Multiscale Habitat Use by Wolverines in British Columbia, Canada

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ABSTRACT Wolverine (*Gulo gulo*) distribution in British Columbia, Canada, includes multiple-use lands where human use and resource extraction may influence habitat selection. We evaluated seasonal habitat use by resident adult wolverines using radiotelemetry locations from 2 multiple-use landscapes in British Columbia. Food, predation risk, and human disturbance hypotheses were considered in logistic regression analyses of used and random landscapes. Male wolverine habitat associations were most supported by the food hypothesis in both summer and winter. Moose (*Alces alces*) winter ranges, valley bottom forests, and avalanche terrain were positively associated with winter male wolverine use. Habitat use by male wolverines in winter was also negatively associated with helicopter skiing areas in the Columbia Mountains. Habitat associations of females were more complex; combinations of variables supporting food, predation risk, or human disturbance hypotheses were included in most supported models from both summer and winter in both study areas. Females were associated with alpine and avalanche environments where hoary marmot (*Marmota caligata*) and Columbia ground squirrel (*Spermophilus columbianus*) prey are found in summer. Roaded and recently logged areas were negatively associated with female wolverines in summer. In the Columbia Mountains, where winter recreation was widespread, females were negatively associated with helicopter and backcountry skiing. Moose winter ranges within rugged landscapes were positively associated with females during winter. Our analysis suggests wolverines were negatively responding to human disturbance within occupied habitat. The population consequences of these functional habitat relationships will require additional focused research. Our spatially explicit models can be used to support conservation planning for resource extraction and tourism industries operating in landscapes occupied by wolverines. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2180–2192; 2007)

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Wolverines are widely distributed across most of British Columbia, Canada, and in mountainous regions of the northwestern United States (Aubry et al. 2007, Lofroth and Krebs 2007). Relatively low densities, poorly understood habitat requirements, and increasing human pressures in wolverine range present conservation challenges to wildlife managers (Banci 1994, Weaver et al. 1996). Previous analyses have considered terrain (slope, aspect, elevation) and vegetation (tree species, forest age, nonforest types) to assess habitat selection (Hornocker and Hash 1981, Whitman et al. 1986, Banci and Harestad 1990). Although results describe patterns of use and avoidance in particular study areas, an approach that emphases functional understanding of habitat selection by wolverines would better support land use decision making and provide a strong base for conservation planning (Ruggiero at al. 1994, Boyce et al. 2002). We developed three nonexclusive hypotheses based on food, predation risk, and human disturbance to explain seasonal habitat selection by male and female wolverines.

The influence of food, particularly winter carrion, on wolverine survival and reproduction has been well documented (Hornocker and Hash 1981, Magoun 1985, Persson 2005, Lofroth et al. 2007). Ungulate (moose [*Alces alces*], caribou [*Rangifer tarandus*], mountain goat [*Oreamnos americanus*], mule deer [*Odocoileus hemionus*], elk [*Cervus elaphus*]) carrion from predator kills, starvation, avalanches, and other sources sustains wolverines in winter (van Zyll de Jong 1975). Winter food supplementation increased reproductive success of adult female wolverines in Sweden (Persson 2005), suggesting reproduction is food limited. Seasonal shifts to higher elevations in summer by male and female wolverines may be a response to seasonal changes in prey distributions (Hornocker and Hash 1981, Whitman et al. 1986, Banci and Harestad 1990, Copeland 1996, Landa et al. 1998). During summer, when ungulates are widely dispersed, alpine- and subalpine-associated sciurids (*Marmota* spp., *Spermophilus* spp.) and bird prey compose a greater proportion of wolverine diet (Magoun 1987, Landa et al. 1997). Our food hypothesis predicts winter use of habitats where ungulate carrion and small mammal prey are available (Lofroth et al. 2007). Ungulate winter ranges (moose, caribou, mountain goat), avalanche paths, and early seral vegetation present in recently logged areas, as well as young forests that support snowshoe hare (*Lepus americanus*) and porcupine (*Erethizon dorsatum*) were expected to be selected by male and female wolverine. We expected that alpine and subalpine–avalanche habitats would be used by wolverines in summer due to the abundance of hoary marmots (*Marmota caligata*); Harrower 2001, Lofroth et al. 2007) and Columbia ground squirrels (*Spermophilus columbianus*) in these areas. We expected that barren habitats, such as glaciers, snow, and rock, supporting very limited prey resources, would be avoided by wolverines during all times of the year.

Predation risk also has been suggested as a factor influencing habitat use by wolverines, especially reproductive females (Magoun and Copeland 1998). Reproductive female

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wolverines are likely under greater energetic and predation pressures than males due to high costs of lactation (Iversen 1972, Persson 2005) and vulnerability of neonates before dispersal (Magoun and Copeland 1998). These differences may be expressed through different patterns of habitat selection. Wolves (*Canis lupus*) have been observed killing adults (Boles 1977) and digging up and killing wolverine young from their natal dens (Burkholder 1962). In contrast to the food hypothesis, the predation risk hypothesis predicts negative habitat associations where access to food comes with a significant risk. In winter, we expected wolverines to avoid ungulate winter ranges, where wolves and cougars (*Puma concolor*) spend the majority of their time, to reduce the probability of encounter with these predators (Allison 1998, Stotyn and Serrouya 2005). We expected positive association with rugged, complex terrain where security is presumably greater (Magoun and Copeland 1998). Under the predation risk hypothesis, we also expected wolverines to avoid roads in winter, because roads may increase predator access to areas in winter (Thurber et al. 1994). During summer, when predator movements are not constrained by snow, we expected roads to be neutral with respect to predation risk.

Studies in North America (Hornocker and Hash 1981, Weaver et al. 1996, Carroll et al. 2001, Rowland et al. 2003) and Scandinavia (May et al. 2006) have suggested that wolverines avoid human activity. Roads, human infrastructure, and human population density are associated with wolverine distribution at broad scales, and they may influence habitat use by individual wolverine at finer scales. Our human disturbance hypothesis predicts negative response by wolverines to human activities, due to potential direct displacement by humans or by motorized vehicles during both winter and summer. We expected wolverines to favor roadless areas year-round and to avoid intensive winter recreation (e.g., skiing and snowmobiling) areas during winter.

We used data from 2 independent wolverine studies completed in British Columbia to 1) evaluate food, predation risk, and human disturbance as hypotheses explaining sex- and season-specific wolverine habitat selection, and 2) develop resource selection function models of wolverine habitat use for land management planning.

STUDY AREA

We collected data between 1995 and 2003 from 2 study areas in British Columbia: Omineca Mountains in north-central British Columbia and Columbia Mountains in southeastern British Columbia (Fig. 1).

The 8,900-km^2 Omineca Mountains study area was located in the Williston Reservoir Basin in north-central British Columbia (Fig. 1). It included Sub-Boreal Spruce, Boreal Black and White Spruce, Spruce–Willow–Birch, Englemann Spruce-Subalpine Fir, and Alpine Tundra biogeoclimatic zones (Pojar and Meidinger 1991). Low-elevation forests were dominated by white spruce (*Picea glauca*), black spruce (*Picea mariana*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). High-elevation forests were primarily Engelmann spruce (*Picea engelmanii*) and subalpine fir. Alpine habitats were dominated by herbaceous meadows, tundra, and nonvegetated communities. Elevations ranged from 675 m to 2,200 m. Extensive forest harvesting, with associated major forestry roads, had occurred in the eastern and northern portions of the study area. The western and southern portions of the study area had relatively little forest harvesting. The study area was bordered on the east by a hydroelectric reservoir (Williston Lake).

The Columbia Mountains study area encompassed 7,000 km^2 of rugged mountainous terrain in the interior wet-belt of southern British Columbia (Fig. 1). Elevation varied from 460 m to 3,385 m. The study area included Interior Cedar–Hemlock, Engelmann Spruce–Subalpine Fir, and Alpine Tundra biogeoclimatic zones (Pojar and Meidinger 1991). Valley bottoms were dominated by dense stands of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Mid- to upper elevations were covered in Engelmann spruce and subalpine fir. Alpine environments were covered by herbaceous meadow, low shrub, tundra, or nonvegetated habitats. Avalanche chutes were common due to steep topography. Extensive forest harvesting had occurred within a large portion of the study area. The study area contained a transportation corridor and a hydroelectric reservoir (Lake Revelstoke). Winter recreation, particularly helicopter skiing, snowmobiling, and backcountry skiing, is a growing sector of the local economy. Fifteen percent of the study area was within Revelstoke and Glacier National parks.

Moose, caribou, and small numbers of mountain goat represented the available large prey in the Omineca Mountains study area. Medium and small prey included hoary marmot, beaver (*Castor canadensis*), red squirrel (*Tamiascurus hudsonicus*), flying squirrel (*Glaucomys sabrinus*), porcupine, and a number of species of mice (*Peromyscus* spp.), shrews (*Sorex* spp.), and voles (*Microtus* spp.). Six species of grouse (*Dendragapus* spp.; *Bonasa umbellus*) and ptarmigan (*Lagopus* spp.) occurred there. Large prey occurring in the Columbia Mountains study area included caribou, moose, elk, mountain goat, and mule deer. Medium- and small-sized prey included hoary marmot, Columbia ground squirrel, red squirrel, flying squirrel, beaver, porcupine, and a number of species of mice, shrews, and voles. Three grouse and one ptarmigan species also were present. Wolves were the main year-round predator present in both study areas, and cougar were present in low numbers in the Columbia Mountains.

METHODS

Wolverine Capture and Monitoring

We captured wolverines during winter–early spring (Jan–Apr) each year using modified box traps (e.g., Copeland 1996, Krebs and Lewis 2000, E. C. Lofroth, British Columbia Ministry of Environment, unpublished data) or barrel traps (Hornocker and Hash 1981, Banci 1987). Traps

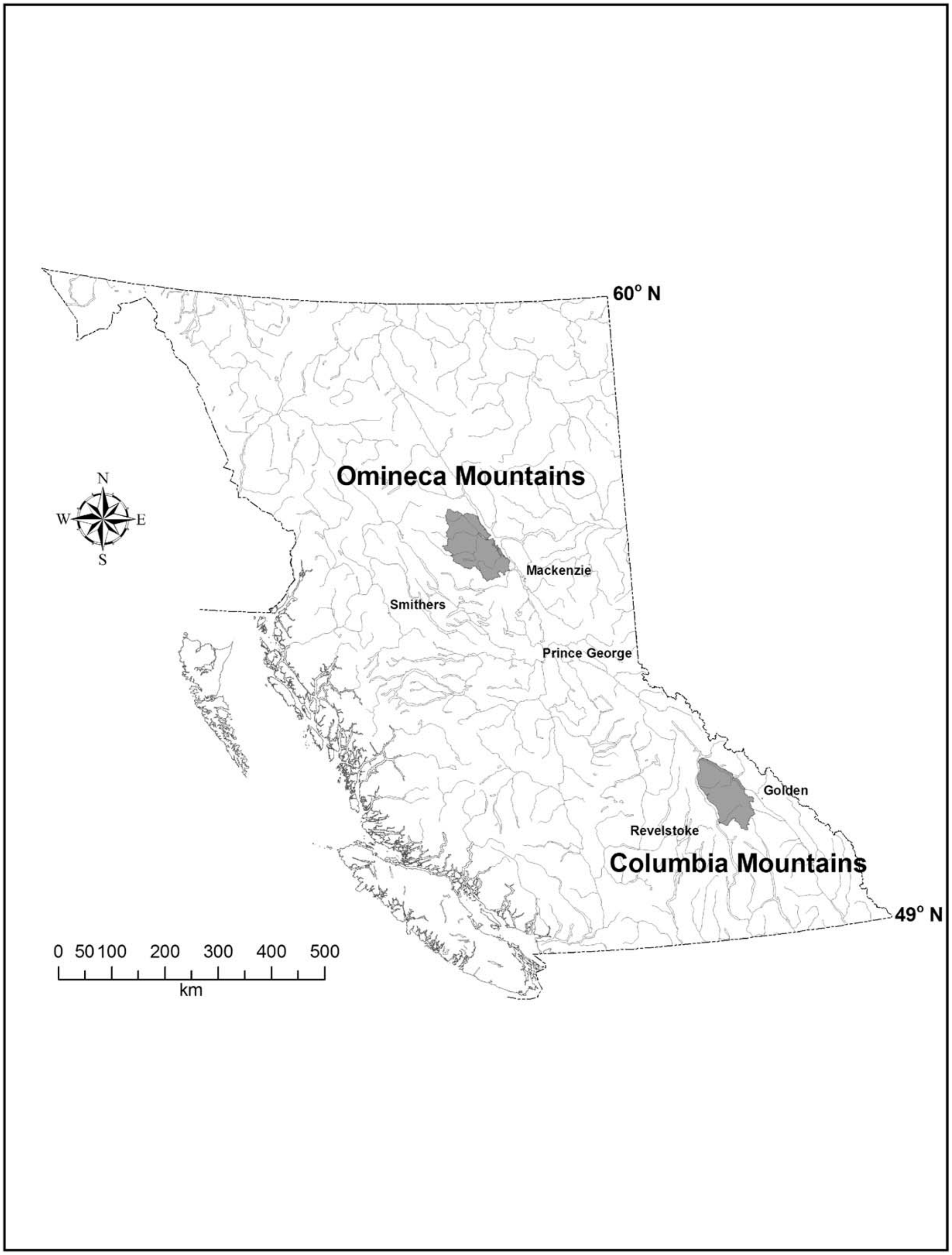

Figure 1. Location of Omineca Mountains and Columbia Mountains study areas for wolverine in British Columbia, Canada 1995–2003.

were located in areas where we thought captures were most likely to occur and in areas that were logistically accessible. We immobilized wolverines using ketamine hydrochloride (HCl; e.g., Hash and Hornocker 1980; Copeland 1996) or mixtures of tiletamine HCl and zolazepam HCl (e.g., Golden et al. 2002), delivered via a pole syringe or blow pipe. Wolverines were radiomarked with Telonics MOD335 very high frequency radiocollars (Telonics, Inc., Mesa, AZ) or surgically implanted with Telonics IMP300 or IMP400 radiotransmitters by a veterinarian. Radiotransmitters were equipped with mortality sensors. All handling procedures followed approved Canadian Council

Table 1. Number of adult wolverines monitored, 95% adaptive kernel (ADK) home ranges and number of radiotelemetry locations and standard errors by sex and season in the Columbia and Omineca Mountain study areas, British Columbia, Canada, 1995–2003.

Study	Sex	Season	Animals	Locations	$\bar{x}$	SE	ADK 95% (km^2)
Columbia	F	Summer	13	486	37	4.5	325
	F	Winter	13	397	31	3.3	
	M	Summer	7	197	28	6.0	772
	M	Winter	7	202	29	5.6	
Subtotal				1,282			
Omineca	F	Summer	10	272	27	6.1	405
	F	Winter	10	260	26	6.3	
	M	Summer	9	131	15	3.9	1,366
	M	Winter	9	180	20	4.7	
Subtotal				843			
Total				2125			

on Animal Care Guidelines and British Columbia Government and Parks Canada animal care protocols.

We classified wolverines as subadults ($\leq$2 yr old) or adults ($>$2 yr old) on the basis of premolar or canine (postmortem) tooth section characteristics, tooth wear, presence of cataracts, pelage appearance, or nipple and testes size (Magoun 1985). We considered adults only in this analysis.

Wolverines were monitored from the air at least every 2 weeks. Locations were recorded on 1:40,000 air photos and 1:50,000 topographic maps to generate Universal Transverse Mercator coordinates (Columbia Mountains) or directly onto 1:20,000 orthophotos (Omineca Mountains). Accuracy was estimated to be 95% within 400 m (Apps et al. 2001) for Columbia Mountains data and 95% within 200 m within the less rugged Omineca Mountains study area (Lofroth 2001). We divided the telemetry data set into summer and winter seasons based on prey availability and wolverine reproduction (Table 1). Summer season commenced in mid- to late May with the emergence of marmots from winter hibernation and the conclusion of natal den use by female wolverines. Summer concluded when marmots began hibernation (Oct). The winter season was the period when there was persistent snow cover at treeline. Winter season was slightly longer in the Omineca Mountains study area due to a cooler, more boreal climate.

Habitat Variables

Habitat data for each study area were assembled as a series of 100-m resolution raster grids in a Geographical Information System (GIS). The data consisted of human use, land cover, winter prey distribution, and terrain variables (Table 2). ArcInfo software on UNIX and Windows operating systems was used for all GIS applications. With the exception of winter recreation variables, choice of source data was limited to those with continuous coverage across both study areas. We developed predictions for food, predation risk, and human disturbance hypotheses to explain habitat associations of wolverines.

We used the low-elevation forest zone (Interior Cedar Hemlock; Pojar and Meidinger 1991) as a surrogate for winter small mammal prey (Houde 1997) in the Columbia Mountains. In the Omineca Mountains, where beavers were a common prey item (Lofroth et al. 2007), we generated a surrogate for a riparian habitat by buffering 1:20,000 terrain resources information management (TRIM; Surveys and Resource Mapping Branch 1992) basemap streams, rivers, and lakes by 100 m. We obtained 1:20,000 ungulate winter range and mountain goat winter range polygons derived for land use planning from aerial surveys and track transects (Serrouya and D'Eon 2002) from British Columbia Government (Integrated Land Management Bureau, Ministry of Agriculture and Lands, Victoria, BC, Canada). Caribou winter range was estimated as 75% adaptive kernel probability polygons of caribou winter telemetry points gathered between 1992 and 2001 (Apps et al. 2001; S. McNay, Wildlife Infometrics, unpublished data). These polygons represented the main winter concentrations of caribou use concurrent with radiotagged wolverines.

We used Landsat Thematic Mapper (Surveys and Resource Mapping Branch 1995) to depict alpine and subalpine–avalanche summer prey habitats as well as glaciers, rock, and barren habitats within both study areas.

We used a Ruggedness Index (Beasom et al. 1983) based on 100-m contours available in 1:20,000 TRIM basemaps to depict security habitat. The index measures the density of contour lines, yielding higher values in steep broken, gullied terrain than in homogenous steep or gentle terrain.

Human use variables included those associated with winter recreation activity, roads, and forest harvesting. Winter recreation data included estimates of snowmobiling, backcountry skiing, and helicopter skiing in the Columbia Mountains study area. Snowmobiling areas included primary use sites mapped as polygons by British Columbia Ministry of Environment at 1:20,000 scale. Helicopter skiing run locations were provided as 1:20,000 GIS polygon coverages by the 2 helicopter skiing companies operating within the Columbia study area. Backcountry ski use was centred on the Trans Canada Highway corridor within and adjacent to Mount Revelstoke and Glacier National parks. In conjunction with National Park staff, we developed ski

Table 2. Human use, prey distribution, and terrain variables considered in wolverine seasonal habitat use analysis of telemetry data collected in Columbia and Omineca mountains, British Columbia, Canada, 1995–2003. Predictions are grouped under food, predation risk, and human disturbance hypotheses. Positive (+) or negative (–) predicted associations are indicated.

		Food		Predation risk		Human disturbance	
Variable	Description	Winter	Summer	Winter	Summer	Winter	Summer
Prey distribution							
Moose	% winter range	+		–			
	% recently logged	+		–			
Caribou	% winter distribution	+					
Mountain goat	% winter range	+					
Avalanche kill ungulate	% avalanche	+					
Marmot	% alpine		+				
	% avalanche		+				
Snowshoe hare (Omineca only)	% recently logged	+		–			
Small mammal (Columbia)	% interior Cedar Hemlock	+					
Beaver (Omineca)	% buffered H_2O	+	+				
All	% glacier, snow, rock	–	–				
Terrain							
Ruggedness	Index			+	+		
Human use							
Snowmobiling and backcountry skiing (Columbia only)	% use polygons					–	
Heli skiing (Columbia only)	% ski runs					–	
Roadless	% roadless			+		+	+

use polygons on 1:50,000 topographic maps using field knowledge of access points, trails, and day use areas and aerial observations of ski tracks during telemetry flights. We made no attempt to categorize intensity of use for any winter recreation variables. Winter recreation was nonexistent in the Omineca Mountains; therefore, it was not considered in the analysis. We combined road data from 1:20,000 TRIM (Surveys and Resource Mapping Branch 1992) and from data sets of forest roads (British Columbia Ministry of Forests, Resources Inventory Branch 1995), and then we edited and augmented the resulting data set using our field knowledge. These vector data were converted to a simple 2-class raster grid depicting roaded and roadless areas (Ferguson et al. 2003). We used baseline thematic mapping data that classifies land cover at scale 1:250,000 using Landsat Thematic Mapper satellite imagery (Surveys and Resource Mapping Branch 1995) to characterize recently logged areas, young forest, old forest, alpine, glacier–snow–rock, subalpine–avalanche habitats (Table 2). Minimum polygon size was 15 ha.

Analysis Approach

We followed Apps et al. (2001) scale-dependent approach, except we evaluated 3 scales instead of 4. Scales were defined based on distances between sequential independent radiotelemetry locations taken ≥1 day apart. The distance between sequential radiolocations did not vary by season ($F = 3.68$, df = 1, $P = 0.06$), but it was greater for males than females ($F = 236.27$, df = 1, $P < 0.001$), and it was greater for Omineca Mountain than Columbia Mountain wolverines ($F = 18.39$, df = 1, $P < 0.001$; Fig. 2). Accordingly, at the broadest scale considered (landscape), we used the 95th percentile of the distance between sequential telemetry locations by study area and sex to establish paired random point separation from telemetry points (Table 3). We considered this to be the maximum radius potentially available to individual wolverines. A factor of 0.3 was applied to this distance to obtain the meso scale, which in turn was multiplied by 0.3 to obtain the fine-scale distance

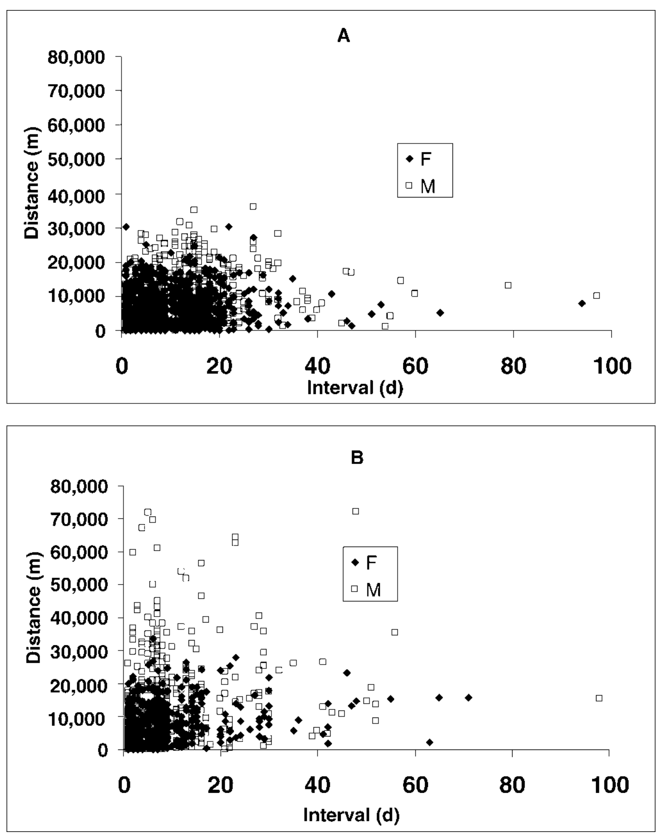

Figure 2. Distance (m) and interval (d) between sequential radiotelemetry locations for male and female wolverines monitored in (A) Columbia Mountains, British Columbia, Canada, 1995–2003, and (B) Omineca Mountains, 1995–2002.

Table 3. Scale definitions for multiscale analyses of habitat selection by wolverines in the Columbia and Omineca mountains, British Columbia, Canada. Distance refers to the separation between used and available sample points. At landscape scale, the distance equals the 95% movement distance between sequential radiotelemetry locations. Radius refers to the circle within which habitat composition is measured (Apps et al. 2001).

Sex	Scale	Columbia distance (km)	Columbia radius (km)	Omineca distance (km)	Omineca radius (km)
M	Landscape	25.2	7.6	37.1	12.4
	Meso	7.6	2.3	12.4	4.2
	Fine	2.3	0.7	4.2	1.4
F	Landscape	16.8	5.0	18.8	6.3
	Meso	5.0	1.5	6.3	2.1
	Fine	1.5	0.5	2.1	0.7

between used and random points. Although the multiplier chosen was arbitrary, it ensured that the radius of the finest scale of analysis was similar or greater than the 95% confidence interval telemetry error (Apps et al. 2001). To acknowledge the structural characteristics of the wolverine population (e.g., occupation and defense of multiannual home ranges), we applied a constraint that at the meso and fine scale, available points had to fall within the individual wolverine's 95% adaptive kernel home range.

Each habitat grid was summarized within a circle around each used and available point at the 3 scales. The radius of this circle equalled the distance between used and random points for that scale multiplied by 0.3. For example, landscape scale use and random points for Columbia males were separated by 25.2 km, and habitat composition was measured in a circle 7.6 km around each point (Table 3; Fig. 3). Large hydroelectric reservoirs that formed portions of the edges of both study areas were not considered available habitat in the analysis. We tabulated the data and exported them from the GIS.

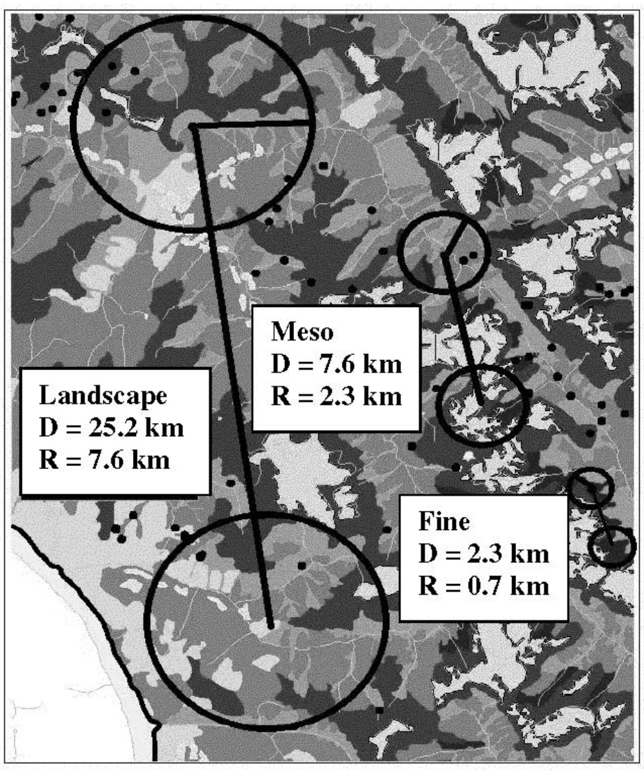

Figure 3. Multiscale (landscape, meso, fine) design used to analyze wolverine habitat selection using Columbia Mountain, British Columbia, Canada, males as an example. "D" refers to distance between used and random points; "R" is the radius within which habitat composition is measured. Baseline Thematic Mapper habitat layer (Surveys and Resource Mapping Branch 1995) is shown. Approximate scale, 1:350,000.

Statistical Analyses

We pooled data by sex, season, and study area to account for our study design, which includes relatively few locations from each sample animal (Table 1). Variables associated with each wolverine habitat selection hypothesis (food, predation risk, human disturbance; Table 2) were screened in a correlation matrix within and across scales. We removed the least significant univariate predictor where $r > 0.6$. We used multivariate logistic regression to develop resource selection functions (Manly et al. 1993) for each set of hypothesis variables, as well as combinations of 2 and all 3 hypotheses. In this way, we developed 7 candidate models for each sex–season–study area, yielding 56 potential models. When parameter estimates opposed the predicted response for a variable, it was removed from that candidate model. In 22 cases, correlation among variables reduced the number of variable sets (Table 4). Models were fitted without constants, consistent with a use or available design (Boyce et al. 2002). We used Akaike's Information Criterion (AIC) to select the best model (Burnham and Anderson 1998), and we calculated AIC weights for each candidate model. Model parameters were not averaged, because we were interested in the hypotheses underlying the models rather than the coefficients themselves. We report likelihood ratio tests for individual variable coefficients in the most supported models to assist in identifying relative importance of variables. We included receiver operator characteristic (ROC) scores (i.e., area under ROC curve) for each selected model as an indicator of model performance. Model parameters were mapped within a GIS following Manly et al. (1993) to generate seasonal models suitable to support resource management planning in wolverine habitat.

RESULTS

Thirty-nine adult wolverines (23 F, 16 M) were located a total of 2,125 times within the 2 study areas (Table 1). Wolverines in the Omineca Mountains moved long distances between locations, frequently >30 km for males (Fig. 2), and their movement distances were greater than wolverines in the Columbia Mountains. Consistent with greater movements, adaptive kernel home ranges for

Table 4. Wolverine seasonal habitat use models (top 3) for adult male and female wolverines monitored between 1995 and 2003 in Columbia and Omineca mountains, British Columbia, Canada. Models are ranked based on relative Akaike's Information Criterion (ΔAIC) values. The AIC weights (w_i), number of parameters (K), log-likelihood value (LL), and AIC values are reported for each model. Variables were grouped under food (FOOD), human disturbance (HUMAN), and predation risk (PREDATION) hypotheses.

Model	Study area	LL	K	AIC	ΔAIC	w_i
F: Winter	Columbia					
PREDATION+ HUMAN + FOOD		–474.66	8	965.32	0.00	>0.99
FOOD + HUMAN		–480.19	8	976.38	11.06	<0.01
FOOD		–497.02	3	1000.04	34.72	<0.01
F: Summer	Columbia					
FOOD + HUMAN		–613.98	4	1235.96	0.00	0.94
FOOD		–615.65	5	1241.30	5.34	0.06
NULL		–673.74	1	1349.48	113.52	<0.01
M: Winter	Columbia					
FOOD + HUMAN		–229.41	7	472.82	0.00	0.71
FOOD		–231.29	6	474.58	1.76	0.29
HUMAN		–276.95	2	557.90	85.08	<0.01
M: Summer	Columbia					
FOOD		–232.79	5	475.58	0.00	>0.99
NULL		–273.10	1	548.20	72.62	<0.01
F: Winter	Omineca					
FOOD + PREDATION		–341.31	4	690.62	0.00	>0.99
FOOD		–356.46	2	716.92	26.30	<0.01
PREDATION		–359.43	2	722.86	32.24	<0.01
F: Summer	Omineca					
FOOD + HUMAN		–336.71	4	681.42	0.00	>0.99
FOOD		–359.39	2	722.78	41.36	<0.01
HUMAN		–373.93	2	751.86	70.44	<0.01
M: Winter	Omineca					
FOOD		–241.72	2	487.44	0.00	>0.99
HUMAN		–248.37	2	500.74	13.30	<0.01
NULL		–249.53	1	501.06	13.62	<0.01
M: Summer	Omineca					
FOOD		–179.25	2	362.50	0.00	0.79
NULL		–181.60	1	365.20	2.70	0.21

Omineca Mountains male and female wolverines were larger than Columbia Mountain wolverines (Table 1). Males from both study areas used more than twice the area used by adult females. Resident wolverines we monitored rarely crossed the hydroelectric reservoirs. One male in the Columbia Mountains occupied a home range that straddled the Trans Canada Highway.

The most supported sex-, season-, and study area-specific multivariate logistic regression habitat use models were all significant ($\chi^2 > 4.7$, df ≥ 2, $P < 0.03$; Tables 5, 6).

Habitat use by male wolverines was most supported by the food hypothesis in 3 of 4 seasonal models (Table 4). Columbia Mountains males were associated with subalpine–avalanche habitat landscapes and negatively associated with glacier–snow–rock habitat at all scales in summer (Fig. 4). Males were associated with moose winter ranges at the meso scale in the Omineca Mountains and with recently logged landscapes in summer (Fig. 5). The food and human disturbance hypothesis combination was most supported for Columbia Mountains male habitat use in winter. Helicopter skiing was negatively associated, and subalpine–avalanche habitat and Interior Cedar Hemlock forests were positively associated with Columbia Mountains male habitat use in winter (Fig. 4).

Female wolverine summer habitat use was most supported by the food and disturbance hypothesis combination in both study areas. Columbia Mountains females were associated with meso-scale roadless areas, and Omineca Mountains females were negatively associated with recently logged landscapes in summer. Alpine habitats at landscape and meso scales were positively associated with use by Omineca Mountains females in summer (Fig. 5). Columbia Mountains females were positively associated with fine-scale subalpine–avalanche habitat and negatively associated with glacier–snow–rock, habitat at meso and fine scales in summer. A combination of food, predation risk, and human disturbance hypotheses were the most supported winter model for Columbia Mountains females. Ungulate winter ranges and subalpine–avalanche habitats were positively associated with use by Columbia Mountains females in winter (Fig. 4). Negative associations with helicopter skiing at the landscape scale, backcountry skiing at the meso scale, and recently logged areas at the landscape scale were also included in the lowest AIC winter model for Columbia Mountains females (Table 5). Habitat use by Omineca Mountains females in winter was most supported by the food and predation risk hypothesis. Moose winter ranges were negatively associated with use by Omineca Mountains females in winter at landscape scale and positively associated at meso scale, suggesting a response to food and predation risk. Omineca Mountains females also were positively associated with terrain ruggedness at the landscape scale (Fig. 5).

Table 5. Variables, coefficients, and receiver operator characteristic (ROC) scores for most supported seasonal logistic regression models of wolverine habitat selection in the Columbia Mountains, British Columbia, Canada, 1995–2003. Variables were grouped under food (FOOD), human disturbance (HUMAN), and predation risk (PREDATION) hypotheses.

Model	Variable	Scale	Hypothesis	Estimate	SE	χ^2	*P*
F: summer	Glacier	Meso	FOOD	–4.02	0.54	71.76	<0.001
ROC score = 0.71	Glacier	Fine	FOOD	–1.90	0.58	12.67	<0.001
	Roadless	Meso	HUMAN	0.35	0.12	9.35	0.002
	Avalanche	Fine	FOOD	0.66	0.24	7.29	0.007
F: winter	Avalanche	Fine	FOOD	0.96	0.29	11.70	0.001
ROC score = 0.75	Glacier	Meso	FOOD	–6.42	0.94	80.31	<0.001
	Moose	Meso	FOOD	0.91	0.44	4.38	0.036
	Heliski	Landscape	HUMAN	–5.54	1.04	30.45	<0.001
	Recently logged	Landscape	PREDATION	–4.12	1.25	12.16	0.001
	Backcountry skiing	Meso	HUMAN	–2.08	1.02	5.04	0.025
	Ruggedness	Meso	PREDATION	0.11	0.02	20.28	<0.001
M: summer	Glacier	Landscape	FOOD	–3.97	1.39	8.49	0.004
ROC score = 0.75	Glacier	Meso	FOOD	–5.11	1.21	23.79	<0.001
	Glacier	Fine	FOOD	–6.59	1.89	32.58	<0.001
	Avalanche	Landscape	FOOD	5.71	1.04	33.45	<0.001
M: winter	Avalanche	Fine	FOOD	1.70	0.45	15.75	<0.001
ROC score = 0.79	Glacier	Landscape	FOOD	–2.94	1.07	7.87	0.005
	Glacier	Meso	FOOD	–8.05	1.78	37.15	<0.001
	Glacier	Fine	FOOD	–4.77	2.70	5.54	0.019
	ICH[a]	Fine	FOOD	0.91	0.21	19.04	<0.001
	Heliski	Meso	HUMAN	–2.59	1.23	4.66	0.031

[a] ICH = Interior Cedar–Hemlock biogeoclimatic zone (Pojar and Meidinger 1991).

DISCUSSION

Despite differences in prey species occurrence, terrain, extent and types of human use, and vegetation cover types between the 2 study areas, our analysis suggests underlying similarities in habitat associations of wolverines. Male wolverines were positively associated with food-related habitat variables in both summer and winter in Omineca and Columbia mountains. Low-elevation forests and moose winter ranges, which likely provide ungulate carrion, were used extensively by wolverines in winter, consistent with other North American studies (Hornocker and Hash 1981, Whitman et al. 1986, Banci and Harestad 1990). Use of mid-elevation subalpine–avalanche and recently logged habitats in summer by male wolverines in our study where marmots, snowshoe hares, and other small bird and mammal prey occur, supports results from Montana, USA (Hornocker and Hash 1981), and British Columbia (Lofroth et al. 2007).

Our models suggest habitat associations of female wolverines are complex; they likely involve responses to food, predation risk, and human disturbance. Females in both study areas were positively associated with moose winter ranges at the meso scale, suggesting food sensitivity. High energetic demands during winter associated with reproduction (Iversen 1972, Magoun and Copeland 1998, Persson 2005) likely influence habitat use during this period. Seasonal habitat use by female wolverines suggests a shift from low-elevation forested environments in winter to high subalpine and alpine habitats in summer, similar to results reported by Whitman et al. (1986), Copeland (1996), and Landa et al. (1998).

Consistent association with avalanche path habitats by wolverines of both sexes in both seasons underscores their importance for wolverines in the rugged terrain of the Columbia Mountains. Prey production in these areas is likely high due to winter avalanche kill of large mammals such as mountain goat and moose (Krebs and Lewis 2000), as well as summer use by hoary marmots, a key late winter and summer prey (Lofroth et al. 2007), especially for reproductive females.

Table 6. Variables, coefficients, and receiver operator characteristic (ROC) scores for most supported seasonal logistic regression models of wolverine habitat selection in the Omineca Mountains, British Columbia, Canada, 1995–2002. Variables were grouped under food (FOOD), human disturbance (HUMAN), and predation risk (PREDATION) hypotheses.

Sex: season	Variable	Scale	Hypothesis	Estimate	SE	χ^2	*P*
F: summer	Alpine	Landscape	FOOD	1.97	0.63	10.17	0.001
ROC score = 0.72	Alpine	Meso	FOOD	0.83	0.41	4.21	0.040
	Recently logged	Landscape	HUMAN	–6.01	1.00	45.35	<0.001
F: winter	Moose	Landscape	PREDATION	–5.67	1.14	30.30	<0.001
ROC score = 0.63	Ruggedness	Landscape	PREDATION	0.09	0.04	5.91	0.015
	Moose	Meso	FOOD	3.76	0.84	22.54	<0.001
M: summer	Recently logged	Landscape	FOOD	2.41	1.13	4.72	0.030
ROC score = 0.64							
M: winter	Moose	Meso	FOOD	2.65	0.70	15.62	0.001
ROC score = 0.70							

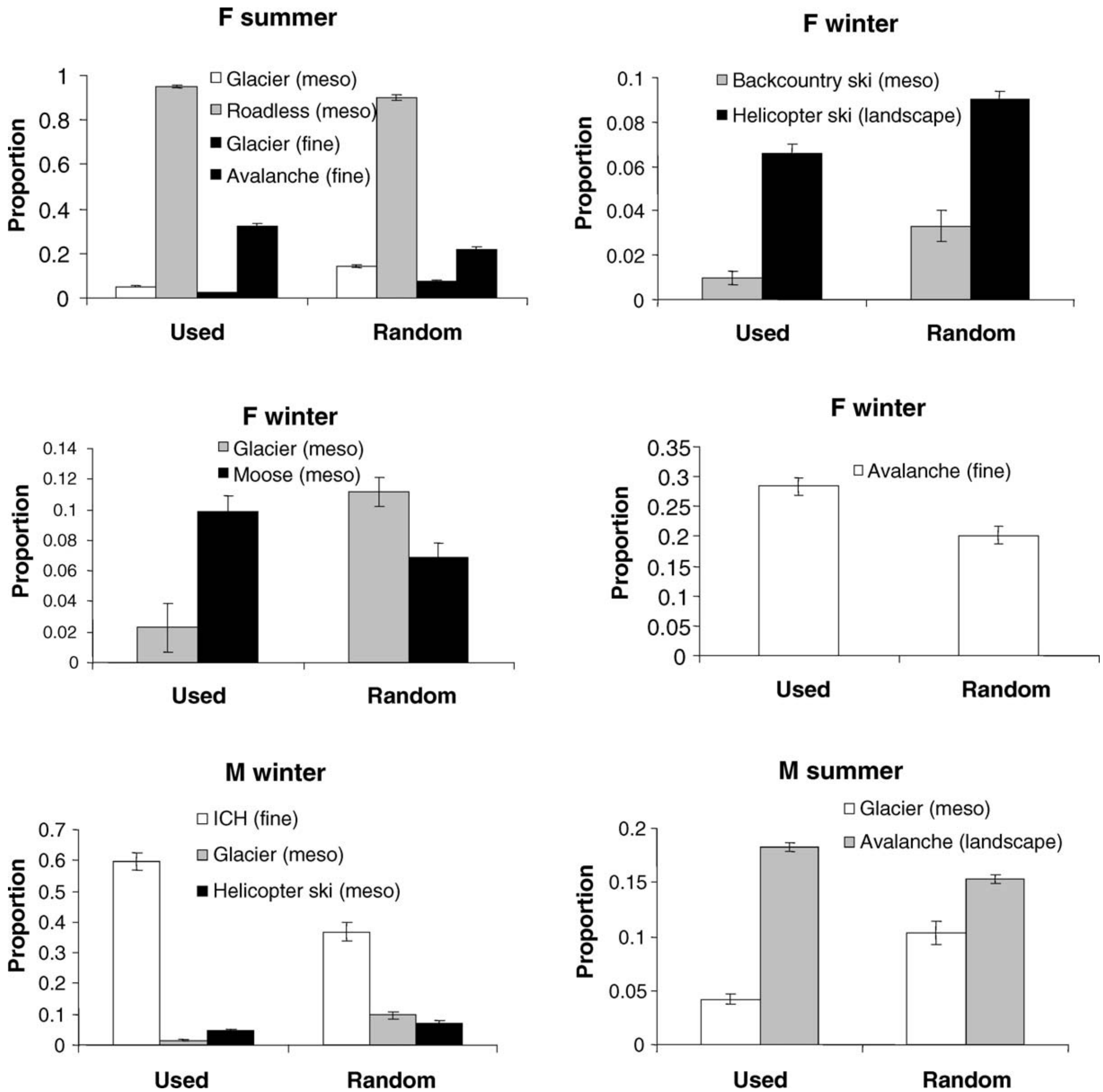

Figure 4. Univariate means and standard errors for selected predictor variables from most supported female and male wolverine seasonal habitat use models for the Columbia Mountains, British Columbia, Canada, 1995–2003. Habitat composition (proportion) was measured in a scale-dependent manner (fine, meso, landscape) around each telemetry location (used) and paired random (random) point.

Food habit evidence from wolverine scat and foraging observations (Lofroth et al. 2007) suggest that our choice of key prey species was appropriate. Although Mountain goat and caribou are known to be important food items for wolverines in winter (Krebs and Lewis 2000, Lofroth et al. 2007), their winter ranges did not contribute to any of the most supported winter models. Our data on winter prey distribution are based on aerial surveys (moose, mountain goat) and telemetry observations (caribou), not from distribution of carrion per se, which may be a more appropriate measure of food availability for wolverines (van Zyll de Jong 1975).

Human use and predation risk-related variables were also strong predictors in all female seasonal models. We expected predation risk to be an important factor during winter denning season when reproductive females must provision and protect developing neonates from predation (e.g., Burkholder 1962, Magoun and Copeland 1998, Persson et al. 2003). Our results support this hypothesis. Females were negatively associated with broad landscapes of winter range where wolves concentrated (Allison 1998, Kunkel and Pletscher 2001) and positively associated with rugged terrain where security habitat is presumably more abundant.

The influence of human activity on wolverine distribution has been assessed at broad regional scales using historical observations and trapping records (Weaver et al. 1996, Carroll et al. 2001, Rowland et al. 2003). May et al. (2006) suggested that human infrastructure was a primary factor for home range location examined in their Norwegian study. Our analysis is the first to consider winter recreation in addition to roads as habitat variables in a use-availability context. In 3 of the 4 female seasonal models and one male model, human use variables contributed to the most supported models. Helicopter skiing and backcountry skiing

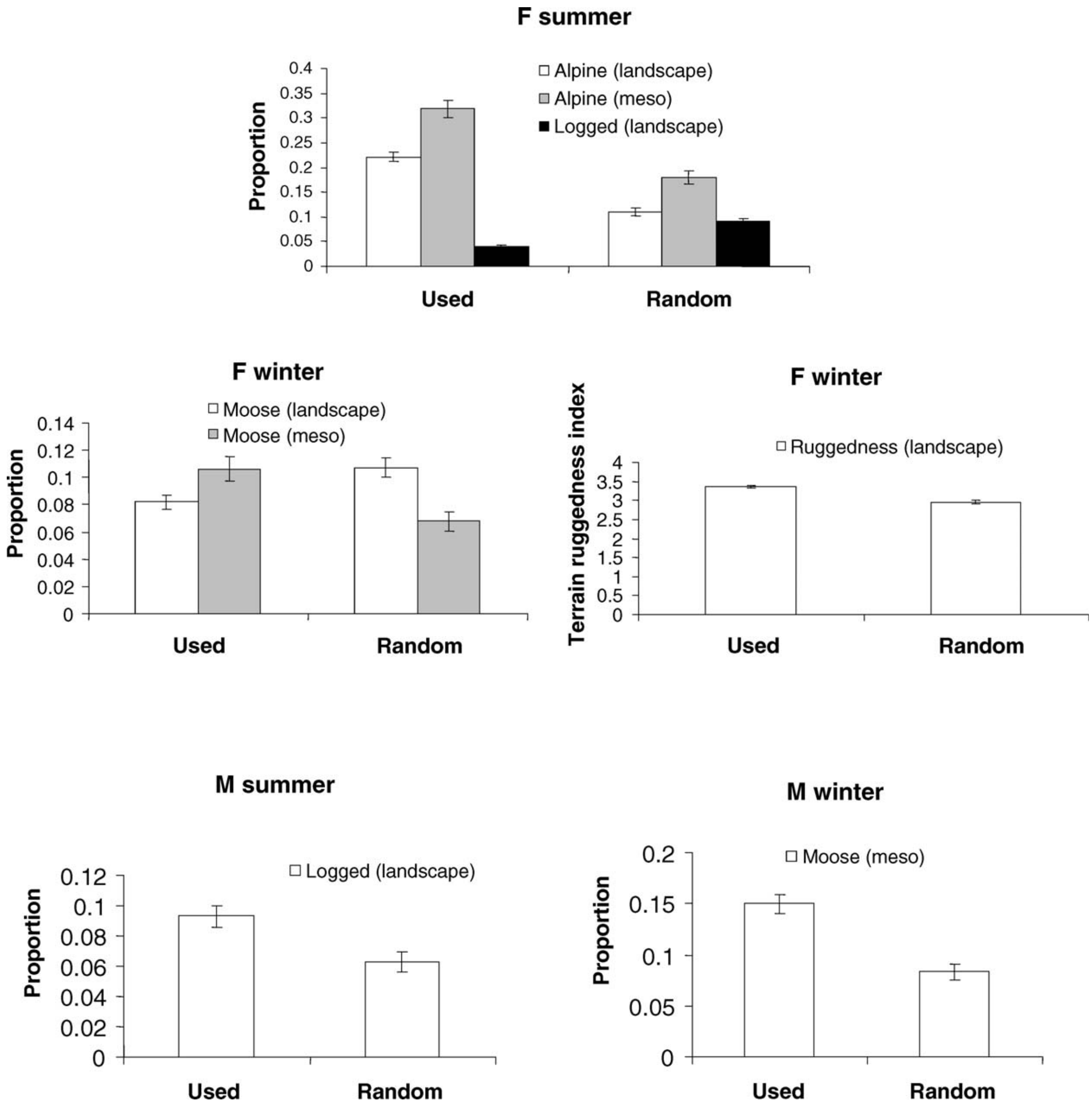

Figure 5. Univariate means and standard errors for predictor variables from most supported female and male wolverine seasonal habitat use models for the Omineca Mountains, British Columbia, Canada, 1995–2003. Habitat composition (proportion) was measured in a scale-dependent manner (fine, meso, landscape) around each telemetry location (Used) and paired random (Random) point.

were negatively associated with Columbia Mountain females' use in winter. In summer, females were positively associated with roadless areas and negatively associated with recently logged areas. Taken together, these results suggest that wolverines, particularly females, are responding negatively to human activities within their home ranges.

Our Columbia Mountains study area included 2 national parks where helicopter skiing was not permitted. Resident females from park areas could potentially bias our results, because these females had much lower overlap with helicopter skiing, and samples were pooled. In addition, we did not consider temporal or frequency-based descriptors of actual use of ski runs. Additional focussed research simultaneously examining wolverine use with helicopter skiing and backcountry skiing activity will be required to adequately assess impacts of this growing land use on wolverines in the mountains of western North America. Summer models for both study areas clearly highlight the value of alpine and subalpine environments, which traditionally have received little use by humans. The future influence of expanded summer recreation on wolverine habitat selection should be considered an unknown cumulative risk. Wolverines may respond in a threshold rather than linear manner once ecological resiliency is exceeded (Peterson et al. 1998).

As a binary variable (e.g., roadless vs. roaded), roads did not seem to influence habitat associations strongly for male wolverines in our analysis. Roads may play a more direct role

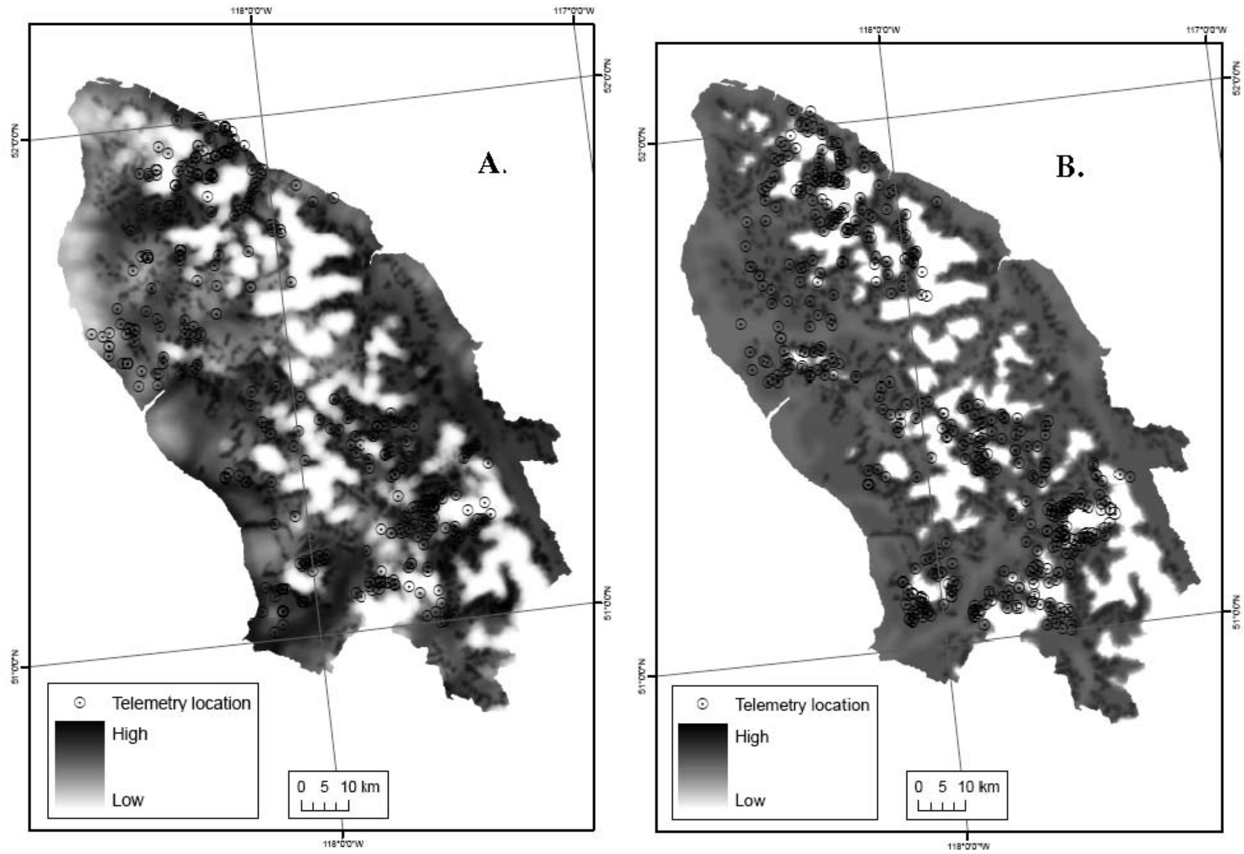

Figure 6. Multivariate logistic regression (resource selection function) models depicting female wolverine habitat quality within the Columbia Mountains study area, near Revelstoke, British Columbia, Canada in A) winter and B) summer. Telemetry points were gathered from radiomarked adult females from the study area, 1995–2003. Darker area represents higher probability of habitat selection.

in population demography via direct mortality and access for trappers (Banci 1994, Krebs et al. 2004). Because we did not consider measures of road use (e.g., traffic volume), we likely reduced the ability to detect a response by wolverines to roads in our analysis.

Previous analyses of habitat selection by wolverines have focussed on evaluating selection among a small suite of vegetative cover types at a single scale (Whitman et al. 1986, Banci and Harestad 1990) or at multiple scales (Copeland 1996). Our analysis followed a functional approach, examining a wider suite of variables potentially influencing habitat associations of wolverines. At levels present in our study areas, human use factors we considered contributed to the most supported female seasonal models, but they were much less influential in male models. Combinations of food-related variables at multiple scales best described habitat associations of male wolverines in our study areas. In the future, as human use (recreation) increases and timber extraction moves to higher elevation forest zones, direct and indirect impacts may become significant. Our models (Figs. 6, 7) provide spatially explicit representation of current habitat quality applicable to our study areas. Testing of the models with independent data sets and improved data on human use and carrion distribution will be necessary to improve understanding for future management.

MANAGEMENT IMPLICATIONS

Female wolverines, in winter and summer, have habitat associations that require careful consideration by land and resource managers. Human use, including winter recreation and the presence of roads, reduced habitat value for wolverines in our studies. Maintaining ungulate distribution and opportunities for spatial separation between wolverines and other large predators such as wolves is also likely important to females during denning and young rearing (Hatler 1989, Magoun and Copeland 1998). We think precautionary steps to protect habitat should be taken until more focussed research examining the behavioral and demographic responses of wolverines to human use is completed to establish thresholds for managers working to resolve conflicts in multiuse landscapes. Land managers need to ensure greater attention is paid to creating and maintaining quantitative map-based data on human use to enable consideration in future habitat analysis, land use planning, and habitat supply forecasts.

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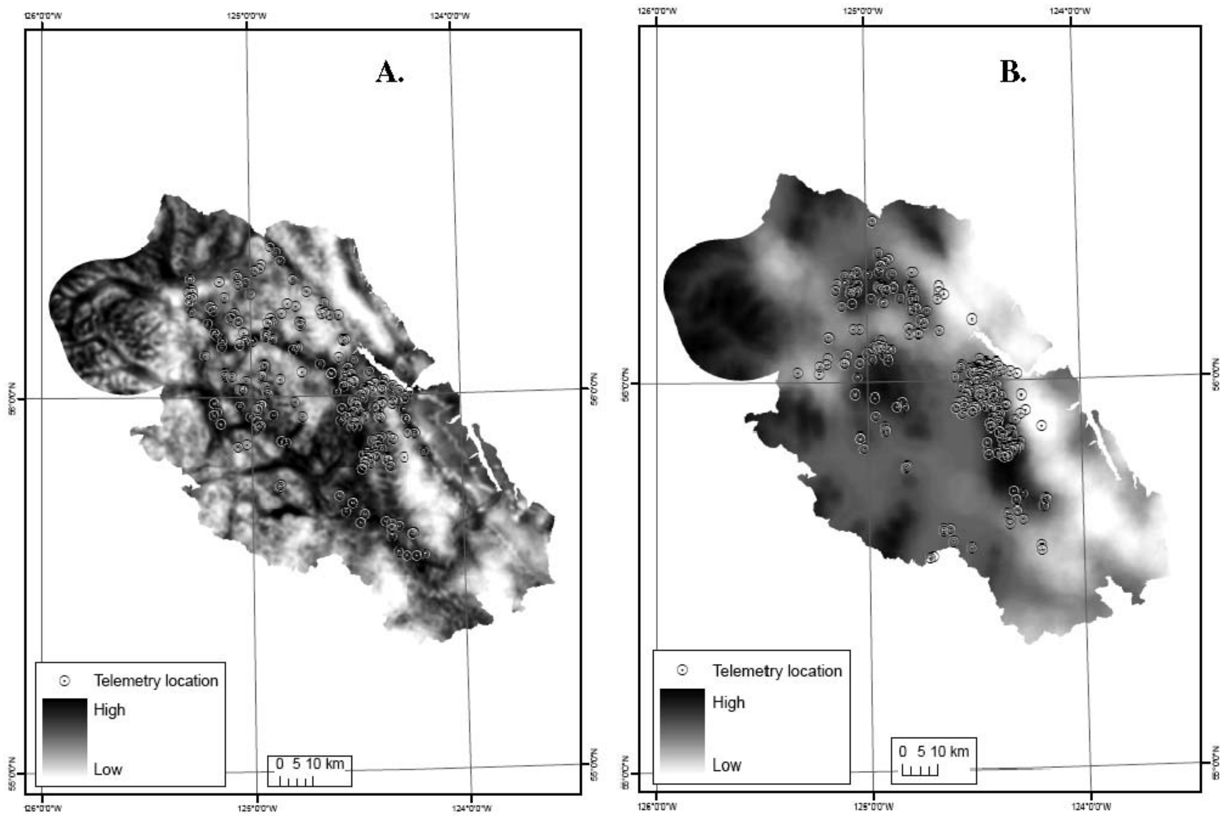

Figure 7. Multivariate logistic regression models depicting female wolverine habitat quality within the Omineca Mountains study area, near Mackenzie, British Columbia, Canada in A) winter and B) summer. Telemetry points were gathered from radiomarked adult females from the study area, 1995–2002. Darker area represents higher probability of habitat selection.

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