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EVALUATION OF LANDSCAPE MODELS FOR WOLVERINES IN THE INTERIOR NORTHWEST, UNITED STATES OF AMERICA

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The wolverine (*Gulo gulo*) is an uncommon, wide-ranging carnivore of conservation concern. We evaluated performance of landscape models for wolverines within their historical range at 2 scales in the interior Northwest based on recent observations ($n = 421$) from Washington, Oregon, Idaho, and Montana. At the subbasin scale, simple overlays of habitat and road-density classes were effective in predicting observations of wolverines. At the watershed scale, we used a Bayesian belief network model to provide spatially explicit estimates of relative habitat capability. The model has 3 inputs: amount of habitat, human population density, and road density. At both scales, the best models revealed strong correspondence between means of predicted counts of wolverines and means of observed counts ($P < 0.001$). Our results can be used to guide regional conservation planning for this elusive animal.

Key words: Bayesian models, carnivores, conservation planning, *Gulo gulo*, habitat evaluation, interior Columbia Basin, models, Northwest, roads, wolverine

The wolverine (*Gulo gulo*) is a wide-ranging, secretive, midsized carnivore that occurs in low densities across its range (Banci 1994; Wilson 1982; Witmer et al. 1998). Wolverines in the conterminous United States often occur in remote, high-elevation mountain basins and cirques, particularly during the breeding season (Banci 1994; Wilson 1982), rendering population surveys difficult. Consequently, the wolverine is rarely observed and is one of the least studied of the midsized carnivores in the United States (Ruggiero et al. 1994; Weaver et al. 1996). Such traits present special challenges for conservation and management of this poorly understood species.

Although the status of the wolverine is considered globally secure, it is uncommon, and local populations likely have been extirpated or reduced throughout its range (Banci 1994; Wilson 1982). In the United States, wolverines no longer occur east of Montana and Wyoming. The species also may have been extirpated from the southern periphery of its former range in Colorado (Nead et al. 1985), and it is extremely uncommon and possibly has been extirpated in California (Kucera and Barrett 1993), with the last verified sighting in 1922 (K. Aubrey, in litt.). Likewise in Canada, the

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species is presumed to have been extirpated in New Brunswick and is considered vulnerable or imperiled in several other provinces (NatureServe 2001, http://www.natureserve.org/explorer).

Despite apparent shrinkage of the species' range, there is evidence of population resurgence within portions of its historical range. For example, although Davis (1939) declared that the species was likely extinct in Idaho, Copeland (1996) trapped and studied 19 wolverines in a population in central Idaho in the 1990s. In Montana, Newby and McDougal (1964) reported an apparent repopulation of areas where wolverines had not been recorded for many years.

Whereas several field studies of the species have been conducted in Alaska and Canada (e.g., Banci 1987; Magoun 1985; Whitman et al. 1986), only 2 studies have been reported for the conterminous 48 states: one in Montana (Hornocker and Hash 1981) and a more recent study in Idaho (Copeland 1996). Thus, basic information about wolverine distribution and habitat relationships in the conterminous United States is scarce. Because populations in this region occur southernmost in the species' range in North America, habitat requirements there may differ from those of populations found in more northern ecosystems. Recent genetic studies of wolverines have suggested that range reductions caused population fragmentation in the southern portions of the species' range in North America (Kyle and Strobeck 2001). Wilson et al. (2000) demonstrated that even relatively close populations (<350 km apart) are genetically distinct, suggesting that large numbers of refugia may be required across broad landscapes to maintain genetic diversity.

Wolverines, especially males, have comparatively large home ranges (100 to >1,000 km^2—Copeland 1996; Hornocker and Hash 1981; Wilson 1982) and select for vast areas of relatively undisturbed habitat, which may be critical for persistence of populations (Carroll et al. 2001). The combined effects of urban development, human disturbance (Austin 1998; Banci 1994; Carroll et al. 2001; Copeland 1996; Ruediger 1998), and overtrapping (Weaver et al. 1996; Witmer et al. 1998) likely contributed to the currently restricted distribution of the wolverine.

Wolverine habitat and population status were assessed recently under the aegis of the Interior Columbia Basin Ecosystem Management Project (hereafter referred to as "Interior Columbia Basin Project"; U.S. Forest Service and U.S. Bureau of Land Management, in litt.). Wisdom et al. (2000) evaluated broad-scale changes in amount of habitat from historical (about 1850–1890) to current (1985–1995) periods for the wolverine and other terrestrial vertebrates in the interior Columbia Basin (hereafter referred to as "Basin"). Raphael et al. (2001) projected effects of various strategies for federal land management on the status of the wolverine population in the Basin with the use of Bayesian belief network (BBN) models (Marcot et al. 2001).

In their assessments, both Raphael et al. (2001) and Wisdom et al. (2000) developed models that predict wolverine distribution and habitat capability from hypothesized habitat relationships. These models were constructed using broad-scale geographic information system data from the Interior Columbia Basin Project (Hann et al. 1997; Wisdom et al. 2000), but their performance has not been evaluated. Evaluation of models developed for the Interior Columbia Basin Project is important because of the potential for these models to influence land management decisions across a large portion of the interior Northwest.

We evaluated performance of 2 models for wolverines, both broad-scale (subbasin—Wisdom et al. 2000) and midscale (watershed—Raphael et al. 2001), to understand better how landscape variables influence the distribution of wolverines. Specifically, we used an independently derived data set of observations on wolverines to

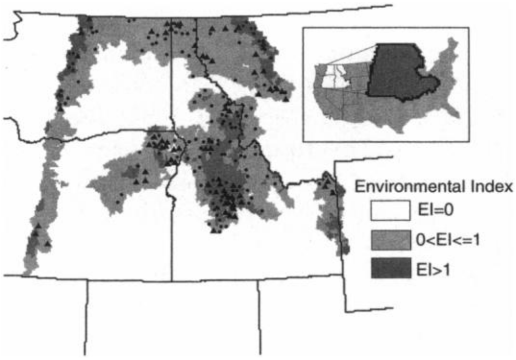

FIG. 1.—Observations of wolverines (1983 to present) and current environmental index values for watersheds in the interior Columbia Basin, northwestern United States. Environmental index values ranged from 0 to 2 and were generated from the Bayesian belief network model developed by Raphael et al. (2001) for wolverines. Dots represent single observations of wolverines; triangles represent >1 observation in a watershed.

evaluate the performance of the 2 models. We also developed and evaluated alternative models to determine whether other combinations of variables explain observed wolverine distribution better than do the subbasin or watershed models. Last, we evaluated the relative importance of landscape variables used in the models for predicting wolverine distribution at the 2 scales.

By examining such broad-scale patterns, our work complements previous, fine-scale research on wolverines (e.g., Copeland 1996). Results of broad-scale and fine-scale research, considered together, could strengthen management inferences and subsequent conservation planning and research for wolverines at multiple spatial scales in the interior Northwest.

MATERIALS AND METHODS

Study area.—The Basin included that portion of the Columbia River Basin east of the crest of the Cascade Range and portions of the Great Basin and the Klamath Basin in Oregon (Fig. 1). This area encompassed a variety of ecosystems across 58 million ha of western United States and was defined as the study area for science assessment of the Interior Columbia Basin Project. More than 50% of the Basin is under public ownership; most of the area was rural, with low densities of humans (slightly >4 people/km^2) compared with the rest of the nation (29 people/km^2—Crone and Haynes 2001).

The Basin supported diverse terrestrial communities, with environments ranging from low-elevation arid shrublands and grasslands to high-elevation subalpine forests and alpine tundra. Details of this environment and the associated flora and fauna are found in Hann et al. (1997), Marcot et al. (1997), and Quigley et al. (1996).

Most landscape variables for the Interior Columbia Basin Project were calculated using a hydrological hierarchy, with subwatersheds nested within watersheds, which are in turn nested within subbasins (Hann et al. 1997). There were 167 subbasins in the Basin, with 2,562 watersheds nested within them. Mean subbasin area was 3,450 km^2 (range = 47–10,805 km^2); this size was comparable with the regional scale over which land management plans may affect distribution of wide-ranging carnivores such as wolverines. Mean watershed area was 230 km^2 (range = 36–881 km^2), a scale comparable with home ranges of wolverines.

The subbasin model.—Wisdom et al. (2000) specifically defined source habitats (sensu Pulliam 1988; Pulliam and Danielson 1991) for wolverines and other vertebrates as vegetation measurable at a pixel size of 1 km^2 that contributes to stationary or positive population growth. To estimate habitat abundance for the subbasin model, Wisdom et al. (2000) modified the vegetation-classification system of cover types and structural stages created for the Interior Columbia Basin Project. This system consisted of 157 combinations of cover type (the dominant vegetation or physical feature occurring in a given 1-km^2 pixel) and structural stage (the dominant structural condition associated with the cover type in the pixel—Hann et al. 1997; J. P. Menakis et al., in litt.). Seventy-six of the 157 combinations were defined as source habitats for wolverines, including most or all cover types and structural stages in montane forest, subalpine forest, and alpine tundra (see Wisdom et al. 2000 for details). The source habitats identified by Wisdom et al. (2000) were intended to include the cover types and structural stages that, in combination, contribute to meeting the year-

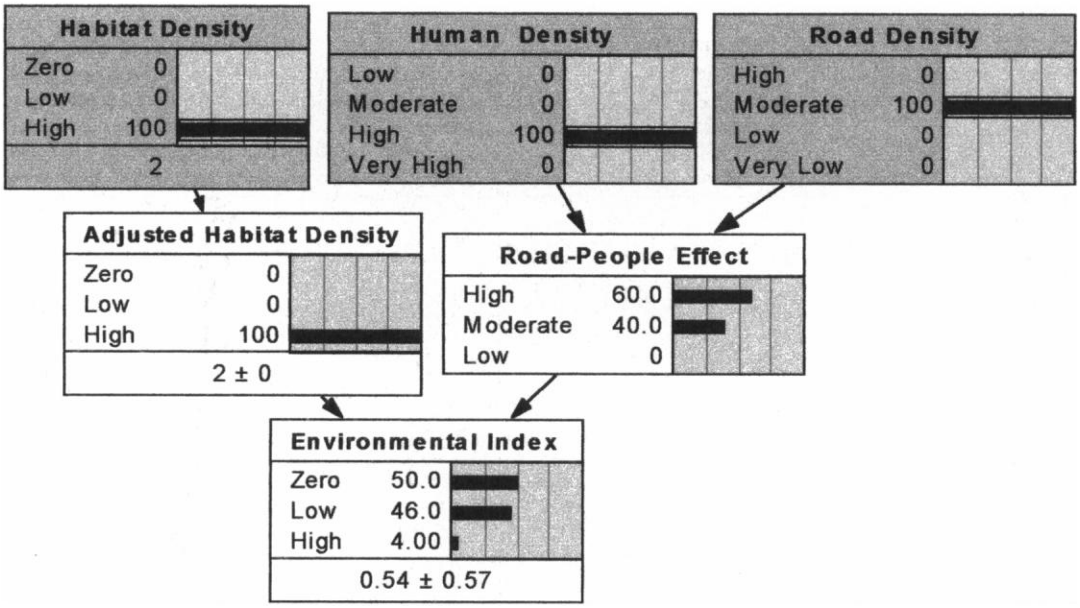

FIG. 2.—Schematic of the environmental index model developed for wolverines (from Raphael et al. 2001). Input variables (see Appendix I) and intermediate and response variables are described in the text.

round needs of wolverines in terms of food, denning, and other life requisites. However, these habitats were not a direct measure of such requisites. Consequently, understanding the utility of such habitats in characterizing coarse-resolution, regional status of conditions for wolverines was a primary focus of our current evaluation.

Wisdom et al. (2000) estimated current abundance of wolverine habitat in 127 subbasins (those with ≥1 km^2 of habitat) and mapped these data in relation to estimated density of roads. Three classes of road density were developed at the scale of the subbasin (Appendix I). The resulting map of habitat abundance and road-density classes, as developed by the above methods, constituted a subbasin model for wolverines that was considered by Wisdom et al. (2000) to reflect relative wolverine density. They specifically hypothesized that subbasins containing moderate to high habitat abundance, and zero to low road density, were associated with greatest density of wolverines and greatest probability of population persistence.

The watershed model.—Raphael et al. (2001) developed a BBN model for wolverines at the scale of the watershed. A BBN model is a type of influence diagram that depicts the causal agents that influence the likelihood that a parameter assumes certain values (Lee 2000; Marcot et al. 2001). BBN models are particularly useful in organizing our thinking about species-habitat relationships (sensu Johnson 2001; Marcot et al. 2001). BBN models have been applied in decision making and management for fisheries, wildlife, and other natural resources (Lee 2000; Marcot et al. 2001).

The wolverine BBN predicts relative habitat capability for each watershed based on 3 input variables: habitat density (expressed as 1 of 3 classes of habitat proportion); road density; and human population density (Fig. 2; Appendix I). Estimates of road density and human population density, summarized into classes (Appendix I), were combined in the wolverine BBN as proxies for human disturbance, which is of particular concern around den sites (Copeland 1996; Raphael et al. 2001; Fig. 2). Other features commonly associated with wolverines, especially during the denning season (e.g., logs, talus, or high-elevation cirques), could not be measured reliably across the Basin (Witmer et al. 1998), nor were we able to model local factors such as abundance of carrion or of primary predators (e.g., mountain lion—*Felis concolor*), which may affect prey availability for wolverines. Such data were not uniformly available across the Ba-

TABLE 1.—Comparison of wolverine models and selection criteria at 2 spatial scales in the interior Columbia Basin, northwestern United States, listed in order of increasing $\Delta QAIC_i$[a] at each scale. ($\Delta QAIC_i$ is the difference between minimum QAIC [Burnham and Anderson 1998] and the QAIC for a particular model.) For all models, the dependent variable is count of wolverine observations.

Scale and model number	Explanatory variables[b]	Number of parameters[c]	$\Delta QAIC_i$
Subbasin			
1S	Log habitat amount, road-density class	5	0
2S	Log habitat amount	3	0.07
3S	Log area, habitat class, road-density class	7	5.80
4S	Log area, habitat class	5	6.06
5S	Log area, road-density class	5	8.82
Watershed			
1W	Log area, environmental index	4	0
2W	Log habitat amount, road-density class	6	2.25
3W	Log area, road-density class	6	2.96
4W	Log area, human-density class	6	3.42
5W	Log habitat amount	3	4.71
6W	Log area, habitat class, human-density class, road-density class	11	7.93
7W	Log area, habitat class	5	10.04

[a] $QAIC_i$ quasi-Akaike's information criterion.

[b] Habitat amount (km^2) is the watershed (or subbasin) area times proportion of habitat; area is the area of the watershed or subbasin (in km^2); and environmental index is the score from the Bayesian belief network model (Raphael et al. 2001), watershed scale only. See Appendix I and text for further descriptions of variables.

[c] Equals 1 + number of parameters fit in model (including intercept).

sin. Thus, the model was structured to depict year-round habitat capability as influenced by broad-scale human disturbances.

Conditional probability tables link the model variables, such as adjusted habitat density and road-people effect (Fig. 2), by incorporating beliefs of experts on how explanatory variables are related (Lee 2000; Marcot et al. 2001). The model yields an environmental index, which for wolverines incorporates habitat density adjusted by effects of human disturbance (Fig. 2). Expected values of the environmental index (an average of the class score of 0, 1, or 2 weighted by the probability of occurrence) ranged from 0 to 2 (Fig. 2).

To explore whether the original models at each scale best combined existing data, we developed alternatives to the subbasin and watershed models based on the same variables, with the addition of a habitat variable that reflected the actual amount of habitat in a watershed or subbasin (i.e., habitat as a continuous variable). Alternative models at the subbasin scale included amount of habitat or habitat class, road density, or both. Alternative models at the watershed scale included various combinations of ≥1 of the 3 explanatory variables used in the BBN (classes of habitat density, road density, and human population density) and amount of habitat (Table 1). Although all possible 2-variable models were developed, we report only the best fitting of those developed at the watershed scale.

Wolverine observation data.—We tested the subbasin, watershed, and alternative models with wolverine observations (counts) from databases maintained by natural heritage programs in Washington, Oregon, Idaho, and Montana under the Natural Heritage Network (Groves et al. 1995). Counts included published observations from Washington, Oregon, and Idaho (Edelmann and Copeland 1999). Counts were not used in constructing the models and thus served as an independent data set by which the models could be evaluated for their ability to predict relative counts of wolverines.

For testing the models, we used only observations occurring within the Basin boundaries (Fig. 1): Washington (n = 55), Oregon (60), Idaho (214), and Montana (92). Each observation was associated with a watershed and its corresponding subbasin. Although observations were obtained from 1933 to 1999, we limited our analyses to 421 observations recorded since 1983 because such observations should correspond better to current vegetation and other environmental attributes used in our analyses.

Because the observations were not derived from systematic sampling, potential biases exist in the counts, particularly from unequal survey effort across the Basin. However, observations were screened for reliability by natural heritage programs for each state with various criteria; records ranged from tracks or other reported evidence of presence to museum specimens. Moreover, Edelmann and Copeland (1999) found a spatial correspondence between confirmed and unconfirmed wolverine sightings in the interior Northwest and noted that standard criteria for screening observations have not been developed (Maj and Garton 1994). Likewise, Carroll et al. (2001) developed separate models for fisher (*Martes pennanti*) and lynx (*Lynx canadensis*), first using more reliable records (e.g., specimens and trapping reports) and subsequently using all records, and found no difference between models. Our data set included only 8 confirmed observations (i.e., those associated with physical evidence); the majority were observations of wolverines (71%) or their tracks (21%). We used all recent observations, regardless of type or source, for the analyses we report in this paper.

Matching scales with wolverine locations.—At the scale of the subbasin, we quantified habitat abundance and road density within 124 of the 127 subbasins identified for the subbasin model (those subbasins containing source habitat for wolverines). The 3 subbasins containing habitat that were excluded were in Wyoming because of the small percentage of the study area in that state. Number of observations per subbasin averaged 2.6 (range 0–32).

At the watershed scale, Raphael et al. (2001) restricted their analyses using the BBN model to the 1,179 watersheds nested within subbasins containing moderate or high amounts of source habitat (see Appendix I, habitat class at subbasin scale). Our results were comparable with those of that study because we used the same constraint in selecting watersheds for testing the models at this scale but also excluded 32 watersheds in Wyoming. Thus, we analyzed 1,147 watersheds where wolverine observations (n = 358) were available. Most watersheds (81%) had no observations; mean number of observations per watershed was 0.3.

Statistical analysis.—In our analyses, we used Poisson regression models and estimated parameters with maximum likelihood methods. We used Akaike's information criterion to identify the most parsimonious models (those with optimal balance of fewest parameters and good fit to the data) among our competing set of models at each scale (Burnham and Anderson 1998). Implicit in the use of this approach is the assumption that a series of ecologically plausible models has been developed, from which the most parsimonious model can be identified (Anderson et al. 2001).

Because the response variable—number of wolverine observations in a watershed or subbasin—was a count, we modeled it as a Poisson variable. The Poisson distribution is a discrete distribution that assumes nonnegative integer values and is often applied to the number of uncommon events, such as wolverine observations, occurring in some time interval or spatial area (Feller 1957). We used generalized linear models (McCullagh and Nelder 1989) to relate counts of wolverine observations to various explanatory variables and used the GENMOD procedure (PROC GENMOD—SAS Institute Inc. 1997) for model fitting.

We would expect the number of observations to relate multiplicatively to area; everything else being equal, we would expect a watershed or subbasin twice as large as another to have twice as many observations from sampling effects alone. Because of this supposition, and because a generalized linear model with a Poisson variable involves a logarithmic transformation of the response variable (number of observations), we used the logarithm of area as an explanatory variable in the models.

The homogeneous Poisson distribution assumes that events (wolverine observations) are independent and equally likely to occur in all units (e.g., watersheds). We tested this assumption by examining counts for their conformance to a homogeneous Poisson distribution. At both scales, variance exceeded the mean, indicating nonhomogeneity of occurrences. A 2nd indicator of overdispersed data, Pearson's chi-square statistic divided by its degrees of freedom (Burnham and Anderson 1998; SAS Institute Inc. 1997), also suggested that the observations were clumped. Thus, we chose a correction for overdispersion (the variance inflation factor, $\hat{c}$—Burnham and Anderson 1998). At each scale, the set of all competing models was developed and then fit to the data with PROC GENMOD. The variance inflation factor, ĉ, was selected from the best-fitting model (i.e., the one with lowest deviance), regardless of the number of parameters in the model. We used Pearson's chi-square statistic divided by its degrees of freedom as our estimate of ĉ (Burnham and Anderson 1998; SAS Institute Inc. 1997). These ĉ values, 1 for each scale, were used to correct for overdispersion, and all models were fit again in PROC GENMOD to obtain the final statistics for model comparisons.

We developed several models to predict observations of wolverines in a watershed or subbasin and assessed the adequacy of competing models for fitting the data with a modified Akaike's information criterion (Anderson et al. 2001; Burnham and Anderson 1998). Values of Akaike's information criterion reflect the goodness of fit of a model to the data by incorporating the log-likelihood, and they reflect the parsimony of the model by incorporating the number of parameters. Because of overdispersion of the data, we used the quasi-Akaike's information criterion value, which adjusts for that overdispersion by dividing the log-likelihood by ĉ (Burnham and Anderson 1998).

We further evaluated performance of the selected model (the model with lowest value of the quasi-Akaike's information criterion) at each scale by comparing model predictions against actual counts. Because of the large sample sizes and the high variability in observed counts, we sorted and grouped sample units (40 per group for watershed-scale models and 10 per group for subbasin models) by their predicted values and then calculated means of predicted and observed counts for each group. We next calculated Pearson correlation coefficients between the 2 sets of means for each of these 2 models and the original model of interest at each scale (i.e., the BBN model at watershed scale and the road-density and habitat class model at subbasin scale). We also visually compared the mean observed and mean predicted counts for these 4 models. Statistical significance was assessed at the alpha = 0.05 level.

RESULTS

Subbasin models.—The 124 subbasins included in the subbasin model of Wisdom et al. (2000) made up 74% of the total study area but captured 99% of all observations in the Basin (Fig. 3). In addition, subbasins that were identified in this model as having greatest potential to support wolverine populations (that is, the 23 with moderate or high amount of habitat and low road density) constituted only 17% of the total area of subbasins with habitat but captured 37% of the wolverine observations (Fig. 3).

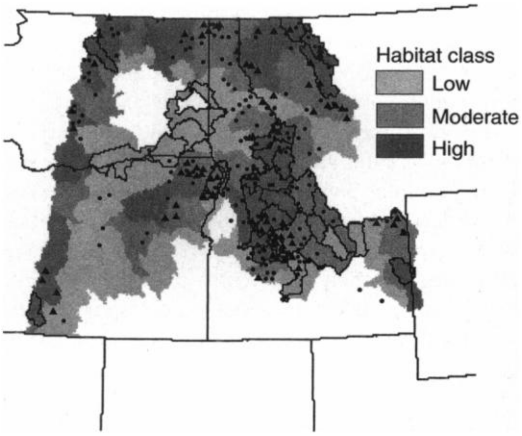

FIG. 3.—Observations of wolverines (1983 to present) and abundance of source habitats in relation to low road densities (outlined in black) within 124 subbasins in the interior Columbia Basin, northwestern United States. See Appendix I for explanation of habitat and road-density classes. Dots represent single observations of wolverines; triangles represent >1 observation in a watershed.

All explanatory variables in the subbasin model (model 3S; Table 1) and the 4 alternative models at this scale were significant ($P \leq 0.003$, type-III likelihood-ratio statistics, PROC GENMOD). Individual regression coefficients for selected models at this scale also were significant (Table 2), with 1 exception: the low level of road density in model 1S did not differ from the moderate level (Table 2).

Of the competing models fitted at this scale, the 2 best ones were nearly identical in their quasi-Akaike's information criterion values (Table 1). The most parsimonious model included the logarithm of habitat amount and road-density class, whereas

TABLE 2.—Statistics (from PROC GENMOD—SAS Institute Inc. 1997) of selected models for predicting counts of wolverines at 2 spatial scales in the interior Columbia Basin, northwestern United States, from 1983 to present. Blank cells for variable level are those for which the variable level is not applicable; the variable is continuous and thus does not have levels.

Scale and model number	Explanatory variable[a]	Variable level	Regression coefficient	*SE*	χ^2	*P*
Subbasin						
1S	Log habitat amount		0.60	0.11	30.00	<0.0001
	Road-density class	Low	0.28	0.21	1.84	0.18
		Moderate	0[b]			
		High	−0.93	0.33	7.75	0.0054
	Intercept		−5.45	1.26	18.79	<0.0001
2S	Log habitat amount		0.60	0.11	31.13	<0.0001
	Intercept		−5.50	1.24	19.48	<0.0001
Watershed						
1W	Environmental index		0.63	0.13	22.36	<0.0001
	Log area		0.57	0.17	11.10	0.0009
	Intercept		−4.68	0.94	24.84	<0.0001
2W	Log habitat amount		0.26	0.08	9.41	0.0022
	Road-density class	Very low	0[b]			
		Low	0.08	0.22	0.12	0.7314
		Moderate	−0.51	0.20	6.43	0.0112
		High	−0.98	0.29	11.52	0.0007
	Intercept		−1.94	0.41	22.76	<0.0001
3W	Log area		0.50	0.17	8.83	0.0030
	Road-density class	Very low	0[b]			
		Low	−0.07	0.22	0.11	0.7430
		Moderate	−0.67	0.20	11.50	0.0007
		High	−1.06	0.29	13.62	0.0002
	Intercept		−3.45	0.92	14.09	0.0002

[a] Habitat amount (km^2) is the watershed (or subbasin) area times proportion of habitat; area is the area of the watershed or subbasin (in km^2); and environmental index is the score from the Bayesian belief network model (Raphael et al. 2001), watershed scale only. See Appendix I and text for further descriptions of variables.

[b] Effects for other levels of the explanatory variable are relative to this level; accordingly, the regression coefficient for this level is set to 0 and *SE*, χ^2, and *P* are not applicable (SAS Institute Inc. 1997).

model 2S included only the log of habitat amount (Table 1). In comparison, other models we examined at this scale (models 3S [original subbasin model], 4S, and 5S) had considerably less support from the data (Table 1). Amount of habitat was a better explanatory variable than was road-density class at this scale. The model (2S) with only log of habitat amount was well supported by the data, whereas the model (5S) with only road-density class and log of area had much weaker support. However, means of predicted counts closely matched means of observed counts for both the best model (1S; $r = 0.97$, $P < 0.0001$; Fig. 4a) and the original subbasin model (3S; $r = 0.91$, $P < 0.0001$; Fig. 4b).

Watershed models.—Watersheds with high scores for environmental index under the BBN model captured a disproportionately large number of wolverine observations (Fig. 1). Moreover, all explanatory variables, except habitat density, in the 7 models at the watershed scale were significant ($P \leq 0.012$, type-III likelihood-ratio statistics, PROC GENMOD). In particular, an effect of road-density class on occurrence of wolverines was evident in the 3 models in which it was included ($P \leq 0.008$, type-III likelihood-ratio statistics,

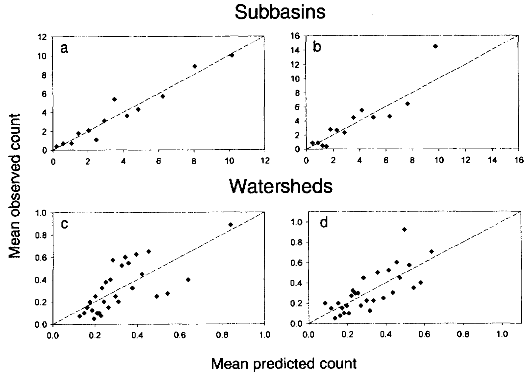

FIG. 4.—Observed counts of wolverines compared with predicted counts within subbasins and watersheds in the interior Columbia Basin, northwestern United States. a) Model 1S, subbasin scale; b) model 3S, subbasin scale (original road density—habitat class model of Wisdom et al. 2000); c) model 1W, watershed scale (Bayesian belief network model of Raphael et al. 2001); and d) model 2W, watershed scale. Observations were sorted into groups of 10 for plots of subbasin data (n = 124 subbasins) and groups of 40 for plots of watershed data (n = 1,147 watersheds). See Table 1 for variables included in each model. Dashed lines indicate $y = x$ for comparison.

PROC GENMOD). The low level of road-density class (see Appendix I for definition) in models 2W and 3W, however, did not differ from the very low level, suggesting that this variable could be collapsed to 3 or fewer levels (Table 2).

The BBN model (1W) appeared to be the most parsimonious among the competing models evaluated at the watershed scale (Tables 1 and 2). The 2nd-ranked model (2W) was the best of the 2-variable models evaluated, and it included log of habitat amount and road-density class. The next 2 models, 3W and 4W, were very similar in strength of evidence, as indicated by values of the quasi-Akaike's information criterion. These models included a single explanatory variable (road-density class or human-density class) and were better supported by the data than were the 2 models (5W and 7W) with habitat as the single explanatory variable.

The 2 models that included habitat-density class, as used in the BBN (Appendix I), were ranked 6th and 7th among the models considered at the watershed scale (Table 1). This variable was not significant in either model ($P > 0.33$). By contrast, amount of habitat was significant ($P < 0.001$) in both models (2W and 5W) in which it was entered.

Mean observed counts of wolverines increased linearly with counts predicted from the BBN ($r = 0.70$, $P < 0.0001$; Fig. 4c). A similar relationship was observed for the 2nd best model (model 2W; $r = 0.76$, $P < 0.0001$; Fig. 4d).

DISCUSSION

Model performance.—Both the subbasin and the watershed models (i.e., the habitat–road density model for subbasins and the BBN for watersheds) performed well, as did many of the alternative models. Close agreement in observed versus predicted counts occurred across scales and models, despite the coarse resolution of the landscape data, the combined use of empirical and hypothesized relations in model development, and the variable quality of wolverine observation data used for model evaluation. Moreover, the low probability of detecting and reporting the presence of wolverines, regardless of sampling method, presents a challenge for model evaluation and could cause lack of fit for even the most "perfect" of models.

All these factors add "noise" to the system we examined; thus, the degree to which the original model predictions matched the observed counts is compelling. This is particularly surprising, considering that wildlife habitat models in general do not have a history of proven performance or validation (Roloff and Kernohan 1999). Carroll et al. (2001) included high road density, precipitation, human population density, cirque habitat, and wetness in their model for wolverines. In testing their model with trapline data from British Columbia, Canada, Carroll et al. (2001) found that predicted habitat value was significantly, but not strongly, correlated with number of wolverines trapped ($r = 0.167$, $P = 0.003$). Potential biases in the trapline data may have accounted for the weak correlation (Carroll et al. 2001).

At the subbasin scale, our study showed that amount of habitat and road-density class were good indicators of the distribution of wolverine observations, as noted in the original subbasin model and alternative models. At the watershed scale, the model based on the BBN output (i.e., the environmental index score) performed as well as any model, indicating that the original BBN combined the explanatory variables in a meaningful way. Some alternative models developed at this scale, however, actually fit the data better (based on log-likelihood values) than did the model that used the BBN output, but at the cost of involving more variables. The Akaike's information criterion procedure penalized the BBN model less than the alternative models because it treated output of the BBN model (i.e., the environmental index score) as a single variable, although computing the score requires that its 3 input variables be measured. That some models we developed fit the data as well as does the BBN model suggests that, at least for the data we had, the component variables could be combined more effectively than is now done with the BBN. As new data become available, the alternative models we developed should be used to revise the wolverine BBN to reflect new knowledge about the relative importance of its input variables.

Although the wolverine BBN was developed to assess broad-scale, year-round habitats across watersheds, model outputs also corresponded to more fine-scale data. In his study of wolverines in central Idaho, Copeland (1996) described 7 dens. The dens occurred in 4 watersheds; environmental index scores for these watersheds (2 each with scores of 1.34 and 1.85) are the 1st and 3rd highest among all scores generated across the 1,179 watersheds with the wolverine BBN. Thus, although the BBN was not developed as a model for denning habitat, watersheds exceeding some threshold score for environmental index may provide an appropriate starting point for surveys of potential reproductive sites. Such sites may be scarce in the Basin (Copeland 1996), and further field investigations are warranted.

Habitat versus human disturbance.—Our results demonstrated that greater amounts of habitat, low road density, and low human population density corresponded closely with observations of wolverines across the Basin. The relative value of these 3 explanatory variables differed, however, across models. At the subbasin scale, the model incorporating amount of habitat alone was nearly as effective as the best model, which incorporated both amount of habitat and road-density class; the similarity in values of the quasi-Akaike's information criterion implies that the data are inadequate for selection of one model over the other. This finding concurs with the suggestion that amount of habitat, as indicated by vegetation cover type, is an adequate predictor of wolverine occurrence at regional scales (M. M. Hart et al., in litt.).

At the watershed scale, however, road density and human population density were better than amount of habitat or habitat class in predicting counts of wolverines. Of the watershed models that included only logarithm of area and 1 explanatory variable, those with either road density or human population density (3W and 4W) performed better than models with only amount of habitat or habitat class (5W and 7W). The habitat class variable used in the BBN, consisting of habitat estimates collapsed to classes of zero, low, and high (Appendix I), was clearly too coarse a measure of habitat and seemed inadequate as an explanatory variable outside the framework of the BBN. Likewise, the habitat class variable at the subbasin scale was inferior to the variable for actual amount of habitat as a continuous variable.

Source habitat for wolverines in the Basin has increased 14% since historical periods and thus may not limit current distribution or populations of the species. Rather, human disturbance may be the driving force behind its present distribution because populations are primarily found in areas relatively free of human disturbance (Banci 1994; Carroll et al. 2001; Weaver et al. 1996).

Further evidence of the importance of road density in predicting habitat quality for wolverines is found in a recently developed and tested model for wolverines in the Rocky Mountain region (Carroll et al. 2001). In their generalized additive-model plot, predicted occurrence of wolverines declined when road densities exceeded approximately 1.7 km/km^2. Our watershed-scale models suggested a lower threshold in the Basin—moderate road densities (from 0.44 to 1.06 km/km^2) were distinguishable from low densities (≤ 0.44 km/km^2) in predicting counts of wolverines but were not different from high densities (>1.06 km/km^2).

Although Wisdom et al. (2000) did not include human population density in their subbasin model, Raphael et al. (2001) included this variable in the BBN model at the watershed scale. Even in a single-variable model (model 4W), this variable performed well. It seems prudent to include both human population and road density as explanatory variables in broad-scale models for wolverines, as was done in the BBN.

Implications for conservation.—Our assessment provides a broad-scale depiction of relative quality of wolverine habitat across a large portion of the species' current and formerly occupied range. Although results from our models were compelling at both subbasin and watershed scales, the latter is likely more appropriate for conservation planning for this species. Wolverine home ranges are of the same order of magnitude as the watersheds used in our analyses, and groups of adjacent watersheds could be surveyed and considered together in conservation planning. The Basin consists of a heterogeneous landscape, and summarizing data over a smaller scale, such as the watershed, may improve model performance (Karl et al. 2000).

Outputs from BBN models could be used to guide systematic surveys of wolverines (e.g., in defining strata for sampling). Systematic surveys across large areas of western North America are needed to further understand the distribution of this elusive species (Banci 1994; Carroll et al. 2001). Because wolverines can cover immense distances, many observations may reflect where the animals travel or disperse rather than areas where wolverines reside to meet life requisites (Carroll et al. 2001).

For wolverines and other wide-ranging carnivores, strategies for regional-level planning and conservation must accompany stand-level studies to manage and conserve these species better (Banci 1994; Noss and Beier 2000; Ruggiero et al. 1994). As noted by Ruggiero et al. (1988), patterns of species abundance may provide the best information for many species on the importance of environments for persistence of populations. Management decisions must be made without absolute knowledge of species requirements as researchers continue to seek better knowledge about uncommon species such as the wolverine.

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APPENDIX I

Explanatory variables in landscape models for wolverines in the interior Columbia Basin, northwestern United States, and associated descriptions, assumptions, rationale, and levels used to assess habitat capability for wolverines at 2 spatial scales, based on current (1985–1995) conditions.

Subbasin scale

Habitat class.—Assigned by ranking all subbasins containing source habitat by proportion of habitat and dividing them into 3 equal classes (see Wisdom et al. 2000). Broad-scale classifications of amount of habitat for wide-ranging carnivores such as wolverines can be useful in management applications. There are 3 levels: low is lowest one-third; moderate is middle one-third; and high is highest one-third of subbasins based on rank ordering.

Road-density class.—Predicted road-density class by subbasin, based on the dominant class among watersheds nested within each subbasin (Wisdom et al. 2000; J. P. Menakis et al., in litt.). Measures of road density can be used as a coarse-scale constraint in developing broad-scale models for wide-ranging species that are sensitive to human disturbance. There are 3 levels of road-density class at this scale: low is ≤ 0.44 km/km^2; moderate is >0.44–1.06 km/km^2; high is >1.06 km/km^2.

Watershed scale

Habitat class.—Habitat-density class as used in the environmental index model for wolverines (Fig. 2, habitat density input; Raphael et al. 2001). Amount of habitat, based on the proportion of habitat in the watershed currently relative to the historical median proportion, with the median calculated across all watersheds in the historical range of wolverines in the Basin. Habitat density is an upper limit to the potential area of habitat within each watershed. Differences in levels of habitat-density (zero, low, and high) index differences in habitat quantity, but not quality, across watersheds. There are 3 levels of habitat class at the watershed scale: zero = habitat absent; low = proportional area of habitat < historical median proportion but >0; and high = proportional area of habitat ≥ historical median.

Road-density class.—Predicted road-density class by watershed, calculated by multiplying the proportion of each watershed in each of 6 original road-density classes (Hann et al. 1997) by the ordinal class number (i.e., 1–6). These products were then summed and the resulting weighted average used to assign each watershed to 1 of 4 final classes. Road-density data for the Interior Columbia Basin Ecosystem Management Project were initially mapped at 1-km^2 resolution using a geographic information system (J. P. Menakis et al., in litt.). High road density, in tandem with moderate to high human populations, yields a high road–people effect in the environmental index model, which may result in increased potential for mortality or displacement of wolverines away from otherwise suitable environments. There are 4 levels of this variable: very low is <0.06 km/km^2; low is ≥0.06–0.44 km/km^2; moderate is >0.44–1.06 km/km^2; and high is >1.06 km/km^2. This variable, in combination with human population density, indexes the degree to which road–people effects are present.

Human-density class.—Human population density class by watershed. Current densities were estimated by summarizing recent federal census block data for 1-km^2 pixels to the watershed level (Raphael et al. 2001; J. P. Menakis et al., in litt.). There are 4 levels of human-density class at this scale: low is <3.9 people/km^2, typically remote from population centers; moderate is ≥3.9 but <23.2 people/km^2, usually dominated by public land ownership, but use may be high if road densities allow access; high is ≥23.2 but <38.6 people/km^2, commonly dominated by private lands in smaller urban areas; very high is ≥38.6 people/km^2, typically urban, with scattered rural areas.