Ecological Applications, 12(6), 2002, pp. 1840–1860

A MULTISCALE BEHAVIORAL APPROACH TO UNDERSTANDING THE MOVEMENTS OF WOODLAND CARIBOU

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Abstract. We assessed the response of woodland caribou (*Rangifer tarandus caribou*) to land-cover type, predation risk, energetic costs of movement, and patch configuration at multiple spatial scales. We applied a nonlinear model to frequent locations collected with Global Positioning System (GPS) collars to identify discontinuities in the scales of movement by caribou found in forested and alpine (above tree line) habitats. We differentiated intra- from interpatch movements and identified collections of patches (multiple-patch scale) where caribou concentrated intrapatch movements. On average, intra- and interpatch movements were 450.7 and 1268.8 m, respectively, and multiple-patch movements occurred over an area of 182 ha. Intrapatch movements were highly correlated, indicative of a strong relationship between behavior and place. Caribou in the forest selected patches of Pine terrace, whereas caribou in the alpine selected patches of Alpine-little vegetative cover. Predation risk was not a factor influencing movements of caribou at the intrapatch scale. Selection of cover types was more variable during interpatch movements. At that scale, caribou selected patches of Pine terrace, Lakes/rivers, Alpine-little vegetative cover, and Alpine-grass. The routes selected by caribou had lower energetic costs relative to surrounding terrain, and during some winters, caribou were subjected to higher levels of predation risk during those movements. At the multiple-patch scale, selection was more specific and encompassed patches of Alpine-little vegetative cover, Alpine-grass, and Pine terrace. Predation risk was relatively unimportant at the multi-patch scale, but animals that moved from forested to alpine habitats reduced their relative risk of predation. Patch configuration was a poor predictor of those areas where caribou concentrated intrapatch movements. There was some evidence of caribou selecting patches of Pine terrace within a matrix of Wetlands and Pine–black spruce/black spruce patches. Caribou in the alpine avoided patches of Alpine-little vegetative cover adjacent to forest types. Our results indicate that forest managers should maintain widely distributed patches of Pine terrace and implement silvicultural regimes that do not stimulate predator populations across areas used for interpatch movements.

Key words: caribou; GPS; habitat patch; heterogeneity; movement patterns; multiscale analysis; patch configuration; predation risk; Rangifer tarandus caribou; *selection.*

INTRODUCTION

Woodland caribou (*Rangifer tarandus caribou*) are a high-priority management species across North America (Cumming 1992). Historical trends of declining populations or extirpated herds have necessitated management schemes that not only conserve and stabilize existing populations, but also possibly enhance others (Edmonds 1988). In British Columbia, Canada, an increased demand for merchantable timber has led to a heightened awareness of the potential conflict between human encroachment and the requirements of caribou. To meet the needs of both industry and caribou, resource managers, planners, and biologists must understand the processes governing movements and distribution of those animals relative to several potentially limiting factors including forage, predators, the energetic costs of movement (i.e., movement routes), and snow (Stevenson and Hatler 1985).

Previous studies of woodland caribou have taken coarse-grained approaches to explaining caribou–habitat relationships. Caribou locations at one or several arbitrarily defined scales have been related to generalized maps of vegetation and topography (Bradshaw et al. 1995, Steventon 1996, Terry and Wood 1999, Poole et al. 2000), with little emphasis on how limiting factors vary at different scales. Because processes were not investigated and can only be assumed, it is difficult to generalize the results of those studies to other time periods or geographic areas where processes may be consistent, but site-specific conditions (e.g., snow depth) differ (Levin 1992).

As with the previously mentioned works, the habitat

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requirements of large mammals are often inferred through resource selection studies that measure the use of resources relative to their availability across some defined area (e.g., Alldredge and Ratti 1992). Although widely used by wildlife ecologists, use vs. availability approaches suffer from several shortcomings (Aebischer et al. 1993). One conceptual limitation is defining used and available resources appropriately. Analyses are frequently designed to recognize habitat selection as hierarchical and patterns of selection as differing between scales or levels within the hierarchy (Johnson 1980). The definitions of those scales, however, are often arbitrary or based on criteria with little direct relationship to the ecological responses of the study species (Porter and Church 1987). Studies should be designed to measure effects at scales specific to the response of species to the environment (Morris 1987, Wiens 1989). The importance of environmental features may, however, remain consistent across appropriately chosen scales of measurement (see Schaefer and Messier 1995).

Many use vs. availability analyses implicitly assume that habitat is the vegetation or cover types occurring across the study area. Habitat is ''the resources and conditions present in an area that produce occupancy—including reproduction and survival—by a given organism'' (Hall et al. 1997:175). Processes that govern the movements, distribution, and habitat use of a species, however, also include factors such as predation risk, snow, parasites, and population density. By including a larger suite of explanatory variables than vegetative associations and assessing their importance across a range of scales, our study encompassed what Lima and Zollner (1996) termed ''a behavioral ecology of ecological landscapes.''

The objectives of this study were (1) to use frequent relocation data to identify three spatiotemporal scales of movement by caribou that were not arbitrarily defined (i.e., not defined a priori by the researchers, but rather by the animals; see Johnson et al. 2002), and (2) to develop parsimonious statistical models allowing us to evaluate selection of environmental features at each of those scales. The three scales of movement and selection are broadly categorized as (1) small-scale intrapatch movements that probably characterize the foraging behaviors of caribou when moving between feeding sites, (2) meso-scale interpatch movements that probably represent movements by caribou between patches of forage where collections of intrapatch movements occur, and (3) multipatch movements that represent the aggregate collection of intrapatch movements that were not distinguishable by an intervening interpatch movement. Here we refer to scale in the ecological, not cartographic, context. Small scales are representative of relatively small areas and temporal periods and large scales represent relatively large geographic areas and longer intervals. We considered a patch to be all levels of heterogeneity larger than the feeding site, but not extending beyond the most dominant and observable ecotone.

We assumed that environmental features would affect caribou movements differently according to scale. Inclusion of environmental features (i.e., independent variables) within our predictive models was guided by field observations (Johnson et al. 2001) and published research of caribou movements and habitat selection. Because our goal was to develop parsimonious models, we did not include all explanatory variables at each of the three scales, but chose models for each scale based on our knowledge of caribou ecology (Burnham and Anderson 1998). We had insufficient knowledge to explicitly predict and test selection of specific cover types, so an exploratory approach was adopted and all cover type classes were initially included for analyses at each scale.

During small-scale movements, which we assumed were representative of foraging bouts, we predicted that caribou would demonstrate correlated foraging movements, select specific cover types depending on occupancy of forested or alpine landscapes, and choose locations to feed that offered a relatively low risk of predation. At one scale larger in the behavioral hierarchy, we predicted that caribou would select specific cover types, areas of low predation risk, and terrain that permitted fewer energetic costs when moving between patches that afforded foraging opportunities. At the third scale, we assessed selection of multiple patches relative to composition and configuration of cover types and predation risk. Relative to the configuration of cover types, we predicted that selection of multiple patches by caribou would be most strongly influenced by the juxtaposition and contagion of those patches. At each of the three scales, we used movements of the animals to delineate resource availability. We present results from the smallest to largest scales of movement. Results are discussed in the context of multiscale analyses, the importance of each independent variable for understanding the movements of caribou, and the conservation implications of our findings.

Because the variety and availability of forage are most limited during the winter and caribou typically spend the summer months at high elevations distant from areas of forest harvesting (Seip 1998), we focused our investigations on the activities of female caribou during winter. Specifics regarding methodology and application of movement rates to identify scales of selection for a small subset of caribou, rather than a biological assessment of movement strategies across animals as presented here, were reported in Johnson et al. (2002).

STUDY AREA AND METHODS

We conducted analyses using movement data from female woodland caribou referred to as the Wolverine herd. Those animals are located in north-central British Columbia, Canada, and are considered part of the

Northern Woodland Caribou ecotype (Heard and Vagt 1998). As with most woodland caribou populations found throughout North America, animals of the Wolverine herd occur in small groups and space themselves widely throughout their range: 0.09 caribou/km^2, range 0.06–0.12 caribou/km^2 (Bergerud 1992, Terry and Wood 1999).

Caribou of the Wolverine herd range over an area of ~5100 km^2. Approximately 7.2% of the caribou's range has been recently disturbed (<20 yr) by forest harvesting. Terrain varies across that area, from valley bottoms at ~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 by shrubs, herbs, bryophytes, and lichens, with occasional trees in krummholz form (Meidinger and Pojar 1991).

Caribou and wolf relocations

We captured and collared 16 individual female caribou from March 1996 through March 1999. At the scales of analysis presented here, the 16 collared caribou probably represented the selection and movement strategies of 40% of the population. This number is contingent on a group size of nine individuals during the winter (Wood 1996; C. J. Johnson, *unpublished data*), the movement of the collared animals being representative of the group, and a total of 361 animals (95% confidence interval = 225–497 animals; Terry and Wood 1999) in the Wolverine herd. Caribou locations were collected using two versions of GPS 1000 collars (small and large battery packs; LOTEK Engineering, Newmarket, Ontario, Canada). Locations were differentially corrected using N3WIN (V. 2.412, LOTEK Engineering). Collars equipped with small battery packs were scheduled to record one location every 3 h for a total of eight locations per day, whereas collars with large battery packs were scheduled to record one location every 4 h.

Depending on the number of unique signals acquired by the receiver during a location attempt and the configuration of the transmitting satellites, differentially corrected GPS locations obtained from more than three satellites can be as accurate as 3–8 m 95% of the time (Johnson 2000). We omitted all locations with a horizontal dilution of precision (HDOP, an index of satellite configuration) of >25 and locations generated with three satellites (two-dimensional locations) that were not differentially corrected. We used very high frequency (VHF, Lotek Engineering, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA), Argos satellite (Telonics, Mesa, Arizona, USA), and GPS collars (Televilt International AB, Lindesberg, Sweden) to monitor the movements and feeding habits of 19 collared wolves (*Canis lupus*) from eight packs throughout the duration of the study.

Identifying scales of movement

We used a nonlinear curve-fitting model to identify small-scale intra- and large-scale interpatch movements of individual caribou (see Sibly et al. 1990; Johnson et al. 2002). Individual movement vectors between successive caribou relocations were transformed to rates and then plotted as $\log_e$ frequency distributions for each caribou by winter combination. A least squares procedure was then used to fit the nonlinear model (i.e., curve) to the distribution of movement rates (STATISTICA Nonlinear Estimation; Statsoft 1997). The nonlinear procedure approximates a broken-stick model, but is more objective and precise (Sibly et al. 1990). Intrapatch movements were assumed to occur at a greater frequency and with lower movement rates relative to interpatch movements. The model takes the form

$$y = \log_e(N_s\lambda_s e^{-\lambda_s r} + N_l\lambda_l e^{-\lambda_l r}) \qquad (1)$$

where y is the estimated number of caribou movements that occur during each discrete interval of movement rates; N is the number of small- and large-scale movements that occur at each rate interval; subscripts s and l indicate small- and large-scale movements, respectively; λ represents the probability that small- or large-scale movement occurs in the next interval; and r is the movement rate.

Following model fit, we used the estimated parameters (N, λ) to identify a bout criterion interval that would allow us to classify individual movements as large or small scale. Sibly et al. (1990) used data that were distributed according to time between events and thus referred to their bout criterion as t_c. We applied the model to movement rates, however, and refer to the breakpoint value as the scale criterion or r_c. The r_c value represents the inflection point of the $\log_e$ frequency distribution of caribou movement rates and is calculated as

$$r_c = \frac{1}{\lambda_s - \lambda_l}\log_e\frac{N_s\lambda_s}{N_l\lambda_l}. \qquad (2)$$

Movement rates of caribou $<r_c$ were considered to be small-scale movements; rates $>r_c$ were large-scale movements. We distinguished an additional scale of selection (areas where caribou concentrate small-scale movements) as the area of all small-scale movements that occur following and before the next large-scale interpatch movement (Fig. 1).

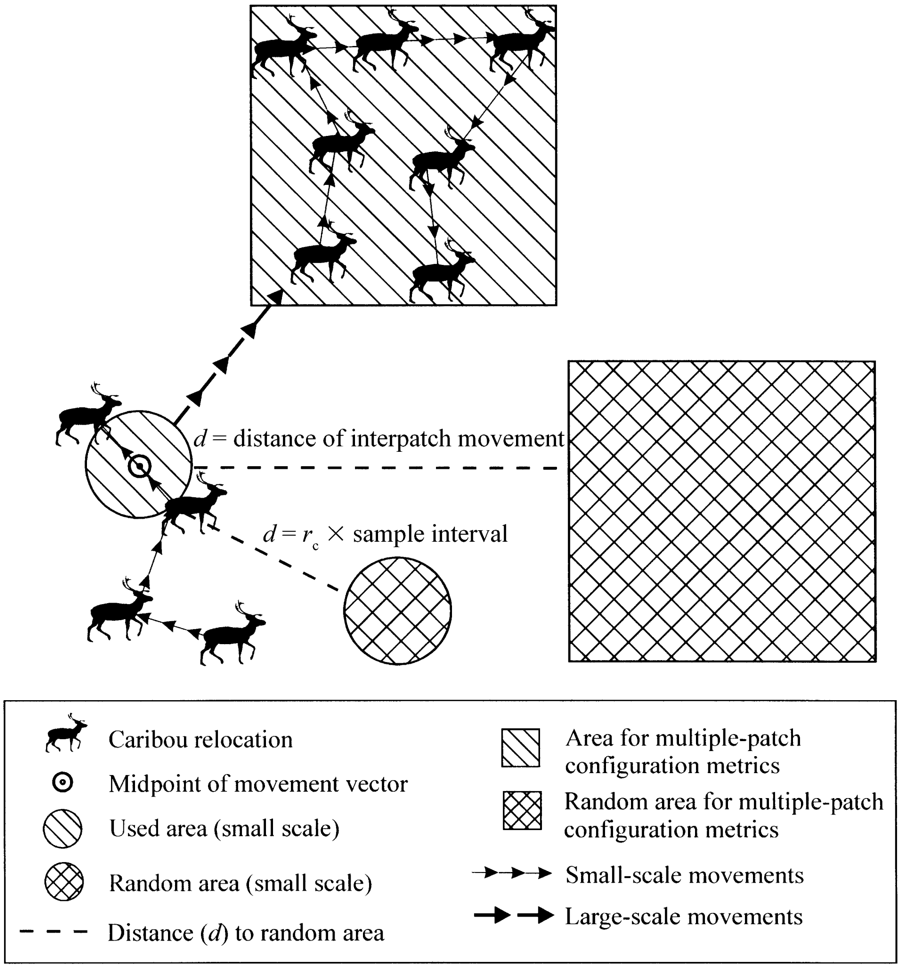

FIG. 1. Schematic representation of the sampling design used to define small-scale intrapatch movements, large-scale interpatch movements, and areas used for multiple-patch configuration metrics, using GPS relocations collected from caribou of the Wolverine herd in north-central British Columbia, Canada (March 1996–April 1999).

Habitat attributes

We developed a series of geographic information system (GIS) routines to quantify environmental features that may influence the movements of caribou at each of the three scales. GIS analyses were conducted with IDRISI (V. 4.1, V. 2, V. 32; Clark Labs 1999).

Cover type.—We used LANDSAT V Thematic Mapper satellite imagery and a Terrain Resource Information Management (TRIM; 25 × 25 m pixel resolution, British Columbia Ministry of Crown Lands 1990) digital elevation model (DEM) to classify the geographic area used by all collared caribou. We identified 13 cover types of unique vegetative and topographical association (Table 1; Johnson 2000).

Distance to predation risk.—We monitored the movements and feeding habits of 19 collared wolves from eight packs throughout the duration of the study. Selection of habitat by wolves was inferred through a comparison of relocations and kill sites to random locations drawn from the area encompassed by the 95% minimum convex polygon showing the range of wolf relocations (Kenward and Hodder 1996). Using the GIS, we centered an error buffer with a radius of 125 m on all wolf relocations and extracted the proportion of each cover type (Leptich et al. 1994). Because wolves select certain habitats for hunting vs. other behaviors (Kunkel and Pletscher 2000), we arbitrarily weighted kill sites (where predation was confirmed) to have twice the influence of nonkill relocations (where wolf presence was a potential risk to caribou).

We used logistic regression to determine which cover types were most associated with wolves and, therefore, associated with high risk of predation (Mladenoff et al. 1999). Predation risk is defined as the probability of encountering or being captured by a predator during some time period (Lima and Dill 1990). The significant positive coefficients of the logistic regression were used to develop a spatial surface describing the weight-

TABLE 1. Description of cover types found across the range of the Wolverine caribou herd in north-central British Columbia, Canada.

Cover type	Percentage of area	Description
Aspen/cottonwood	5.8	Primarily (97%) stands of *Populus tremuloides* that may be associated with *Pinus contorta*; includes floodplains dominated by *Populus balsamifera, Salix* spp., and *Alnus incana*.
Pine terrace	3.0	Level glaciofluvial terraces and other well-drained soils consisting of *P. contorta* and an understory of *Cladina* and *Cladonia* spp.
Pine	7.5	Dominated by *P. contorta* (80%), but may occur with some component of *Picea mariana* or *Picea engelmannii* × *P. glauca* in older stands; prevalence of feather mosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*) and, to a lesser extent, *Cladina* or *Cladonia* spp.
Spruce	7.0	Dominated by *P. engelmannii* × *P. glauca* (80%), but may be a minor component of *P. mariana, P. contorta, P. tremuloides*, or *P. balsamifera*; typically at lower elevations (<1100 m) on wetter sites.
Pine–spruce	4.5	Level to steep slopes at lower elevations consisting of *P. engelmannii* × *P. glauca* and *P. contorta*; poorly to moderately developed shrub and herb layers and a continuous cover of feather mosses.
Pine–black spruce/black spruce	9.6	Primarily (78%) older *P. contorta*–*P. mariana* stands found on level to moderate slopes; some *Cladina* and *Cladonia* spp., but characteristically feather mosses; also areas consisting of open, stunted forests of *P. mariana* with abundant arboreal lichens.
Wetland	5.3	Shrub/sedge- and forb-dominated wetlands on depression landscapes with high water tables.
Lakes/rivers	7.2	Permanent and ephemeral water bodies.
Mid-elevation coniferous	36.1	Mid-elevation stands (1100–1600 m) composed of *Abies lasiocarpa, P. engelmannii*, and *P. contorta* on moderate to steep slopes.
Krummholz	6.8	Shrub cover of *A. lasiocarpa* on gentle to moderate slopes at elevations of 1300–1600 m; associated with abundant arboreal lichens.
Alpine-shrub	2.1	Moderate to steep slopes with extensive cover of *Betula glandulosa* or *Salix reticulata*; *Altai fescue, Carex, Stereocaulon,* and *Cetraria* spp. found in openings.
Alpine-grass	0.3	Windswept slopes and ridges dominated by *A. fescue,* associated with *Stereocaulon, Cetraria,* and *Cladina* spp.
Alpine-little vegetative cover	4.8	Flat to steep rocky terrain with sparse vegetation restricted to pockets of soil among rock outcrops; lichen-dominated cover of *Umbilicaria, Cetraria, Cladina,* and *Stereocaulon* spp.

ed distance of every cell to high-risk cover. This operation involved three steps: (1) for each cover type with a positive coefficient, we generated a GIS surface where every 25 × 25 m cell in the study area was assigned a risk value equal to the shortest distance to that cover type; (2) each risk value was then multiplied (weighted) by the inverse of the coefficient produced from the logistic regression; and (3) the risk values of all cells were averaged to produce one surface representing the overall proximity to risk for each cell within the study area. The greater these values, the greater the distance to high-risk cover types and the lower the risk of predation for caribou.

Costs of movement.—We used equations developed by Fancy and White (1987) to model the energy expended by a 100-kg female caribou moving across variable terrain. We used a DEM generated from TRIM data to estimate whether an animal was moving up or down slope, the mean slope of the movement path, and the change in elevation between caribou relocations. The energy costs (in kilojoules per kilogram$^{0.75}$) of walking on a horizontal snow-covered surface were calculated as the distance traveled multiplied by the cost per kilometer (1.696 $\mathrm{kJ \cdot kg^{-1} \cdot km^{-1}}$) corrected for sinking depths in snow of 12–47 cm (($0.02416 \times e^{0.0635}$) + 1) (Fancy 1986). The net energy costs of moving uphill were calculated as the mean cost of lifting 1 kg of body mass (1.957 $\mathrm{kJ \cdot kg^{-1} \cdot m^{-1}}$), adjusted for slope of terrain, multiplied by the total vertical distance ascended. Energy recovered during downhill movements was calculated as the efficiency of recovery (0.412 $\mathrm{kJ \cdot kg^{-1} \cdot m^{-1}}$) corrected for slope, multiplied by the potential energy stored while lifting 1 kg of body mass 1 m (9.79 kJ) and total vertical distance (Fancy 1986).

Spatial autocorrelation.—When animal relocations at one point in time and space are dependent or partially the product of previous relocations, the statistical assumption of independence is violated. Lack of independence can distort measures of variance and invalidate inferential statistics. From an ecological perspective, the degree of correlation can be used to measure the strength of selection for specific environmental features. For example, a caribou spending a relatively long period in one area leads to an aggregation of relocations and indicates that the animal is attracted to a specific feature of the environment. As distances among relocations increase, the strength of the relationship between behavior and place decreases. To model dependence of animal locations, we developed a distance-weighted estimate of the spatial correlation of relocations of individual caribou (Augustin et al. 1996). We assumed that autocorrelation decreased as distance between relocations and rate of movement increased. Creation of the autocorrelation surface was a three-step process: (1) we stratified the caribou relocation data by animal; (2) a surface was then created where the inverse distance from each cell to the nearest relocation was calculated; and (3) a weighted averaging filter of variable size was passed over the distance surface. Filter size ranged from 3 × 3 to 13 × 13 pixels, with larger filters applied to animals with faster median rates of movement (Augustin et al. 1996).

Patch configuration.—Because of the large number of landscape metrics available (see McGarigal and Marks 1995), we a priori selected two measures that may be related to caribou behavior. We used a contagion index to determine if caribou select areas dominated by large patches of a single type (Baskent and Jordan 1995). Large values are generated for collections of patches that predominantly consist of few cover classes; small values arise from collections of patches that consist of many different cover types in approximately equal proportions (for the formula, see Mladenoff and DeZonia 1999:13). We also calculated adjacency matrices to determine if caribou select arrangements of juxtaposed cover types. Values ranged from 0% to 100% and represented the proportion of cells of one cover type that were neighbored by a second cover type (see Mladenoff and DeZonia 1999:9 for formula). We used APACK (V. 2.11) to calculate landscape metrics (Mladenoff and DeZonia 1999).

Selection analyses

Caribou relocations were stratified by individual, year, and scale of selection according to the corresponding r_c. For intra- and interpatch movements, the midpoint of each vector between successive relocations was calculated and a circular buffer with a diameter equal to the distance between the two relocations was generated (Fig. 1). We assumed that the circular buffer represented the potential area over which a caribou may have ranged (i.e., used habitat) between relocations and accommodated bias associated with the failure of the GPS collars to acquire signals from at least three satellites at each attempt (Johnson 2000). The buffer was superimposed on each data layer (cover type, predation risk, spatial autocorrelation, cost of movement) and the mean value or, for cover type, the percentage of each cover type within that buffer, was extracted for analysis as used habitat. Multiple-patch composition consisted of the proportion of cover types or predation risk averaged across all successive intrapatch movements separated by large-scale interpatch movements (Fig. 1).

To identify selection for habitat variables at each scale, we compared used areas with corresponding random areas. The spatial extent of the random area was set to not exceed the maximum expected linear distance that a caribou could move relative to the paired used area. For intrapatch movements, this was calculated as the r_c multiplied by the relocation interval (e.g., 4 h; Fig. 1); for interpatch movements, the third quartile of interpatch rates was multiplied by the corresponding relocation interval. We considered the third quartile rate to be more conservative and representative than the maximum recorded rate because maximum rates could be related to larger scales than we examined (e.g., migration). The buffer size of each random location was equal in area and did not overlap the paired caribou relocation. For selection of multiple-patch areas, a location was randomly chosen from the circumference of a circle centered on the last recorded intrapatch movement and of a radius equal to the distance of the next interpatch movement. The random location was equal in size to the summed area of all previous intrapatch locations.

We pooled locations for animals by scale, year, and occupation of forested habitats, alpine habitats, or both. Exclusive occupation of one habitat was arbitrarily defined as a ratio of 5:1 locations below or above 1650 m (tree line). Where sample sizes permitted, we developed a logistic regression of selection for each component of the landscape (i.e., forest, alpine, forest–alpine) for each of the four winters (Type III Analysis; Manly et al. 1993). For each regression, selected and random locations served as the dichotomous dependent variable and, contingent on the movement scale analyzed, cover type, predation risk, energetic costs of movement, and land-cover configuration served as the independent variables. We tested the influence of correlated movements, cover types, and predation risk on intrapatch movements; cover types, predation risk, and the energetic costs of movement on interpatch movements; and cover types, predation risk, and land-cover configuration (patch contagion and adjacency) on the selection of areas consisting of multiple patches. Relative to configuration, we tested whether cover types selected at that scale occurred in a matrix of lesser used types, as identified by published reports and our on-site field investigations (Johnson et al. 2001).

We used Akaike's Information Criterion (AIC) to rank and identify the cover-type variables that were most reliable for making inferences about the movement processes (Burnham and Anderson 1998). This method is best suited for a small subset of a priori hypotheses, but the large number of cover types and inter-animal variability led us to use a best subsets approach. We ranked all cover-type regressions from lowest AIC score to highest. For those with a difference in scores of less than two from the lowest, we calculated Akaike weights (w), which serve as a normalized measure, and summed the w's for each cover type (Burnham and Anderson 1998). Cover types that occurred frequently or with low AIC scores would, therefore, have a large summed w value. Those cover types with a w greater than 0.15 were retained and used with the other independent variables for final regression comparisons.

We evaluated reliability of logistic regressions using log likelihood χ^2 tests, non-cross-validated classification accuracy, and Nagelkerke R^2 values (Menard 1995). We used a derivation of the Relative Pratt index to assess the importance and relative strength of independent variables (Thomas and Zumbo 1997, Thomas et al. 1998). Explained variation (R^2) of each logistic model was partitioned among the independent variables, using $d_f = \beta_j r_j / R^2$, where d_j represents the proportion of model R^2 attributed to variable j, β_j is the jth standardized regression coefficient calculated using a weighted least squares procedure, and r_j is the simple Pearson correlation between the response and the jth explanatory variable in the logistic regression model (Thomas and Zumbo 1997). Variables with a score of $d_j > 1/(2p)$ were considered important, where p represents the number of variables in the model (Thomas and Zumbo 1996). We used tolerance scores to reveal variables with excessive collinearity (threshold of <0.2; Menard 1995), and leverage statistics and Pearson standardized residuals to diagnose cases that fit the model poorly or had a large influence on model coefficients. Independent variables were log-ratio transformed to reduce the effects of collinearity and decrease the influence of large values (Aebischer et al. 1993). All statistical analyses were performed with STATISTICA (V. 5.5; Statsoft 1997). Unless otherwise noted, we considered tests to be statistically significant at an α of 0.05.

Snow depth

Throughout three of the four winters (excluding 1995–1996), we collected snow depths at 12 stations located across the range of the collared caribou; measurements, however, were inconsistently made because of travel logistics. Data were insufficient to model regional snow depths and to include as a variable within the logistic-regression analyses. Therefore, we used linear regression to explore those data for trends in depth from south to north, east to west, and over time. Snow depths were averaged across two-week periods resulting in eight periods for each winter (1 December–31 March). Only those snow stations with data for at least four periods in a year were analyzed.

RESULTS

Caribou locations

Over four winters, we collected 7218 caribou locations from 16 individual caribou. We collected GPS data from seven of the 16 animals for more than one winter. Because animals ranged over a large study area (5100 km^2) with variable topography, snow conditions differed between years, and collared caribou did not consistently select the same habitat (forest, alpine, forest–alpine) across winters, we considered data from each winter to be independent. Consequently, we developed models of selection for 25 ‘‘animals’’ (Table 2).

Eight caribou spent most of the winter in forested habitats, eight spent winter in alpine habitats, and nine spent some portion of winter in both alpine and forested habitats. Of those animals with continuous location data over a winter (approximately four months), four, four, and five caribou resided in the forest, alpine, and mixed forest–alpine habitats, respectively. Scale criteria (r_c) separating small- from large-scale movements ranged from 0.95 to 3.89 m/min. Using those values and the most frequently recorded sampling interval (4 h) resulted in average intra- and interpatch movements of 450.67 ± 46.78 m and 1268.78 ± 98.69 m (mean ± 1 SE), respectively. For animals with few locations, model fit often was inconclusive (see Johnson et al. 2002). In those instances for which there were <150 relocations or data collection occurred for less than one month ($n = 8$), we applied the mean r_c of the models fit to the other caribou (1.88 m/min).

Predation risk

We recorded 650 wolf relocations and 13 kill sites. Of the total, 200 relocations and seven sites where moose (*Alces alces*) had been killed by wolves were treated as independent (excluding individuals traveling together or multiple relocations at den or kill sites), and were located within the range of the collared caribou and used for these analyses. Because there were no differences in the percentage of cover types used during snow or snow-free periods (Rao's $R = 0.907$, df = 11, 402, $P = 0.533$), we pooled all wolf relocations for logistic regression analysis (Table 3; $\chi^2 = 99.452$, df = 11, $P < 0.001$, $R^2 = 0.28$; classification accuracy = 72%). Patches of Pine, Spruce, and Wetlands/lakes/rivers (with significant positive regression coefficients) were areas in which caribou were most likely to encounter wolves and consequently, to be subjected to greater risk of predation (Fig. 2).

Intrapatch selection

Caribou were located in, and thus made small-scale movements in, each of the three habitats (forest, alpine, forest–alpine) in all four winters, except for the forest during the first year of the study (1995–1996). Results from the forest reflect low sample size. All logistic models of intrapatch selection were significant (Table 4). While in the alpine, caribou selected patches of Alpine-little vegetative cover (Table 5). Animals in the forest consistently selected Pine terrace, whereas caribou ranging across both the forest and alpine selected a combination of the former two cover types. To a lesser extent, small-scale movements occurred in Wetlands and Pine–black spruce/black spruce areas. During the winter of 1995–1996, caribou also demonstrated se-

TABLE 2. Summary of movements of adult female caribou of the Wolverine caribou herd in north-central British Columbia, Canada (March 1996–April 1999) and scale criteria (r_c) used for logistic regression analyses.

Model (year, habitat)	Individual caribou	Date collected (dd/mm)	r_c (m/min)	No. movements†		Forest : alpine movements‡
				SS	LS	
1995–1996, forest–alpine	771A	01/03–31/03	1.26	136	59	62:133
1995–1996, forest–alpine	BA1A	01/03–31/03	1.33	120	25	100:45
1995–1996, alpine	831A	13/03–31/03	1.88	94	27	8:113
1995–1996, alpine	851A	12/03–31/03	1.88	127	15	0:142
1995–1996, alpine	B91A	12/03–31/03	1.88	118	16	0:134
1996–1997, forest	041A	01/12–11/02	1.25	168	58	226:0
1996–1997, forest	1D1A	01/12–23/12	1.88	59	13	72:0
1996–1997, forest	771A	01/12–25/12	1.88	37	12	49:0
1996–1997, forest	772B	21/02–31/03	0.95	146	33	179:0
1996–1997, forest–alpine	0E2B	23/02–27/03	1.88	68	22	31:59
1996–1997, forest–alpine	E41A	01/12–31/03	1.47	369	108	103:374
1996–1997, alpine	852B	01/12–25/03	1.53	420	55	6:469
1996–1997, alpine	B91A	01/12–31/03	1.45	521	62	0:583
1997–1998, forest	1D2B	01/12–24/03	2.18	351	20	371:0
1997–1998, forest	832B	10/12–31/03	3.89	516	32	547:1
1997–1998, forest	E41A	01/12–31/03	3.62	229	2	231:0
1997–1998, forest–alpine	772B	01/12–31/03	2.87	526	85	433:178
1997–1998, alpine	042B	01/12–31/03	2.18	505	82	43:544
1997–1998, alpine	B91A	01/12–31/03	2.13	316	56	40:332
1998–1999, forest	852B	11/12–31/03	1.40	247	64	271:40
1998–1999, forest–alpine	042B	10/12–31/03	1.13	297	59	98:258
1998–1999, forest–alpine	1D2B	19/12–31/03	1.59	338	39	223:154
1998–1999, forest–alpine	843C	01/12–31/03	1.69	528	100	155:473
1998–1999, forest–alpine	B94D	26/03–31/03	1.88	22	5	11:16
1998–1999, alpine	B91A	11/03–31/03	1.88	98	8	0:106

† SS and LS refer to small-scale intrapatch and large-scale interpatch movements, respectively.

‡ All movements above 1650 m were considered to occur in alpine habitats.

lection for Mid-elevation coniferous patches. Predation risk had little influence on selection at the intrapatch scale, but during the winter 1998–1999, caribou occurring in the alpine chose areas with a relatively greater distance to high-risk cover types (i.e., $d_j >$ importance criterion). The autocorrelation variable explained a large amount of the variation captured by all models. That variable had a mean importance rating (i.e., $\Sigma d_j/$ total number of models [alpine or forest or mixed]) across all winters of 0.74. In order of decreasing importance, values were 0.13 for patches of Pine terrace and Alpine-little vegetative cover; 0.030 for Pine–black spruce/black spruce; 0.021 for Mid-elevation coniferous; and <0.02 for Wetland, Alpine-grass, and Distance to predation risk.

Interpatch selection

Large-scale movements by caribou occurred in the same habitats as intrapatch selection and were significant for all combinations of year and habitat, but sam-

TABLE 3. Logistic regression model differentiating wolf relocations and kill sites from random locations relative to cover types in the Wolverine caribou herd study area of north-central British Columbia, Canada (March 1996–April 1999).

Variable	β	χ^2	*P*
Intercept	0.341		
Mid-elevation coniferous	−0.185	24.315	<0.001
Wetland/lakes/rivers	0.071	22.113	<0.001
Pine	0.037	18.147	<0.001
Spruce	0.068	14.601	<0.001
Alpine	−0.206	7.925	0.005
Krummholz	−0.077	4.783	0.029
Aspen/cottonwood	−0.039	3.272	0.071
Pine–black spruce/black spruce	0.047	2.379	0.123
Spruce–pine	−0.073	1.169	0.280
Pine terrace	−0.094	0.741	0.389
Roads/clearcuts	0.006	0.007	0.935

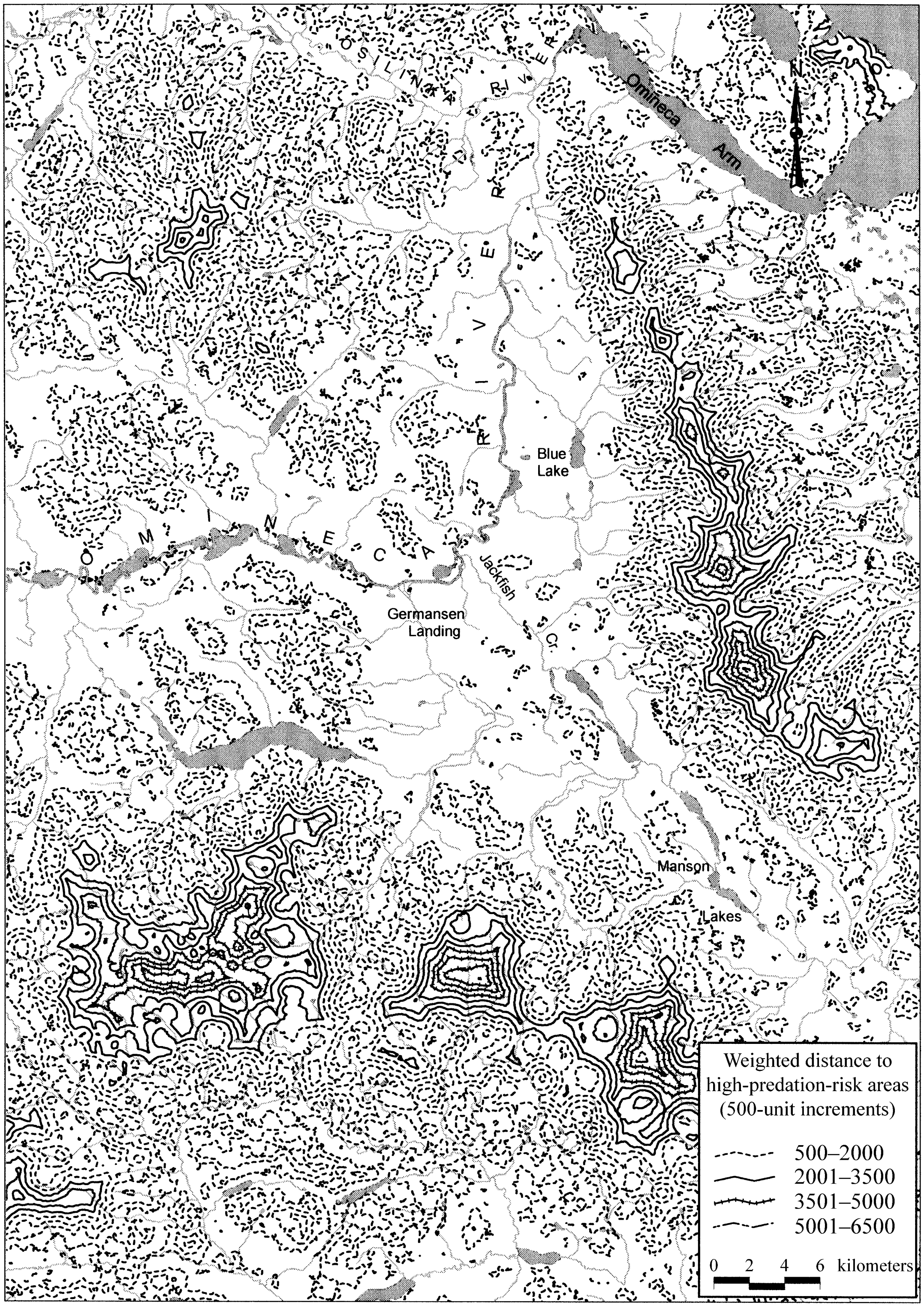

FIG. 2. Distribution of predation risk, as determined from wolf relocations, across the range of the Wolverine caribou herd of north-central British Columbia, Canada (March 1996–April 1999). Predation risk decreases as distance from high-risk patch types (Pine, Spruce, and Wetlands/Lakes/Rivers) increases.

TABLE 4. Statistical summary of logistic regression models (observed vs. random movements) of selection by caribou in north-central British Columbia, Canada (March 1996–April 1999) at scales of intra- and interpatch movements and collections of patches.

					Classification accuracy	
Model (year, habitat)	χ^2	df	P	R^2	Random locations	Caribou locations
Intrapatch selection						
1995–1996, forest–alpine	110.53	9	<0.001	0.26	63.8	64.1
1995–1996, alpine	234.35	8	<0.001	0.39	78.1	70.0
1996–1997, forest	149.87	9	<0.001	0.22	66.3	64.2
1996–1997, forest–alpine	258.97	12	<0.001	0.34	74.1	64.1
1996–1997, alpine	765.90	9	<0.001	0.34	76.9	73.1
1997–1998, forest	708.14	13	<0.001	0.28	77.3	71.7
1997–1998, forest–alpine	304.65	10	<0.001	0.34	71.5	69.2
1997–1998, alpine	332.63	10	<0.001	0.18	71.1	64.6
1998–1999, forest	132.91	9	<0.001	0.32	77.1	67.9
1998–1999, forest–alpine	427.70	12	<0.001	0.17	68.5	62.5
1998–1999, alpine	76.40	6	<0.001	0.44	78.7	75.3
Interpatch selection						
1995–1996, forest–alpine	38.80	7	<0.001	0.28	57.3	78.1
1995–1996, alpine	71.41	7	<0.001	0.64	82.1	88.9
1996–1997, forest	33.63	9	<0.001	0.18	60.9	74.6
1996–1997, forest–alpine	76.07	11	<0.001	0.35	67.7	79.2
1996–1997, alpine	84.36	8	<0.001	0.41	70.7	92.0
1997–1998, forest	19.76	6	0.003	0.23	57.7	73.6
1997–1998, forest–alpine	50.39	7	<0.001	0.35	65.1	80.5
1997–1998, alpine	56.56	8	<0.001	0.25	57.4	76.8
1998–1999, forest	31.88	7	<0.001	0.30	65.6	87.3
1998–1999, forest–alpine	91.05	9	<0.001	0.26	60.2	74.9
Patch composition						
1995–1996, forest–alpine	27.85	7	<0.001	0.35	75.6	76.6
1995–1996, alpine	44.34	8	<0.001	0.59	81.6	89.5
1996–1997, forest	50.28	7	<0.001	0.44	70.3	79.0
1996–1997, forest–alpine	67.66	9	<0.001	0.52	73.5	88.6
1996–1997, alpine	76.24	7	<0.001	0.54	69.4	93.4
1997–1998, forest	21.26	8	0.007	0.34	83.8	80.0
1997–1998, forest–alpine	25.67	6	<0.001	0.27	64.9	64.4
1997–1998, alpine	43.10	7	<0.001	0.29	59.6	79.8
1998–1999, forest	31.86	7	<0.001	0.43	70.7	70.7
1998–1999, forest–alpine	27.62	7	<0.001	0.12	58.5	70.2
Patch configuration						
1995–1996, forest–alpine	6.30	5	0.278	0.09	53.3	55.3
1995–1996, alpine	2.80	3	0.557	0.04	45.7	61.5
1996–1997, forest	7.46	4	0.114	0.08	59.4	67.7
1996–1997, forest–alpine	22.55	8	0.004	0.20	38.0	87.5
1996–1997, alpine	31.30	4	<0.001	0.25	47.4	89.3
1997–1998, forest	7.27	5	0.201	0.13	67.6	54.3
1997–1998, forest–alpine	19.95	6	0.003	0.21	67.2	54.2
1997–1998, alpine	11.71	5	0.039	0.08	46.7	63.4
1998–1999, forest	5.98	4	0.200	0.09	64.3	58.1
1998–1999, forest–alpine	12.77	5	0.030	0.06	33.3	83.0

ple size was insufficient to test movements recorded for alpine habitats during the winter of 1998–1999 (Table 4). Cover types selected by caribou for interpatch movements included Pine terrace and Alpine-little vegetative cover, as well as Lakes/rivers, Alpine-shrub, Alpine-grass, Wetland, Pine–black spruce/black spruce, and Aspen/cottonwood (Table 6). Costs of movement were typically less across selected terrain. Caribou making interpatch movements through alpine habitat during the winter of 1995–1996 and through forest during the winters of 1996–1997 and 1997–1998 chose routes with a greater risk of predation, although caribou moving across forest–alpine areas during the winter of 1996–1997 were subjected to lower risk of predation. Of all the independent variables across all models and winters, the cost of movement was most important (mean $d_j = 0.198$), although patches of Pine terrace (mean $d_j = 0.177$) and Alpine-little vegetative cover (mean $d_j = 0.166$) contributed almost equally.

Composition of multiple-patch areas

For intrapatch movements, caribou selected multiple-patch areas that were on average 182 ha, but extremely variable (1 SD = 2844 ha). Composition of

TABLE 5. Influence of cover types, distance to predation risk, and correlated locations on small-scale intrapatch movements by caribou in north-central British Columbia (March 1996–April 1999). Models are defined by year, habitat (forest, alpine, or mixed forest–alpine), and importance criterion (in parentheses).

Model and variable†	β†	1 SE	d_j
1995–1996, forest–alpine (0.056)			
Autocorrelation	0.034	0.005	0.71
Mid-elevation coniferous	0.104	0.025	0.15
Alpine-grass	0.076	0.021	0.05
1995–1996, alpine (0.063)			
Autocorrelation	0.050	0.005	0.86
Alpine-little vegetative cover	0.123	0.026	0.17
1996–1997, forest (0.056)			
Autocorrelation	0.024	0.003	0.66
Pine terrace	0.088	0.014	0.31
1996–1997, forest–alpine (0.042)			
Autocorrelation	0.044	0.005	0.61
Alpine-little vegetative cover	0.132	0.025	0.13
Pine terrace	0.167	0.034	0.12
Wetland	0.085	0.035	0.03
1996–1997, alpine (0.056)			
Autocorrelation	0.051	0.003	0.82
Alpine-little vegetative cover	0.142	0.017	0.14
Alpine-grass	0.118	0.014	0.04
1997–1998, forest (0.039)			
Autocorrelation	0.068	0.004	0.75
Pine terrace	0.106	0.012	0.17
Wetland	0.095	0.014	0.06
1997–1998, forest–alpine (0.05)			
Autocorrelation	0.092	0.008	0.69
Alpine-little vegetative cover	0.119	0.020	0.11
Pine–black spruce/black spruce	0.097	0.019	0.08
Pine terrace	0.073	0.019	0.06
Distance to predation risk	−0.011	0.005	0.03
1997–1998, alpine (0.05)			
Autocorrelation	0.038	0.003	0.63
Alpine-little vegetative cover	0.123	0.013	0.37
1998–1999, forest (0.056)			
Autocorrelation	0.119	0.015	0.75
Pine terrace	0.150	0.026	0.23
Pine–black spruce/black spruce	0.047	0.021	0.04
Distance to predation risk	0.032	0.016	0.03
1998–1999, forest–alpine (0.042)			
Autocorrelation	0.028	0.002	0.83
Pine–black spruce/black spruce	0.164	0.022	0.09
Alpine-little vegetative cover	0.031	0.011	0.03
1998–1999, alpine (0.083)			
Autocorrelation	0.140	0.023	0.86
Distance to predation risk	0.095	0.035	0.10
Alpine-little vegetative cover	0.129	0.054	0.09

Notes: Patch selection was determined by logistic regression of observed and random locations. Variables are considered important if d_j is greater than the importance value (given in parentheses in column 1); d_j represents the proportion of model R^2 attributed to each explanatory variable.

† Only those cover types associated with selection (i.e., positive regression coefficient β) and variables with an importance value ≥ 0.025 are listed.

cover types and distance to predation risk differed between selected and random areas (Table 4). Caribou in the forest chose collections of patches consisting of Pine terraces, whereas animals in the alpine selected areas of Alpine-little vegetative cover (Table 7). Animals ranging across both the forest and alpine selected collections of patches consisting of the former two cover types. During the winters of 1995–1996 and 1998–1999, caribou in forest–alpine areas were farther from areas of high predation risk than were randomly avail-

TABLE 6. Influence of cover types, movement terrain, and distance to predation risk on large-scale interpatch movements by caribou in north-central British Columbia (March 1996–April 1999). Models are defined by year, habitat (forest, alpine, mixed), and importance criterion (in parentheses).

Model and variable†	β†	1 SE	d_j
1995–1996, forest–alpine (0.071)			
Alpine-grass	0.088	0.040	0.37
Cost of movement	−0.001	0.001	0.29
Alpine-shrub	0.076	0.049	0.22
1995–1996, alpine (0.071)			
Alpine-little vegetative cover	1.24	0.347	0.52
Distance to predation risk	−0.188	0.052	0.20
Cost of movement	−0.001	0.001	0.11
Wetland	0.398	0.168	0.10
1996–1997, forest (0.056)			
Pine terrace	0.130	0.103	0.17
Lakes/rivers	0.093	0.049	0.17
Distance to predation risk	−0.016	0.032	0.06
Spruce	0.024	0.056	0.05
Aspen/cottonwood	0.066	0.052	0.05
Cost of movement	−0.001	0.001	0.03
1996–1997, forest–alpine (0.046)			
Alpine-grass	0.148	0.052	0.21
Distance to predation risk	0.065	0.035	0.21
Pine terrace	0.138	0.071	0.13
Cost of movement	−0.001	0.001	0.11
Wetland	0.068	0.071	0.03
1996–1997, alpine (0.063)			
Alpine-little vegetative cover	0.918	0.265	0.60
Cost of movement	−0.001	0.001	0.22
1997–1998, forest (0.083)			
Pine terrace	0.166	0.063	0.46
Distance to predation risk	−0.091	0.04	0.43
Cost of movement	−0.001	0.001	0.07
Krummholz	0.146	0.071	0.04
1997–1998, forest–alpine (0.071)			
Pine terrace	0.289	0.098	0.38
Lakes/rivers	0.211	0.108	0.18
Cost of movement	−0.001	0.001	0.18
1997–1998, alpine (0.063)			
Cost of movement	−0.001	0.001	0.42
Lakes/rivers	0.098	0.049	0.07
Pine terrace	0.226	0.114	0.04
1998–1999, forest (0.071)			
Lakes/rivers	0.223	0.075	0.33
Cost of movement	−0.001	0.001	0.17
Pine–black spruce/black spruce	0.133	0.113	0.15
Pine terrace	0.040	0.075	0.06
Alpine-little vegetative cover	0.184	0.076	0.04
1998–1999, forest–alpine (0.056)			
Cost of movement	−0.001	0.001	0.38
Alpine-grass	0.064	0.025	0.17
Aspen/cottonwood	0.118	0.038	0.16
Lakes/rivers	0.046	0.041	0.04

Notes: Patch selection was determined by logistic regression of observed and random locations. Variables are considered important if d_j is greater than the importance criterion (shown in parentheses in column 1).

† Only those cover types associated with selection (i.e., positive regression coefficient β) and variables with an importance value ≥ 0.025 are listed.

TABLE 7. Influence of cover types and distance to predation risk on selection of multiple-patch areas by caribou in north-central British Columbia (March 1996–April 1999).

Model and variable†	β†	1 SE	d_j
1995–1996, forest–alpine (0.071)			
Alpine-little vegetative cover	0.150	0.055	0.53
Alpine-grass	0.074	0.055	0.18
Distance to predation risk	0.034	0.035	0.12
Pine terrace	0.080	0.132	0.03
1995–1996, alpine (0.063)			
Alpine-little vegetative cover	0.505	0.153	0.70
1996–1997, forest (0.071)			
Pine terrace	0.181	0.039	0.61
1996–1997, forest–alpine (0.056)			
Pine terrace	0.399	0.107	0.30
Alpine-little vegetative cover	0.226	0.076	0.29
Alpine-grass	0.150	0.061	0.03
1996–1997, alpine (0.071)			
Alpine-little vegetative cover	0.497	0.144	0.54
1997–1998, forest (0.063)			
Pine terrace	0.141	0.085	0.33
Pine–black spruce/black spruce	0.047	0.100	0.09
Distance to predation risk	−0.020	0.041	0.07
Pine	0.117	0.130	0.03
1997–1998, forest–alpine (0.083)			
Alpine-grass	0.252	0.096	0.28
Pine terrace	0.094	0.042	0.25
1997–1998, alpine (0.063)			
Alpine-little vegetative cover	0.128	0.048	0.39
Alpine-grass	0.050	0.042	0.05
1998–1999, forest (0.071)			
Pine terrace	0.242	0.070	0.63
Spruce	0.108	0.057	0.12
Alpine-little vegetative cover	0.101	0.136	0.05
Distance to predation risk	0.050	0.040	0.04
1998–1999, forest–alpine (0.071)			
Distance to predation risk	0.020	0.022	0.23
Alpine-little vegetative cover	0.021	0.035	0.15
Alpine-grass	0.039	0.039	0.10
Pine terrace	0.058	0.036	0.04

Notes: Patch selection was determined by logistic regression of observed and random locations. Variables are considered important if d_j is greater than the importance criterion (shown in parentheses in column 1).

† Only those cover types associated with selection (i.e., positive regression coefficient β) and variables with an importance value ≥ 0.025 are listed.

able. Across winters, areas of Alpine-little vegetative cover had the largest mean importance rating (0.379) to models describing multiple-patch selection, followed by Pine terraces (0.313).

Configuration of multiple-patch areas

In general, configuration of patches was most important when caribou ranged across alpine habitats. In contrast to the other three scales of selection, several of the models (including all forest models) describing differences in the configuration of patches across selected and random areas were nonsignificant (Table 4). Patches of Alpine-little vegetative cover adjacent to Krummholz or Mid-elevation coniferous areas were consistently avoided. Caribou in the alpine habitat selected patches of Alpine-grass adjacent to Mid-elevation coniferous patches, but animals in forest–alpine areas avoided that juxtaposition of patch types (Table 8). Instead, those caribou selected for Pine terraces adjacent to Wetlands and Pine–black spruce/black spruce areas, and in the winter of 1997–1998 avoided patches adjacent to Lakes/rivers. Patch contagion was important for three of the five significant models. There was no consistent trend, however, to suggest that caribou chose multiple-patch areas consisting of larger patches of fewer cover types (i.e., with positive contagion values).

Snow depth

Snow depths were recorded during at least four of eight 2-wk periods in winter during 1996–1997 (seven

TABLE 8. Influence of patch adjacency and contagion on selection of multiple-patch areas by caribou in north-central British Columbia (March 1996–April 1999); "→" indicates that patch type 1 was adjacent to patch type 2.

Model and variable†	β	1 SE	d_j
1996–1997, forest–alpine (0.063)			
Alpine-little vegetative cover → Krummholz	−0.124	0.055	0.64
Alpine-little vegetative cover → Mid-elevation coniferous	−0.078	0.081	0.16
Pine terrace → Wetland	0.022	0.025	0.13
Alpine-grass → Mid-elevation coniferous	−0.080	0.178	0.05
Contagion	0.291	0.337	0.04
1996–1997, alpine (0.125)			
Alpine-little vegetative cover → Krummholz	−0.094	0.041	0.43
Alpine-grass → Mid-elevation coniferous	0.160	0.081	0.27
Contagion	0.493	0.310	0.17
Alpine-grass → Krummholz	−0.032	0.024	0.14
1997–1998, forest–alpine (0.083)			
Pine terrace → Pine–black spruce/black spruce	0.023	0.012	0.34
Pine terrace → Wetland	0.068	0.042	0.22
Alpine-grass → Krummholz	0.323	0.255	0.16
Contagion	−0.574	0.410	0.15
Pine terrace → Lakes/rivers	−0.128	0.094	0.09
Alpine-grass → Mid-elevation coniferous	0.163	0.286	0.03
1997–1998, alpine (0.1)			
Alpine-little vegetative cover → Krummholz	−0.033	0.015	0.47
Contagion	−0.450	0.272	0.25
Alpine-grass → Krummholz	−0.014	0.013	0.14
Alpine-grass → Mid-elevation coniferous	0.073	0.053	0.13
1998–1999, forest–alpine (0.1)			
Alpine-grass → Krummholz	−0.031	0.015	0.49
Alpine-little vegetative cover → Mid-elevation coniferous	−0.028	0.017	0.30
Alpine-grass → Mid-elevation coniferous	−0.029	0.050	0.07
Contagion	0.243	0.218	0.07
Alpine-little vegetative cover → Krummholz	−0.004	0.008	0.06

Notes: Patch selection was determined by logistic regression of observed and random locations. Variables are considered important if d_j is greater than the importance value (given in parentheses in column 1); d_j represents the proportion of model R^2 attributed to each explanatory variable.

† Only those variables with an importance value ≥ 0.025 are listed.

stations), 1997–1998 (nine stations), and 1998–1999 (three stations). During winter 1996–1997, we did not collect snow depths at the most southern portion of the caribou range, as we did in 1997–1998 and 1998–1999. In 1996–1997, snow depths did not differ between stations relative to their north to south ($F = 2.88$, df = 1, 49, $P = 0.096$, $r^2 = 0.06$) or east to west ($F = 2.51$, df = 1, 49, $P = 0.12$, $r^2 = 0.05$) orientations, but increased significantly over time ($F = 41.95$, df = 1, 49, $P < 0.001$, $r^2 = 0.46$). The average range of depths between stations was 25.8 ± 4.9 cm (mean ± 1 SE). Snow depths increased in 1997–1998 from north to south ($F = 10.66$, df = 1, 45, $P = 0.002$, $r^2 = 0.19$) and over time ($F = 37.49$, df = 1, 45, $P < 0.001$, $r^2 = 0.46$), but showed no trends relative to the east to west direction ($F = 1.91$, df = 1, 45, $P = 0.174$, $r^2 = 0.04$). The average range of snow depths between stations was 31.7 ± 6.6 cm. Sample size was insufficient to perform analyses for the 1998–1999 winter.

DISCUSSION

Relative to other boreal and sub-boreal ungulates, woodland caribou characteristically demonstrate frequent movements and seasonal or interseasonal migrations (Cumming 1992). Movements may be in response to predation risk, avoidance of insects, forage accessibility as dictated by snow, forage availability as dictated by grazing intensity and season, or social aggregations such as during rut (Helle and Tarvainen 1984, Bergerud and Page 1987, Ion and Kershaw 1989, Nellemann 1996). Caribou in north-central British Columbia spent some time at locations making a series of small-scale movements, presumably while foraging, followed by less frequent moves of longer distance to other patches or locations on the landscape (Table 2). Others have noted similar patterns of movements of ungulates using GPS-collar data (Rodgers et al. 1996, Pastor et al. 1997) and direct observations (Ward and Saltz 1994).

Scales of selection

We used movement rate as an index of animal behavior to identify scales of selection, and compared selection at spatial scales defined by caribou, not the researcher (Morris 1987, Pastor et al. 1997). Where previous habitat studies identified multiple scales of selection by caribou, analyses only differentiated use and availability of habitat types within and outside home ranges (Bradshaw et al. 1995, Terry and Wood 1999, Poole et al. 2000). The movement rates of caribou permitted us to explicitly define availability relative to the behavior of an individual caribou.

Depending on the questions asked and phenomena measured, the scale or scales of investigation may determine findings and alter conclusions (Wiens 1989). We recognize that our study only examined a subset of the possible scales representing the movements and selection habits of caribou (Allen and Starr 1982). For example, while trailing caribou through winter habitats, we observed finer scales of selection that were a response to heterogeneity greater than our habitat maps (Johnson et al. 2001). Caribou also make choices that result in scales of selection larger than those measured at a series of individual movements. Animals may choose alpine habitats over forested habitats or migrate to portions of their range to meet seasonal requirements (e.g., calving). Terry and Wood (1999) reported that caribou in the south of our study area made northerly movements from early- to late-winter ranges and that caribou were more likely to winter in the forest during years of less snow. Six of our collared caribou also spent December in the south of the study area before moving north toward areas with alpine habitats. During 1997–1998, snow depths decreased from the south to the north of the study area. Although the absolute differences in snow depths between snow stations were small, they may have exceeded a threshold for which the energetic gains of cratering were less than the costs (Fancy and White 1985). During our on-site field investigations, we observed alpine habitats with shallower snow relative to forested habitats (Johnson et al. 2001). Those animals that moved to the alpine may have selected snow conditions that permitted greater access to terrestrial lichens. That scale of selection is larger than the scales of movement we identified, and would only be apparent after several cumulative interpatch movements.

Selection of cover types

Particular cover types were selected consistently across the four winters and three spatial scales that we identified. Schaefer and Messier (1995) also noted consistent selection affinities of muskoxen (*Ovibos moschatus*) across scales. In our case, patches of Pine terrace and Alpine-little vegetative cover were prevalent at intrapatch, interpatch, and multiple-patch scales. Our smaller scale site investigations revealed that caribou selected feeding sites across Pine terraces that provided abundant *Cladina* and *Cladonia* lichens (Johnson et al. 2001). Similarly, within patches of Alpine-little vegetative cover and Alpine-grass, caribou selected feeding sites on windswept ridges with *Stereocaulon*, *Cladina*, *Cetraria*, and *Thamnolia* lichens. There also were notable among-scale differences in selection of cover types. Wetlands and patches of Pine–black spruce/black spruce were selected during intra- and interpatch movements more frequently than at the multiple-patch scale. Lakes/rivers and patches of Alpine-shrub and Aspen/cottonwood were important cover types exclusively during interpatch movements.

The cover types selected by caribou in our study during winter are in general agreement with those of other studies of woodland caribou in central British Columbia. Terry and Wood (1999) also reported that caribou of the Wolverine herd selected stands of lodgepole pine, wetlands, and alpine habitats. Caribou in west-central British Columbia selected stands of dry lodgepole pine, meadows, and alpine habitats (Cichowski 1993), or were associated with old forest on sites of poor productivity and with wetland mosaics (Steventon 1996). Caribou of the Takla herd, south of our study animals, selected spruce–fir forests and alpine habitats during winter (Poole et al. 2000). Our multiscale approach, however, revealed differences in cover type between scales and allowed us to test a wider range of variables while linking the behavior (movement patterns) of the animals at smaller scales to those areas selected (Johnson et al. 2001). Furthermore, where previous studies used forest inventory data with little sensitivity to caribou–vegetation relationships, our map of cover types was developed to represent ecological types (e.g., Pine terraces) with likely relevance to caribou biology (Johnson 2000). Large numbers of relocations per individual also allowed us to consider a greater number of cover types.

Distance to predation risk

The spatial separation hypothesis (James 1999) asserts that to minimize predation risk, caribou should distance themselves from moose and their principal predator, wolves. Studies of caribou–moose–wolf interactions in Alberta, British Columbia, and Ontario showed that caribou and moose selected different habitats, wolves and moose were associated with similar habitats, and moose were the primary prey of wolves (Bergerud 1985, Seip 1992, Cumming et al. 1996, James 1999). We did not monitor the locations of moose, but assumed that wolves mimicked the habitat affinities of their principal prey species, as was observed by James (1999). The premise of our risk variable is that caribou have knowledge of, and avoid, locations where the probability of encountering a predator is high. Three assumptions govern this relationship: (1) wolves preferentially select specific locations to hunt, concentrating their efforts in the most productive locations for prey abundance or ease of capture; (2) prey location is related to vegetation; and (3) independent of cover type, actual or perceived wolf distribution encompasses the entire study area. Bouskila and Blumstein (1992) assumed that knowledge of predation risk was exercised through simple rules. Using an optimization model, they concluded that animals attempt to track fluctuations in predation risk despite incomplete or inaccurate knowledge, but rules that overestimate risk should lead to lower mortality. Jedrzejewski and Jedrzejewska (1990) demonstrated that bank voles (*Clethrionomis glareolus*) were just as likely to avoid pens scented with weasel (*Mustela nivalis*) as those that actually contained weasel. Similarly, caribou may use vegetation to evaluate risk (sensu Hirth 1977). Because wolves cannot be in all patches at all times, such a rule would overestimate actual risk, but perhaps would represent perceived risk.

Particular cover types in our study area presented a greater risk to caribou or moose of encountering a predator, as demonstrated by logistic regression analysis of wolf relocations and kill sites (Table 3). With the exception of one winter, predation risk was unimportant at the scale of intrapatch movements. Although distance from high-risk patches will differ among locations within any one patch, variation over what was considered available might have been too small to detect selection or avoidance of low-risk areas. This outcome is consistent with our implicit assumption that caribou evaluate predation risk at scales larger than the patch (i.e., we assigned risk values to patches of a specific type).

Predation risk was most important during interpatch movements. This resulted from animals transiting higher risk cover types such as Lakes/rivers, patches of Spruce, and Wetlands (Tables 3 and 6) when moving between patches. Fuller and Keith (1980) reported that most wolf kills of moose during the winter occurred in lowland habitats, despite an equal distribution of moose across lowland and upland areas. Nelson and Mech (1991) noted that white-tailed deer (*Odocoileus virginianus*) were more vulnerable to wolf predation during large-scale migratory movements.

Predation risk at the scale of multiple patches was unimportant for three of the four winters studied. Only in 1997–1998 did caribou in the forest tend to be in areas of higher predation risk (Table 7). Alternatively, during the winters of 1995–1996 and 1998–1999, caribou occupying both forest and alpine habitats selected areas of lower predation risk. This result reflects the cumulative within-winter movements of caribou from high-risk valley bottoms to low-risk alpine areas.

Our data illustrate that risk is scale dependent and that it must be considered relative to the range of cover types occupied by caribou. For movements at the interpatch scale, risk occurs relative to short-term occupancy of risk-prone cover types. Caribou also may respond to predation risk at scales beyond what we defined as multiple-patch selection. Distance to risk was the greatest between low- and high-elevation habitats (Fig. 2). Selection of alpine habitats may be a strategy to maximize the distance from high-risk valley bottoms (Bergerud and Page 1987). Little variation in risk across low-elevation forested areas, but strong selection by wolves for particular patch types across those areas, suggests that caribou should adopt nonlinear strategies when responding to risk: caribou should avoid patches where moose are typically found, or at a much larger scale, should occupy alpine or mid-elevation habitats.

Research across a large number of terrestrial and aquatic species has demonstrated that predation risk is an important component of animal behavior (for a review, see Lima and Dill 1990). We can, however, only speculate about how individuals perceive or measure risk. Our results do not reveal whether caribou were actively choosing low-risk habitats or fortuitously experienced lower risk through the selection of habitats associated with a greater abundance or accessibility of desirable forage species. Furthermore, if caribou were actively reducing their risk, we are unsure whether they were avoiding moose or wolves. Within the constraints of available data, we are confident that wolves were not hunting within habitats strongly selected by caribou as foraging areas (i.e., Pine terrace, Alpine-little vegetative cover; Table 3). From our observations, wolves appeared to hunt the more abundant and spatially predictable moose. Caribou selecting low-risk patches adjacent to high-risk cover types or traveling through high-risk patches, however, may increase their probability of becoming secondary prey (Holt 1984). The complexity of choice increases when animals attempt to minimize risk while meeting daily or seasonal nutritional requirements (Ferguson et al. 1988, Heard et al. 1996, Bowyer et al. 1999, Kie et al. 1999).

Correlated movements

Small-scale intrapatch movements of caribou were highly correlated relative to random locations (Table 5). Frequent sampling of animal relocations for movement analyses can violate the statistical assumption of independence of error terms. One solution has been to use a statistical test based on Schoener's (1981) ratio to decrease the sampling interval to the point at which relocations are considered independent (Swihart and Slade 1985). McNay et al. (1994) demonstrated that for animal movements with skewed distributions, an independence interval based on Schoener's ratio was excessive and led to the classification of most data as dependent. Although our average relocation interval (~7.5 h) was greater than that used to indicate independence for pronghorns (*Antilocapra americana*, >4 h), coyotes (*Canis latrans*, >6 h), and white-tailed deer (>4 h) (Reynolds and Laundré 1990, Holzenbein and Marchinton 1992), we still chose to explicitly model autocorrelated movements. This reduced the potential for violating statistical assumptions (Neter et al. 1990) and permitted an exploration of the biological meaningfulness of autocorrelation.

A large portion of the variation between random and recorded intrapatch movements by caribou was explained by autocorrelation. This outcome suggests that caribou responded to resource heterogeneity at a finer scale than we mapped ($<25 \times 25$ m pixel or 625 m^2). These findings also suggest that resources have a patchy rather than random distribution (Kotliar and Wiens 1990). Our investigations at smaller scales showed that caribou are selective at fine scales (i.e., feeding sites) based on the presence of certain lichen species and snow conditions, which may limit access to those lichens (Johnson et al. 2001).

Energetic costs of movement

Anecdotal observations and theoretical works suggested that, independent of predation risk, caribou should transit flat valley bottoms with little topographic relief during large-scale movements (Wiens et al. 1997). Relative to surrounding mountainous terrain, those areas offer lower energetic costs and are more likely to be associated with foraging habitats, e.g., Pine terrace (White and Yousef 1978, Fancy and White 1987). Our approach of calculating the energetic costs of moving up slope, down slope, or across flat terrain did not consider all factors affecting those costs (e.g., sinking depth in snow, speed of travel), but we believed it to be more representative than comparisons based only on differences in slope and elevation (Krist and Brown 1994). For all winters, caribou moved across topography with lower energetic costs relative to what was available (i.e., caribou selected terrain that facilitated level or downhill movements more often than uphill movements). This is consistent with features such as valley bottoms and lowlands associated with Lakes/rivers, a cover type selected at that scale (Table 6).

Composition and configuration of patches

Researchers typically quantify the composition of available and selected habitats, but do not report spatial configuration of those same habitat patches. Numerous landscape metrics, however, are available to quantify spatial arrangement, size, and shape of individual patches and collections of patches (Baskent and Jordan 1995, McGarigal and Marks 1995, Gustafson 1998). Most tests of patch configuration have been relative to habitat requirements of avian species (McGarigal and McComb 1995, Bellamy et al. 1998, Saab 1999), although Stuart-Smith et al. (1997) calculated several measures for distinct landscapes occupied by caribou in northeastern Alberta.

We did not describe patterns of patch configuration, but tested for differences in configuration between what was selected by caribou and what was available. Our analyses were designed using information from previous studies (Paré and Huot 1985, Cichowski 1993, Terry and Wood 1999) and our observations. We tested whether cover types selected at the scale of multiple-patch areas occurred in a matrix of lesser used Wetlands, Pine–black spruce/black spruce areas, or Lakes/rivers. Wetland complexes consisting of those cover types contain sedges (*Carex* spp.), abundant arboreal lichens (*Bryoria* spp.), and mineral licks, all of which may have value to caribou. We also assessed whether cover types selected in alpine habitat occurred adjacent to forested patches (Krummholz or Mid-elevation coniferous) containing arboreal lichens.

Relative to patch composition, and in contrast to studies of other faunà (Hokit et al. 1999, Saab 1999), indices of patch configuration served as poor indicators of those collections of patches chosen by caribou. For those significant logistic models containing forest adjacencies (1996–1997, 1997–1998), caribou selected patches of Pine terrace adjacent to Wetlands and Pine–black spruce/black spruce stands. Site investigations revealed some foraging activity within those cover types, but it was less frequent than cratering for terrestrial lichens in adjacent Pine terrace patches (Johnson et al. 2001). We speculate that, although their distribution is limited, sedges in wetlands may serve as a protein supplement (Skoog 1968, Klein 1982, Bradshaw et al. 1995) for a diet dominated by high-energy, but low-protein lichens (Thing 1984, Dannell et al. 1994).

Patch configuration was more important to caribou ranging across the alpine habitat. Caribou consistently avoided patches of Alpine-little vegetative cover adjacent to forest patches (Table 8). This may be a strategy to maximize distance from predators, or to select more exposed windswept slopes. Adjacencies of Alpine-grass were inconsistent across winters. During some winters, animals selected areas adjacent to forest cover whereas in other winters, they avoided them. We observed caribou foraging in Krummholz patches on arboreal lichens on only one occasion, and Mid-elevation coniferous cover was important at the intrapatch scale during only one winter, 1995–1996 (Johnson et al. 2001). Differences between winters may be due to inter-animal variation in selection.

During some winters, large patches of a single type (i.e., positive coefficients for contagion; Table 8) dominated areas selected by caribou, whereas other winters were characterized by collections of smaller patches. This suggests that the distribution of patch types and sizes varies across the study area and that caribou selected a range of patch collections.

CONSERVATION IMPLICATIONS

Resource managers attempting to meet conservation objectives for woodland caribou are concerned principally with the negative effects of forest practices. Relative to natural disturbance, forest harvesting alters the composition and seral distribution of commercial tree species across large areas, leading to at least a temporary reduction in the availability of suitable forage for caribou while increasing that available for moose (Cumming 1992, Seip 1998). The distribution and abundance of wolves can be expected to increase in proportion to moose (Messier 1994). Studies of caribou–forestry interactions have reported that caribou may abandon or avoid harvested and partially harvested areas for >12 yr (Darby and Duquette 1986, Chubbs et al. 1993, Cumming and Beange 1993).

Our research suggests that caribou respond to the environment hierarchically and that forest practices should recognize a range of scale-dependent requirements. Caribou occurred in either forest, alpine, or a combination of forest and alpine habitats during any one winter. Across those broad geographic areas, caribou were most restrictive in their general choice of collections of patches, but within those areas they selected a wider variety of cover types for making intra- or interpatch movements. For forest-dwelling caribou, patches of Pine terrace, comprising only 3% of the study area (Table 1), were important at the three scales that we analyzed. There also was weak evidence that patches of Pine terrace contained within a matrix of Wetlands and Pine–black spruce/black spruce stands were desirable. Caribou in the alpine zone used patches of Alpine-little vegetative cover (<5% of the study area), which were spatially distinct from the forest. Although alpine habitats are not of interest to the forest industry, mining development and the needs of animals occupying both forest and alpine habitats must be recognized. Road building adjacent to alpine and krummholz habitats may also facilitate the movements of predators and increase the risk of predation to caribou occupying high-elevation areas (James 1999).

Connectivity of cover types across the landscape should be defined relative to animal responses to cover type and arrangement (Wiens et al. 1997). The female caribou that we monitored were selective when making interpatch movements, but chose a wider range of cover types than at the other two scales. This indicates that animals may be less constrained by cover type during large-scale movements. The prevalence of Lakes/rivers and level topography indicates that valley bottoms may serve as movement corridors, although large-scale movements were not restricted to low elevations. When animals did make interpatch movements, they were subject to a greater risk of predation. Successional changes influencing moose and wolf numbers would have their greatest influence on caribou at that scale, and could possibly create population sinks, fragment their range, or isolate alpine from forested habitats (Lord and Norton 1990, Harrison and Voller 1998). Low-elevation areas that connect disparate portions of a caribou range should be recognized during forest development planning and treated as special management zones.

Our recommendations are facilitated by the coarse-filter ecosystem management approach of Seip (1998). He recommended that areas managed for caribou maintain large, unfragmented patches of older forest that support terrestrial lichens and serve to spatially separate caribou from early seral habitats where moose and wolves may be encountered. When forest harvesting is conducted across the range of northern caribou, Seip (1998) suggested abandoning many small clearcuts and adopting a harvesting regime of a few large clearcuts that roughly approximate the natural disturbance patterns (i.e., fires) of boreal and sub-boreal forests, while ensuring that large, unfragmented patches of older forest also are retained.

The breadth of biotic and abiotic stimuli that affect individual animals and ultimately populations occurs across a wide spatial and temporal range. Failing to account for such spatial and temporal variation may have implications for study objectives, results, and conservation initiatives (Bergin 1992). In our study, we used animal-centered measures to distinguish between different scales of selection, and included dynamic attributes such as predation risk and the energetic costs of movement with vegetative characteristics to identify how selection by caribou varied between scales. The knowledge gained from identifying scale-dependent factors can be used to improve conservation strategies for caribou inhabiting heterogeneous landscapes.

ACKNOWLEDGMENTS

We thank G. Althoff and G. Watts for expert flying, net-gunning, and animal handling; L. Frey and E. Stier skillfully flew relocation and GPS upload flights. B. Zumbo and D. Ayers provided statistical advice and N. Alexander was instrumental in producing the supervised classification of the study area. R. T. Bowyer and two anonymous reviewers provided insightful comments on an earlier version of this manuscript. This work was funded by an Inventory Grant from Forest Renewal British Columbia, a Grant-in-aid from the Boone and Crockett Club, a British Columbia Ministry of Environment, Lands, and Parks Environmental Scholarship, a University of Northern British Columbia Natural Resources and Environmental Studies Scholarship, and a Natural Sciences and Engineering Research Council Post Graduate Scholarship.

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