegetation, debris, and snow variables discriminated between feeding sites. The first discriminant function differentiating between terrestrial and arboreal sites (Fig. 1) accounted for 75% of the between-site variation (χ^2=722.86, *df*=48, *P*<0.001; *r*=0.687). Eleven variables were statistically important in discriminating those sites with the most important being *Pleurozium schreberi*, moss species, and debris (Table 1). In general, there were greater amounts of moss and debris,

and deeper snow at the arboreal sites and more biomass of lichens at the crater sites (Table 1). In interpreting this function, it is important to consider that differences in group centroids result largely from our averaging those variables at terrestrial feeding and random sites and applying those means to arboreal sites on the same transect. Thus, if the two terrestrial site types had different values, their average, applied to their corresponding arboreal foraged and random sites, would show correspondingly large differences in group centroids.

Craters and random terrestrial sites were differentiated by a second discriminant function (Fig. 1), accounting for 17.6% of the between-site variation (χ^2=217.77, *df*=30, *P*<0.001; *r*=0.416). On average, cratered sites had a greater biomass of lichens (*Cladonia* spp., *Cladina mitis*), less moss and lower snow depths than sites where caribou did not feed (Table 1).

Arboreal feeding and random arboreal sites were differentiated by a third discriminant function (Fig. 1),

Table 1 Variables identified by discriminant function (DF) analysis as important (threshold=0.031) in defining each successive DF and separating terrestrial feeding sites used by caribou, random terrestrial sites, arboreal feeding sites used by caribou, and random arboreal sites at forested locations in north-central British Columbia (December 1996–April 1998). Variables are ranked according to their importance using the parallel discriminant ratio coefficient (DRC, Thomas and Zumbo 1996). Mean measures of lichens (g dry weight m^{-2}) and mosses/debris (cm^2) are calculated by site type

Discriminant function	Variable	Parallel DRC score	Terrestrial feeding site		Random terrestrial site		Arboreal feeding site		Random arboreal site	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1st DF	*Pleurozium schreberi*[b]	0.223	264.60	440.59	721.11	909.25	549.90	566.63	512.85	536.40
	Moss spp.[b]	0.218	162.53	219.20	277.16	450.46	328.92	494.94	250.48	331.49
	Debris	0.102	380.03	382.87	470.61	512.56	384.57	248.04	431.98	254.72
	Cladina rangiferina[a]	0.065	22.91	42.06	23.72	56.90	15.97	18.74	24.41	32.61
	Stereocaulon alpinum[b]	0.063	28.05	71.29	16.53	59.61	24.51	53.49	24.45	47.55
	Peltigera aphthosa[a]	0.054	28.74	54.79	28.91	55.24	27.03	24.52	28.64	28.04
	Cladonia uncialis[a]	0.047	9.76	28.47	5.96	20.30	5.69	14.00	8.03	16.88
	Cladina mitis[a]	0.041	121.68	112.61	65.10	93.06	93.16	65.85	87.05	68.05
	Cladonia ecmocyna[b]	0.040	76.71	106.40	50.71	86.11	58.33	57.05	61.41	55.57
	Cetraria ericetorum[a]	0.039	4.24	10.86	2.92	7.86	3.28	4.91	3.58	4.81
	Snow depth (cm)	0.032	55.59	17.61	57.67	18.65	69.05	17.78	57.56	17.64
2nd DF	*Cladonia* spp.[b]	0.357	76.71	78.62	41.73	62.08	46.98	36.37	54.15	40.04
	Cladina mitis[a]	0.346	121.68	112.61	65.10	93.06	93.16	65.85	87.05	68.05
	Pleurozium schreberi[b]	0.132	264.60	440.59	721.11	909.25	549.90	566.63	512.85	536.40
	Snow depth (cm)	0.053	55.59	17.61	57.67	18.65	69.05	17.78	57.56	17.64
	Moss spp.[b]	0.034	162.53	219.20	277.16	450.46	328.92	494.94	250.48	331.49
3rd DF	*Bryoria* spp.[b]	0.560	2.82	2.95	2.88	3.46	4.76	6.20	2.26	3.66
	Snow depth (cm)	0.158	55.59	17.61	57.67	18.65	69.05	17.78	57.56	17.64
	Snow density (g cm^{-3})	0.138	22.25	5.02	21.93	5.47	24.78	4.24	22.51	4.56
	Cladina mitis[a]	0.071	121.68	112.61	65.10	93.06	93.16	65.85	87.05	68.05
	Snow hardness (g cm^{-2})	0.047	0.639	0.100	0.634	0.343	0.681	0.162	0.643	0.001

[a] Distinct moss or lichen class (single species)
[b] Composite moss or lichen class

accounting for 7.5% of the between-site variation (χ^2=67.47, df=14, P<0.001; r=0.286). Mean differences in the amount of *Bryoria* spp. and *C. mitis*, and snow characteristics indicated that caribou fed on arboreal lichens at trees where there was more *Bryoria* spp., and when the surrounding area had more *C. mitis* and deeper, denser, and harder snow, relative to transects where caribou did not arboreal feed (Table 1).

The discriminant function model correctly classified 62.2% of the samples into their appropriate sites compared to a classification accuracy of 27.5% based on chance alone. The highest misclassification (81.7%) occurred for the arboreal feeding sites, which often were misclassed as random arboreal sites.

The statistical and interpretative outcome of the biomass×location model was similar to that reported for the previous noninteraction lichen biomass model (Table 1). The biomass×time model differed in that the third discriminant function was responsible for explaining a larger proportion of the overall between-site variation (11.2%). Some minor reordering occurred in the ranking of variables for the two interaction models (biomass×time, biomass×location), and several variables were included or excluded as important when describing their respective discriminant functions. For the biomass×time model, *Bryoria* spp. (parallel DRC=0.051) and *Cladonia ecmocyna* (parallel DRC=0.043) were included as important and moss spp. was unimportant when explaining the second discriminant function, whereas snow hardness (parallel DRC=0.005) became unimportant relative to the third discriminant function. When compared to the noninteraction model, neither variable inclusion nor order of importance differed for the second and third discriminant functions of the biomass×location model.

The biomass of important lichen species measured at feeding sites showed a weak, but significant linear rela-

596

Table 2 Variables identified by DF analysis as important (threshold=0.042) in differentiating terrestrial feeding sites used by caribou from random terrestrial sites at alpine locations in north-central British Columbia (December 1996–April 1998). Variables are ranked according to their importance with the parallel discriminant ratio coefficient (DRC) (Thomas and Zumbo 1996). Mean measures of lichens (g dry weight m^{-2}) are presented by site type

Variable	Parallel DRC score	Terrestrial feeding site		Random terrestrial site	
		$\bar{x}$	SD	$\bar{x}$	SD
Snow depth (cm)	0.169	15.52	7.72	22.50	14.94
Cladina rangiferina	0.162	13.60	27.65	2.12	7.33
Cetraria cucullata	0.160	9.34	10.89	4.91	6.94
Cladina mitis	0.158	32.00	29.39	20.19	35.42
Thamnolia spp.	0.114	4.68	15.92	0.51	2.50
Stereocaulon alpinum	0.109	113.67	105.74	105.74	91.20
Debris (cm^2)	0.053	497.77	416.63	937.50	662.91

Fig. 2 Mean discriminant function scores (centroids±SE) for alpine locations in north-central British Columbia (December 1996–April 1998) illustrating the separation of terrestrial feeding sites used by caribou (*n*=70) from random terrestrial sites (*n*=68). Variables are listed below each function with the direction of influence indicated by *arrows*
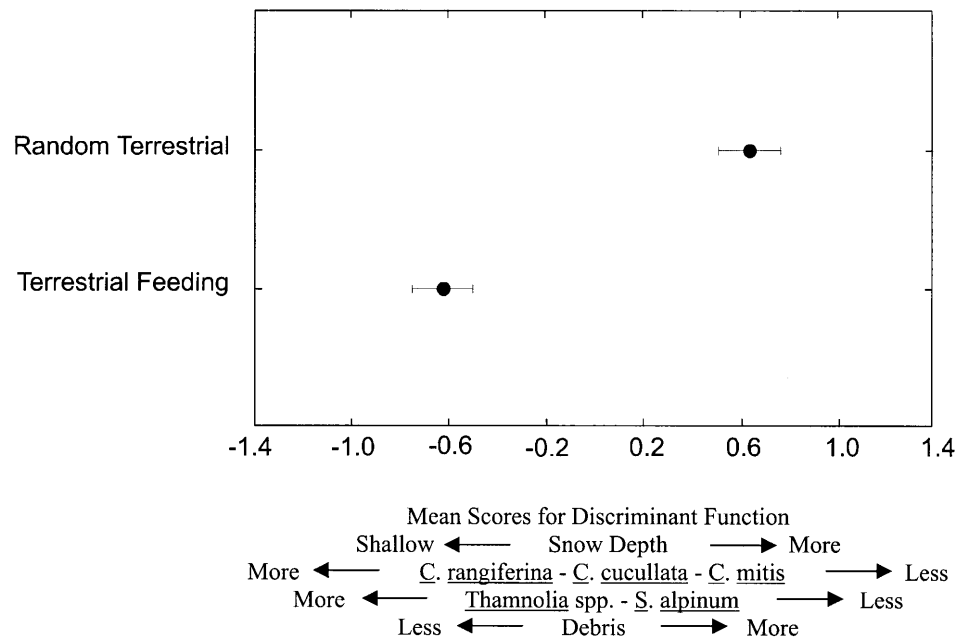
tionship with snow depth (*Cladina mitis*: *F*=16.71, *df*=1, 169, *P*<0.001; *r*^{2}=0.090; *f*^{2}=0.100; *Cladonia* spp.: *F*=15.49, *df*=1, 164, *P*<0.001, *r*^{2}=0.086; *f*^{2}=0.094).

At alpine sites, craters measured in the alpine were distinguished from random sites with a classification accuracy of 78.7% relative to a 50.1% classification accuracy based on chance alone (χ^2=59.18, *df*=12, *P*<0.001; *r*=0.608) (Fig. 2). Caribou fed at sites with more lichens (*Cladina rangiferina*, *C. mitis, Cetraria cucullata*, *Thamnolia* spp., *Stereocaulon alpinum*), less deep snow, and less debris than random sites (Table 2). With the exception of small differences in the χ^2 statistic, the interaction models of biomass×time (χ^2=57.00, *df*=12, *P*<0.001; *r*=0.600) and biomass×location (χ^2=54.66, *df*=12, *P*<0.001; *r*=0.590) in the alpine did not differ from the noninteraction model. Biomass of *Cladina rangiferina* measured at feeding sites was linearly related to snow depth (*F*=10.30, *df*=1, 21, *P*=0.004, *r*^{2}=0.329; *f*^{2}=0.490). Regression equations for the other important lichens (*Cetraria cucullata, Cladina mitis, Thamnolia* spp., and *S. alpinum*) were not significant (all *P*>0.05).

Patch selection

In the forest, there were approximately 4 times more craters ($\bar{x}$=8.5±0.94 SE) than arboreal feeding sites ($\bar{x}$=2.1± 0.39) per patch (*n*=85). The path model used to describe patch use (Fig. 3) included lichens, snow, and moss and was identified by the 2nd and 3rd discriminant functions (Table 1) of the noninteraction discriminant function analysis, as well as the estimated number of animals using the patch. Our model did not statistically differ from empirical data (χ^2=12.01, *df*=6, *P*=0.062), with the indices of fit also suggesting a good fit between hypothesized and empirical models (Steiger-Lind RMSEA index=0.109; McDonald noncentrality index=0.965; RMS standardized residual=0.049). Snow depth (*T*=−5.24, *P*<0.001), *Cladina mitis* (*T*=4.27, *P*<0.001), and *Cladonia* spp. (*T*=4.42, *P*<0.001) contributed to explaining the number of terrestrial feeding sites within the patch, while snow depth (*T*=5.28, *P*<0.001) and snow hardness (*T*=2.45, *P*=0.014) were significant predictors of the number of arboreal feeding sites in the patch (Fig. 3).
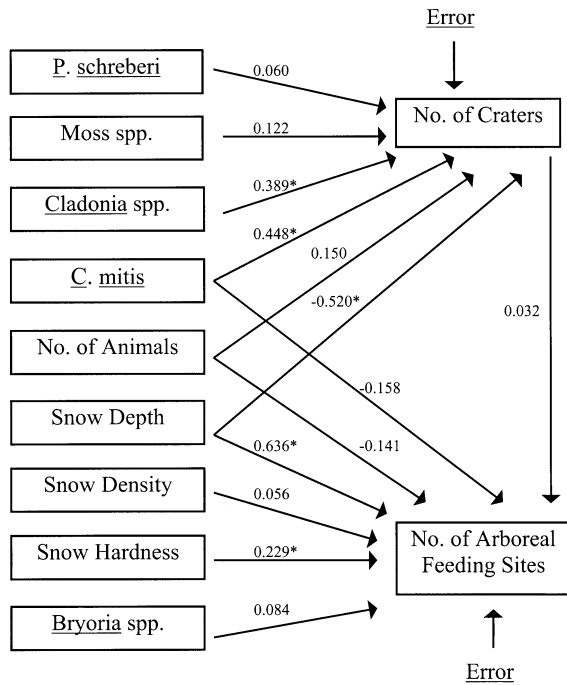
Fig. 3 Path diagram illustrating a hypothesized linear scalar relationship between the variables identified as important to the selection of feeding sites at forested locations and the selection of feeding patches by woodland caribou in north-central British Columbia (December 1996–April 1998). *Numerals* near each path indicate standardized path coefficients; *asterisks* indicate values significantly different from 0
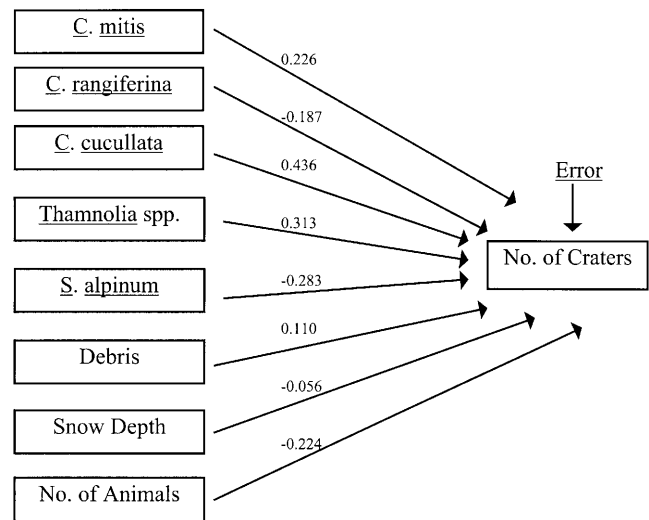

Fig. 4 Diagram illustrating a hypothesized linear scalar relationship between the variables identified as important to the selection of feeding sites at alpine locations and the selection of feeding patches by woodland caribou in north-central British Columbia (December 1996–April 1998). *Numerals* near each path indicate standardized regression coefficients; all variables were nonsignificant

Number of craters did not significantly contribute to the explanation of the number of arboreal feeding sites and the number of animals in a patch did not affect the number of arboreal or terrestrial feeding sites.

In the alpine, number of craters averaged 31.8±5.2 per patch (*n*=23). Five species of lichen, debris, and snow depth, each identified as important in influencing foraging decisions at the feeding site, and the number of animals sighted at each patch were included in our model predicting the use of alpine patches by caribou (Fig. 4). The regression model was not significant (*F*=1.178, *df*=8, 13, *P*<0.381, r^2=0.420; f^2=0.725).

Landscape selection

Lichen biomass was summed for *Cladina rangiferina*, *C. mitis*, *S. alpinum*, *Peltigera aphthosa*, *Cladonia* spp., *C. uncialis*, *Cetraria ericetorum*, and *Cladonia ecmocyna* at forested terrestrial feeding sites and for *Cladina mitis*, *C. rangiferina*, *Thamnolia* spp., *Cetraria cucullata*, and *S. alpinum* at alpine sites. Caribou foraging at forested sites ($\bar{x}$=345.9±11.65 g m^{-2}) had access to twice as much biomass of important lichen species relative to animals foraging at alpine sites ($\bar{x}$=173.3± 13.88 g m^{-2}, *t*=8.80, *df*=127.26, *P*<0.001). Lichen biomass also was less variable at forested sites (CV=0.48) relative to alpine feeding sites (CV=0.67). Snow depth

was deeper and less variable at feeding sites in the forest ($\bar{x}$=55.1 cm, CV=0.32) when compared with those sampled in the alpine ($\bar{x}$=15.5 cm, CV=0.50, *t*=18.34, *df*=83.11, *P*<0.001). Snow hardness was greater and more variable in the alpine ($\bar{x}$=3.3 g cm^{-2}, CV=1.71) than in the forest ($\bar{x}$=0.7 g cm^{-2}, CV=0.52, *t*=12.62, *df*=96.23, *P*<0.001).

Relative to patches on the landscape, biomass of the previously listed lichens (Table 1), with the addition of *Bryoria* spp. for forested patches, was summed across foraged and random sites for each transect. On average, lichen biomass was greater and less variable at forested patches ($\bar{x}$=270.0 g m^{-2}, CV=0.48) when compared with alpine patches ($\bar{x}$=34.7 g m^{-2}, CV=0.85, *t*=15.77, *df*=68.25, *P*<0.001). Snow depth also differed significantly between the two landscapes, being deeper and less variable at forested patches ($\bar{x}$=57.8 cm, CV=0.31; $\bar{x}$=19.6 cm, CV=0.36; *t*=14.77, *df*=46.04, *P*<0.001). Snow at forest patches was less hard and less variable ($\bar{x}$=0.6 g cm^{-2}, CV=0.44) than the snow measured at alpine patches ($\bar{x}$=3.4 g cm^{-2}, CV=0.90, *t*=8.99, *df*=25.97, *P*<0.001).

Discussion

Effects of spatial scale on foraging decisions

Ecologists have advocated a multi-scale hierarchical approach for studies of resource selection and animal behavior to incorporate the breadth of biotic and abiotic stimuli that affect the choices and decisions of individuals and ultimately populations (Delcourt et al. 1983; Senft et al. 1987; O'Neill et al. 1989; Kotliar and Wiens 1990). We addressed two related questions in our study:

(1) do woodland caribou exhibit trade-off decisions between forage abundance and accessibility, and (2) does spatial scale affect the foraging behavior of caribou? Our analyses of the foraging decisions by woodland caribou at four spatial scales confirm the importance of using a multi-scale approach and the potential for interactions between both time and space affecting trade-off decisions.

At the finest scale we measured, caribou selected specific species of terrestrial lichens (*Cladonia* spp., *Cladina mitis*) (Table 1). These herbivores chose sites to feed where selected lichens were the most abundant and snow depths least deep. When snow conditions limited accessibility, animals in the forest began feeding on the more accessible, yet less abundant arboreal lichens (*Bryoria* spp.) (Table 1, Fig. 1). Thereafter, the choice of feeding site was the consequence of abundance of arboreal lichens, snow depth, density, and hardness, and was likely independent of the smaller-scale use of terrestrial lichen species which because of snow were less accessible. *C. mitis* was, however, still present at transects where animals had chosen to feed on arboreal lichens. We interpret this result as an interaction between the forage species and the feeding site, where selection of *C. mitis* occurred concurrently with *Bryoria* spp. when snow depths neared the limit for cratering by caribou. Our data also revealed that when choosing arboreal lichens, caribou selected those trees with the greatest abundance of *Bryoria* spp. (Table 1). We believe, therefore, that caribou in forested areas decide between terrestrial feeding sites, which are favored, and the alternate arboreal feeding sites based on two interacting effects: accessibility as limited by snow depth, density, and hardness, and availability of arboreal lichens on individual trees. We originally predicted that the amount of favored terrestrial lichens might act as a third interacting variable in the choice of feeding sites. Our regression analyses, however, indicated that the abundance of terrestrial lichens had little affect on the amount of snow that caribou would excavate to access lichens. With the exception of *C. rangiferina*, the same held for alpine sites.

At one scale higher, lichen species and variables describing snow characteristics, which were important to caribou choosing discrete feeding sites, did not always explain selection of a patch. Of the eight variables statistically significant at the scale of the feeding site, only two lichen species (*C. mitis*, *Cladonia* spp.) and snow depth were important in explaining number of terrestrial feeding sites in a patch, and only snow depth and hardness explained the number of arboreal feeding sites in a patch (Fig. 3). The influence of snow on patch use supports the assertions of other researchers that caribou select areas of relatively shallow snow (Pruitt 1959; LaPerriere and Lent 1977; Skogland 1978; Darby and Pruitt 1984). Where snow conditions restricted access to terrestrial lichens, caribou in our study fed on arboreal lichens (*Bryoria* spp.), regardless of their total availability across the patch (Fig. 3). This outcome is contrary to behavior demonstrated at the scale of the feeding site

(Table 1), and indicates that an interaction likely occurred between the feeding site and patch. Where caribou do not select patches based on the abundance of arboreal lichens, they may instead select those trees with the greatest biomass of *Bryoria* spp. within currently occupied patches. This likely occurs following some limit in the accessibility of terrestrial lichens. This result demonstrates that trade-off decisions occur at multiple spatial scales, and that foraging decisions at the scale of the patch may be dictated by a simpler suite of variables than present at the scale of the feeding site.

At the scale of the patch, the alpine model was not significant. Neither biomass of lichens nor snow influenced patch use in the alpine environment. This result is counterintuitive when considering the relatively high variability in lichen biomass and snow depths among alpine patches. Other factors, aside from forage biomass and accessibility, probably drive patch selection in the alpine environment. Furthermore, our comparison of the importance of variables at the feeding site and patch demonstrated that the foraging behavior of caribou varies across scales and that conclusions cannot necessarily be extrapolated from one scale to another (Gardner et al. 1989; Turner et al. 1989; Turner 1990).

At the largest spatial scale we measured, woodland caribou chose between two landscapes that differed in biomass and accessibility of lichens. Relative to the forest, animals in the alpine landscape foraged across an environment with shallower, more variable snow cover and less abundant, more variably distributed lichens. Animals in the forest likely encountered higher energetic costs of obtaining food (Fancy and White 1985) with the nutritional advantage of greater forage biomass. We were not, however, able to estimate the energetic costs of cratering in different snow conditions (e.g., Fancy 1986) or the intake rates of foraging animals (e.g., Parker et al. 1999).

There are likely factors, other than those related to foraging decisions, that affect the choice of a landscape at which to spend a large portion of winter (Senft et al. 1987). For example, caribou may reduce the risk of predation from wolves by distancing themselves from other prey species such as moose or seeking refuge in terrain that is relatively inaccessible to predators (Bergerud et al. 1984; Bergerud 1985; Cumming and Beange 1987; Seip 1992). Inhabiting alpine locations would segregate caribou from moose and potentially decrease the probability of encountering wolves (Seip 1992; Johnson 2000; but see Dale et al. 1994). Responding to predation risk at the scale of the landscape also may affect behavior at smaller scales (Stephens and Krebs 1986; Lima and Dill 1990). Caribou in the alpine may be more risk-averse, weighing lower forage accessibility and abundance against factors such as escape terrain and visibility that would reduce the risk of being surprised or captured by a predator (Ferguson et al. 1988; Bowyer et al. 1999). This is one possible explanation for the inferior fit of the hypothesized model of patch use by caribou in the alpine environment relative to the forest.

Trade-off decisions at multiple scales: implications for optimal foraging

Forage abundance and accessibility at the level of the individual animal are necessary to maintain productive populations of caribou. Skogland (1985, 1986) documented the density-dependent effects of food limitation during winter on recruitment rate and adult female body size of wild reindeer in a predator-free environment; pregnancy rates increase with increasing fat and protein reserves in female Peary caribou (*R. t. pearyi*) and barren-ground caribou (*R. t. granti*, *R. t. groenlandicus*) (Thomas 1982; Allaye-Chan 1991; Ouellet et al. 1997). Furthermore, White (1983) reported that selective feeding strategies facilitating even small gains in quality or intake can have significant "multiplier effects" on the weight gain of reindeer. Although the individual roles of energy, protein, and digestibility are often difficult to separate, forage quality has been shown to influence diet selection in both wild and captive ungulates (Kyriazakis and Oldham 1993; Wang and Provenza 1996; Berteaux et al. 1998). Therefore, if caribou adopt foraging strategies that maximize nutritional gain, those strategies should be observable at the scale of the individual forage species.

Caribou and other sub-species of *Rangifer* have evolved physiological mechanisms to subsist on a diet low in protein (Klein and Schønheyder 1970; Westerling 1970). Most fruticose lichens, however, contain 2–5% crude protein, which is less than the 6–8% recommended by Van Soest (1982) as necessary for a positive protein balance (Scotter 1965; Russell et al. 1993). Considering the relatively high digestible energy content of lichens and the suspected negative over-winter protein budget of caribou, the optimal diet likely would be one highest in digestible protein (DP), although energy also has been reported to be limiting during winter (Cameron 1972; Pulliainen 1971; Huot 1989; Allaye-Chan 1991).

From previously published values used to calculate DP and digestible energy (Hanley et al. 1992), lichen species highly selected by caribou in this study likely were not the most "nutritious" of those available. For example, *Bryoria* spp. (~0.9% DP; 14.7 kJ g^{-1}), *S. alpinum* (~2.3% DP; 8.8 kJ g^{-1}), and *P. aphthosa* (~10.7% DP; 8.4 kJ g^{-1}) are higher in digestible protein and energy than *Cladina mitis* (~–1.6% DP; 8.2 kJ g^{-1}) and higher in digestible protein than *Cladonia* spp. (~–0.5% DP; 7.6 kJ g^{-1}) (C.J. Johnson, unpublished work; Solberg 1967; Bergerud 1972; Scotter 1965, 1972; Thing 1984; Thomas et al. 1984; Dannell et al. 1994). Assuming that caribou had the choice of all lichen species at each foraging location, this result is contrary to an optimal diet model predicting that caribou should select lichen species that rank highest in digestible protein and energy (Stephens and Krebs 1986).

One possible explanation for why caribou did not select the most nutritious species is that caribou do not respond to dietary feedback and the associated affects on fitness at such a fine scale (Galef 1991). Alternatively, caribou may be selecting forage species for reasons other than maximizing nutritional gain per unit biomass. As caribou locate lichens through the snow using olfactory cues, selecting the most conspicuous lichens would reduce search time and increase foraging efficiency. Animals would maximize net gain by increasing intake of those species that are the easiest to detect. We have no knowledge of the detection thresholds of individual species, but perhaps those lichens that are selected have a stronger scent. As the snow deepens, however, terrestrial lichens may become more difficult to detect (Bergerud and Nolan 1970; Bergerud 1974) and a switch to an alternative, more conspicuous and consequently more dense forage, arboreal lichens, would become the optimal strategy (Dukas and Ellner 1993).

A third factor that may influence the selection of lichen species by caribou is the availability of lichen. Even if caribou are capable of selecting forage based on nutrient content, it may be more advantageous to increase intake and reduce search time by selecting the most abundant species, especially if discrimination errors are large and nutritional differences are small (Yoccoz et al. 1993). Unlike for some types of plants, there is a positive relationship between availability of lichens and intake by reindeer (Trudell and White 1981). With some exceptions, our ranking of importance of lichens to site selection in the forest corresponded with abundance of the individual species across feeding and random terrestrial sites (Tables 1, 2). Our interaction models, which were designed to test the prediction that foraging caribou would adjust their behavior to match temporal and spatial changes in the abundance and accessibility of lichens, further support this explanation. As the winter advanced, *Bryoria* spp. and *Cladonia ecmocyna* (~0.03% DP; 7.6 kJ g^{-1}) became more important and snow hardness less important in discriminating terrestrial and arboreal feeding sites, respectively. Because both of those lichen species are of lower nutritional value than other lichens, this shift likely resulted from caribou selecting the most accessible or abundant species over time. As snow depths increased, which correlated with time during winter, animals cratered as well as selected trees with greater amounts of arboreal lichens (*Bryoria* spp.). *C. ecmocyna* was more abundant at locations frequented by caribou during the later portions of the winter, suggesting an interaction between both time and space. Snow hardness was statistically displaced by other lichen variables that, when combined with time, explained a higher proportion of the variation between feeding and random arboreal sites. In the alpine environment, the importance of individual lichen species and snow conditions did not vary across time or space.

At the scale of the patch, caribou foraging intensity (as measured by the number of feeding sites) was explained by abundance of favored lichens and snow depth. If foraging intensity is considered synonymous with time in a patch, our results agree with the predictions of several optimal patch use models (Charnov 1976; Parker and Stuart 1976; Iwasa et al. 1981). At the

600

scale of the landscape, caribou feeding patterns showed a trade-off between abundance, accessibility, and variability of lichen biomass and snow conditions. Choosing between forest or alpine landscapes, however, may offer no distinct nutritional advantage with ecological or evolutionary consequences. Rather, the two landscapes exemplify two potential solutions for a species that shows extreme behavioral and physiological plasticity across a wide variety of mid- to high-latitude habitats (Williams and Heard 1986). Caribou are well adapted for dealing with extreme snow conditions (Telfer and Kelsall 1984) and have evolved an energetically efficient technique for travelling over and obtaining terrestrial lichens from beneath the snow (Fancy and White 1985). The depth for cratering by caribou and reindeer ranges from 50 to 80 cm (Formozov 1946; Pruitt 1959; Stardom 1975; LaPerriere and Lent 1977; Helle and Saastamoinen 1979; Darby and Pruitt 1984), although craters as deep as 123 cm have been reported (Brown and Theberge 1990); we observed craters as deep as 97 cm in the forest. As to the selection and availability of lichens, field studies commonly report different results (DesMeules and Heyland 1969). This is not to say that caribou are unselective within a chosen landscape, or that they do not choose between landscapes, just that they can forage effectively across a wide range of environmental conditions.

Conclusion

At the scale of the forage species and feeding site, caribou chose terrestrial sites with the shallowest snow (prediction 2) and trees with the greatest amount of arboreal lichen (prediction 4), but did not select specific lichens based on nutritional value (prediction 1) or compensate for deep snow conditions by selecting sites with the greatest biomass of favored lichens (prediction 3). At the scale of the patch, the biomass of terrestrial lichens (prediction 5) and snow (prediction 6) affected the frequency of cratering in the forest, but not the alpine, whereas foraging on arboreal lichens was only influenced by snow depth and hardness rather than biomass of lichens (prediction 7). At the scale of the landscape, a trade-off may have occurred where reduced accessibility in the forest relative to the alpine environment could be balanced by increased biomass of terrestrial and arboreal lichens (prediction 8). Taken together, these observations reveal that there is likely no single "optimal strategy" that a foraging animal should adopt, but rather a variety of strategies to meet changing needs and circumstances.

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