

# Interpreting Resource Selection at Different Scales for Woodland Caribou in Winter

**DAVID D. GUSTINE**,<sup>1,2</sup> *Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada*

**KATHERINE L. PARKER**, *Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada*

**ROBERTA J. LAY**,<sup>3</sup> *Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada*

**MICHAEL P. GILLINGHAM**, *Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada*

**DOUGLAS C. HEARD**, *British Columbia Ministry of Environment, Prince George, BC V2N 1B3, Canada*

## Abstract

Scientists commonly use resource selection functions (RSFs) to identify areas important to large herbivores. Defining availability of resources is scale dependent and may limit inference on biological mechanisms of selection, particularly if variation in selection of resources is high among individuals within a population. We used logistic regression, the information-theoretic approach, and Global Positioning System (GPS) radiotelemetry data from 10 female woodland caribou (*Rangifer tarandus caribou*) and 5 wolf (*Canis lupus*) packs to model resource selection by individual caribou in the winter and late-winter seasons. We evaluated the influence of spatial scale on the relative importance of cost of movement and components of predation risk. We examined attributes of the risk of wolf predation within availability data at 2 spatial scales, and quantified variation in resource selection among individual caribou. Energetic cost of movement was the most important covariate for all caribou at a spatial scale defined by seasonal movement. Increasing distance to areas of high wolf risk was more important at the larger spatial scale of home range. Variation was high in the selection of resources among caribou, although commonalities among individuals enabled pooling data on use and availability into 2 selection strategies. Researchers and managers should conduct multiscale analyses with varied definitions of availability, quantify variation among individuals, and pool data into common selection strategies to identify mechanisms of selection and to map a population's selection for resources on the landscape. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1601–1614; 2006)

## Key words

*Caribou, energetic cost, movement, predation risk, Rangifer, reproductive condition, resource selection, scale.*

Evaluating mechanisms in ecological processes may be confounded by the influence of both spatial and temporal scales (Wiens 1989, Levin 1992). Animals typically respond to environmental factors in a hierarchical fashion (Johnson 1980, Senft et al. 1987, Schaefer and Messier 1995) and therefore, inferences about ecological mechanisms are likely to vary with the scale of analyses (Wiens 1989, Danell et al. 1991, Johnson 2000). The selection of resources may vary among individuals by age (Nielsen et al. 2002), sex (McLoughlin et al. 2002), and reproductive condition (Rachlow and Bowyer 1998) within a population (Aebischer et al. 1993), which adds further complexity to the issue of scale. Variation in the selection of habitats among individuals may be an important life-history trait for the species (Bowyer et al. 1999, Gustine et al. 2006). Factors that influence selection of habitats by ungulates include year (Wood 1996), time of year (i.e., season; Apps et al. 2001), forage abundance and availability (Schaefer and Messier 1995), cover (Boyce et al. 2003), anthropogenic disturbance

(Nellemen and Cameron 1998), energetic cost of movement (Johnson 2000), and predation risk (Lima and Dill 1990). Factors may vary in relative importance across scales (Wiens 1989), with those most limiting to individual fitness possibly important at coarser scales (Rettie and Messier 2000).

Researchers have used resource selection functions (RSFs) to identify and model characteristics of areas selected by ungulate populations at a variety of scales and therefore inferred these characteristics as important to ungulate populations (Schaefer and Messier 1995, Boyce et al. 2003, Johnson et al. 2004). They often define RSFs with the use of logistic regression in use versus availability designs (Boyce et al. 2002). Researchers commonly limit availability to the study area (McClellan et al. 1998) or home range(s) of a population (Johnson 1980). Consequently, they typically make inferences relative to the selection of resources by a population and rarely make inferences relative to the selection of resources by individuals (Aebischer et al. 1993) within that population (i.e., Type I or II vs. Type III design; Thomas and Taylor 1990), particularly for large mammals (Nielsen et al. 2002). Defining availability as the study area, or as the sum of the availabilities of individual animals, to model selection across animals may provide good predictive models (Boyce et al. 2003) but could be limited in delineating mechanisms of resource use if variation in

<sup>1</sup> E-mail: [ftddg@uaf.edu](mailto:ftddg@uaf.edu)

<sup>2</sup> Present address: Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000, USA

<sup>3</sup> Kenai Peninsula Borough, Spruce Bark Beetle Mitigation Program, Soldotna, AK 99669, USA

resource selection is high among individuals (Manly et al. 2002, Nielsen et al. 2002). Johnson et al. (2002a,b) suggested using parameters of movement to define availability for woodland caribou (*Rangifer tarandus caribou*) because movement events (i.e., migration, and intra- and interpatch movements) could provide insights into scale-dependent mechanisms of selection, and they advised conducting future research at multiple scales to identify important habitats. Management agencies, however, frequently have few resources or limited locational data to conduct multiscale analyses. Recent research, therefore, has attempted to ascertain the best scale of analysis in predicting habitats important to large herbivores (Apps et al. 2001, Boyce et al. 2003). Although a best scale is unlikely to exist for examining mechanisms that underlie selection behavior(s) (Wiens 1989), some scales, particularly the patch scale (the Johnson 1980 third order of selection), and corresponding definitions of availability (i.e., home ranges) may be more appropriate and useful to managers. Woodland caribou are an excellent species to evaluate the importance of different covariates in resource selection at different scales, the interaction between scale and definitions of availability, and the variation in the selection of resources among individuals. Caribou require large areas to overwinter (Cumming 1992, Zimmerman et al. 2002), exhibit scale-dependent responses to habitat factors (Johnson 2000, Rettie and Messier 2000), and appear sensitive to biological (e.g., energetic cost of movement; Johnson et al. 2002a) and ecological parameters (i.e., predation risk; Bergerud et al. 1984, Johnson et al. 2002a).

The northern ecotype of woodland caribou in British Columbia (Heard and Vagt 1998) overwinters in windswept alpine areas (Cichowski 1993, Wood 1996), in low-elevation lodgepole pine (*Pinus contorta*)–lichen stands when snow depths are low (Johnson 2000, Zimmerman et al. 2002) or in intermediate- to high-elevation spruce (*Picea* spp.)–fir (*Abies lasiocarpa*) forests (Cichowski 1993, Poole et al. 2000). Sizes of winter home ranges (Wood 1996, Poole et al. 2000) and movement rates (Johnson et al. 2002a,b) vary among regions and individuals and may be largely dependent on the availability of habitats, as well as the scale(s) examined by researchers (Levin 1992). Minimizing energetic costs in winter, however, appears important for female caribou moving among patches that are often in areas with high predation risk (Johnson 2000). The importance of minimizing energetic costs also may be influenced by body condition, which affects movement rates, the availability of resources, and, subsequently, resource selection.

Woodland caribou appear sensitive to distribution of other ungulates and wolves during the winter (James 1999, Johnson et al. 2002a). Increased densities of caribou often stimulate a functional response in wolf populations (Seip 1991, Bergerud 1992, Dale et al. 1994). Dispersal by caribou over large areas may be an effective life-history strategy against wolf predation during all times of the year (Bergerud et al. 1984, Seip 1991), and the ability of caribou to increase their distance from wolves may affect survival (Seip 1992,

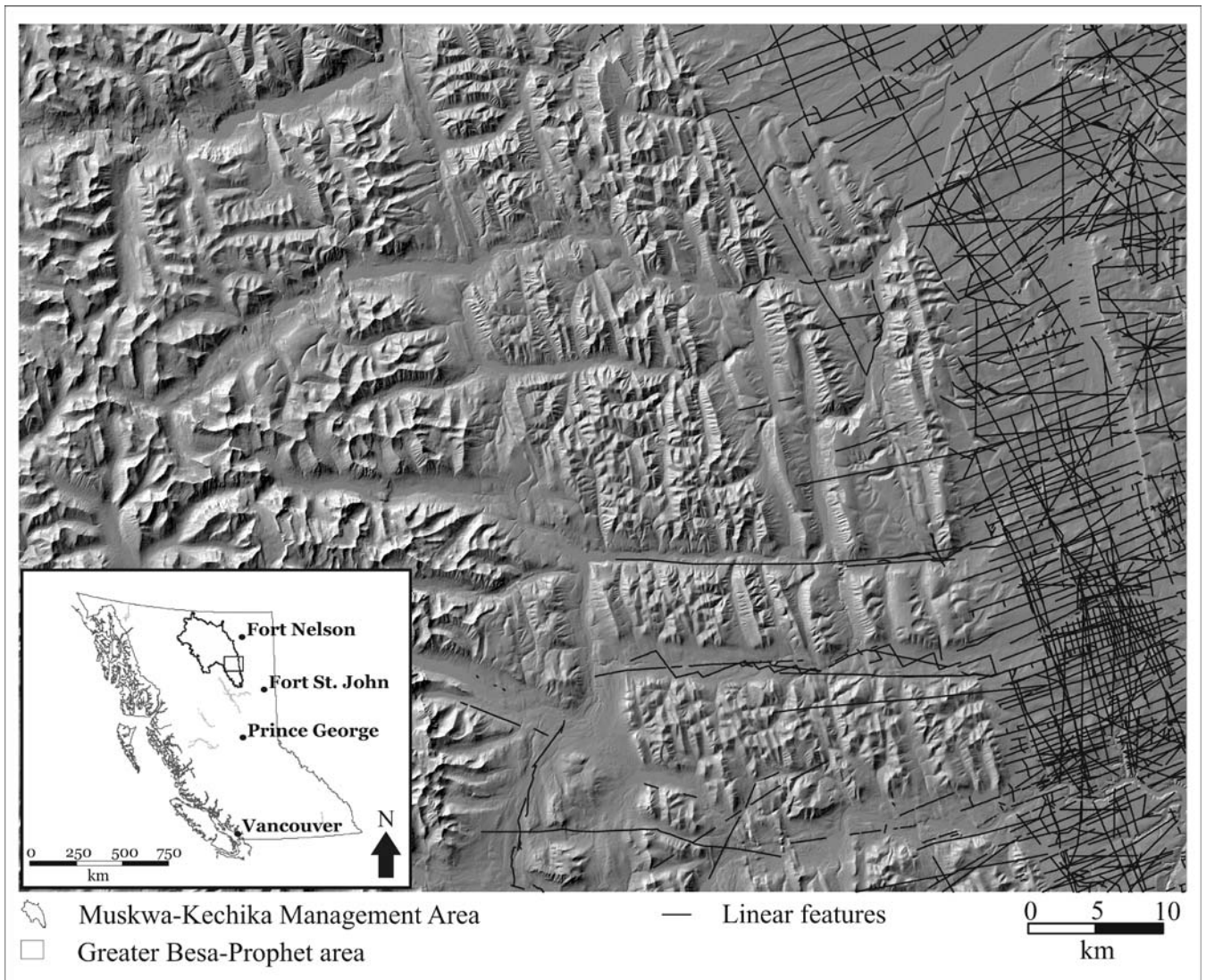
Wittmer 2004). By increasing the distance between conspecifics, other ungulates (e.g., moose [*Alces alces*]), and wolves, dispersal by individual caribou increases search time and lowers encounter rates for wolves, thereby decreasing hunting efficiency (Bergerud et al. 1984, Bergerud and Page 1987, James 1999).

The goal of this study was to identify habitats and ecological parameters important to female woodland caribou during the winter (Nov–Feb) and late-winter seasons (Mar–Apr) in a multipredator–multiprey ecosystem in northern British Columbia, Canada. Our objectives were: 1) to identify the relative importance of energetic cost of movement, predation risk, and distance to areas of high predation risk for pregnant and nonpregnant animals at a relatively small spatial scale defined by seasonal movement, 2) to identify the consequences of defining availability at two different scales (seasonal movement vs. seasonal home range) to the relative importance of components of predation risk, and 3) to quantify selection of resources among individual caribou at the management-oriented scale of the seasonal home range and identify common selection strategies among individuals.

## Study Area

The Greater Besa–Prophet area (GBPA; approx. 741,000 ha) is part of the 6.4-million-ha Muskwa–Kechika Management Area in northern British Columbia, Canada, and is located between 57°11' and 57°15'N, and 121°51' and 124°31'W (Fig. 1). Elevations range from 630 m to 3,025 m, with tree line occurring between approximately 1,450 m and 1,600 m. The eastern portion of the GPBA had relatively little topographic relief (approx. 630–800 m) and was covered by hybrid spruce (*Picea mariana* × *glauca*), black spruce (*Picea mariana*), or both. Sedge (*Carex* spp.) meadows with willow (*Salix* spp.) and alder (*Alnus* spp.) were common along watercourses and seismic lines (Fig. 1). There were quaking aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) stands at drier sites along the eastern edge of the mountains. In the mountainous western portion of the GBPA, riparian white spruce (*Populus glauca*) complexes with poorly drained willow–birch (*Betula glandulosa*) communities and sedge meadows dominated valley bottoms (approx. 800–1,300 m; Lay 2005). Mature lodgepole pine associations were uncommon. Low-productivity white spruce stands typically covered north-facing slopes. Fuzzy-spiked wild rye (*Elymus innovatus*), quaking aspen, and balsam poplar occurred on southern exposures, which often were frequently and recently burned (Lay 2005). Subalpine vegetation (1,400–1,700 m) varied with aspect, but generally consisted of willow–birch and infrequent spruce or fir trees. These latter species often occurred in krummholz form on windswept areas or upper elevations. Alpine areas consisted of permanent snowfields, glaciers, barren rock with sparse or mat vegetation, and grasslands (Demarchi 1996). Mountain avens (*Dryas integrifolia*), alтай fescue (*Festuca altaica*), arctic white heather (*Cassiope tetragona*), moss campion (*Silene acaulis*), and a variety of





**Figure 1.** The Greater Besa-Prophet area of the Muskwa-Kechika Management Area in northern British Columbia, Canada, 2004.

mosses were the most common alpine species. Lichens were abundant at drier alpine sites and common species included various reindeer (*Cladonia* spp.) and pixie-cup lichens (*Cladonia* spp.), Iceland lichens (*Cetraria* spp.), foam lichens (*Stereocaulon* spp.), rockworm (*Thamnolia vemicularis*), and furled-paper doll (*Flavocetraria cucullata*).

Repeated east-west drainages and south-facing slopes that support one of the most diverse ungulate predator-prey ecosystems in North America characterized the GBPA. Large mammals found in the area included woodland caribou, Stone's sheep (*Ovis dalli stonei*), mountain goats (*Oreamnos americanus*), moose, elk (*Cervus elaphus*), wolves, grizzly (*Ursus arctos*) and black bears (*Ursus americanus*), coyotes (*Canis latrans*), wolverines (*Gulo gulo*), and lynx (*Lynx canadensis*). The GBPA was mostly unaffected by large-scale industrial activity, although seismic oil exploration has been common in the eastern portion of the GBPA (Fig. 1). Human activities in the area primarily consisted of hunting, guide-outfitting, and prescribed burning. Terrestrial access was restricted except for low levels of all-terrain

vehicle and snowmobile activity in the southern portion of the study area.

## Methods

### **Animal Capture and Locational Data**

We captured 25 female caribou and 23 wolves from 5 packs and fitted them with GPS collars (Simplex™, Televilt, Lindesberg, Sweden) on 21–23 November and 18–19 December 2001. We captured and handled all animals in accordance with the guidelines of the Canadian Council on Animal Care (2003). Based on tooth eruption and wear, we considered caribou  $\geq 2$  years to be adults. We programmed collars to acquire locations every 6 hours for 2 years to maximize the potential number of fixes for a multiyear study while addressing the trade-off with battery size. We targeted areas for animal capture based on previous telemetry data on wintering female caribou (J. Elliot, British Columbia Ministry of Environment, unpublished data) and territories of wolf packs in the GBPA. Wolf data were from a concurrent research study in the GBPA (B. Milakovic,

University of Northern British Columbia, unpublished data). We captured caribou and wolves from a helicopter (Bell Jet Ranger II-206B); we used a net gun to capture caribou, and darted and sedated wolves using Telazol™ (tiletamine and zolazepam; Fort Dodge Laboratories, Fort Dodge, Iowa). We took blood samples (2 10-mL tubes) to determine reproductive condition of caribou via serum progesterone concentrations (Ropstad et al. 1999; Prairie Diagnostics Services, Saskatoon, Canada).

We recovered GPS data via remote download and by collar retrieval. We did not include locations acquired on the day of and after capture in our analyses because preliminary analyses suggested movement rates immediately after capture tended to be atypical (D. Gustine, University of Northern British Columbia, unpublished data). We included data on individual caribou in analyses if there were locational data from the date of capture to the date of download. We screened all GPS data for erroneous easting and northing coordinates (D'Eon et al. 2002) using Spatial Viewer (M. P. Gillingham, University of Northern British Columbia, unpublished data). We examined the distances between concurrent GPS locations of collared individuals to evaluate the independence of locational data. We defined fix rate per caribou (i.e., per GPS collar) as the number of nonerroneous fixes acquired from capture to the end of the late winter season divided by the total number of possible fixes within that time period.

We used trends in movement rates (m/hr) of caribou and changes in snow depth from November to April to define 2 caribou seasons: winter (mid-Nov–Feb) and late winter (Mar–Apr). To identify these general trends, we averaged movement rates (m/hr) per individual (i.e., distance between consecutive 6-hr fixes divided by 6) by month and then across individuals for an average monthly movement rate;  $n$  for the SE was the number of caribou.

We used movement rates and seasonal home ranges to define the availability of resources for individual caribou and wolf packs. We defined availability at 2 scales for caribou, both within Johnson's (1980) third order of selection: seasonal movement and seasonal range. Seasonal movement was an individual caribou's potential for movement within a season. Movement potential was a circle, centered on each use point (a GPS location), with a radius equal to the distance determined from the 95th percentile movement rate for 6-hour fixes; we randomly selected 5 points for availability locations within this distance from the use point (C. Johnson, University of Northern British Columbia, personal communication). A seasonal range was the home range defined by the 100% minimum convex polygon (MCP; Mohr 1947) of an individual caribou for that season, buffered by the movement potential distance. We also defined resource availability for wolf packs using 100% MCPs for each pack by caribou season (winter and late winter). We estimated MCPs using the animal movement extension (Hooge et al. 1998) in Arcview 3.2™ (Environmental Systems Research Institute, Redlands, California). We excluded data outside the boundaries of the GBPA from

analyses. We randomly removed all but one of any duplicate wolf locations within a pack (i.e., same date and time) to address issues of data independence. We randomly selected 5 availability points per use point within each MCP for each wolf pack and individual caribou using the random point generator extension (Jenness 2003) in Arcview 3.2 (Environmental Systems Research Institute, Redlands, California).

#### **Inputs to Resource Selection Models for Caribou**

**Vegetation, topography, and distance to linear features.**—Vegetative and topographical covariates in resource selection model sets for caribou and wolves were 25-m resolution raster Geographic Information System (GIS) data. We used a digital elevation model (DEM) from the 1:20,000 British Columbia Terrain and Resource Inventory Management program (British Columbia Ministry of Crown Lands, 1990) to create slope and aspect layers. For wolves, we categorized aspect into north (316–45°), east (46–135°), south (136–225°), and west (226–315°) directions to address problems with northerly values having the same aspect but different values (0° and 360°). We did not assign an aspect to pixels with slope  $\leq 1^\circ$ . For caribou, we maintained aspect as 2 continuous variables (i.e., northness and eastness; Roberts 1986) to minimize issues of perfect separation between used and available data sets.

We identified 15 vegetation classes with the use of an August 2001 Landsat Enhanced Thematic Mapper image (Lay 2005). We combined these classes, with a minimum mapping unit of  $75 \times 75$  m, into 9 classes (Table 1) to allow for accuracy levels  $>80\%$  and complete separation in logistic regression models while maintaining biologically important differences. Because measures of vegetative diversity or juxtaposition may be an important component of resource selection (Johnson 2000), we created an index of vegetation fragmentation from the 15 satellite-image-derived vegetation classes (Lay 2005) that categorized fragmentation as open, closed, or unique cover types. Open cover types included water, rock, and the alpine vegetation class. The closed coniferous cover types were Pine, Spruce, and Riparian spruce classes. We considered Snow–glacier areas and Subalpine shrubs, Shrubs, Burned–disturbed, and *Carex* spp. classes as separate cover types. We used a moving  $7 \times 7$  pixel-sized window to classify each pixel relative to the proportions of different cover types in that window. We categorized these values into low-, medium-, and high-fragmentation classes, as in Gustine (2005).

Because linear features may be important travel routes for wolves in winter (James and Stuart-Smith 2000), we created a distance to linear features layer with the use of existing 1997–2000 databases (G. Haines, British Columbia Oil and Gas Commission, unpublished data). Linear features were generally associated with oil and gas exploration (e.g., roads, seismic lines, pipelines). We rasterized and buffered all linear features by 10 m to address locational error. We based the distance-to-linear-features surface (25-m pixel size) for the GBPA on the perpendicular distance from each pixel to the edge of the closest linear feature.



**Table 1.** Nine classes of vegetation used for analyses of resource selection by caribou (*Rangifer tarandus caribou*) in the Greater Besa–Prophet area, northern British Columbia, Canada, 2001–2002.

Vegetation classes	Portion of study area (%)	Description
Carex spp.	6.0	Wetland meadows dominated by sedges, typically at low elevations
Riparian spruce	11.8	Low elevation areas with black and hybrid spruce, often with standing water in spring or summer; gravel bars adjacent to rivers and creeks
Spruce	23.2	White and hybrid spruce-dominated communities
Pine	4.6	Lodgepole pine-dominated communities
Shrubs	5.8	Deciduous shrubs <1,600 m dominated by bog-birch and willow and some cinquefoil ( <i>Potentilla fruticosa</i> )
Subalpine shrubs	9.2	Deciduous shrubs >1,599 m; spruce–shrub transition zone at middle to upper elevations (white and hybrid spruce, and dominated by birch and willow)
Burned–disturbed	10.2	Previously burned areas, grass, deciduous trees, or avalanche chutes
Nonvegetated	23.7	Rock; rock habitats with black crustose lichens; permanent snow fields or glaciers and water bodies
Alpine	5.4	Herbaceous alpine vegetation

### *Predation risk and distance to areas of high predation risk.*

—We defined predation risk to caribou by wolves (i.e., wolf risk) as the likelihood of encountering a wolf pack during a season (Lima and Dill 1990). We quantified wolf risk with the use of logistic regression to form RSFs that identified habitats selected by wolves in the GBPA from 21 November 2001 to 30 April 2002. Ecologically plausible models incorporated wolf GPS data, elevation (km), categorized aspect, slope, vegetation class, distance to linear features (km), and the index of fragmentation. We calculated coefficients of selection (i.e., beta coefficients,  $\beta_i$ ) with the use of logistic regression (Menard 2002) and identified the most parsimonious models with the use of the information-theoretic approach (Burnham and Anderson 2002) and  $k$ -fold cross validation (Boyce et al. 2002). We formed 9 RSFs to define predation risk by wolf pack and season (winter and late winter), as in Gustine (2005). Because MCPs of radiomarked wolf packs did not provide full coverage of the GBPA, and because there was at least one other known uncollared pack in the GBPA, we used pooled RSFs to predict selection values for wolves for those few areas without data. In areas where pack boundaries overlapped, we assigned the lower RSF value to that pixel because of probable decreased vigilance by pack members and subsequently lower predation risk (e.g., Mech 1994).

We developed a wolf-risk layer by applying the  $\beta_i$  in the logistic regression models and the log-linear model to each 25 × 25-m pixel in the GBPA, based on its topographic and vegetation features, using a raster GIS (PCI Imageworks 9.1™, Richmond Hill, Ontario, Canada; Gustine et al. 2006). We then determined the distance to high-risk predation areas from each pixel in the GBPA. We defined areas of high wolf risk as pixels in the top quarter of all risk values by season. We converted these high-risk areas into polygons in Idrisi32™ (Clark Labs, Worcester, Massachusetts). We created another surface of the distances from each pixel to the nearest area (polygon) of high wolf risk, which we defined as the perpendicular distance (km) to the edge of the high-risk area.

*Estimated cost of movement for caribou.*—We used the change in elevation and the distance between use and available points to model the energetic cost of movement

(kJ/kg/hr) by female caribou across variable terrain (Johnson et al. 2002a). We estimated cost of movement from equations developed by Fancy and White (1987). We did not make corrections for snow depth and slope because the time between fixes (6 hr) probably allowed access to numerous different microsite conditions. We used the DEM (British Columbia Ministry of Crown Lands 1990) to determine if a caribou moved uphill, horizontally, or downhill from one location to the next. Therefore, use cost was from use location<sub>*x*</sub> to use location<sub>*x*+1</sub>, and available costs were from use point<sub>*x*</sub> to each of the 5 available points within the potential for movement distance around use point<sub>*x*</sub>. We multiplied the cost of locomotion for moving uphill (3.640 kJ/kg/km), on a horizontal surface (1.722 kJ/kg/km), or downhill (1.293 kJ/kg/km) by the distance (km) between points divided by the duration of time between GPS fixes to give an estimate per unit time (kJ/kg/hr).

### *Relative Importance of Covariates and Scale*

We used logistic regression and Akaike's Information Criterion for small sample sizes ( $AIC_c$ ) to form RSFs that identified habitats important to individual female caribou in the GBPA from 21 November 2001 to 30 April 2002. For all caribou, we entered elevation and wolf risk as quadratic (i.e., linear and squared terms) and linear terms, respectively. We evaluated the effects (linear versus Gaussian or bell-shaped) of slope and distance to areas of high wolf risk (km) for each individual caribou by examining the change in  $AIC_c$  after adding or removing the squared term of the quadratic. If the addition of the quadratic term to the saturated model decreased  $AIC_c$ , then we entered the variable as a quadratic. We did not include vegetation classes that were rare or did not occur in use or available data in formulation of the models (Menard 2002).

We evaluated the relative importance of the predation-risk and cost of movement covariates at the scale of seasonal movement and of the predation-risk covariates at the scale of seasonal range by examining Akaike weights ( $w_i$ ) after adding each of these covariates to a core model set (e.g., higher  $w_i$  and lower  $AIC_c$  suggested model improvement; Burnham and Anderson 2002). There were 9 ecologically plausible core models that included elevation, aspect, slope, vegetation class, and the index of fragmentation. We

validated the most parsimonious core model(s) with the use of  $k$ -fold cross validation (Boyce et al. 2002). We added wolf risk, distance to areas of high wolf risk, and cost of movement (kJ/kg/hr) covariates individually to each model in the core set for each caribou by season. At the scale of seasonal range, we added only the predation-risk covariates because we could not effectively evaluate energetic cost at this scale. We estimated the relative importance of covariate<sub>*j*</sub> (i.e., cost of movement, wolf risk, or distance to areas of high wolf risk) by summing the  $w_{i,s}$  across all models for individual caribou by season for which we included covariate<sub>*j*</sub> in the model ( $w_{+}[j]$ , Burnham and Anderson 2002). As the  $w_{+}(j)$  increased, the importance of covariate<sub>*j*</sub> increased relative to the other covariates. We averaged  $w_{+}(j)$  across caribou by season ( $\overline{w_{+}[j]}$ ) to evaluate the relative importance of covariate<sub>*j*</sub> among all caribou. We also averaged significant  $\beta_{i,s}$  ( $\pm$  SE) for both pregnant and nonpregnant animals to examine the potential role of reproductive status relative to the most important variable(s) of the model set at the scale of seasonal movement.

To examine the importance of the predation risk components at both scales in reference to the core model set, we calculated the change in  $AIC_c$  ( $\Delta AIC_c$ ) when we added covariate<sub>*j*</sub> to the best core model for each caribou by season and scale. For models that included covariate<sub>*j*</sub>, we then averaged the  $\Delta AIC_c$  across animals within a season and scale ( $\overline{\Delta AIC_c}$ ). We used frequency histograms and  $t$ -tests (Zar 1999) to compare the attributes of available wolf risk and distance to areas of high wolf risk between scales (seasonal range and seasonal movement) by season for each individual caribou.

### **Quantifying Variation in the Selection of Resources Among Individuals**

We determined resource selection by individual caribou from the most parsimonious models that performed the best at the scale of the seasonal range (i.e., defined by an averaged Spearman's rank correlation coefficient  $\overline{r_s}$ ) from  $k$ -fold cross validation for each individual caribou by season; Boyce et al. 2002). We used the scale of seasonal range because 1) this is the scale most commonly used by management agencies, 2) all covariates are easily transferable to habitat maps, and 3) selection at larger spatial scales is typically easier to detect (McClellan et al. 1998, Apps et al. 2001). Models at the larger scale (i.e., without energetic cost) therefore should enable easier classification of resource selection strategies among individuals. If selection or avoidance of resources was similar among animals within a season, we pooled data on use and availability (Nielsen et al. 2002) and re-evaluated models (i.e., identified, selected, and validated most parsimonious models). We used the Wald's statistic to determine if the  $\beta_i$  differed from zero, which identified significant selection ( $\beta_i > 0$ ) or avoidance ( $\beta_i < 0$ ) of a resource (Boyce and McDonald 1999, Manly et al. 2002). We graphically evaluated selection coefficients of the best model(s) that differed from zero for similarities (i.e., value and sign of  $\beta_i$ ) within and between seasons. We used a log-linear model (Manly et al. 2002) to estimate RSFs by season.

To facilitate comparisons among caribou or between pooled models, however, we scaled the RSFs from 0 to 1 (RSF<sub>0-1</sub>; Boyce and McDonald 1999). Values approaching 1.0 indicated a greater likelihood of selection of a resource by caribou, whereas values nearing 0.0 indicated avoidance. We plotted RSF<sub>0-1</sub> values as a function of use data for continuous covariates (i.e., elevation, slope, and distance to areas of high wolf risk), using the best model when we held other covariates in the model constant. We qualitatively compared significant  $\beta_i$ s among caribou or between pooled models by season for aspect, fragmentation, and vegetation. We assumed significance of all tests at  $\alpha = 0.05$ . We used Stata for all statistical procedures (Stata 2001).

## **Results**

### **Reproductive Condition of Caribou, Collar Performance, and Movement**

Of the 25 female caribou we captured and collared, 24 were adults; 22 of 24 adult caribou were pregnant ( $\bar{x} = 91.7\%$ , binomial SE = 5.8%). Eleven of the 25 GPS collars on female caribou functioned as programmed from date of capture to 30 April 2002, but because  $>90\%$  of the locations for one animal was east of the GBPA, we used data for 10 individuals (8 pregnant, 2 nonpregnant) in our analyses. We captured 6 animals from 21–23 November and 4 animals on 18 and 19 December 2001. During winter and late winter, most (95.4%) concurrent GPS locations of these animals were  $>0.50$  km apart, but some (2.5%) were  $<0.10$  km apart. There were never  $>2$  animals within 0.10 km of each other, however, and they only remained together for short periods of time. Fix rates were high ( $\bar{x} = 91.3\%$ , SE = 2.1%), resulting in 3,254 locations (552 for nonpregnant animals) during winter and 2,123 locations (452 for nonpregnant animals) from late winter for analysis.

Movement rates were variable within and among individuals at all temporal scales (i.e., day, week, and month). Average monthly movement rates (m/h) declined from November ( $\bar{x} = 98$ , SE = 29.2) to April ( $\bar{x} = 39$ , SE = 12.3) (Jan:  $\bar{x} = 60$ , SE = 14.3; Feb:  $\bar{x} = 44$ , SE = 12.4; Mar:  $\bar{x} = 43$ , SE = 12.4).

### **Performance of Predation-Risk Models**

Most models for predation risk by wolf pack and season performed adequately (all  $\overline{r_s} > 0.70$ , all  $P < 0.024$ ) in the  $k$ -fold cross validation, with few exceptions. Variation was high in the use of resources among packs, but most packs selected for Shrubs (all  $\beta_i > 0.821$ , all  $P \leq 0.001$ ) and Burned-disturbed classes (all  $\beta_i > 0.605$ , all  $P \leq 0.004$ ), while avoiding Pine (all  $\beta_i < -0.743$ , all  $P \leq 0.027$ ) and Spruce (all  $\beta_i < -0.407$ , all  $P \leq 0.031$ ).

### **Relative Importance of Covariates and Scale**

The best core models for all caribou in all seasons at all scales cross-validated well (all  $\overline{r_s} > 0.69$ ; all  $P < 0.025$ ). At the scale of seasonal movement, wolf risk and distance to areas of high wolf risk contributed little information to the core model set as explanatory covariates of resource selection by caribou (all  $w_{+}[j] < 0.059$ ). Wolf risk was not a

parameter in any of the most parsimonious selection models for any caribou in either season. At the scale of seasonal movement, cost of movement (kJ/kg/hr) contributed the most information as an explanatory covariate in both seasons for 9 of 10 caribou (all  $w_+[j] > 0.912$ ). These individuals strongly minimized the energetic cost of locomotion in winter (pregnant:  $\bar{\beta}_i = -0.627$ ,  $\overline{SE} = 0.145$ , all  $P < 0.05$ ; nonpregnant:  $\bar{\beta}_i = -1.134$ ,  $\overline{SE} = 0.287$ , all  $P < 0.05$ ) and late winter (pregnant:  $\bar{\beta}_i = -1.157$ ,  $\overline{SE} = 0.371$ , all  $P < 0.05$ ; nonpregnant:  $\bar{\beta}_i = -1.804$ ,  $\overline{SE} = 0.417$ , all  $P < 0.001$ ).

At the scale of seasonal range, the relative importance of wolf risk varied among individual caribou but generally contributed little information to the core model set as an explanatory covariate during winter or late winter (all  $w_+[j] \leq 0.282$ ). We included wolf risk in the final models for only 3 caribou in both seasons. Conversely, distance to areas of high wolf risk was more important in models for most caribou in both seasons (all  $w_+[j] \geq 0.706$ ; winter,  $n = 8$ ; late winter,  $n = 7$ ).

### Effect of Scale on the Components of Predation Risk in Resource Selection

Wolf risk marginally improved the selected core models in winter and late winter (both  $\overline{\Delta AIC_c} > -1.574$ ) at the scale of seasonal movement but also increased the  $AIC_c$  for 6 animals in each season (Table 2). In contrast, at the scale of seasonal range, wolf risk (with few exceptions) generally improved the core models in winter ( $\overline{\Delta AIC_c} = -38.687$ ) and late winter ( $\overline{\Delta AIC_c} = -3.783$ ) (Table 2). Distance to areas of high wolf risk also generally improved the best core model for each caribou and season at the scale of seasonal movement (all  $\overline{\Delta AIC_c} < -2.935$ ) but provided redundant information (higher  $AIC_c$ ) for 3 animals in late winter (Table 2). At the scale of seasonal range, the distance covariate, with few exceptions, improved the core models in winter ( $\overline{\Delta AIC_c} = -54.424$ ) and late winter ( $\overline{\Delta AIC_c} = -17.301$ ) (Table 2).

Availability data for the components of predation risk (i.e., wolf risk and the distance to areas of high wolf risk) varied with the definition of scale (Fig. 2). In both seasons, the distribution of available points for wolf risk at the scale of seasonal movement shifted to the left (i.e., consistently lower in risk) of available points in the seasonal range. Conversely, the distribution of available points for the distance to areas of high wolf risk shifted to the right (i.e., farther from areas of high risk). Available points for 7 of the 10 caribou at the seasonal movement scale were lower in wolf risk than at the scale of seasonal range in both the winter and late-winter seasons (all  $P < 0.026$ ). Relative to the distance to high wolf-risk areas, available points at the scale of seasonal movement were farther away than at the scale of seasonal range for 7 caribou in the winter (all  $P < 0.002$ ) and for 5 caribou in the late winter (all  $P < 0.001$ ).

### Variation in the Selection of Resources Among Caribou

Although we noted variation among individual caribou in the selection for topographic variables and components of

wolf risk at the scale of seasonal range, we observed similar patterns in the selection of elevations (i.e., the direction of the quadratic form as determined by the signs [+ or -] of the squared and linear terms), slopes, and vegetation classes. Therefore, we pooled use and available data into 2 groups: animals that resided in the eastern (East,  $n = 2$ ) and mountainous (Mountain,  $n = 8$ ) regions of the GBPA. These pooled models cross-validated well in both seasons (Table 3).

**Elevation.**—Elevation was an important parameter for wintering caribou in both seasons (Table 3). Caribou in the East model showed greater selection for lower elevations in winter (Fig. 3a) and for relatively higher elevations (approx. 1,200–1,300 m) in late winter (Fig. 3b; all  $P < 0.001$ ). Mountain animals selected for higher elevations in both seasons (approx. 1,400–1,750 m) (Fig. 3a,b; all  $P < 0.001$ ).

**Slope.**—Slope was not an important parameter in the East model in winter (Table 3), whereas caribou in the Mountain model avoided steep slopes (Fig. 3c;  $P < 0.001$ ). In late winter, caribou in the East selected for steeper slopes and the Mountain animals selected for more moderate slopes (Fig. 3d; all  $P < 0.045$ ).

**Aspect and fragmentation of vegetation.**—Aspect was only important in the Mountain model in winter, but the selection coefficients for northness and eastness did not differ from zero (all  $P > 0.097$ ). Fragmentation was important only in the best East and Mountain models in winter (Table 3), but it was not a significant parameter for the East model (all  $P > 0.076$ ). Caribou in the Mountain model avoided areas of high fragmentation ( $\beta_i = -0.074$ ,  $SE = 0.032$ ,  $P = 0.022$ ).

**Vegetation.**—Vegetation class was important in resource selection in both seasons (Table 3). In winter, caribou in the East and Mountain models selected for the *Carex* spp., Riparian spruce, and Spruce classes (all  $P < 0.004$ ) (Fig. 4). Caribou in the East avoided Nonvegetated and Alpine classes (all  $P < 0.040$ ), whereas individuals in the Mountains selected the Alpine ( $P < 0.001$ ) and avoided Shrubs, Subalpine shrubs, and Burned-disturbed classes (all  $P < 0.001$ ) (Fig. 4). During late winter, caribou in the East selected for Shrubs ( $P < 0.001$ ) and avoided Pine ( $P = 0.003$ ). Caribou in the Mountains selected the Non-vegetated and Alpine types and avoided Subalpine shrubs and Burned-disturbed classes (all  $P < 0.001$ ) (Fig. 4).

**Components of predation risk.**—Wolf risk was not an important parameter in either the East or Mountain models in either season. Distance to areas of high wolf risk, however, was significant (all  $P < 0.032$ ) in both models in both seasons (Table 3). Responses to distance to areas of high wolf risk followed a Gaussian function (Fig. 3e,f). In winter, caribou selected for distances from high wolf-risk areas of approximately 0.50–2.25 km in the East and 0.50 to 1.50 km in the Mountains (Fig. 3e). In late winter, the East and Mountain models both indicated selection for distances of approximately 0.50–1.50 km from high wolf risk (Fig. 3f).



**Table 2.** Change in the Akaike's Information Criterion corrected for small sample size ( $\Delta AIC_c$ ) when we added the risk of wolf predation and distance to areas of high wolf risk to the most parsimonious core model for individual caribou by season (winter [Nov–Feb] and late winter [Mar–Apr]) and scale (seasonal movement and seasonal range) in the Greater Besa–Prophet area, northern British Columbia, Canada, 2001–2002.

Season	Caribou	$\Delta AIC_c$ (core models + risk of wolf predation)		$\Delta AIC_c$ (core models + distance to areas of high wolf risk)	
		Seasonal movement	Seasonal range	Seasonal movement	Seasonal range
Winter	2	1.553	-69.052	-8.558	-48.073
	6	-2.358	-3.510	-13.091	-121.435
	10	-11.347	-25.091	-24.010	-32.439
	11	-0.744	-3.594	-1.714	1.422
	16	1.923	-32.329	-8.639	-115.103
	17	4.641	-2.346	-2.506	-9.000
	20	0.729	-72.601	-3.842	-18.166
	22	0.749	-122.963	-5.406	-98.040
	23	1.740	-23.851	-7.101	-93.582
	25	-0.575	-31.535	-0.693	-9.823
	$\overline{\Delta AIC_c^a}$	-0.369	-38.687	-7.556	-54.424
Late winter	2	0.126	0.901	-10.192	-14.473
	6	-3.079	-1.812	1.477	-71.670
	10	-5.572	-11.667	-3.257	-8.077
	11	0.063	0.732	-12.849	-3.880
	16	1.903	3.391	-4.301	-21.433
	17	0.969	0.699	-1.540	-32.995
	20	-7.112	-4.090	-0.037	-10.024
	22	1.814	-27.296	1.776	1.167
	23	0.830	-0.513	1.013	-9.627
	25	-5.687	1.825	-1.444	0.699
	$\overline{\Delta AIC_c^a}$	-1.574	-3.783	-2.935	-17.031

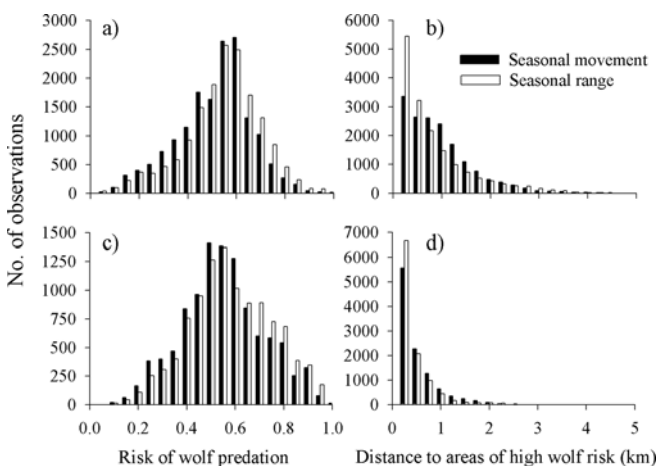
<sup>a</sup> Denotes the average contribution of information by a covariate for a season across all individuals.

## Discussion

Selection of resources varied among individual caribou in the highly diverse GBPA. Our interpretation of the relative importance of different factors contributing to resource selection by female caribou was scale-dependent and complicated by the variation in selection among individuals. Multiscale analyses, however, helped define mechanisms for selection strategies.

### Relative Importance of Predation Risk, Energetic Cost of Movement, and Scale

At the scale of seasonal movement, minimizing the cost of movement appeared to be more important to most caribou individuals in both seasons than predation risk, to which they generally did not respond. Other researchers also have identified minimizing the energetic cost of movement as the most important parameter in selection models for adult female caribou during interpatch movements at several temporal scales in winter (Johnson et al. 2002a). Nonpregnant individuals appeared to be more sensitive to minimizing costs in winter, and possibly late winter, than the pregnant animals, although our sample size was low for nonpregnant animals ( $n = 2$ ). Data from ultrasound measurements of back fat from animals in the GBPA (Gustine 2005) and necropsy data from Dauphiné (1976) showed that nonpregnant caribou have less fat than pregnant individuals do in winter. High mobility has high energetic costs associated with snow depth (Parker et al. 1984, Fancy and White 1987). Females in poorer condition might attempt to minimize energetic costs earlier in winter than animals with higher fat reserves, but in doing so, they may be unable to capitalize on food resources distributed over large areas (Barrett 1982). An increased sensitivity to minimizing energetic costs of movement and the trend toward reduced movement rates in late winter may be in response to changes in snow depth (Stuart-Smith et al. 1997), low or declining body condition (Dauphiné 1976), or reduced movement rates of wolves (B. Milakovic, University of Northern British Columbia, unpublished data). Our



**Figure 2.** Frequency distributions of wolf risk and distance to areas of high risk from availability data for female woodland caribou at 2 scales (seasonal movement and seasonal range) in winter (Nov–Feb, [a], [b]) and late winter (Mar–Apr, [c], [d]) in the Greater Besa–Prophet area, northern British Columbia, Canada, 2001–2002.



**Table 3.** Final pooled resource selection models at the scale of the seasonal range for female caribou during winter (Nov–Feb) and late winter (Mar–Apr) in the Greater Besa–Prophet area, northern British Columbia, Canada, 2001–2002.

Season	Pooled model	Selection model	$n^a$	$K^b$	LL <sup>c</sup>	AIC <sub>c</sub> <sup>d</sup>	$w_i^e$	$E_r^f$	$\bar{r}_s^g$	SE
Winter	East <sup>h</sup> ( $n = 2$ )	Distance to areas of high wolf risk <sup>2i</sup> + vegetation + elevation <sup>2</sup> + fragmentation	4,071	14	-1,536.4	3,101	0.29	1.00	0.840	0.020
		Distance to areas of high wolf risk <sup>2</sup> + vegetation + elevation <sup>2</sup>	4,071	12	-1,538.6	3,101	0.26	1.11	0.840	0.050
	Mountain ( $n = 8$ )	Distance to areas of high wolf risk <sup>2</sup> + vegetation + aspect + elevation <sup>2</sup> + slope + fragmentation	15,384	18	-6,108.0	12,252	0.51	1.00	0.980	0.010
Late winter	East ( $n = 2$ )	Distance to areas of high wolf risk <sup>2</sup> + vegetation + elevation <sup>2</sup> + slope <sup>2</sup>	2381	10	-944.6	1,909	0.89	1.00	0.790	0.040
	Mountain ( $n = 8$ )	Distance to areas of high wolf risk <sup>2</sup> + vegetation + elevation <sup>2</sup> + slope	10,296	14	-4,297.1	8,622	0.64	1.00	0.960	0.010

<sup>a</sup> Sample size.

<sup>b</sup> Number of parameters.

<sup>c</sup> Log-likelihood.

<sup>d</sup> Akaike's Information Criterion corrected for small sample size.

<sup>e</sup> Akaike weights.

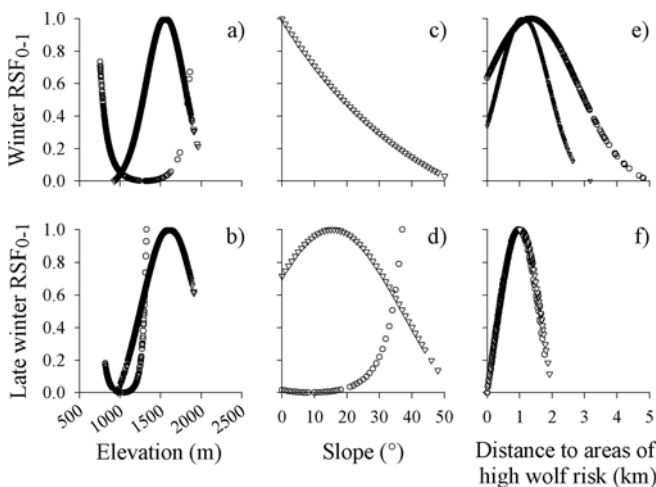
<sup>f</sup> Evidence ratio.

<sup>g</sup> Spearman's correlation coefficient from the  $k$ -fold cross validation ( $n = 5$ , all  $P$  for  $< 0.050$ ).

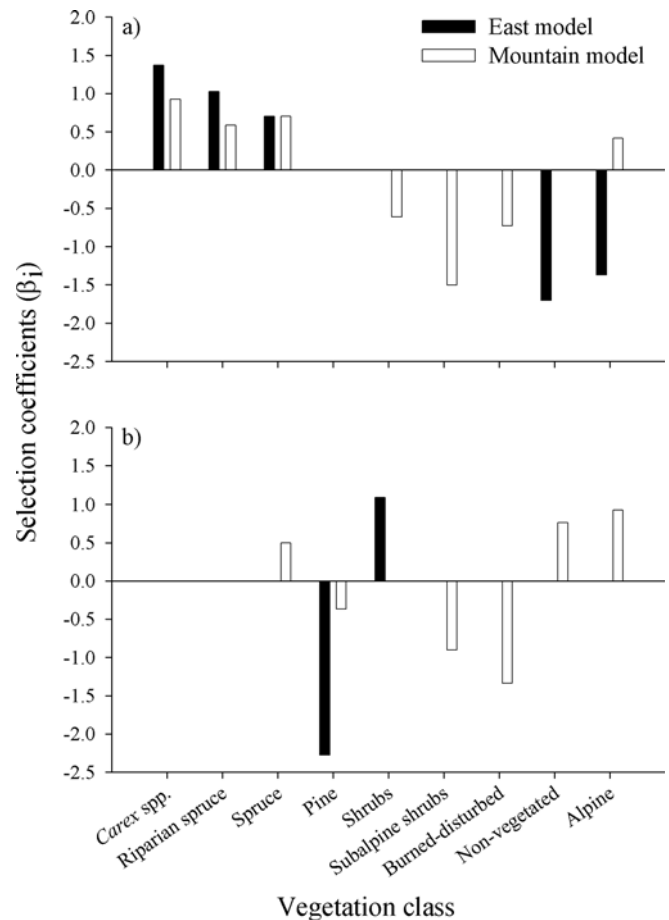
<sup>h</sup> Model was averaged as in Burnham and Anderson (2002:150–162).

<sup>i</sup> Squared terms include the linear term (e.g., elevation<sup>2</sup> = elevation + elevation<sup>2</sup>).

measure of the energetic cost of movement is conservative because we did not incorporate snow depths and steepness of slopes in the equations for cost. In rare cases when animal movements were beyond the 95th-percentile movement, the random distances chosen for available points would be relatively short, resulting in lower estimates of energetic cost. Therefore, given that we likely underestimated costs, the actual importance of minimizing energetic cost of movement in selection of resources by female woodland caribou in winter and late winter is probably even higher.



**Figure 3.** Relative likelihood of female woodland caribou selecting elevations (a), (b), slopes (c), (d), and distances to areas of high wolf risk (e), (f) during winter (Nov–Feb) and late winter (Mar–Apr) assuming other covariates are constant in the final resource selection models for animals living in the East (○) and Mountain (▽) regions of the Greater Besa–Prophet area, northern British Columbia, Canada, 2001–2002. Resource selection functions were scaled 0–1 (RSF<sub>0–1</sub>) as in Boyce and McDonald (1999) to evaluate selection of resources among individuals and pooled models. We did not include slope in the final pooled East model in the winter (c); points are data from Global Positioning System locations.



**Figure 4.** Strength of significant ( $P < 0.050$ ) coefficients of selection for the pooled resource selection models for woodland caribou living in the eastern (East,  $n = 2$ ) and mountainous (Mountain,  $n = 8$ ) portions of the Greater Besa–Prophet area during (a) winter (Nov–Feb) and (b) late winter (Mar–Apr), in northern British Columbia, Canada, 2001–2002.

At the scale of seasonal range, spacing out from areas of high wolf risk was an important parameter for female woodland caribou in both seasons. With few exceptions, the distance to high-wolf-risk areas contributed substantial information to final resource-selection models. Wolf risk provided little additional information to the core model set in winter, although its importance increased in late winter. These data support the importance of increasing the distance to high-risk areas at larger scales (Bergerud 1992, James 1999, Rettie and Messier 2000), but as in Johnson (2000), they also support the importance of minimizing the energetic cost of movement by female woodland caribou in a mountainous environment in the winter and late winter months. Because of the impracticality of defining the energetic cost of movement at such a large scale, we were unable to conclude which parameter was more important in selection of seasonal ranges by caribou.

Given that the spatial scale of availability had a prominent effect on the importance of the components of predation risk in the selection of resources by female caribou, researchers should consider it when evaluating any inferences from RSFs (McClellan et al. 1998). Caribou made selection decisions in a hierarchical fashion (Johnson 1980), with increased sensitivity to components of predation risk at the larger scale (Johnson 2000, Rettie and Messier 2000). The distributions of availability data were sensitive to scale (Fig. 2), suggesting that at the scale of seasonal movement, caribou had already selected areas lower in wolf risk and farther from areas of high wolf risk within the seasonal range (Ferguson et al. 1988, Rettie and Messier 2000). There were some inconsistencies in attributes of availability between scales among individuals, suggesting further that individuals respond variably to wolf risk at different spatial scales. Differential responses to wolf risk could be due, in part, to body condition, because females in poorer condition may take a higher predation risk in their wintering foraging strategy to slow the depletion of body reserves throughout the winter (Clark 1994, Lima 1988, Skogland 1991, Sweitzer 1996). A female with more body reserves could afford to have reduced intake in a relatively safer area. Finer scale data on body condition (e.g., change in body reserves throughout the winter months) and predation risk are necessary to evaluate this asset-protection hypothesis (Clark 1994).

### **Variation in the Selection of Resources Among Caribou**

Use of resources by woodland caribou populations typically varies among regions (Cichowski 1993, Wood 1996, Johnson 2000, Poole et al. 2000). This may result, in part, from different availability of resources (Garshelis 2000) and different distributions of predators among regions (Seip 1998). It is also difficult to compare patterns in resource selection by caribou in the GBPA to areas with less topographic relief east of the Rocky Mountains (e.g., Gaspé Peninsula, Mosnier et al. 2003) or with increased industrial disturbance (e.g., northern Alberta, Canada; James and Stuart-Smith 2000) where land-management activities have

altered distributions of other ungulates and large carnivores. Historic industrial activity in the eastern portion of the GBPA may have affected selection of habitats by caribou, but we assumed that higher predation risk would reflect this (i.e., distance to linear features in wolf-risk models; James and Stuart-Smith 2000). Currently, the GBPA is mostly free of industrial activity during winter, and therefore, we did not include distance to anthropogenic edge in selection models for caribou. We primarily compared our results with the few studies that have examined both biotic and abiotic factors in the selection of resources in the winter by the northern ecotype of woodland caribou in British Columbia (Cichowski 1993, Wood 1996, Johnson 2000, Poole et al. 2000, Zimmerman et al. 2002). Additionally, because of our small sample size, we focused discussion on the strongest patterns in selection behavior.

*Elevation, slope, aspect, fragmentation, and vegetation.*—There were both similarities and differences in the selection of topographic, vegetation, and wolf-risk variables for animals in the eastern (i.e., East model) and more mountainous (i.e., Mountain model) regions of the GBPA. Although caribou in both regions selected for the *Carex* spp., Riparian spruce, and Spruce classes in winter (Fig. 4a), this selection occurred at different elevations, and caribou in the mountains avoided steeper slopes (Fig. 3a,c). Selection for these vegetation classes, elevations, and slopes was similar to caribou near Takla Lake (Poole et al. 2000) and in the Tweedsmuir-Entiako, Itcha-Ilgachuz, and Rainbow herds (Cichowski 1993). Studies on those herds suggested that animals may have foraged on arboreal lichens and sedges (*Carex* spp.), but we conducted no feeding-site investigations and did not observe stands with abundant arboreal lichens in the GBPA. As noted in Johnson et al. (2000), sedges may be an important source of supplemental protein (Skoog 1968) to lichen diets typically low in protein and high in digestible energy (Russell et al. 1993). Not surprisingly, animals in the east did not select for Non-vegetated and Alpine classes because of the relatively flat boreal forest landscape, whereas mountain-dwelling individuals avoided Shrubs, Subalpine shrubs, and Burned-disturbed classes (Fig. 4a). Selection against the Subalpine shrubs and Burned-disturbed classes occurred in both seasons, which was likely in response to predation risk because wolf packs consistently selected these vegetation classes in the GBPA (Gustine 2005). Researchers have documented avoidance by caribou of areas burned within 50 yr in Alaska (Joly et al. 2003) and Manitoba (Schaefer and Pruitt 1991). In the short term, burns appear to negatively affect population productivity either directly (i.e., loss of forage; Seip 1990) or indirectly (e.g., increases in moose populations and wolves; Bergerud and Elliot 1986, Seip 1991), but fires may benefit caribou in the long term (>100 yr; Klein 1982).

In late winter in the GBPA, caribou avoided the Pine vegetation class, and instead selected for Shrubs (Fig. 4b) at 1,200–1,300 m on steeper slopes (Fig. 3b,d) in the east, and for Spruce, Alpine, and Nonvegetated classes (Fig. 4b)

between 1,400–1,750 m on moderate slopes (Fig. 3b,d) in the mountains. The strong avoidance of Pine was in contrast to other research on woodland caribou in winter (Cichowski 1993, Wood 1996, Johnson 2000) and the lack of mature, lichen-producing pine stands in the GBPA may be a partial explanation for this avoidance. Animals in the mountains that selected the Nonvegetated and Alpine classes may have benefited from terrestrial lichens in windswept areas (Cichowski 1993, Wood 1996), lower predation risk (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1991, 1992), or both.

**Components of predation risk.**—Caribou were not sensitive to modeled wolf risk but instead responded to distances to areas of high wolf risk (James 1999). In both seasons, animals did not respond to this parameter in a linear fashion. Instead, selection fit a Gaussian function (Fig. 3e,f). Caribou likely did not perceive distances past a threshold (i.e., the slope of the Gaussian function begins to approach zero) as safer. Their responses probably related to other components of habitat, such as feeding areas, where animals could not disperse themselves the farthest away from areas of high wolf risk all the time. In late winter, caribou in both the East and Mountain models showed a remarkably similar response in selecting for areas approximately 0.50–1.50 km away from areas of high wolf risk. Dyer et al. (2001) observed avoidance distances (0.25–1.00 km) that were comparable. The importance of spacing out from areas of high wolf risk in resource selection at the scale of seasonal range is consistent with other research on caribou (Bergerud 1992, James 1999, Rettie and Messier 2000).

### **Interpreting Resource Selection Between Scales**

Modeling resource selection at one scale would have severely limited interpretation of our selection models (Wiens 1989, Levin 1992). Our two definitions of availability were within Johnson's (1980) third order of selection but still resulted in different interpretations of responses by caribou to biological (i.e., energetic cost of movement) and ecological factors (e.g., predation risk). For example, selection at the scale of seasonal movement suggested that components of wolf risk were unimportant to female woodland caribou, whereas at a larger spatial scale, the importance of spacing out from areas of high wolf risk was apparent (Bergerud 1992, James 1999).

Interpreting the importance of modeled risk was difficult, particularly in the framework of the information-theoretic approach. We modeled wolf risk using the same covariates that we included in the model set to determine resource selection for caribou. Although no variables were strongly collinear, the continuous risk covariate might have contributed little additional information to the suite of covariates already in the model (i.e., if animals selected against wolf risk, a suite of habitat factors within the most parsimonious models may have already provided refugia from predation; Burnham and Anderson 2002). For all individuals, the models with risk as the only covariate were never the most parsimonious in the model set.

Modeling resource selection by individuals, as well as

pooled strategies, with a small sample size may have introduced bias into availability data. Small sample sizes with restrictive definitions of availability increase sensitivity of models to lower variation in biotic and abiotic factors in use and availability data (i.e., spatial autocorrelation; Apps et al. 2001, Nielsen et al. 2002, Boyce et al. 2003), to rare cases of categorical covariates (e.g., vegetation; Menard 2002), and in individual animal responses to unidentified habitat factors at finer scales (Johnson 2000). Spatial autocorrelation could be an artifact of restrictive definitions of availability (e.g., reduced movement would lead to smaller areas of availability) or of the sociality of animals within a sample. Animals that herd together may artificially inflate sample size and therefore lead to bias in coefficients of selection for pooled models. Because of the small sample (approx. 2.5%) of concurrent GPS locations of caribou that were near each other (<0.10 km) and the small numbers of animals together (2) at one time, it is highly unlikely that our inclusion of these data biased estimates of pooled models. Future studies may clarify these issues as more researchers examine the sources of variation in selection behavior among individuals in a population. Another concern for interpreting model results includes bias in locational data, which may lead to an increase in Type I (overestimate selection) or Type II (underestimate selection) error rates (Frair et al. 2004). Our fix rates were high ( $\bar{x} = 91.3\%$ ), which suggested low bias (Frair et al. 2004), although some locational bias was probably present for individuals with the lowest fix rates.

Before pooling use and availability data, researchers should quantify variation in the selection of resources among individuals (Thomas and Taylor 1990, White and Garrott 1990, Aebischer et al. 1993). Quantifying variation among individual animals is an important first step in modeling resource selection for a population (White and Garrott 1990, Aebischer et al. 1993). We based our justification for pooling models on large-scale geographic differences in abiotic factors, and on similarities in the selection of biotic and abiotic factors. By grouping animals, we placed subjective constraints on what appeared to be a selection strategy. Not identifying commonalities in selection among groups of individuals, however, probably would have provided a model with little biological or potentially predictive value (Nielsen et al. 2002). Animals that resided in the flatter eastern portion of the GBPA clearly responded to abiotic factors differently than animals living in the mountainous region. If we pooled our data into one model set that incorporated locations from animals in the east and in the mountains, it is likely that we never would have identified the varied responses to topography, vegetation, and elevation.

Variation in resource selection among individual caribou is a source of concern relative to the utility of pooled models, particularly in the context of interpreting mechanisms behind selection (Aebischer et al. 1993). This variation may be important to ecosystem integrity and researchers should address this in study design, model formulation



(Nielsen et al. 2002), and associated conservation tools (e.g., maps). One of the benefits of RSFs is that researchers can examine variation in selection among individuals within a particular time period, yet researchers rarely conduct or rarely publish Type III designs (Thomas and Taylor 1990) for large mammals (Nielsen et al. 2002). Selection of resources probably varies with year, month, age, sex, reproductive condition, experience, predation risk, body condition, as well as scale of the investigation and corresponding definitions of availability. Researchers modeling selection of resources by large herbivores should account for as many of these variables as possible prior to pooling locational data among individuals within a population. Models from pooled data are essentially an average animal, but prior to pooling, researchers should identify whether an average animal properly represents the population in question (White and Garrott 1990, Aebischer et al. 1993). We recommend that even with some of the above concerns, future studies should interpret selection for ecological factors within and across individuals at multiple scales (Wiens 1989, Aebischer et al. 1993). Identifying scale-dependent responses is most likely to help us understand the mechanisms behind selection of resources (Wiens 1989, Danell et al. 1991).

## Management Implications

Caribou in the GBPA responded to habitat factors at multiple scales during winter. At a small scale defined by

typical movement rates, they were influenced strongly by energetic costs of travel. At the larger scale of their seasonal range, increasing the distance from areas of high wolf risk was more important. These findings have implications for managers relative to the impacts of disturbance on wintering caribou at both small and large scales. Even though there was variability among individuals, there were 2 general patterns of selection for elevations, slopes, and vegetation classes. These patterns distinguished caribou that resided in the eastern region from those in the more mountainous region of the GBPA. Our multiscale analyses should help managers better identify areas of high value for both selection strategies.

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