Special Section: Wolverine

Seasonal Habitat Associations of the Wolverine in Central Idaho

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ABSTRACT Although understanding habitat relationships remains fundamental to guiding wildlife management, these basic prerequisites remain vague and largely unstudied for the wolverine. Currently, a study of wolverine ecology conducted in Montana, USA, in the 1970s is the sole source of information on habitat requirements of wolverines in the conterminous United States. The Montana study and studies conducted in Canada and Alaska report varying degrees of seasonal differences in wolverine habitat use. This article provides an empirical assessment of seasonal wolverine habitat use by 15 wolverines (*Gulo gulo*) radiotracked in central Idaho, USA, in 1992–1996. We controlled for radiotelemetry error by describing the probability of each location being in a habitat cover type, producing a vector of cover type probabilities suited for resource selection analysis within a logistic regression framework. We identified variables that were important to presence of wolverines based on their strength (significance) and consistency (variability in coeff. sign) across all possible logistic regression models containing 9 habitat cover types and 3 topographic variables. We selected seasonal habitat models that incorporated those variables that were strong and consistent, producing a subset of potential models. We then ranked the models in this subset based on Akaike's Information Criterion and goodness-of-fit. Wolverines used modestly higher elevations in summer versus winter, and they shifted use of cover types from whitebark pine (*Pinus albicaulis*) in summer to lower elevation Douglas fir (*Pseudotsuga menziezii*) and lodgepole pine (*Pinus contorta*) communities in winter. Elevation explained use of habitat better than any other variable in both summer and winter. Grass and shrub habitats and slope also had explanatory power. Wolverines preferred northerly aspects, had no attraction to or avoidance of trails during summer, and avoided roads and ungulate winter range. These findings improve our understanding of wolverine presence by demonstrating the importance of high-elevation subalpine habitats to central Idaho wolverines. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2201–2212; 2007)

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The wolverine has been the subject of increasing interest in the conterminous United States. Public concerns regarding the species' historical and current status in the western United States elicited petitions to list the wolverine under the Endangered Species Act in 1995 and 2000. In both cases, the petitions addressed the potential effects of habitat alteration and increasing use of public lands on the wolverine. A single study of wolverine ecology conducted in Montana, USA, in the 1970s (Hornocker and Hash 1981), however, provides the only published scientific information on life history and habitat requirements of wolverines in the conterminous United States.

Isolation from human presence and association with subalpine habitats (Aubry et al. 2007) characterize our general understanding of wolverine–habitat associations at the southern extent of the species' North American range. Current wolverine literature suggests wolverines move to high-elevation summer habitats to find cool temperatures (Hornocker and Hash 1981) or to find prey (Gardner 1985, Whitman et al. 1986, Landa et al. 1998, Krebs and Lewis 2000). Winter shifts to somewhat lower elevations may follow increased availability of carrion (Gardner 1985, Whitman et al. 1986, Landa et al. 1998). Banci and Harestad (1990), however, reported no seasonal variation in use of habitats by wolverines in Yukon, Canada, arguing that seasonal movement was unnecessary due to cool summer temperatures and a lack of high-elevation prey. Where wolverines do change use of habitats seasonally, understanding those seasonal changes is important to land managers faced with assessing the effects of recreation, timber harvest, or livestock grazing in summer, and snowmobiling and skiing during winter.

We report analysis of wolverine radiotelemetry data collected in 1992–1996 in central Idaho, USA. We correct for telemetry error and assess all-possible models as a multivariate approach to identifying individual variables strongly associated with seasonal wolverine presence. We use this reduced variable set to evaluate the hypothesis that wolverines' habitat associations vary seasonally and to provide a suite of candidate variables for model selection.

STUDY AREA

Our study area included 9,315 km^2 in central Idaho (44°N, 115°W; Fig. 1). National Forest lands constituted 99% (9,216 km^2) of the study area, of which 81% were federally

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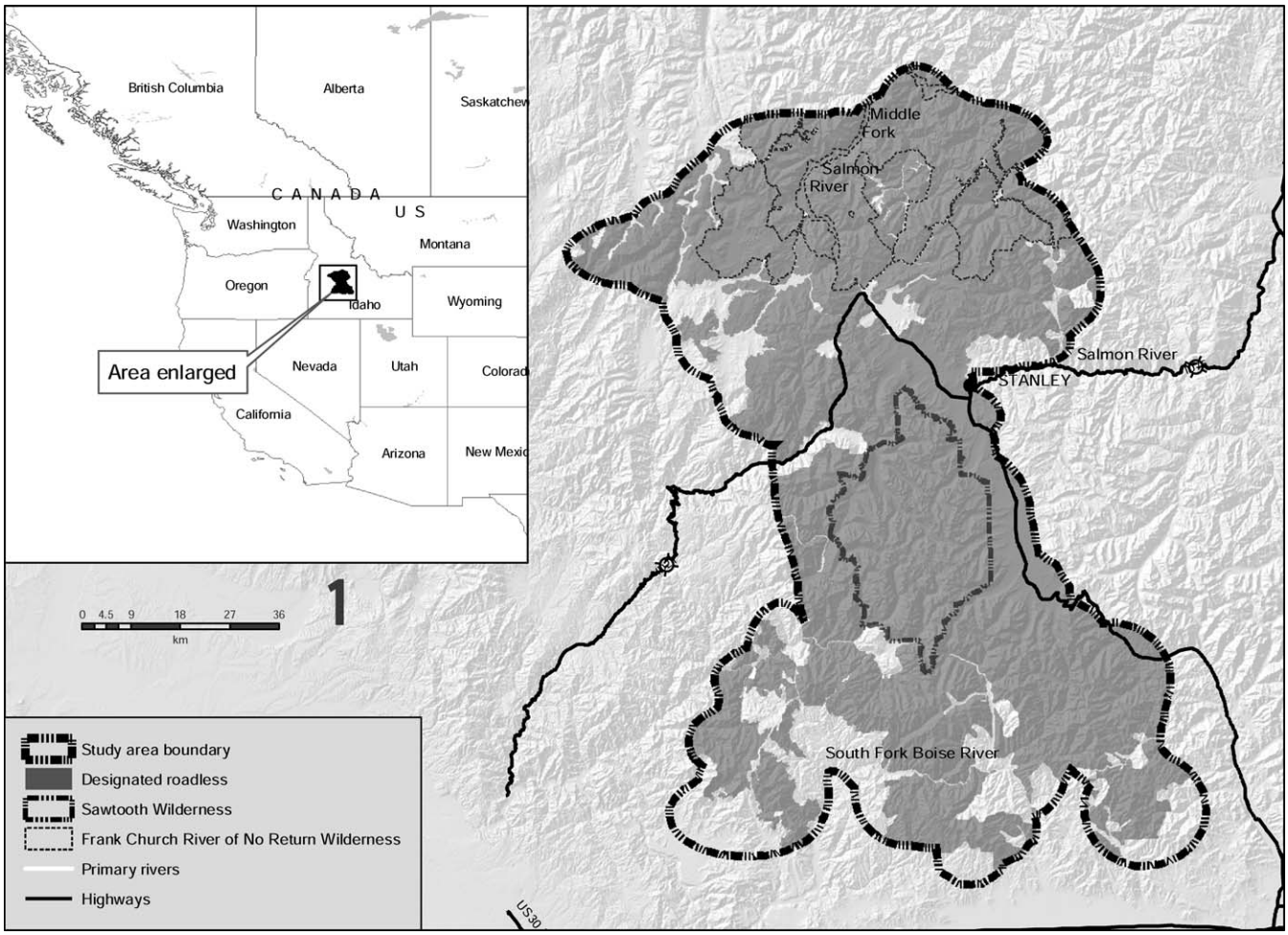

Figure 1. Wolverine project study area in central Idaho, USA, 1992–1996.

designated roadless (7,540 km^2) or wilderness (2,369 km^2; Frank Church River of No Return Wilderness, Sawtooth Wilderness). Other lands (Bureau of Land Management, State Lands, private) constituted the remaining 1% (92 km^2) of the study area.

The climate was generally temperate, but extreme low winter temperatures did occur (−41° C, Dec 1990). Mean temperatures ranged from −8° C in January to 15° C in July. Mean annual precipitation was 58 cm with 48 cm as snow. Elevations ranged from 1,400 m to 3,279 m.

Vegetative communities were diverse, with xeric sagebrush (*Artemesia* sp.)–grass and Douglas fir (*Pseudotsuga menziezii*)–ponderosa pine (*Pinus pondersosa*) associations dominant at lower elevations interspersed with willow (*Salix* sp.)–meadow communities on more mesic sites. Dense lodgepole pine (*Pinus contorta*) interspersed with Douglas fir and subalpine fir (*Abies lasiocarpa*) occurred at mid-elevations along with Engelmann spruce (*Picea engelmannii*)–fir forests interspersed with savanna grassland mosaics. Subalpine forests associated with talus and glacial cirque basins included whitebark pine (*Pinus albicaulis*) and subalpine fir interspersed with open, grass and forb montane–park characterizing upper slopes. Alpine scree habitats associated with talus and open mountaintops above timberline generally occurred >2,700 m.

METHODS

Data Collection and Organization

We captured study animals in log box traps (Copeland et al. 1995) and instrumented them with intraperitoneal implant transmitters, radiocollars, or both. We relocated study animals by aerial and ground tracking from 1992 through 1996. Telemetry flights occurred during daylight hours throughout the year between 0700 hours and 1900 hours. We considered relocations that occurred >24 hours apart independent (wolverines were capable of crossing their home range in 24 hr). We measured aerial relocation error by arbitrarily placing test transmitters throughout the study area on 86 occasions, which were subsequently relocated by other technicians during telemetry flights. We only included ground-based telemetry relocations in which the animal was observed or if the technician was confident he or she was within 100 m of the animal.

A raster-based analysis of landsat Thematic Mapper (TM) images identified 29 cover types within our study area (Redmond et al. 1997). We dropped from the analysis urban and agricultural cover types (0.04% of available) as well as

Table 1. Codes and definitions for central Idaho, USA, wolverine project habitat variables, 1992–1996.

Variable	Habitat code	Habitat description
Douglas fir	DF	Low- to mid-elevation conifer stands dominated by Douglas fir.
Douglas fir–lodgepole pine	DFLP	Dominated by both Douglas fir and lodgepole pine together within the stand.
Douglas fir–ponderosa pine	DFPP	Dominated by both Douglas fir and ponderosa pine together within the stand.
Grass–shrub	GS_SHB	Includes upland native grasslands, valley mesic shrubs and shrub dominated riparian, and upland bitterbrush (*Purshia tridentata*) and sagebrush.
Lodgepole pine	LP	Dominated by mid- to high-elevational lodgepole pine.
Mixed subalpine fir	MX_SA	Upper elevation forest dominated by subalpine fir but may include Engelmann spruce, lodgepole pine, or Douglas fir.
Montane–park	MNT_PRK	Regions with <10% tree cover, <15% shrub cover, and grass cover >15%. Dominated by upper elevation mesic grass or forb species.
Rock-barren	ROCK	Regions dominated by exposed rock, talus, or scree. Patches of trees, shrubs, or grass may occur within the rock areas.
Whitebark pine	WP	High-elevation conifer stands dominated by whitebark pine. May include subalpine fir, Engelmann spruce, and lodgepole pine.

cover types classified as water. We pooled the remaining cover types into 22 types for investigative analyses, and we condensed them to 9 types for the final analysis (Table 1).

Investigators often fail to account for telemetry inaccuracies when using radiotelemetry data to estimate habitat use patterns (Samuel and Kenow 1992). If average telemetry error is larger than the grain of a vegetation coverage map, then habitat associations with reported locations become probabilistic: the organism could have been in cells other than the cell associated with the point location and therefore in different cover types. When this occurs, assigning use to only one cover type associated with the point location frequently results in error, the effects of which vary by configuration, classification success, juxtaposition, and rarity of neighbor cover types (Samuel and Kenow 1992, McKelvey and Noon 2001). The effect of this error, however, can be mitigated by replacing each location with a probability distribution that describes the likelihood of where the animal was located. Rather than associating the animal with a single cover type, the animal is associated with several probable types, with the likelihood of association based on the area of each cover type across a local probability neighborhood defined by the estimated telemetry error distribution (McKelvey and Noon 2001).

We applied this method in the following manner. Thematic Mapper-based cover type-maps (30-m resolution) were used to describe habitat availability. To account for telemetry error, we generated a bivariate normal probability distribution function (pdf) based on the mean relocation error (291 m). As such, the probability of habitat association decreased in a half-normal curve as distance from the acquired telemetry location increased, allowing 50% of the distribution to fall above and 50% below the mean. Scaling the function to fit the 30-m resolution of the habitat layers and extending the grid to incorporate >99% of the volume resulted in a 57×57-cell grid covering an area of 292.4 ha. We scaled the pdf such that the values in each grid cell (the ht of the function at that location) summed across all grid cells and divided by the total number of cells = 1.0 (100% likelihood animal was located within this area). We then separated the cover types into individual grid layers composed of ones where the cover type was present and zeros elsewhere, which we transformed into probability layers using ArcInfo's focalmean function. Focalmean determines the mean of the values in a grid for the cells in its specified neighborhood weighted by a kernel, in this case the grid representing the error-derived pdf (Fig. 2). The result of this process was to produce separate layers for each cover type composed of cell values between 0.0 and 1.0, with values being the probability that a location occurring in that cell was, in fact, located in the cover type represented (McKelvey and Noon 2001). We then extracted the probability value corresponding with our wolverine occurrence and random point layers in each cover type focal mean layer to produce a vector of cover type occurrence probabilities for each point across all available cover types.

We derived topographic variables, elevation, slope, and aspect from a raster-based 30-m digital elevation model (DEM). Before this, we smoothed the DEM with a 5×5-cell focalmean to remove banding (Brown and Barra 1994), and we linearized aspect (radial degrees) by subtracting the value of aspect >180° from 360° (McKelvey et al. 2000). We adjusted topographic values for telemetry error by

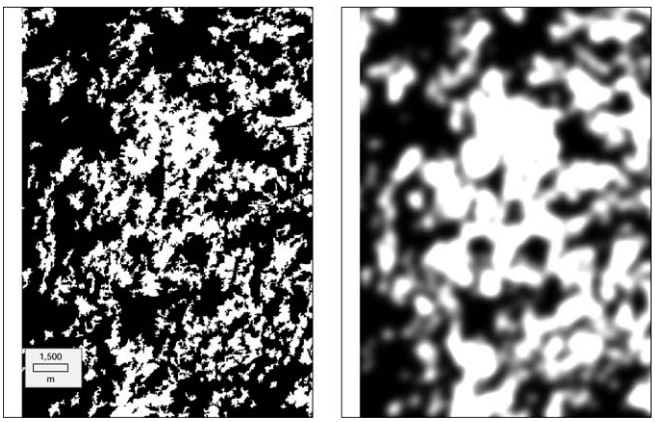

Figure 2. Habitat grid layers (30-m resolution) before (left) and after (right) focalmean analysis. Before focalmean analysis, cells in the image on the left were coded as 1 for habitat presence (black pixels) and 0 for no presence (white pixels). Focalmean analysis converted each cell value to a probability ranging from 0 to 1 (right image).

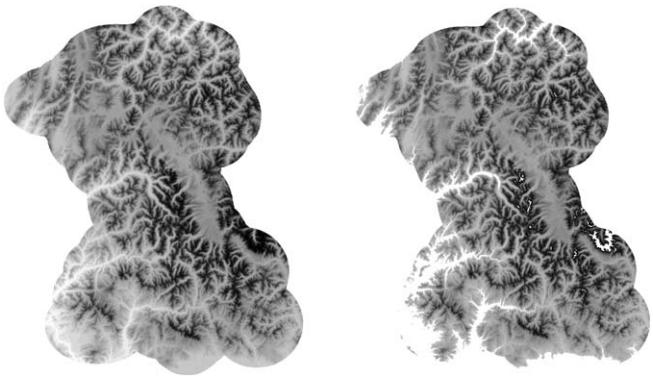

Figure 3. Thirty-meter digital elevation model of the project study area (left) reduced in extent by eliminating pixels occurring <1,600 m and >3,000 m (right). We considered only use and random points occurring within the remaining area for use-availability analysis for wolverine in central Idaho, USA, 1992–1996.

applying the error-derived focalmean kernel producing a weighted average value for each pixel.

We measured elk (*Cervus canadensis*) winter range (Rocky Mountain Elk Foundation 1999) and linear features of perennial streams, roads, and trails (Idaho Water Resources 2005) as nearest distance from telemetry locations. In these cases, we adjusted for telemetry error by computing the focalmean distance of each cell in each layer from the entity of interest (elk winter range, streams, roads, trails).

We investigated habitat relationships for data pooled 1) across all individuals, 2) within seasons, 3) within age and sex, and 4) within age and sex by season. Our models compared wolverine use points with 7,000 random points from across the entire study area. Although this approach arguably violates equal availability assumptions, our intent was to investigate habitat relationships that could be generalizable for wolverines across the range of habitat variation for our study area. We considered variation within age and sex classes to help recognize how each influenced seasonal relationships. Age classes included adults (>2 yr of age; see Rausch and Pearson 1972) and subadults, defined as prebreeding age individuals between 8 months and 2 years of age, because wolverines reach growth cessation at approximately 8 months of age (Iversen 1972); young we monitored became independent of their mother at about 8 months of age. For seasonal analyses, we classified our data into summer (Jun–Nov) and winter (Dec–May) based primarily on periods of snow cover.

In defining available habitat, we recognized that most of our wolverine relocation points occurred within a relatively narrow elevation band. We classified our elevation data into 200-m zones, and we compared proportions of presence to availability. We removed from the analysis areas occurring in zones with expected values of <5 locations. This refined our universe of availability to a 1,400-m elevation band and removed low- and high-elevation habitats that experienced little wolverine use (Fig. 3). Random points were uniformly located within the remaining area.

Statistical Analysis and Model Building

Exploratory and univariate analysis.—We tested for multicollinearity considering variable pairs with Pearson correlation coefficients >0.60 as collinear, which resulted in removal of one of the pair. We performed univariate logistic regression for each independent variable (Hosmer and Lemeshow 2000) to reveal relationships within individual animals and within classes. We used *t*-tests to investigate seasonal differences in elevation use. We condensed distance-to values into arbitrary categories rather than including these variables in our logistic regression modeling, because this provided a more meaningful understanding of the wolverine's relationship with these variables. We used these variables to develop selection indices (Manly et al. 1993), which we evaluated for significance based on Bonferonni-adjusted confidence intervals (Neu et al. 1974). We developed selection indices for elevation and aspect as well. We also used the 200-m elevation bands used to define availability as elevation categories for selection indices. For our regression analysis of elevation, we pooled areas with elevations >2,600 m, which contained both little area and few wolverine locations, into a >2,600-m category to improve the linearity of the data.

We analyzed distances to trails and winter range only for wolverine data associated with summer and winter seasons, respectively. We analyzed distances to roads and streams for the entire data set.

Multivariate analyses.—We used logistic regression to investigate relationships between wolverine presence and a suite of habitat variables. Our primary goals were to identify variables that reliably correlated with seasonal habitat associations and to use these variables to develop models of habitat use. Developed in this manner, and given that we were comparing used locations to random locations rather than to unused locations, understandings concerning correlations with independent variables are limited to evaluation of their relative contributions to separation between used and random data sets and consistency in the signs of the associated coefficients.

To control for differences in sample sizes within and across classes and between use and random points, we added a relative weight value to each point, equalizing the influence on model selection among individuals within a class and between total use points and random points. We calculated weights for random points by dividing the total use points by total random points. To calculate weights for use points for each individual, we first divided the total number of use points for all individuals within a class by the number of individuals to create an equal weighting value. We then divided the number of points for each individual by the equal weighting value. We then used these values in SAS LOGISTIC procedure (SAS Institute Inc., Cary, NC) to weight the corresponding values of the response variable. Applying weights according to the relative difference between number of telemetry locations and random locations provided a 50:50 chance for animals to select random versus use while still maintaining a high-resolution

Table 2. Composition of the wolverine relocation sample in central Idaho, USA, 1992–1996.

Class	Season	Individuals (*n*)	Pooled locations (*n*)	Range of locations/individual
Ad F	Summer	4	205	37–66
	Winter	4	177	17–96
Ad M	Summer	3	124	23–59
	Winter	3	120	29–56
Subad	Summer	6	193	18–57
	Winter	8	184	10–41

measurement of available habitat with a large number of random points.

To investigate the importance of wolverine association with individual variables in multivariate space, we modeled every possible combination of variables in logistic regression using PROC LOGISTIC (SAS Institute Inc.), and then we evaluated performance of each variable across all models. We considered the importance of individual variables based on strength and consistency. We defined strength as the proportion of times each variable was significant ($P < 0.25$; Hosmer and Lemeshow 2000), and we defined consistency as the number of times the slope coefficient changed sign. Thus, a perfect variable would be significant in all models in which it occurred and would never shift sign. In general, these 2 attributes are linked; a nonsignificant variable will tend to change sign due to chance more than a highly significant variable. Where variables were strong but inconsistent, we examined the variable sets associated with coefficient sign changes to determine whether we could understand where and why a variable was changing sign. If sign changes were clearly linked to the inclusion of other variables, we considered the behavior to be interpretable. For each data set, we ranked variables based on these criteria.

To investigate seasonal models predicting wolverine presence in our study area, we evaluated models from our seasonal data set using the 6 best variables based on significance and interpretability (50% of the variables we analyzed). We ranked models based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002); we did not correct for small sample size bias, because the ratio of sample to parameters exceeded 40 (Burnham and Anderson 2002). We secondarily evaluated models that provided equivalent AIC scores (ΔAIC scores < 2.0; Burnham and Anderson 2002) for fit based on the Hosmer and Lemeshow (2000) goodness-of-fit statistic ($\hat{C}$).

RESULTS

Capture and Monitoring

We collected relocation samples from 15 wolverines captured and instrumented in winter from February 1992 to May 1995. We monitored study animals through December 1996. From February 1992 through December 1995, 7 females and 8 males provided 1,185 relocations of which we considered 1,003 independent (Table 2). Telemetry flights occurred during daylight hours throughout the year, averaging 5.9 (SD = 2.83) flights per month. We collected 58 (5.7%) of our relocations by ground-based telemetry. We plotted study animal locations on 7.5-minute topographic maps or logged them on global positioning system for later plotting. Aerial telemetry error was 291 m (SD = 277 m).

Habitat Relationships

All possible combinations of 12 independent cover type variables produced 4,096 logistic regression models. Because each variable could be present in only 50% of the possible models, our analysis of individual variable performance was based on 2,048 models.

Elevation was the key variable for distinguishing wolverine presence. It was the strongest and most consistent variable across all logistic regression models (Table 3). Wolverines preferred higher elevations (positive coeff.; $P > 0.25$) in almost all models in which it was present. Use of high elevation was most notable during summer when all elevations >2,400 m were used more than expected and elevations <2,200 m used less than expected (Fig. 4). During winter, use shifted to the 2,400–2,600-m elevation zone with only the lowest elevations used less than expectation (Fig. 4). Although a seasonal shift in elevation was evident and significant, it was relatively minor, with wolverines shifting <100 m, on average, from summer to winter (Table 4). Adult males and subadults accounted for most of the variation in seasonal elevation use, whereas seasonal shift for adult females was not significant (Table 4). Aspect was seldom significant in either season, although very stable across all models (Table 3), indicating greater use than expected for northerly aspects (Fig. 5). Steep slopes were a strong indicator of wolverine presence in summer, most notably in adults (Table 5).

The key differences in seasonal models were summer presence in whitebark pine and an association with steep slopes and a winter shift to lodgepole pine and Douglas fir communities, along with a strong avoidance of rock (Table 3). Grass–shrub was a consistently strong negative indicator of wolverine presence (Table 4); the coefficient was negative in ≥99% of models across both seasons, and it was significant ($P < 0.25$) in all summer models and 94% of winter models (Table 3). Whitebark pine was an important summer variable for adult females and subadults (Table 5); strong and consistent in ≥94% of the models (Table 3). Douglas fir was a strong-use variable in subadult winter models, whereas use of Douglas fir–lodgepole pine was favored by females (Table 4). Douglas fir–ponderosa pine consistently indicated nonuse, primarily during summer, but it was not strongly significant (Table 3). Rock, a generally strong variable, was largely unstable in summer models (Table 3). Although rock was only moderately correlated with elevation (Pearson correlation coeff. = 0.48), the sign of its coefficient was clearly linked to elevation. When elevation and rock were both in the model, rock was uniformly negative, whereas when elevation was not in the model, rock was negative in only 11% of models.

Table 3. All-possible logistic regression models summary for 9 vegetative variables and 3 topographic variables by season for 15 wolverines in central Idaho, USA, 1992–1996.

	Summer[a]					Winter[a]			
	Coeff. proportions[b]					Coeff. proportions[b]			
Variable[c]	Sig. <0.25	Prop. +	Prop. −	Shift sign	Variable[c]	Sig. <0.25	Prop. +	Prop. −	Shift sign
ASP[d]	0.16	0.09	0.91	0.10	SLP[e]	0.17	0.75	0.25	0.33
DFLP	0.29	0.78	0.22	0.28	ASP[d]	0.23	0.00	1.00	0.00
MIX_SA	0.34	0.73	0.27	0.37	WP	0.45	0.47	0.53	0.90
LP	0.42	0.59	0.41	0.71	DFLP	0.50	0.96	0.04	0.05
DFPP	0.50	0.07	0.93	0.08	DFPP	0.51	0.16	0.84	0.20
DF	0.53	0.58	0.42	0.71	MIX_SA	0.56	0.79	0.21	0.26
MT_PRK	0.55	1.00	0.00	0.00	DF	0.70	0.95	0.05	0.05
ROCK	0.74	0.51	0.49	0.95	MT_PRK	0.72	1.00	0.00	0.00
WP	0.94	1.00	0.00	0.00	LP	0.76	0.97	0.03	0.03
GS_SHB	1.00	0.00	1.00	0.00	ROCK	0.92	0.01	0.99	0.01
ELEV[f]	1.00	1.00	0.00	0.00	GS_SHB	0.94	0.01	0.99	0.01
SLP[e]	1.00	1.00	0.00	0.00	ELEV[f]	1.00	1.00	0.00	0.00

[a] Winter = 1 Dec–31 May; summer = 1 Jun–30 Nov.
[b] Positive (+) and negative (−) signs indicate the proportion (prop.) of all-possible models in which each variable was significant (sig.) at the stated level, the coeff. was positive or negative, and the proportion of times the coeff. sign shifted.
[c] DF = Douglas fir, DFLP = Douglas fir–lodgepole pine, DFPP = Douglas fir–ponderosa pine, GS_SHB = grass–shrub, LP = lodgepole pine, MIX_SA = mixed subalpine fir, MT_PRK = montane–park, ROCK = rock-barren, WP = mixed whitebark pine, ASP = aspect, ELEV = elevation, SLP = slope.
[d] Negative proportions indicate preference for northerly aspects.
[e] Positive proportions indicate preference for steeper slopes.
[f] Positive proportions indicate preference for higher elevations.

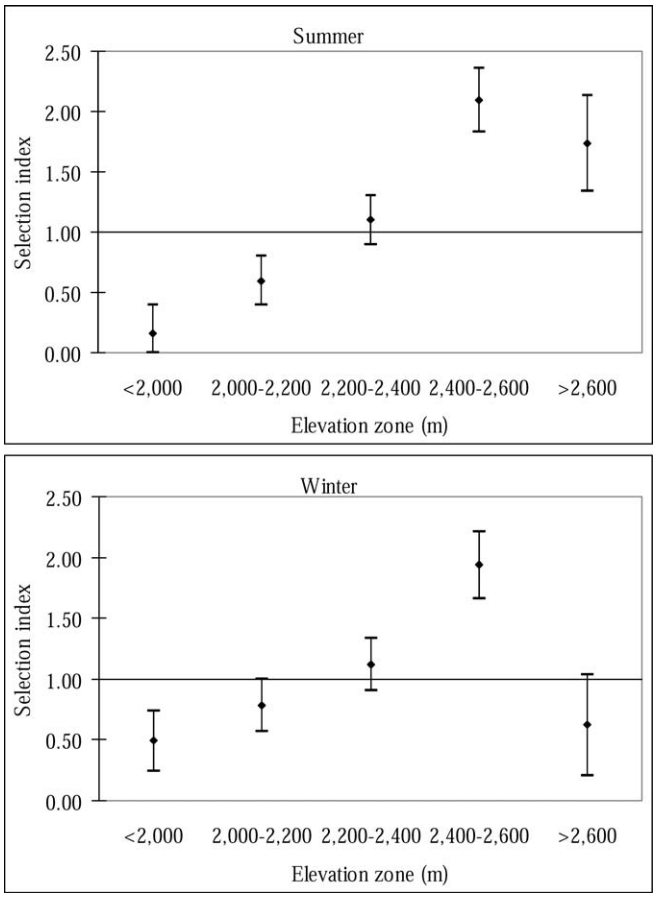

Figure 4. Selection indices (95% CI) for seasonal wolverine use points versus random points for elevational zones in central Idaho, USA, 1992–1996. Intervals occurring >1.00 or <1.00 indicate use or nonuse, respectively. Intervals that include 1.00 indicate no selection.

Adult sexes were most easily differentiated by female presence in whitebark pine during summer and male use of lodgepole pine during winter (Table 5). Subadults were most readily distinguished from the adults by their winter presence in Douglas fir and absence on steep slopes (Table 5).

We found wolverines closer to streams than expected during winter and farther from streams than expected during summer (Fig. 6). No relationship was evident regarding distance to trails. We did not find wolverines close to elk winter range nor were they found close to roads (Fig. 7).

Descriptive Models

The 6 variables that were most strongly associated with wolverine presence among the seasonal models included 4 variables common to both seasons: elevation, grass–shrub, montane–park, and rock (Table 6). Summer models included the addition of whitebark pine and slope, whereas winter models included Douglas fir and lodgepole pine. Selecting only models that included these 6 variables resulted in 63 models for each season. The best models within each subset included 6 winter and 3 summer models with equivalent ($\Delta AIC \leq 2$) seasonal AIC scores (Table 6). The 2 summer models that produced the best AIC scores were also the highest ranked models from the original 4,096 models. For the winter subset, the 2 best AIC models ranked fifth and sixth in the original 4,096 models.

To differentiate between models having equivalent AIC scores, we evaluated their fit based the $\hat{C}$ of Hosmer and Lemeshow (2000). Winter models provided a better overall fit (Table 6), indicating that winter habitat associations were better predictors of wolverine presence than were summer

Table 4. Variable class preference-avoidance rankings for wolverine in central Idaho, USA, 1992–1996. Rankings summarize variable behavior (significance and coeff. stability) over all-possible models.

	Variable classes rankings[b]											
Variable[a]	Pooled overall	Pooled winter	Pooled summer	Ad F	Ad F winter	Ad F summer	Ad M	Ad M winter	Ad M summer	Subad	Subad winter	Subad summer
DF		X			–					X X	X X	
DFLP	X	X		X	X X						X	X
DFPP			–			–			–	–		
GS_SHB	– – –	– –	– – –	– –	– –	– –	– – –	– – –	– – –	– –	–	– –
LP		X			X		X	X X			X	
MIX_SA												
MT_PRK	X X	X	X	X	X					X		X
ROCK		– –					X		X		– – –	
WP			X X	X X X	X	X X X					–	X X
ASP[c]								–	X			–
ELEV[d]	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X	X X X	X X X	X X	X X X
SLP[e]	X X		X X X	X X	X X	X	X X X	X X	X X X			

[a] DF = Douglas fir, DFLP = Douglas fir–lodgepole pine, DFPP = Douglas fir–ponderosa pine, GS_SHB = grass–shrub, LP = lodgepole pine, MIX_SA = mixed subalpine, MT_PRK = montane park, ROCK = rock-barren, WP = whitebark pine, ASP = aspect, ELEV = elevation, SLP = slope.

[b] Preferred (XX)-avoided (– –), significant ($P < 0.25$) in ≥80% of models, and coeff. sign stable in ≥90% of models. Preferred (XXX)-avoided (– – –), significant ($P < 0.25$) in 100% of models, and coeff. sign stable in ≥90% of models.

[c] Aspect is linearized such that the (–) notation indicates preference for northerly aspects, and the (X) notation indicates preference for southerly aspects.

[d] X = preference for higher elevation.

[e] X = preference for steeper slopes.

models. The most parsimonious models also provided the best fit in both seasons (Table 6). We applied the parameters of the best fitting models for each season across the modeled landscape to provide a visual assessment of the models predictions across our study area (Fig. 8).

DISCUSSION

Habitat Relationships

Topographic variables.—Wright et al. (1932:44) characterized the wolverine as "being restricted to the higher life zones" and recommended protection and "enlargement of park areas in the upper Canadian and Hudsonian zones" to ensure wolverine persistence. Our results support this characterization and refine our understanding of the communities associated with wolverine presence. This Hudsonian life zone signature may define a niche that is limited to high-elevation mountain ranges in the conterminous United States and critical to wolverine persistence.

The positive correlation between increasing elevation and wolverine presence in our study area was central to our findings. Excluding the mountaintops, wolverines favored high elevations in nearly all our models; 83% of all wolverine use points occurred in the 2,200–2,600-m elevation zone. Moreover, this preference was not restricted to either season. Although a seasonal shift in elevational use occurred, it was relatively minor. The mean drop in elevation from summer to winter was only 99 m (Table 4) within an available universe with an elevation range of >2,400 m. Along with a general affinity for high elevations, vertical migrations in mountainous areas have been commonly noted for the wolverine (Hatler 1989). Central Alaska wolverines shifted their seasonal elevation use by 225 m within an available range of 1,500 m (Whitman et al. 1986). This, like the modest shift in our study area, was likely due to prey availability in the form of ungulate carrion at lower elevation and upslope movement to locate rodents at higher elevations in summer (Whitman et al. 1986). Hornocker and Hash (1980) described a seasonal shift of 549 m within an elevational gradient of nearly 2,000 m and reasoned that summer movement to higher elevations might provide escape from hot summer temperatures in addition to increasing prey availability. Seasonal vertical migration was apparent in Norway as well, where wolverines shifted 149 m on average (Landa et al. 1998). In Yukon, seasonal migration was not generally apparent, although it was observed in some individuals (Banci and Harestad 1990). Banci and Harestad (1990) reasoned that a lack of prey availability at high elevations during summer, along with moderate summer temperatures throughout their study area, precluded the need for such movements. Regarding the wolverine's general affinity for high elevations, Magoun and Copeland (1998) contended that high elevations provide deep and persistent snow cover necessary for the presence and maintenance of late winter reproductive dens; we found no significant downward winter shift in elevation use in adult females (Table 4).

Wolverines, except for adult males in the summer, preferred northerly aspects in both seasons (Fig. 5; Table 3), contrasting with preference for southerly aspects reported for Montana wolverines (Hornocker and Hash 1980). Based on the assertion of Hornocker and Hash (1980) that wolverines seek out cooler habitats in summer, we would expect preferences for northerly aspects to strengthen during summer. Although confidence intervals associated with aspect selection were tighter during summer, Idaho wolverines preferred northerly aspects in winter as well. In our multivariate analyses, the sign of the coefficients consistently indicated preference for northerly aspects, but

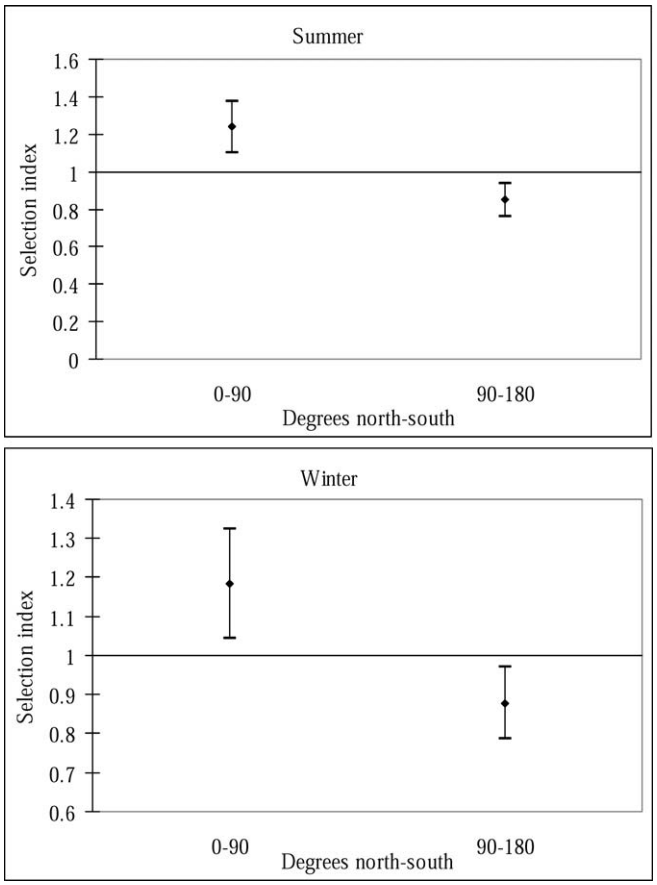

Figure 5. Selection indices (95% CI) for aspect depicting wolverine use points versus random points in central Idaho, USA, 1992–1996. Intervals occurring >1.00 or <1.00 indicate use or nonuse, respectively. Intervals that include 1.00 indicate no selection.

the variable contributed little to predicting wolverine presence (Table 3).

The wolverine's selection for steep slopes in summer, excepting subadults (Table 5), might simply reflect a preference for higher elevation habitats, which were positively correlated with steeper slopes ($R = 0.24$, $P = 0.001$). This is supported by the fact that the coefficient for slope was strongest in models not including elevation. This may also relate to the wolverine's preference for avalanche chutes (Krebs and Lewis 2000), which are common to steep slopes.

Cover type variables.—Wolverine use of habitat varied by season, but when viewed from the perspective of all variables tested, seasonal variation in cover type was relatively minor; wolverines moved from high-elevation whitebark communities in summer to mid-elevation Douglas fir and lodgepole pine in winter. Female's home ranges are much smaller (Banci and Harestad 1990) and therefore less diverse than those of males, likely reflecting fundamental necessities of food procurement and the rearing of offspring in areas proximal to reproductive den sites. Adult females accounted for most of the summer association with whitebark pine and lower elevation Douglas fir–lodgepole pine types in winter (Table 5). Adult males were the only class that preferred rock (during summer) and displayed a preference for lodgepole pine during winter. Lodgepole pine tended to dominate the lower fringes of the subalpine zone in our study area, providing good habitat for ungulates and probably a good source of carrion for wolverines. It was also not uncommon to find wolverines visiting lodgepole forest sites used as hunter camps where they might expect to find hides and bones left from the previous hunting season. In addition, adult males tend to travel more widely than females, and as such, they are more likely found in lower, coniferous-dominated habitats simply by chance. Montane coniferous forest types accounted for 70.2% of adult male wolverine relocations in our study area. Hornocker and Hash (1981) also reported 70% of their relocations occurring in medium-to-scattered timber.

Subadults displayed a wide variation in habitat use (Table 5) that may reflect preferences by both their mother and father. Even though subadults become independent of their mother at about 9 months of age, they remained associated with their natal area until sexual maturity at about 2 years of age (Copeland 1996). Early association with their mother would likely contribute to their selection of habitat as would subsequent association with their father, which we observed with several individuals (Copeland 1996).

Grass–shrub communities were predominately low-elevation communities, but occasionally they extended nearly to mountaintops on southern exposures. Wolverine's universal avoidance of these types may be related to a lack of snow, hot

Table 5. Mean seasonal elevation use (m) and seasonal differences, with 95% confidence limits, standard deviation, and significance of mean separation ($Pr > |t|$) by age and sex class for wolverine relocations (n) in central Idaho, USA, 1992–1996.

Class	Season	n	$\bar{x}$	Lower CL	Upper CL	SD	$Pr > \|t\|$
Age-sex Pooled	Winter	481	2,308	2,288	2,329	237	
	Summer	526	2,407	2,389	2,426	211	
	Difference		99	127	72		<0.001
Ad F	Winter	181	2,415	2,386	2,445	180	
	Summer	209	2,446	2,420	2,472	161	
	Difference		31	70	8		0.124
Ad M	Winter	131	2,274	2,233	2,315	226	
	Summer	152	2,403	2,365	2,441	229	
	Difference		130	185	74		<0.001
Subad	Winter	169	2,264	2,231	2,297	270	
	Summer	165	2,383	2,350	2,416	242	
	Difference		120	167	72		<0.001

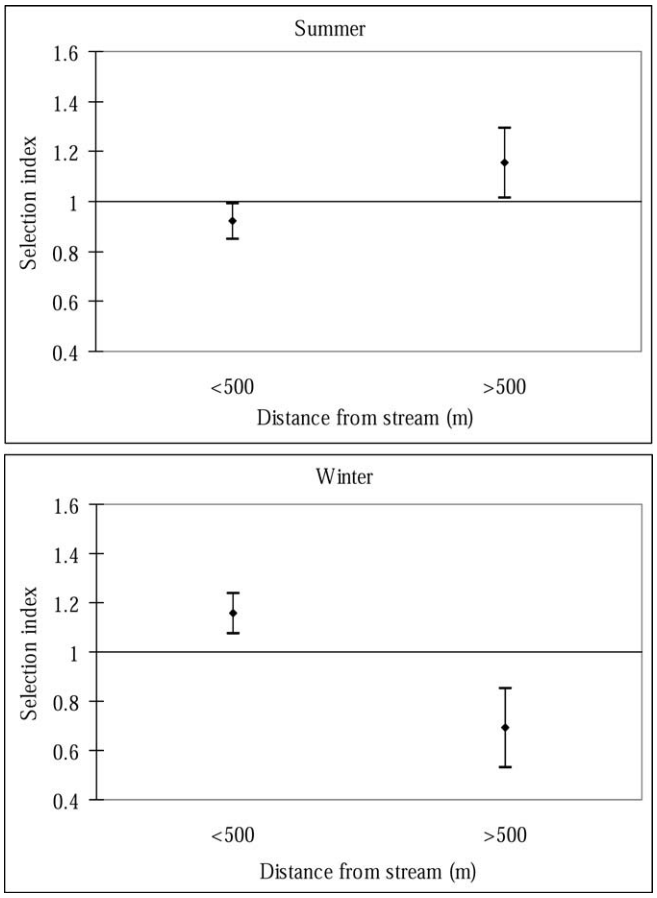

Figure 6. Selection indices (95% CI) depicting distance from streams during summer and winter for wolverine use points versus random points in central Idaho, USA, 1992–1996. Intervals occurring >1.00 or <1.00 indicate use or nonuse respectively. Intervals that include 1.00 indicate no selection.

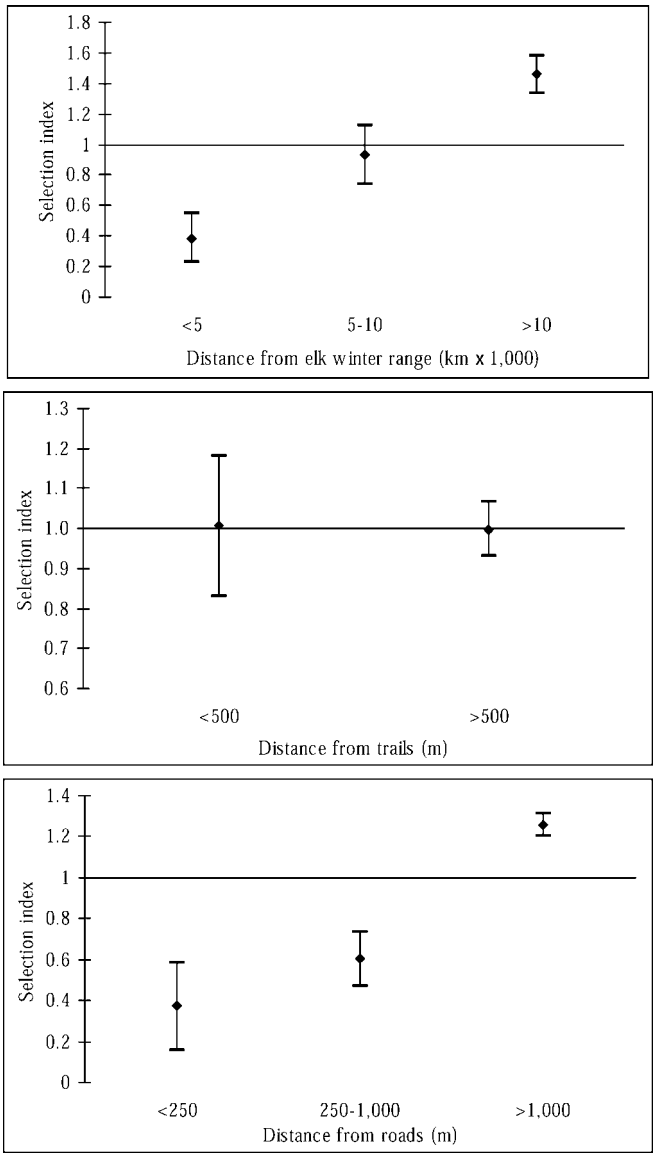

Figure 7. Selection index (95% CI) depicting distance from trails, elk winter range, and roads for wolverine use points versus random points in central Idaho, USA, 1992–1996. Intervals occurring >1.00 or <1.00 indicate use or nonuse, respectively. Intervals that include 1.00 indicate no selection.

temperatures, and a general lack of prey availability and likely contributed to wolverine preference for northerly aspects.

Rock habitats were generally used at proportions less than available across all classes, contrary to results reported in Copeland (1996). This is particularly interesting in that our univariate analyses found a positive association with rock ($P < 0.10$) for all data pooled and for the adult female class during summer (Table 5), as did the compositional analysis conducted by Copeland (1996), which reported a strong use of rock during summer. In this analysis, we found that rock functioned primarily as a surrogate for elevation; hence, it provided a positive estimate in the absence of elevation. Wolverines used high-elevation habitats, but the higher elevation mountaintops, characterized by rock, were not used beyond availability. Conversely, talus rock commonly occurs within and adjacent to high-elevation whitebark pine communities. May et al. (2006) reported similar findings in Norway, wherein rock–ice and alpine tundra habitats were positively associated with wolverine home range location at broad scales, but they were avoided at within-home range scales.

Our distance variables indicated wolverines were not spatially associated with elk winter range. Winter range occurs on the periphery of our study area primarily along low-lying portions of the Middle Fork and main Salmon rivers on the northern and eastern edge of the study area, and at several artificial elk feeding sites along the South Fork of the Boise River in the southern portion of the study area. Carrion use in winter, observed during snow-tracking sessions, was generally located in mid-elevation forests, and in many cases it was associated with hunter wounding mortality. The study area, which was open for elk and deer (*Odocoileus* spp.) hunting during fall, may provide ample carcasses through wounding mortality and butchering remains to sustain members of a low-density species, such as the wolverine, through winter without the need to move to the winter ranges. Wounding mortality rates have been reported as high as 7% of hunter harvest for male elk

Table 6. Logistic regression models predicting seasonal presence (P), change in Akaike's Information Criterion (ΔAIC), and Hosmer and Lemeshow goodness-of-fit statistic ($\hat{C}$) for wolverine in central Idaho, USA, 1992–1996.

Model coeff.[a]	Season[b]	ΔAIC	$\hat{C}$
P = (Intercept + LP − ROCK + DF − GRS_SHB + ELEV)	Winter	0.00	8.10
P = (Intercept − ROCK + DF − GRS_SHB + ELEV)	Winter	0.09	7.98
P = (Intercept + LP − ROCK + DF − GRS_SHB + MT_PRK + ELEV)	Winter	0.71	7.95
P = (Intercept − ROCK − GRS_SHB + ELEV)	Winter	0.83	4.09
P = (Intercept − ROCK + DF − GRS_SHB + MT_PRK)	Winter	1.52	13.21
P = (Intercept + LP − ROCK + DF + ELEV)	Winter	1.73	9.89
P = (Intercept − ROCK − GRS_SHB + ELEV + SLP)	Summer	0.00	24.13
P = (Intercept + WP − ROCK − GRS_SHB + ELEV + SLP)	Summer	0.64	31.20
P = (Intercept + DFLP − ROCK− GRS_SHB + MT_PRK + ELEV + SLP)	Summer	1.75	25.82

[a] LP = lodgepole pine, ROCK = rock-barren, DF = Douglas fir, GS_SHB = grass–shrub, ELEV = elevation, MT_PRK = montane park, SLP = slope, WP = whitebark pine, DFLP = Douglas fir–lodgepole pine.
[b] Winter = Dec–May; summer = Jun–Nov.

(Unsworth et al. 1993) and 27% for female elk (Leptich and Zager 1991). In addition, nonuse of ungulate wintering areas would help maintain spacing between wolverines and other predator competitors such as mountain lion (*Puma concolor*), grey wolf (*Canis lupus*), and coyote (*Canis latrans*).

Why wolverines stayed in proximity to streams during winter, distancing themselves from streams during summer, is not clear, although it may indicate spatial differences in seasonal food availability or that stream channels provide easier travel corridors during winter. Our distance-to-trails statistics indicated no relationship between wolverine presence and maintained trail systems. This may reflect a lack of sensitivity of wolverines to human presence, or it may be related to a low frequency of human presence on the trail systems. It was not uncommon to find study animals near trails and active campgrounds during summer. Our distance-to-road statistics indicated nonuse of areas near roads, but because most roads occur at lower elevations and on the periphery of the study area, this may be an artifact of unequal availability across the study area. Unmaintained winter roads commonly used by our field crew for snowmobile access to trapping sites were frequently used for travel by wolverines. The wolverine has long been considered sensitive to human presence based largely on the

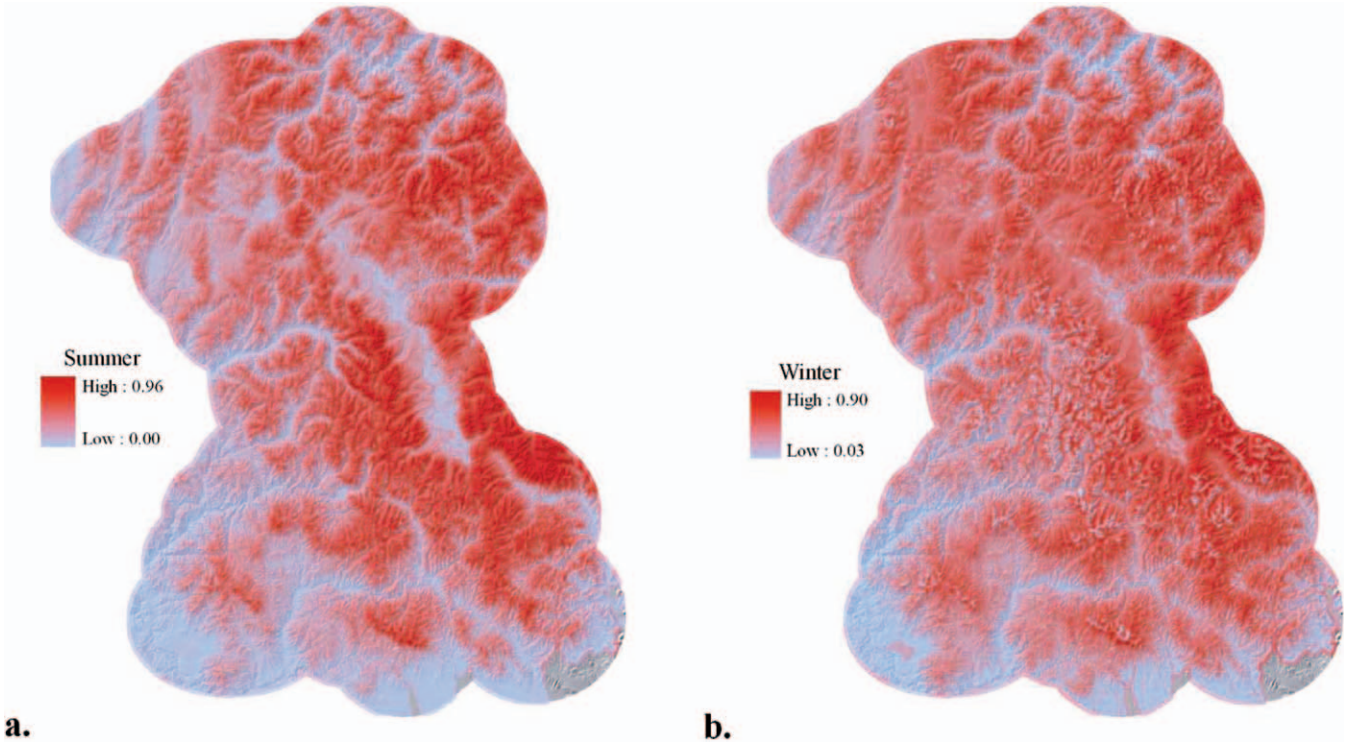

Figure 8. Logistic regression model output layers depicting seasonal probability of wolverine use. We selected models based on strength ($P < 0.25$) and consistency (stability of coeff. sign) of variables derived from summer (a) and winter (b) relocation data in central Idaho, USA, 1992–1996. Model content differed by only a single variable, slope, present in the summer model {summer P = [−7.5167 − (rock × 0.9056) − (grass–shrub × 1.7870) + (elevation × 0.00293) + (slope × 0.0525)], winter P = [−3.9239 − (rock × 2.0071) − (grass–shrub × 1.1273) + (elevation × 0.00187)]}. Modeled output reflects preference for high-elevation, steep slopes in summer, followed by a modest downward shift in elevation during winter. Seasons are distinguished primarily by periods of snow cover as summer (Jun–Nov) and winter (Dec–May).

species' contemporary presence within remote, isolated areas. Several empirical studies have also come to the same conclusion, reporting spatial separation of wolverine and human-related infrastructure (Carroll et al. 2001, Rowland et al. 2003, May et al. 2006), but it is still unclear whether this is truly a cause–effect relationship or simply a description of the species' tendency to reside in areas that are generally inhospitable to human development. Wolverines were most commonly associated with high-elevation remote habitats in our study area, which is 81% roadless. As such, presence cannot likely be attributed to the avoidance of people, roads, or development.

Descriptive models.—Although we conclude that seasonal differences in wolverine habitat preferences were relatively minor, a graphic representation of our best seasonal models clearly displays a varying pattern of use (Fig. 8). Strength of the coefficient for elevation along with the incorporation of steep slopes favors high-elevation habitats in the summer model. In the winter model, high elevation is still preferred, but to a lesser degree, whereas slope is absent and the negative coefficient for rock is 2 times greater than in the summer model, leading to modeled avoidance of high-elevation, rock-dominated cover types. This is consistent with our field observations. The only vegetative component necessary to either model is grass–shrub. Although our 9 vegetative variables provide some insight into wolverine habitat relationships, their contribution to predicting wolverine presence in central Idaho is limited in comparison with topographic variables. Although predictive modeling provides a useful tool for extrapolation of relationships, model fit is a function of the composition of response variables specific to the data used in its development. Generalization beyond this extent will not necessarily be valid.

Conclusions and recommendations.—Seasonal variation in habitat use was evident for wolverines in Montana (Hornocker and Hash 1981) and Alaska, USA (Gardner 1985, Whitman et al. 1986), but less apparent in Yukon (Banci and Harestad 1990). In investigating this relationship in central Idaho, we concur that wolverines exhibited a shift in seasonal habitat use. Nonetheless, the shift was relatively minor in terms of both vertical movement and changes in habitat associations. Wolverine presence was largely limited throughout the year to a 400-m elevational band wherein habitat preferences shifted from whitebark pine communities in summer to Douglas fir and lodgepole pine associations in winter. We think it is reasonable to assume that the wolverine's association with particular vegetation types had less to do with the vegetative species than with some other ecological component provided by or associated with a particular habitat. We speculate, as have others, that seasonal variation in habitat use is a response to varying food availability. Additional study of seasonal food associations might help address this question.

Furthermore, central Idaho wolverines displayed no affinity for ungulate winter range. This could be due to either an adequate food supply outside of these areas or to an avoidance of larger predators that frequent ungulate wintering areas. Although the wolf and mountain lion are commonly cited as predators of the wolverine, neither this relationship nor its influence on wolverine habitat or spatial use is explicit in the literature. The influence of interspecific associations on wolverine habitat selection warrants further study.

Year-round use of high-elevation habitats may be associated with the affinity of female wolverines for persistent snow cover for denning (Magoun and Copeland 1998, Aubry et al. 2007). The character of wolverine reproductive dens has been described for only 5 female wolverines across North America (Magoun and Copeland 1998), only 2 of which were in the contiguous United States (Copeland 1996). If the availability of denning habitat drives female habitat use, a more comprehensive understanding of den site characteristics is essential.

Additionally, our knowledge of wolverine habitat associations would benefit from a more specific understanding of how wolverines use the landscape. Copeland (1996) suggested that wolverines move in response to patchy resources, moving long distances in relatively short periods to resource sites where they remain for an extended period. As such, wolverine habitat associations may vary by the temporal and spatial character of movement and the influence of landscape resistance (Forman and Godron 1986). How landscape resistance and the spatial structure of resources influence wolverine habitat preferences are also opportunities for further study.

MANAGEMENT IMPLICATIONS

Central Idaho wolverine presence within high-elevation communities throughout the year indicates preference for subalpine habitats rather than avoidance of anthropogenic features. Wolverine may be impacted by management practices that influence subalpine communities, particularly those that reduce the presence and opportunity for carrion availability.

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