# CARNIVORES AS FOCAL SPECIES FOR CONSERVATION PLANNING IN THE ROCKY MOUNTAIN REGION

Carlos Carroll,[1,4] Reed F. Noss,[2] and Paul C. Paquet[3]

[1]*Klamath Center for Conservation Research, Orleans, California 95556 USA*
[2]*Conservation Science, Inc., Corvallis, Oregon 97330 USA*
[3]*World Wildlife Fund-Canada, Meacham, Saskatchewan S0K 2V0 Canada*

*Abstract.* Viability analysis of well-selected focal species can complement ecosystem-level conservation planning by revealing thresholds in habitat area and landscape connectivity. Mammalian carnivores are good candidates for focal species because their distributional patterns often strongly reflect regional-scale population processes. We incorporated focal species analysis of four carnivore species, fisher (*Martes pennanti*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), and grizzly bear (*Ursus arctos*), into a regional conservation plan for the Rocky Mountains of the United States and Canada. We developed empirical habitat models for fisher, lynx, and wolverine based on a geographically extensive data set of trapping and sighting records. Predictor variables derived directly from satellite imagery were significantly correlated with carnivore distribution and allowed us to predict distribution in areas lacking detailed vegetation data. Although we lacked similar distributional data for grizzly bear, we predicted bear habitat by adapting and extrapolating previously published, regional-scale habitat models. Predicted habitat for grizzly bear has high overlap with that for wolverine, intermediate overlap with fisher, and low overlap with lynx. High-quality habitats for fisher and lynx, unlike those for wolverine and grizzly bear, are not strongly associated with low levels of human population and roads. Nevertheless, they are naturally fragmented by topography and vegetation gradients and are poorly represented in existing protected areas. Areas with high biological productivity and low human impact are valuable habitat for all four species but are limited in extent. Predicted habitat values for lynx and wolverine are significantly correlated with trapping data from an area outside the extent of the original data set. This supports the use of empirical distribution models as the initial stage in a regional-scale monitoring program. Our results suggest that a comprehensive conservation strategy for carnivores in the region must consider the needs of several species, rather than a single, presumed umbrella species. Coordinated planning across multiple ownerships is necessary to prevent further fragmentation of carnivore habitat, especially in the U.S.–Canada border region.

*Key words: carnivores; conservation plans; fisher; focal species; grizzly bear; habitat models; landscape ecology; lynx; resource selection functions; Rocky Mountains; spatial analysis; wolverine.*

## INTRODUCTION

Many mammalian carnivores are sensitive to landscape change because of their low population density, low fecundity, limited dispersal ability across open or developed habitat, and other traits that lower ecological resilience (Weaver et al. 1996). This makes them potential focal species for use in regional conservation planning, in which the conditions necessary for the long-term persistence of native carnivores form one set of criteria by which to evaluate planning options. Carnivores with the largest area requirements, e.g., the grizzly bear (*Ursus arctos*), are often suggested as umbrella species, on the theory that the area of habitat

required to support viable populations will protect sufficient habitat for other species with smaller area requirements (Noss et al. 1996). Nevertheless, the effectiveness of this strategy, which relies on high overlap between species in habitat requirements, has been evaluated rarely, even within the suite of native carnivore species.

The native mammalian carnivores in the Rocky Mountains of the United States and Canada include grizzly bear, black bear (*Ursus americanus*), gray wolf (*Canis lupus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), puma (*Puma concolor*), bobcat (*Lynx rufus*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), otter (*Lutra canadensis*), fisher (*Martes pennanti*), American marten (*Martes americana*), and several smaller species. Although still present throughout much of the region, many of the large and medium-sized carnivore species are threatened by human activities, such as il-

legal killing, highway and rail mortality, legal control efforts, competition for prey species (e.g., ungulates), and loss of habitat (Clark et al. 1996). These threats, if not averted, may lead to significant range contractions in the near term and regional extinctions of some species within the foreseeable future (Noss et al. 1996).

Although direct, human-caused mortality remains important, loss of habitat increasingly limits populations of carnivores in the region (Clark et al. 1996). Some suitable carnivore habitat in the United States remains unoccupied because of the legacy of predator control programs. Without information on regional-scale trends in habitat, population indices from intensive demographic studies often provide only delayed and ambiguous information on declining viability (Craighead et al. 1995, Doak 1995). Although the basic ecology and habitat requirements of some carnivore species in the region are well known, knowledge is minimal for other species, such as the wolverine. Even less is known about the among-species interactions that determine coexistence. It might be expected that interspecific competition would result in low spatial overlap in source habitats between different species. Interspecific interactions within the carnivore guild, however, combine both competitive and facilitative elements (Buskirk 1999). Species that consume the same prey species may lessen their competition through temporal avoidance or differences in hunting strategies (Schoener 1971). Even in species pairs that compete strongly, such as the gray wolf and coyote, regional sympatry may be possible through local allopatry (Peterson 1995).

Regional planning can facilitate human–carnivore coexistence by identifying spatial refugia or core areas with a level of protection sufficient to buffer populations against conflicts with humans (Merrill et al. 1999). It can also identify optimal locations of buffer zones that will expand the effective size of core areas by allowing use of semi-developed lands while reducing the probability of human-caused mortality. Potential zones of human–carnivore conflict often are in areas of highly productive habitat that have above-average human use, are spatial buffers between large core habitat areas and zones of high human use, or are likely to experience increased human influence in the future, based on land-use and population trends (Corsi et al. 1999, Merrill et al. 1999).

Land management agencies increasingly have advocated ecosystem-level regional planning, for example in the Northwest Forest Plan (USDA and USDI 1994). Viability analysis of individual species, however, allows planners to evaluate the effectiveness of conservation strategies in a way not possible with composite indicators of ecosystem function. Ecosystem change affects viability of carnivores through factors operating on the individual, population, and metapopulation scales (Weaver et al. 1996). Demographic processes operating on the regional scale include the rescue of small, isolated populations by immigration from regional sources. Emigration from core areas into unsuitable matrix habitat may be a significant demographic sink in smaller populations. Less evidence exists for the importance of regional-scale gene flow, but some isolated carnivore populations, such as grizzly bears in Yellowstone, show reduced genetic diversity (Paetkau et al. 1998).

Most existing models for carnivores in the Rocky Mountains are conceptual models that have evolved out of a site-level planning paradigm. In contrast, empirical models, which make use of geographically extensive data sets of species distribution, allow the incorporation of variation in habitat relations across a region and exploration of the fit between alternate models and the data. Although the results of regional-scale empirical modeling often are not easy to interpret mechanistically, they can provide initial estimates of species distribution and abundance, as averaged over coarse spatial and temporal scales through the use of resource selection functions and other techniques (Manly et al. 1993, Boyce and McDonald 1999). Regional-scale empirical models also can provide such data as habitat patch size or potential dispersal frequency for parameterizing dynamic, individual-based models.

The four species considered in our habitat analysis (grizzly bear, lynx, wolverine, and fisher) encompass a range of taxa and habitat associations. We used geographically extensive data sets of species occurrences from trapping reports or sightings to develop distribution models for the lynx, wolverine, and fisher. Although we were not able to compile geographically extensive occurrence data for the grizzly bear, we mapped grizzly bear habitat by adapting and extrapolating previously published regional-scale models (Mace et al. 1999, Merrill et al. 1999).

Our study area extends from the Banff-Yoho-Jasper-Kootenay complex of national parks in Alberta and British Columbia (B.C.), Canada, to the Greater Yellowstone Ecosystem in Montana, Wyoming, and Idaho, USA (Fig. 1). Mountainous topography and low human population density have helped the region to retain populations of all native carnivore species, which are often widely distributed across the landscape in both protected and unprotected management categories. The area is a geographic link between U.S. and Canadian populations of carnivores (Forbes and Boyd 1996). Existing levels of habitat protection and the level of societal support for preserving native carnivores are high. Nevertheless, current protected areas alone are probably insufficient to ensure the viability of many carnivore populations (Paquet and Hackman 1995, Noss et al. 1996). By comparing the viability requirements of several at-risk species and assessing the availability of their habitat across all land ownerships and jurisdictions, our analysis helps to provide the information
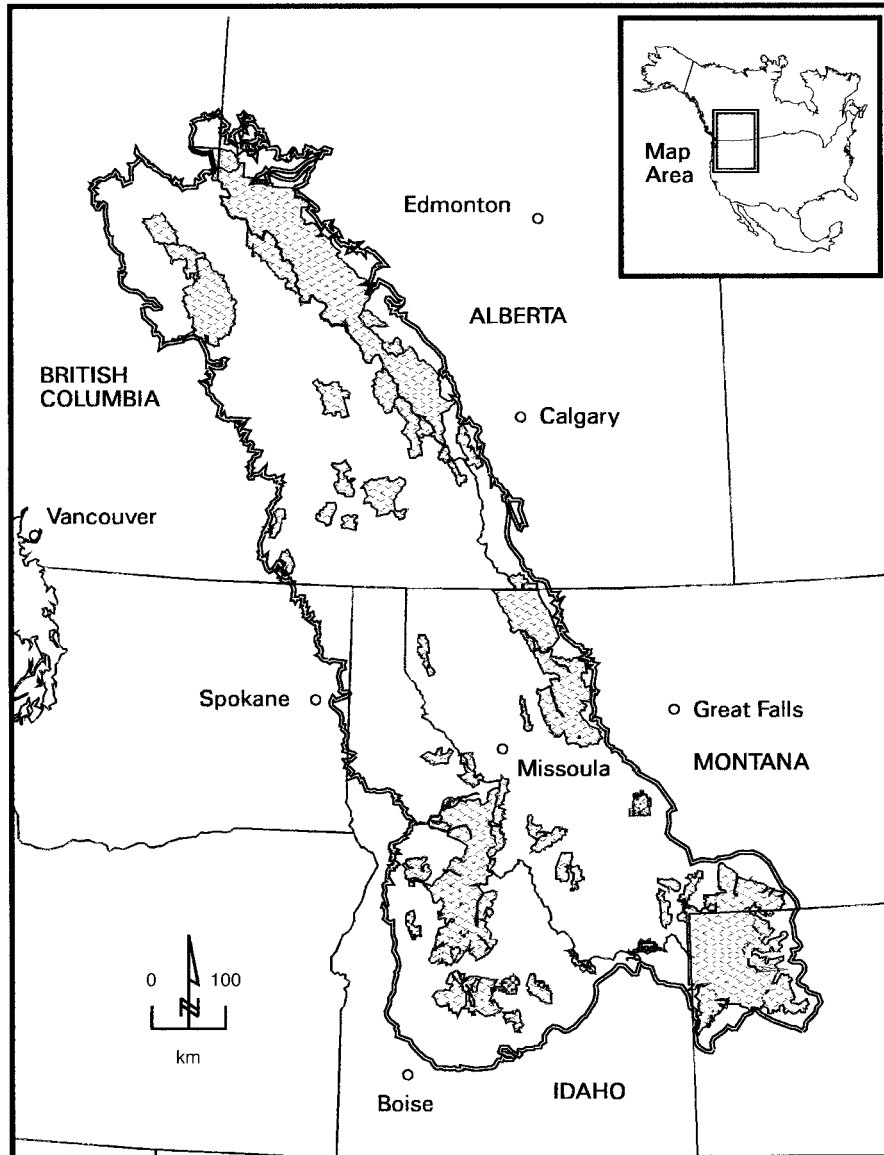
Fɪɢ. 1. Map of study area in the Rocky Mountains of the United States and Canada. The study area boundary is outlined by a double line. Major protected areas are identified by cross-hatching.

necessary to develop a comprehensive conservation strategy for carnivores in the Rocky Mountains.

## Mᴇᴛʜᴏᴅs

### Study area

The study area covers 450 000 km² in the Rocky Mountains of the northern United States and southern Canada (Fig. 1). Study area boundaries approximate those of the Shining Mountains and Northern Rocky Mountain Forest ecoprovinces (Demarchi 1994). The Continental Divide bisects the region. Mean elevation is 1700 m, ranging from ∼200 m along the Columbia Trench in British Columbia to ∼3600 m in the moun-

tains of Mount Robson National Park, Yellowstone National Park, and the Sawtooth Range in Idaho. The climate to the west of the continental divide is more maritime than in areas east of the divide, with higher precipitation and a lower seasonal contrast in temperatures. Mean annual precipitation is 950 mm, ranging from 200 mm in the arid portions of eastern Idaho to >2000 mm in the headwaters of the Columbia River in British Columbia. Much precipitation falls as snow.

Major vegetation types include evergreen needleleaf forests, aspen (*Populus* spp.) parklands, sagebrush (*Artemisia* spp.) shrublands, and grasslands (Achuff 1998). Coniferous forests of the montane zone include species such as Douglas-fir (*Pseudotsuga menziesii),* ponde-

rosa pine (*Pinus ponderosa*), limber pine (*Pinus flex-ilis*), and lodgepole pine (*Pinus contorta*). The subalpine zone may include Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine, western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). Alpine tundra and bare rock and ice cover large areas at higher elevations.

Land ownership is ~33% private, 26% in publicly owned reserves, and 41% in publicly owned nonreserve areas (Strittholt and Frost 1997). Three major protected-area complexes exist in the United States in the areas of Greater Yellowstone (20 900 km²), the Northern Continental Divide (4100 km²), and central Idaho (15 800 km²). In Canada, the Rocky Mountain national parks encompass an area of 23 800 km², with additional smaller protected areas such as Wells-Gray Provincial Park (5500 km²), the Purcell Wilderness (2100 km²), and Glacier National Park, British Columbia (1400 km²).

### Data on carnivore species distributions

We used data on sightings, specimens, and trapping records of fisher, lynx, and wolverine (Fig. 2) from the Natural Heritage Database programs of the states of Montana, Idaho, and Wyoming (Groves et al. 1995). Records provide the species, date, source of the report, and other details of the occurrence. Using this information, we assigned the records to a scale of reliability similar to that used in previous publications (Aubry and Houston 1992, Maj and Garton 1994). We rated specimens and trapping records as of highest reliability, followed by sightings and tracks grouped according to the expertise of the observer. In addition to problems of reliability or verifiability, the records show strong spatial sampling bias, e.g., toward roads, that was addressed by methods described later. Records of highest reliability constitute 44.8% and 28.6% of the fisher and lynx data, respectively, allowing us to compare models constructed from limited data sets of high reliability with those from less reliable, but more extensive data sets. This was not possible for the wolverine records, which are predominantly (89.7%) sightings or tracks.

After removal of duplicate and unreliable records, the total numbers of occurrences that overlapped the area for which we had complete habitat data were 346, 413, and 503 for fisher, lynx, and wolverine, respectively. Of these records, 176, 232, and 348, for fisher, lynx, and wolverine, respectively, were collected after 1982. We selected this historical threshold to be consistent with previous work (Maj and Garton 1994). We adapted our grizzly bear habitat model from previous work (Mace et al. 1999, Merrill et al. 1999) because geographically extensive occurrence records were not available.

### Habitat data

The habitat variables (defined in Table 1) were developed in a GIS format (Table 2). They can be grouped
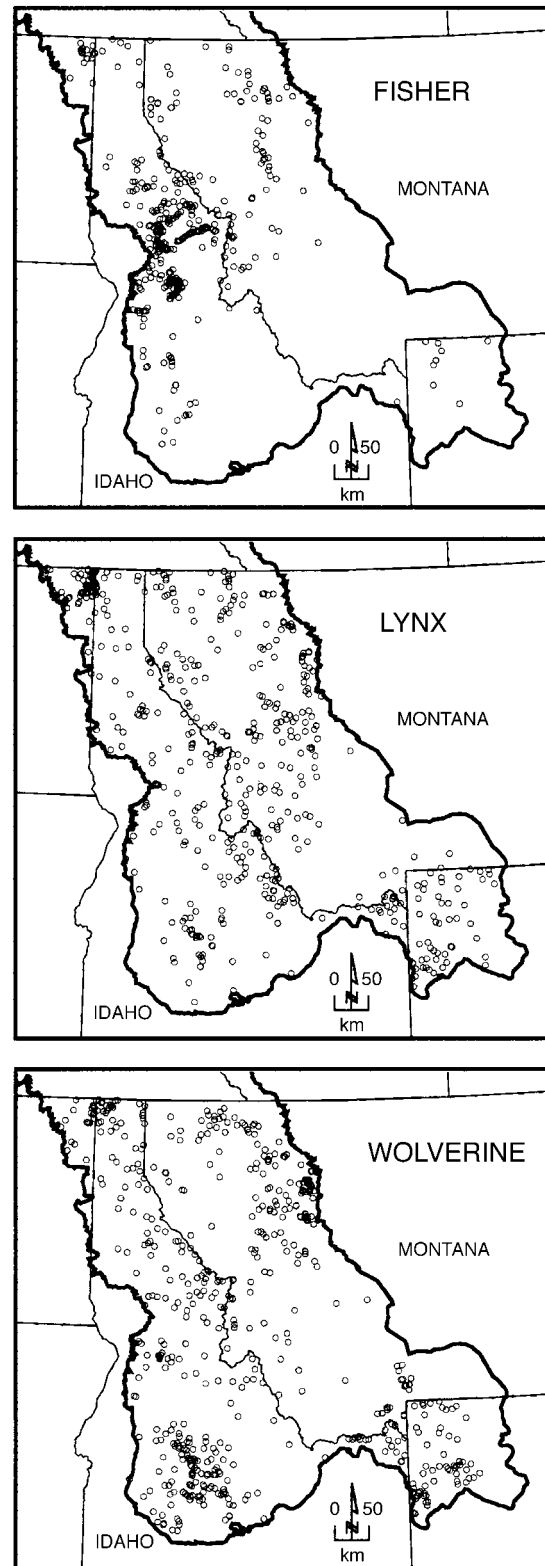


FIG. 2. Occurrence data used in developing habitat models for fisher, lynx, and wolverine. Total numbers of occurrence locations, including historical (pre-1983) records, are 368, 529, and 584 for fisher, lynx, and wolverine, respectively.

TABLE 1. Description of terms used in tests of habitat variables.

| Term | Abbreviation | Definition |
| --- | --- | --- |
| Akaike information criterion | AIC | model-fitting statistic that incorporates penalties for addition of variables |
| Advanced Very High Resolution Radiometer | AVHRR | satellite-based sensor that provides multispectral images of the earth at low spatial and radiometric, but high temporal, resolution |
| Bayesian Information Criterion | BIC | model-fitting statistic that is similar to AIC, but with larger penalties for overfitting |
| Cliford-Richardson-Hemon test | CRH | test of significance of associations between spatially autocorrelated variables |
| Generalized additive model | GAM | nonparametric function that estimates the relationship between variables using a smoothing algorithm |
| Gap Analysis Projects vertebrate model | GAP vertebrate model | predictive model of potential habitat for vertebrate species, developed by state Gap Analysis Projects from vegetation cover type maps, elevation data, range boundaries, and literature on species–habitat associations |
| Moderate-Resolution Imaging Spectrometer | MODIS | sensor, launched on the Terra satellite, that provides multispectral images of the earth at low spatial, but high temporal and spectral, resolution |
| Moving window | | method of deriving composite measurements of variables averaged over an area surrounding each pixel in a GIS data layer |
| Normalized Differenced Vegetation Index | NDVI | transformed ratio of near infrared and red spectral bands in a satellite image, used to measure vegetation condition. The Modified NDVI metric adds information from an additional spectral band to control for variation in soil reflectance |
| Resource selection function | RSF | function that is proportional to the probability that a resource unit, such as an area of habitat, will be used by an animal |
| Somers' Dxy | | measure of the correlation between observed and predicted values that can be used to assess the explanatory power of a model |
| Tasseled-cap transformation | | transformation of six of the reflectance bands of TM imagery into three indices (brightness, greenness, and wetness), that represent major axes of variation in TM data. Similar to principal components transformation except that axes are fixed for all TM data rather than dependent on a particular data set |
| Topographic complexity | | measure of the ruggedness of terrain, derived by multiplying scaled values for slope and for aspect curvature |
| Thematic Mapper | TM | sensor on the Landsat series of satellites that records seven spectral bands at high spatial, but low temporal, resolution |

into five categories of vegetation, satellite imagery metrics, topography, climate, and human-impact related variables. Although acquired at a range of resolutions (Table 2), all variables were generalized to 1-km resolution for the final analysis.

Vegetation variables were GIS vegetation layers developed from supervised classification of Landsat Thematic Mapper (TM) satellite imagery. Data from three mapping projects completed by the Wildlife Spatial Analysis Lab at the University of Montana were merged to create a layer covering >90% of the U.S. portion of our study area (Redmond et al. 1996, 1997, 1998). The resolution of the data was 30 m, whereas the average size of the regions given attributes during the classification process was ~6.25 ha. These regions were categorized as to vegetation cover type (Redmond et al. 1998), tree canopy closure class, and tree size class. Absolute thematic accuracy for cover type was 61.4% (Redmond et al. 1998). The coverage also included data on the original reflectance values from the TM imagery.

We derived secondary variables from the original vegetation data layer. Edge areas within 100 m of ecotones between forest and shrubland or grassland were delineated. The association of species with groupings of vegetation cover types was assessed by classifying the cover type information into a binary layer of preferred and nonpreferred cover types, according to the cover type element of the vertebrate habitat models developed by the Montana GAP (Gap Analysis Project) program (Redmond et al. 1998). The complete GAP vertebrate models incorporate several additional factors. A binary map of forest types strongly associated with lynx habitat (subalpine fir, Engelmann spruce, and lodgepole pine; Koehler and Aubry 1994) was created as an alternative to the more inclusive habitat definition in the GAP model.

Comparable vegetation data derived from satellite

TABLE 2.  Data layers evaluated in the development of the carnivore distribution models for the Rocky Mountains.

| Data layer | Resolution | Reference | Extent | Source† |
|---|---|---|---|---|
| Vegetation variables | | | | |
| Tree canopy closure | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Tree size class | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Proportion of hardwood cover types | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Standard deviation of tree closure | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Standard deviation of tree size | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Forest edge with shrub or grasslands | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Lynx cover types | 30 m | Redmond et al. (1998) | U.S. | 9 |
| GAP vertebrate model, lynx | 30 m | Redmond et al. (1998) | U.S. | 9 |
| GAP vertebrate model, fisher | 30 m | Redmond et al. (1998) | U.S. | 9 |
| GAP vertebrate model, wolverine | 30 m | Redmond et al. (1998) | U.S. | 9 |
| Average annual NPP | 2 km | Keane et al. (1996) | U.S. | 4 |
| Forest average annual NPP | 2 km | Keane et al. (1996) | U.S. | 4 |
| Satellite imagery metrics | | | | |
| Average daily NDVI | 1 km | James and Kalluri (1993) | All | 3 |
| Modified NDVI | 30 m | Nemani et al. (1993) | All | 3, 9 |
| Brightness | 30 m | Crist and Cicone (1984) | All | 3, 9 |
| Greenness | 30 m | Crist and Cicone (1984) | All | 3, 9 |
| Wetness | 30 m | Crist and Cicone (1984) | All | 3, 9 |
| Topographic variables | | | | |
| Elevation | 90 m | | All | 1, 7, 8 |
| Topographic complexity | 90 m | | All | 1, 7, 8 |
| Cirque denning habitat | 90 m | Hart et al. (1997) | All | 1, 7, 8 |
| Climatic variables | | | | |
| Average annual precipitation | 2 km | Daly et al. (1994) | All | 5 |
| Average annual snowfall | 2 km | Daly et al. (1994) | U.S. | 5 |
| Human impact related variables | | | | |
| Human population density | 2 km | | All | 2, 6 |
| Interpolated human population density | 1:100 000 | Merrill et al. (1999) | All | 6, 8 |
| Road density | 1:20 000–1:100 000 | | All | 1, 7, 8 |

† *Data sources:* 1, Alberta Environmental Protection, Edmonton, Alberta, Canada; 2, Center for International Earth Science Information Network (CIESIN), Palisades, New York, USA; 3, EROS Data Center, U.S. Geological Survey, Sioux Falls, South Dakota, USA; 4, Interior Columbia Basin Ecosystem Management Project (ICBEMP), Walla Walla, Washington, USA; 5, Oregon Climate Survey, Corvallis, Oregon, USA; 6, Statistics Canada, Ottawa, Ontario, Canada; 7, Terrain Resource Information Management (TRIM), Victoria, British Columbia, Canada; 8, U.S. Geological Survey, Reston, Virginia, USA; and 9, Wildlife Spatial Analysis Laboratory, University of Montana, Missoula, Montana, USA.

imagery are not yet available for most of the Canadian portion of our study area. We used imagery-based metrics to develop variables that were not limited by the extent of the vegetation data, but could be applied to the entire study area. We acquired Landsat TM imagery for most of the Canadian portion of our study area, and merged it with reflectance data contained in the U.S. vegetation database. TM scenes from the United States date from 4 June to 25 September and the years 1991–1995. Canadian TM scenes span a seasonal range of 23 June to 25 September and the years 1989–1998. This large temporal range, due to the acquisition of imagery from several sources, created some problems with normalization between adjacent scenes. Four satellite scenes whose season of acquisition differed greatly from the remainder of the imagery were processed with a histogram-matching algorithm to increase inter-scene normalization (ERDAS 1998).

We derived from TM imagery the indices of brightness, greenness, and wetness (Crist and Cicone 1984). These "tasseled-cap" indices are a standardized means of representing the three principal axes of variation in the values of six TM spectral bands. "Pseudo-habitat" variables such as greenness that are derived directly from unclassified satellite imagery are correlated, to varying degrees, with ecological factors such as net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997), and have proved useful in modeling wildlife distributions (Mace et al. 1999). Vegetation variables and imagery metrics such as greenness may be expected to be correlated with abundance of prey species through their relationships to primary productivity. However, the relationship between such variables and productivity in the Rocky Mountains is weakened by phenological variation between years and spatial variation in percentage of bare ground and percentage of dry biomass (Merrill et al. 1993).

We also derived the modified Normalized Difference Vegetation Index (NDVI) metric, which is an index that combines three spectral bands of TM imagery in order to measure changes in vegetative cover and condition (Nemani et al. 1993). Our second source of imagery, the Advanced Very High Resolution Radiometer

(AVHRR) sensor, has low spatial and spectral resolution compared to the Landsat TM sensor (Eidenshink 1992). Its daily temporal resolution, however, may allow improved estimation of ecological factors that show seasonal variation. Maximum daily NDVI values from the AVHRR sensor were acquired for the entire study area for each month in 1995 (James and Kalluri 1993). We also evaluated average annual net primary productivity (NPP) values, as estimated from AVHRR data and a biogeochemical model (Keane et al. 1996).

We derived topographic variables from a digital elevation model assembled at 90-m resolution. A topographic complexity variable was derived by combining the values for aspect curvature and slope (ESRI 1998). High values of this variable indicate steep or irregular terrain. We derived a variable representing the occurrence of the north-facing cirques suitable for wolverine denning from aspect and curvature data. This attribute, which does not incorporate data on soil type or vegetative cover, is a simplified version of the cirque denning habitat metric developed by Hart et al. (1997).

We acquired data on mean annual precipitation throughout the study area at ~2-km resolution (Daly et al. 1994). Mean annual snowfall data were also available for the U.S. portion of the study area. These climatic data were derived from meteorological records and elevation data by means of the PRISM model (Daly et al. 1994).

Variables that may serve as surrogates for the effects of humans on wildlife at the regional scale include road density and human population density (Mladenoff et al. 1995, Merrill et al. 1999). GIS data on roads, trails, and railroads were assembled for the study area and grouped into classes based on the degree of expected use. Road density calculations, performed at the 1-km resolution, incorporated weights based on this classification, with highways weighted two to three times the weight of unpaved roads. Trails and other routes were rated at 0.35 that of unpaved roads (Merrill et al. 1999). Road data were available at varying scales: 1:100 000 for the United States, 1:50 000 for Alberta, and 1:20 000 for British Columbia. This discrepancy might be expected to underestimate road density in the United States. Actual road density, however, is greatest in the United States and least in British Columbia. Thus, the effect is expected to be conservative in that it underestimates the contrasts in habitat conditions between jurisdictions.

We acquired data on human population at the scale of census blocks (United States) and enumeration areas (Canada). The average area of a census block in this region is 4 km$^2$ when urban areas are included, but most of the area is contained in blocks >100 km$^2$ in size. A data layer representing all population centers as points was interpolated using an inverse distance weighting algorithm (ESRI 1998). This provides an approximation of the effects of population centers over

distance, for example, as they might affect the level of recreational use of adjacent public lands (Merrill et al. 1999).

### Modeling methods

We used multiple logistic regression to compare habitat variables at sighting locations with those at random points (Hosmer and Lemershow 1989). Before building the multiple-variable models, we conducted exploratory analysis of univariate relationships between potential predictor variables and the occurrence data, using nonparametric significance tests and generalized additive modeling (Hastie 1993). Spearman rank correlation tests were used to compare occurrence locations with random locations. A large number (4500) of random points was used as a comparison set to increase the precision of the estimates for regression coefficients in the multivariable models. Positive autocorrelation in our spatial data violated the assumption of independent observations of standard significance tests, resulting in artificially high levels of significance (Haining 1990). We used the Cliford-Richardson-Hemon (CRH) method to adjust the effective sample size used in significance tests, based on a measure of the spatial covariance of the variables (Cliford et al. 1989, Thomson et al. 1996).

Generalized additive modeling (GAM) plots were used to assess curvature and thresholds in the univariate models. A large set of alternate multivariable models was constructed and evaluated with the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC), diagnostic statistics that penalize for overfitting (Akaike 1973, Schwarz 1978). We allowed models to contain variables that did not appear highly significant in univariate tests, if this resulted in lower AIC values. We also considered interpretability and field knowledge of the species when choosing among competing models that had similar AIC values. Models were not allowed to contain more than one of a pair of highly correlated variables. Collinearity among variables may be problematic when using derived metrics, such as the topographic variables used here. The percentage of variance explained by the model was assessed with Somers' Dxy (Harrell et al. 1996). Because many candidate models were considered, the multiple regression analysis should be considered exploratory. Predicted habitat values can be seen as map-based hypotheses subject to refinement and validation by future survey data (Murphy and Noon 1992, Carroll et al. 1999).

The spatial correlation structure of wildlife distribution data can be modeled as a combination of coarse-scale trend and mesoscale variation (Bailey and Gatrell 1995). Although we did not incorporate trend surface variables derived from geographic coordinates directly into our models, the significance of coarse-scale factors, particularly precipitation, is probably partially due to trend surface effects. We modeled mesoscale envi-

ronmental covariates with a moving-average function that assigns to each cell the mean value of the attributes within a surrounding circular moving window (Haining 1990, ESRI 1998). A moving window 30 km² in size was used based on previous work with mesocarnivore habitat models (Carroll et al. 1999). A function that computes the standard deviation within the moving window was used as an estimate of landscape diversity (ESRI 1998). Because our occurrence data set consisted of irregularly spaced sample sites, we reduced the effect of uneven sampling effort by differentially weighting points in the model-fitting algorithm, based on the area of the space-filling Thiessen polygon that surrounds each point.

Because the occurrence data had varying levels of reliability, we built alternate models that either excluded or included occurrences with lower reliability ratings (sightings and tracks). To examine potential differences between historical (pre-1983) and recent occurrence data, we included variables representing this threshold and its interactions in the model, and fit alternate models that excluded historical data.

We used the coefficients from the final model to calculate a resource selection function (RSF) $w(x)$ for used (occurrences) and available (random) resources (Manly et al. 1993, Boyce and McDonald 1999), using the equation

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i).$$

Because the number of used vs. unused resource units is not known, the RSFs represent only a relative probability of occurrence of a species at a location (Manly et al. 1993). The resulting RSF values are therefore mapped as quantiles (e.g., the most suitable one-third of the study area) rather than actual values.

To compare the results of our mesocarnivore models with a regional-scale model for a large carnivore, we mapped predicted habitat value for grizzly bears by adapting a model previously developed for Idaho from sightings data (Merrill et al. 1999). This model integrates information on density of roads and human population into a composite habitat effectiveness metric representing the level of security or lack of human presence. Habitat effectiveness is then combined with an estimate of habitat productivity to predict grizzly bear distribution. Because vegetation data of the type used by Merrill et al. (1999) to estimate habitat productivity were not available outside of Idaho, we substituted a habitat productivity index based on tasseled-cap greenness. Greenness has been shown to be significantly associated with landscape-scale grizzly bear distribution in Montana and Alberta (Mace et al. 1999, Gibeau 2000).

The system of registered traplines in British Columbia (B.C.) allows data to be collected on the number of animals trapped per year for a specific area (Fig. 3). Mean trapline area in our study region is 300 km². We
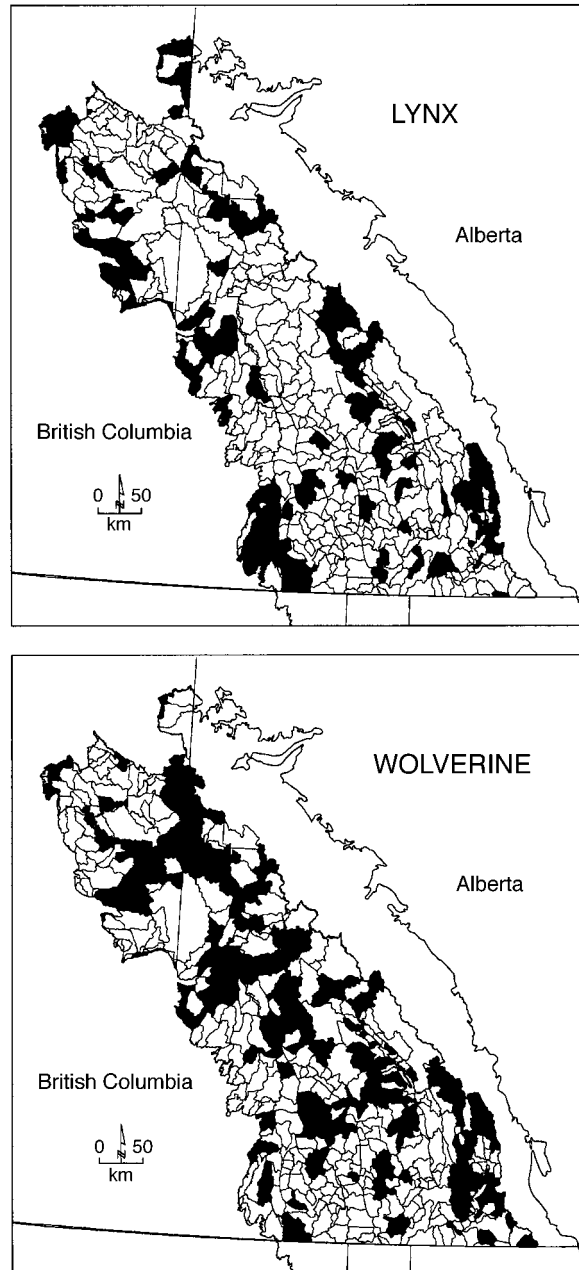


FIG. 3. Trapping data used to validate lynx and wolverine models. Areas in southeastern British Columbia reporting trapping of lynx or wolverine for the period 1986–1996 are shown in black. Boundaries of registered trapline areas are outlined.

validated the models by testing the significance of the correlation between the habitat value predicted by the models developed from U.S. records and the number of animals per unit area trapped per reported trapping year in the B.C. portion of the study area. The B.C. trapping data had unknown, but probably substantial, biases in effort and reporting. However, because these might be expected to be of a somewhat different nature

than bias associated with sightings data, the B.C. data provide a useful validation data set. A more accurate estimate of relative abundance would require supplementary information on effort, gathered by trapper questionnaires. There were 354 registered traplines that overlapped the area covered by our model of predicted lynx habitat in British Columbia and that had at least one year of trapping data reported ($8.56 \pm 2.39$ yr, mean $\pm 1$ SD) from 1986 to 1996. Of these traplines, 313 also overlapped the area covered by our model of predicted wolverine habitat. Of these, numbers of traplines reporting capture of the species were 14, 76, and 105 for fisher, lynx, and wolverine, respectively. The low number of traplines reporting fisher reflects both the species' scarcity and trapping restrictions, precluding use of these data to validate the fisher habitat model.

In order to assess the degree of spatial overlap between predicted habitat for the four species, we measured the value of the four predicted habitat GIS layers at 12 000 random locations. The resulting data were analyzed with Spearman rank correlations and principal-components analysis (PCA). Although the correlation and PCA output tables provide a quantitative assessment of similarity of habitat across species, PCA plots are useful for visual assessment of similarity patterns.

## RESULTS

### Univariate analysis

Although 53 of 81 correlations between species occurrences and predictor variables were significant at the $P < 0.05$ level using standard significance tests, only 37 remained significant at that level after correction for spatial autocorrelation (Table 3). Results of the univariate generalized additive modeling suggested that probability of occurrences was reduced for fisher and lynx below a road density threshold of ~0.6 km/km². In contrast, wolverine occurrences showed a negative relationship with road density >1.7 km/km² (Fig. 4).

The positive correlation between sighting probability and tree canopy closure leveled out at 40% closure in the wolverine and lynx models, but fisher occurrences continued to increase in probability until the 60% canopy closure level. A negative correlation between lynx occurrences and topographic complexity was evident at above the 35% level of topographic complexity, but was not evident for the fisher and wolverine. The generalized additive models for precipitation suggested a quadratic curvature in this variable for the fisher and wolverine multiple regression models.

### Multiple regression models

Model coefficients, standard errors, and significance values for the selected models for each of the three species are listed in Table 4. Differences between models including and excluding historical records were ev-

ident for the wolverine, but not for lynx and fisher. Interactions between the factor for date of record and the road density and interpolated human population density variables were highly significant ($P < 0.01$) for the wolverine. In order to maintain consistency between species models and to make occurrence data relatively contemporaneous with the satellite imagery data (1989–1998) and the trapping data used in model validation (1986–1996), we fit the final models for all three species using only recent (1983–1998) occurrence records.

Models that did not use the spatial weighting factor were similar to the reported models, which used weights derived from Thiessen polygons. Models for fisher and lynx that excluded sightings and tracks were similar to those using all records. We chose to include records of sightings and tracks in the final models, as excluding them greatly reduces sample size and geographic representation.

The final model for fisher included variables representing precipitation as a quadratic function, elevation, wetness, greenness, and a variable for the low road density (<0.6 km/km²) threshold (−2 log-likelihood (LL) = 859.2, $\chi^2$ = 359.5, df = 6, $P$ = 0.000, Dxy = 0.667). Allowing the inclusion of variables only available for the United States resulted in a model with the addition of tree canopy closure and standard deviation in tree size (−2LL = 852.4, $\chi^2$ = 366.3, df = 8, $P$ = 0.000, Dxy = 0.668).

The final model for the lynx included variables representing modified NDVI, brightness, topographic complexity, and the low road density threshold (−2LL = 1345.8, $\chi^2$ = 359.1, df = 4, $P$ = 0.000, Dxy = 0.353). Allowing the inclusion of variables only available for the United States resulted in a model with the addition of variables for snowfall and precipitation (quadratic) (−2LL = 1332.4, $\chi^2$ = 372.5, df = 7, $P$ = 0.000, Dxy = 0.401).

The final model for the wolverine included variables representing precipitation as a quadratic function, interpolated human population density, a high road density effect, cirque habitat, and wetness (−2LL = 1721.0, $\chi^2$ = 398.3, df = 6, $P$ = 0.000, Dxy = 0.363). Allowing the inclusion of variables only available for the United States resulted in a model that added variables for forest edge, tree canopy closure, and snowfall, while dropping the precipitation, wetness, and cirque habitat variables (−2LL = 1722.0, $\chi^2$ = 397.3, df = 5, $P$ = 0.000, Dxy = 0.385). Values of Somers' Dxy were thus substantially lower for the lynx and wolverine models than for the fisher models.

Use of detailed vegetation information rather than unclassified satellite imagery improved model fit, but the degree of improvement varied among species. The most limited model was fit with AVHRR-derived variables in place of either vegetation or TM-derived metrics. Improvement in fit as measured by change of AIC

INVITED FEATURE

TABLE 3. Habitat attributes at occurrence and random sites used in development of the carnivore distribution models. Values are means ($\pm$ 1 SD). Occurrence sites do not include historic (pre-1983) records.

| Variable | Fisher ($n = 176$) | Lynx ($n = 232$) |
|---|---|---|
| $X$-coordinate (Lambert projection) | $-93\ 317$ (70 217) | $-32\ 235$ (117 539) |
| $Y$-coordinate (Lambert projection) | 512 633 (112 688) | 546 840 (160 369) |
| Tree canopy closure (%) | 45.76 (12.55)* | 42.13 (17.54)* |
| Tree size class | 2.0187 (0.4734) | 1.8508 (0.6359)* |
| Percentage hardwood types | 11.81 (19.01) | 17.15 (34.91) |
| SD of canopy closure | 24.29 (3.95) | 23.40 (5.42) |
| SD of tree size | 1.0907 (0.1791) | 0.9711 (0.2172) |
| Forest edge (% of total area) | 28.76 (17.08) | 22.33 (16.55) |
| Lynx cover types | 0.166 (0.214) | 0.257 (0.262)* |
| GAP fisher cover types | 0.605 (0.186)* | 0.542 (0.277)* |
| GAP lynx cover types | 0.537 (0.227) | 0.603 (0.279)* |
| GAP wolverine cover types | 0.723 (0.165) | 0.688 (0.273)* |
| Annual NPP carbon (g/m²) | 593.58 (164.81)* | 521.34 (169.93) |
| Forest area NPP carbon (g/m²) | 475.38 (195.60)* | 402.78 (201.76)* |
| Average daily NDVI | 145.30 (8.35)* | 140.09 (12.10)* |
| Modified NDVI | 301.19 (103.25)* | 281.57 (191.70)* |
| Brightness | 90.38 (17.11) | 88.48 (21.16)* |
| Greenness | 13.29 (11.75)* | 7.36 (8.54)* |
| Wetness | $-4.80$ (15.81)* | $-8.33$ (14.23) |
| Elevation (m) | 1427.4 (368.6) | 1600.3 (468.9) |
| Topographic complexity (%) | 20.52 (17.69) | 21.46 (17.18) |
| Cirque denning habitat | 0.032 (0.015) | 0.034 (0.016) |
| Mean annual precipitation (mm) | 1054.3 (281.8)* | 883.6 (330.8) |
| Mean annual snowfall (mm) | 2310.3 (1067.8) | 2216.6 (1250.3)* |
| Human population density (no./km²) | 1.255 (3.377) | 2.669 (12.225) |
| Interpolated human density | 278.14 (312.49) | 385.51 (310.30) |
| Road density (km/km²) | 1.284 (0.733)* | 1.036 (0.697)* |

*Notes:* Attributes that differ significantly between occurrence and random sites at the 0.05 level in a Spearman rank correlation test are marked by an asterisk. Sample size for significance tests was corrected for spatial autocorrelation using the CRH method (Cliford et al. 1989).

from these AVHRR models to models using TM-derived variables was 11.6, 4.8, and 1.6 for the fisher, lynx, and wolverine, respectively. Improvement in fit from AVHRR models to models using both vegetation and TM-derived variables was 15.1, 4.8, and 3.4 for the fisher, lynx, and wolverine, respectively.

### Validation results

Mean predicted wolverine habitat value for traplines in the British Columbia portion of our study area was significantly correlated with the number of wolverines trapped per trap-year per unit area ($r_S = 0.167$, df = 311, $t = 2.99$, $P = 0.003$). Mean predicted lynx habitat value was also significantly correlated with the number of lynx trapped per trap-year per unit area ($r_S = 0.132$, df = 352, $t = 2.50$, $P = 0.013$). We mapped predicted values (Fig. 5) without incorporating the low road density threshold effect that we attribute to sampling bias. Prediction without the effects of this variable should produce values that more closely approximate actual
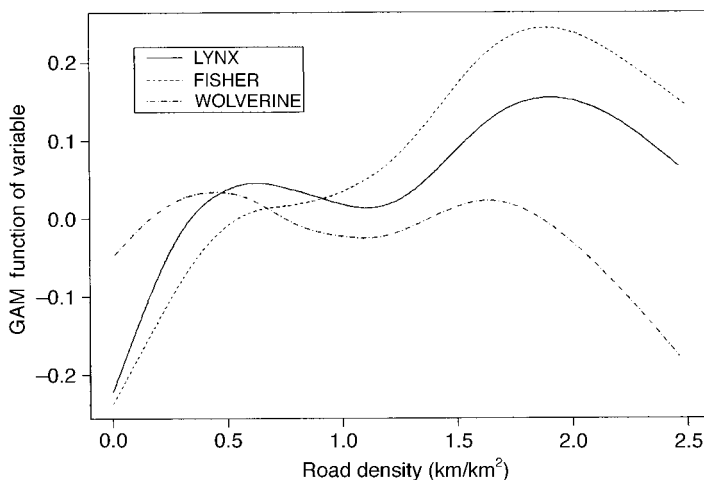


FIG. 4. Generalized additive modeling (GAM) plot of the univariate relationship of road density to probability of occurrence for fisher, lynx, and wolverine.

TABLE 3. Extended.

| Wolverine ($n = 348$) | Random ($n = 4531$) |
|---|---|
| −19 603 (117 144) | −14 991 (116 900) |
| 456 099 (192 137) | 464 817 (169 287) |
| 36.71 (16.72) | 32.65 (20.84) |
| 1.6362 (0.6320) | 1.5029 (0.8414) |
| 14.82 (36.11) | 12.38 (28.13) |
| 23.78 (5.79)* | 20.96 (7.92) |
| 1.0283 (0.2010)* | 0.9372 (0.3225) |
| 26.37 (16.55)* | 22.45 (17.77) |
| 0.347 (0.281)* | 0.220 (0.269) |
| 0.456 (0.279) | 0.411 (0.318) |
| 0.600 (0.272)* | 0.488 (0.332) |
| 0.684 (0.268)* | 0.566 (0.347) |
| 498.93 (190.65) | 461.03 (184.95) |
| 361.72 (208.91)* | 302.12 (220.69) |
| 135.53 (8.95) | 136.43 (16.10) |
| 229.23 (149.64) | 195.27 (217.12) |
| 95.32 (23.39) | 100.03 (28.29) |
| 4.92 (10.33) | 3.69 (11.81) |
| −10.66 (12.86) | −13.61 (16.53) |
| 1865.6 (486.5)* | 1714.7 (523.3) |
| 27.91 (20.65)* | 24.38 (21.40) |
| 0.041 (0.018)* | 0.034 (0.017) |
| 965.1 (340.4)* | 804.9 (375.9) |
| 2725.8 (1368.7)* | 1973.7 (1459.5) |
| 1.733 (9.486)* | 5.141 (28.242) |
| 261.22 (251.66)* | 354.26 (309.26) |
| 0.691 (0.560) | 0.875 (0.747) |

species distributions. A comparison of mapped habitat value with the distribution of protected areas (Fig. 6), shows that mean quantiles of predicted habitat values are markedly higher within protected areas for grizzly

bear (62.4 vs. 46.4) and wolverine (65.2 vs. 45.7), but not for fisher (50.3 vs. 48.8) or lynx (42.1 vs. 49.2). Correlations between predicted habitat values for the four species are shown in Table 5. The highest correlations are of the wolverine with the fisher ($r_S = 0.56$) and with the grizzly bear ($r_S = 0.54$).

This relationship is also evident in results of the principal-components analysis of predicted habitat values. Wolverine and grizzly bear show similar loadings on the first and second component axes (Table 6, Fig. 7). These two axes constitute 81.8% of the total variance. Loadings for the lynx on these axes contrast strongly with those for wolverine and grizzly bear, with fisher occupying an intermediate position. The third axis (12.0% of variance) distinguishes grizzly bear habitat from that of the other three species. The wolverine and fisher have strong contrasts on the fourth axis (6.2% of variance).

## DISCUSSION

The analysis of species–habitat associations for the fisher, lynx, and wolverine suggests that regional-scale vegetation, climatic, topographic, and human-impact variables may be limiting factors governing mesocarnivore distributional patterns. Predictions from the regional-scale models may allow map-based conservation planning at a spatial scale that is relevant to the population processes of wide-ranging carnivores, and may allow initial plans to be refined as new data become available. The large amount of unexplained variance in our analysis, however, suggests that regional-

TABLE 4. Variables contained in multiple logistic regression models, showing coefficients, standard errors, and significance values from the Wald test.

| Variable | Coefficient | 1 SE | $t$ | $P$ |
|---|---|---|---|---|
| Fisher | | | | |
|   Intercept | −10.8476 | 1.2871 | −8.4280 | 0.0000 |
|   Precipitation | 0.0135 | 0.0023 | 5.9285 | 0.0000 |
|   Precipitation (quadratic) | $-5.0400 \times 10^{-6}$ | $1.0319 \times 10^{-6}$ | −4.8843 | 0.0000 |
|   Elevation | $-9.6500 \times 10^{-4}$ | $3.2589 \times 10^{-4}$ | −2.9611 | 0.0031 |
|   Low road density† | −3.0540 | 0.8585 | −3.5574 | 0.0004 |
|   Wetness | −0.0431 | 0.0100 | −4.3075 | 0.0000 |
|   Greenness | 0.0508 | 0.0137 | 3.7051 | 0.0002 |
| Lynx | | | | |
|   Intercept | −2.3227 | 0.5662 | −4.1026 | 0.0000 |
|   High topographic complexity† | −0.0362 | 0.0153 | −2.3659 | 0.0180 |
|   Modified NDVI | 0.0011 | 0.0006 | 1.7957 | 0.0725 |
|   Brightness | −0.0148 | 0.0049 | −3.0417 | 0.0024 |
|   Low road density† | −1.4485 | 0.6070 | −2.3863 | 0.0170 |
| Wolverine | | | | |
|   Intercept | −5.9952 | 0.5976 | −10.0329 | 0.0000 |
|   Precipitation | 0.0048 | 0.0011 | 4.5167 | 0.0000 |
|   Precipitation (quadratic) | $-1.7225 \times 10^{-6}$ | $0.4735 \times 10^{-6}$ | −3.6379 | 0.0003 |
|   Interpolated population | −0.0013 | 0.0003 | −4.1081 | 0.0000 |
|   High road density† | −0.5974 | 0.5269 | −1.1339 | 0.2569 |
|   Cirque habitat | 6.7243 | 4.6514 | 1.4456 | 0.1483 |
|   Wetness | −0.0119 | 0.0061 | −1.9598 | 0.0500 |

*Note:* Models shown used only recent (1983–1998) occurrence records.
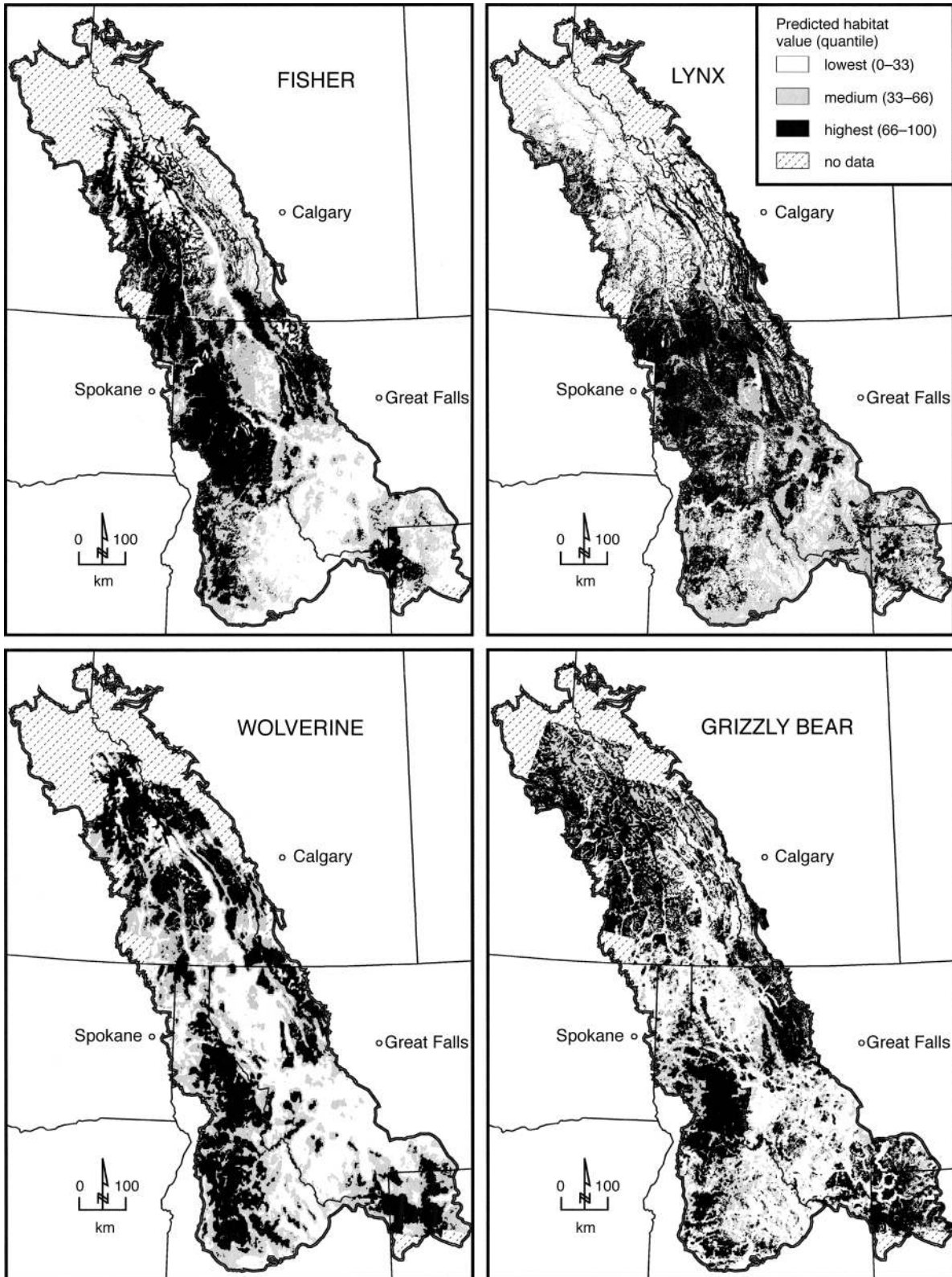† Variables incorporating thresholds that are described in *Results*, *Univariate analysis*.

FIG. 5. Distribution of fisher, lynx, and wolverine habitat in the Rocky Mountain study area as predicted by the RSF (resource selection function) analysis, and distribution of grizzly bear habitat as predicted by a regional-scale habitat model adapted from previously published work.

TABLE 5. Spearman rank correlations between predicted habitat maps for the four carnivore species.

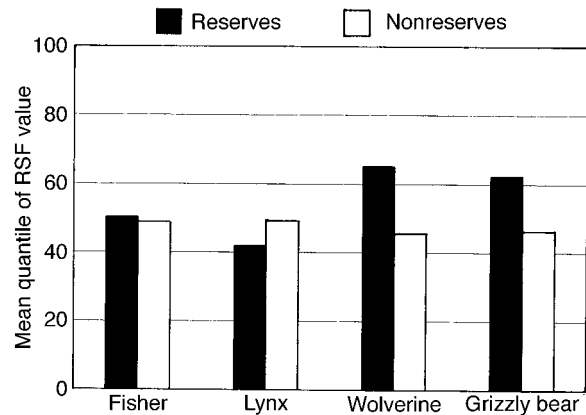| Species | Species | | |
|---|---|---|---|
| | Lynx | Fisher | Wolverine |
| Fisher | 0.3581 | | |
| Wolverine | −0.0833 | 0.5635 | |
| Grizzly bear | 0.0712 | 0.4699 | 0.5376 |



FIG. 6. Comparison among the four carnivore species of mean quantiles of RSF values for reserves and nonreserved management categories in the study area. Reserves constitute ~26% of the study area.

scale models alone are not sufficient for the development of detailed conservation plans. Given the strong sampling bias and low reliability inherent in unverified occurrence data sets, a large percentage of unexplained variance is probably unavoidable. The combination of multiple GIS habitat layers leads to spatial error propagation and increased levels of uncertainty (Heuvelink 1998). In addition, some percentage of the variation in the distribution and abundance of a species will be determined by factors unrelated to habitat quality, such as historical effects and stochastic variability in habitat occupancy. Our analysis also does not attempt to quantify the relationships between probability of occurrence and population density, or between density and individual survival and reproduction (Van Horne 1983).

The sampling bias associated with occurrence data may be most problematic when evaluating the effects of variables such as road density, which may be correlated with both sampling effort and habitat quality. We have used knowledge of the species, in combination with univariate GAM plots (Fig. 4), to attempt to separate these two factors. In the correlation tests (Table 3), both fisher and lynx detections showed a significant positive association with roads. The decrease in detection probability at low road densities for both fisher and lynx was judged to be an artifact of reduced observer effort in non-roaded areas, an unavoidable bias in sightings data that obscures potential relationships between species distribution and lower levels of road density. Wolverine detections showed no significant association with roads in the univariate tests, but appear to be negatively associated with higher levels of road density in the GAM plot (Fig. 4). Although Wald test values for this variable show low significance (Table 4), addition of road density to the multiple regression model for wolverine does result in a better model as measured by the AIC statistic. The significant effects

on model estimates of human impacts in the wolverine model when pre-1983 occurrences are included also suggest that these associations are biologically important, rather than artifacts of a spatial coincidence with other unmeasured factors. Although our interpretation is biologically plausible based on species knowledge, a more rigorous evaluation of the effects of road density on these mesocarnivores must await development of systematic survey data sets.

The degree of fit of the models varies greatly among species. Fit of the fisher model to the data (0.667), as measured by Somer's Dxy, is similar to that reported for grizzly bear (Merrill et al. 1999) and for a fisher model derived from presence–absence survey data (Carroll et al. 1999). Model fit for the wolverine (0.363) and lynx (0.353) is much poorer. Two factors contribute to this contrast. First, fisher occurrences are concentrated in a relatively small portion of the study area compared with occurrences of the lynx and wolverine (Fig. 2). Spatial autocorrelation in environmental variables would cause model fit to be higher in the fisher, independent of actual habitat associations. Maximum dispersal distances for the fisher (100 km) are much less than those for the wolverine (378 km) and especially the lynx (1100 km) (Craighead et al. 1999). Thus sightings of the latter two species are more likely to occur in habitat that is suitable for travel but not for

TABLE 6. Loadings and proportion of variance for principal-components analysis of predicted habitat values for the four carnivore species.

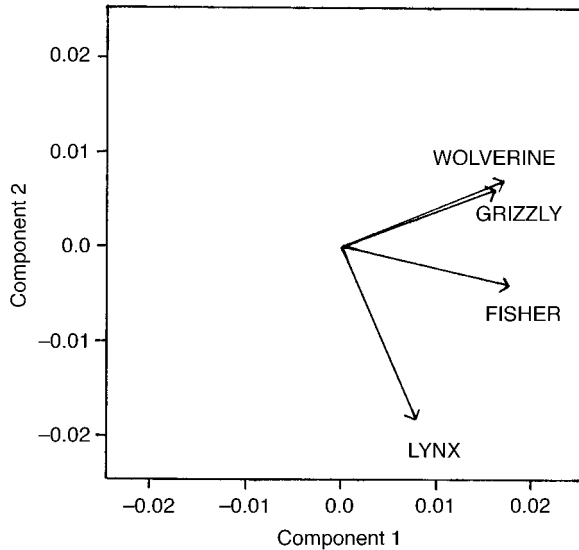| Species | Component | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| Fisher | 0.5855 | −0.2345 | 0.4495 | 0.6326 |
| Lynx | 0.2006 | −0.8825 | −0.1777 | −0.3865 |
| Wolverine | 0.5687 | 0.3436 | 0.3601 | −0.6549 |
| Grizzly bear | 0.5418 | 0.2195 | −0.7980 | 0.1469 |
| Proportion of variance | 0.5416 | 0.2762 | 0.1200 | 0.0622 |

FIG. 7. Results of the principal-components analysis of predicted habitat values for the four carnivore species. The arrows labeled by species indicate loadings on the first and second component axes.

residence. Use of systematic survey data that could document presence and absence would probably result in a greater increase in model fit in wolverine and lynx than in fisher. Such data sets are currently being created for the lynx (McKelvey et al. 1999). Techniques for regional-scale surveys are less developed for the wolverine (but see Hart et al. 1997).

The second factor influencing differences among species in model fit is the complexity of the habitat associations for a particular species, and how well the GIS metrics used represent underlying limiting factors. For the fisher, pseudo-habitat variables such as greenness appear to serve as adequate proxies for habitat data if prediction is the primary aim. Better interpretability remains an advantage of models containing vegetation variables. Lack of data on difficult-to-measure habitat variables such as forest structure may limit the power of the models for lynx or wolverine.

### Interpretation of individual models

*Fisher.*—The strong association between fisher and low- to mid-elevation, biologically productive forests has been noted in previous studies in the western United States. In Montana, reintroduced fishers preferred low-elevation mesic forests, especially riparian areas, and dense young mixed-conifer stands (Roy 1991, Heinemeyer 1993). In northern California, regional-scale fisher distribution was strongly associated with high levels of tree canopy closure (Carroll et al. 1999). Although canopy closure is consistently important across studies, selection for size class and forest type is more variable. Mixed-conifer and mixed-conifer–hardwood types generally are favored. Fishers are legally trapped

in British Columbia, Alberta, and Montana, and incidental trapping risk may be high in other areas (Powell and Zielinski 1994). Nevertheless, human-impact variables have not been significant in regional-scale models.

Indices of greenness and wetness seem to represent important correlates of fisher distribution. Interpretation of changes in these metrics is complex. The cover type class (e.g., forest vs. grassland) and topographic position of a site will affect the manner in which the metric changes in response to changes in ecological attributes such as productivity. As they age, forest stands may first increase and then decrease along the tasseled-cap axes. Brightness often corresponds to the amount and reflectivity of exposed soil. Greenness, as its name suggests, is often a correlate of green phytomass. Closed hardwood–conifer forest typically has higher greenness than do pure conifer stands. Wetness is often highest in young conifer stands, with hardwoods and older conifers having lower wetness (Cohen et al. 1995). The negative coefficient for wetness and the positive coefficient for greenness in the fisher model may reflect association with productive mixed forest.

Fisher dispersal distances average 10–33 km, much less than those of the lynx and wolverine, and long-distance (~100-km) dispersal is infrequent (Arthur et al. 1993, Powell and Zielinski 1994). This may limit rapid recolonization of areas where fishers have been extirpated and may reduce regional viability in regions, such as the intermountain west, where habitat areas are small and isolated (Heinemeyer and Jones 1994). We speculate that the highly aggregated pattern of fisher distribution in both the Rockies and Pacific coastal regions reflects a threshold in habitat area or population size below which subpopulations have low persistence.

*Lynx.*—We might expect that the strong association of lynx with a single prey species, the snowshoe hare (*Lepus americanus*), would simplify the development of habitat models. Although patch-level foraging habitat requirements for lynx may reflect the distribution of its prey, landscape- and regional-scale requirements for viability are more complex. Optimal foraging habitat probably is found in early seral stands, whereas mature forest is important for denning; more field data are needed to document these generalizations (Koehler and Brittell 1990).

Snowshoe hare densities peak in stands that provide dense cover and large quantities of browse that are accessible above the snowpack (Koehler and Brittell 1990). These qualities are found in 15- to 40-yr-old conifer stands in our study region (Koehler and Aubry 1994). Hares occur at relatively low densities in this region because of the fragmented distribution of boreal forest types at the southern end of their range, and the greater diversity of lagomorph species and hare predators (Wolff 1980).

The negative association of lynx distribution with

brightness in our model may be attributable to avoidance of sparsely vegetated areas or to selection for particular cover types. Positive association with modified NDVI suggests selection for highly productive forests. The negative association of lynx with areas of high topographic complexity is consistent with field studies (Koehler and Aubry 1994, Apps 2000, McKelvey et al. 2000). The evident contrast between areas in British Columbia where lynx were trapped vs. those where wolverine were trapped (Fig. 3) supports the existence of contrasting topographic effects on these two species.

Direct mortality from roadkill was the major cause of low survival for reintroduced lynx in New York State (Brocke et al. 1991), but this factor may be less important in resident populations. In a study of relative habitat abundance of grizzly bear, wolverine, and lynx in the U.S. northern Rockies, Wisdom et al. (1999) also noted that lynx distribution seemed less correlated with low road density than did that of the other two carnivore species. Trapping mortality can be high, and Hatler (1988) has suggested that the higher viability of lynx populations in British Columbia than in Alberta is due to the spatial refugia from trapping provided by mountainous areas. Although our results cast doubt on the favorability of highly mountainous areas, some trapping refugia may contain areas of less rugged terrain.

*Wolverine.*—The wolverine is often characterized as a wilderness species whose persistence is linked to the presence of large areas of low human population density. Only recently, however, have field data become available to document more specific habitat requirements (Hornocker and Hash 1981, Banci 1987, Copeland 1996).

The dependence of the wolverine on temporally variable and unpredictable food resources (e.g., ungulate carrion) means that individuals must maintain home ranges much larger than those of other carnivores of similar size (Copeland 1996). The combination of large area requirements and low reproductive rate make the wolverine vulnerable to human-induced mortality and habitat alteration. Populations probably cannot sustain rates of human-induced mortality greater than 7–8%, lower than that documented in most studies of trapping mortality (Banci 1994, Weaver et al. 1996).

Female wolverines must leave their kits for lengthy foraging trips, and often select natal den sites in deep talus in remote alpine cirques with snow cover late into spring (Copeland 1996). These sites allow wolverines to construct snow tunnels that provide thermoregulatory benefits for kits, are secure from excavation by predators, and are located in habitat that is used by few other carnivores and that provides an abundance of small-mammal prey for rearing kits (Magoun and Copeland 1998). The inclusion of the cirque habitat variable, which is a crude approximation of known natal den requirements, suggests that these areas may also be important limiting factors at coarser scales. Although elevation was not included in the final multiple regression model, the positive association with both snowfall and cirque habitat highlights the importance of alpine areas. A positive association with forest edge may indicate the importance of subalpine parkland landscapes. The biological significance of precipitation is less interpretable than that of snowfall, and the alternate model incorporating snowfall has proved more generalizable to other areas for which snowfall data are available (Carroll et al., 2001).

The wolverine shows more generalized use of open areas and a wider variety of vegetation types than do the marten and fisher (Banci 1994, Copeland 1996). Canopy closure thresholds in our analysis are lower than those of the fisher and similar to those of the lynx. Thus, the present distribution of the wolverine, like that of the grizzly bear, may be more related to regions that escaped human settlement than to vegetation structure. The relative adequacy of models based on AVHRR data for wolverine, in contrast to fisher and lynx, is consistent with generalized cover type associations.

*Grizzly bear.*—Although based on previously published models, our results for the grizzly bear represent an extrapolation of previous work to a region twice the size (Fig. 5), and show increasing fragmentation of habitat areas along a north–south gradient in British Columbia, as well as along the Columbia Trench. This is likely to affect the long-term viability of bears occupying smaller refugia within southern British Columbia, and to increase isolation of bear populations in the United States. The distribution of the grizzly bear, which was relatively continuous in the pre-settlement era, is increasingly fragmented into small, isolated populations with potential risks of genetic isolation and demographic stochasticity (Craighead and Vyse 1996). Although island populations of 100–300 bears have persisted with occasional immigration, completely isolated populations may require ≥1000 bears to persist (Craighead and Vyse 1996). To be effective, a grizzly conservation strategy must consider the status of the entire regional metapopulation over an area that encompasses both source and sink populations.

### Validation results

The significant correlation between predicted lynx and wolverine habitat and the trapping data supports the conclusion that those models, despite having lower fit than the fisher model, do identify biologically important limiting factors. Despite contrasts in management status of the species between the United States and Canada, road density and human population data emerge as relatively robust surrogates for human impacts on the wolverine. Overall, surrogates for human impact factors are likely to be more generalizable than surrogates for ecological factors, and the distribution

of those species strongly limited by human impacts will be easier to predict (Mladenoff et al. 1999).

### Conservation planning for multiple species

Results of the principal components analysis and correlation analysis (Tables 5–6, Fig. 7) highlight the contrast between priority areas for the lynx and for the grizzly bear and wolverine. The fisher appears to be intermediate between these extremes. This contrast may be due to use (grizzly bear and wolverine) or avoidance (lynx) of rugged terrain. The contrasts between species sensitive to direct human impacts but able to use open habitats (grizzly bear and wolverine) and those species associated with forest habitats (lynx and fisher) is also evident (Mattson et al. 1996). This conceptual framework may aid multispecies conservation strategies by suggesting combinations of focal species, such as the grizzly bear and lynx, that can be more effective umbrellas than any species alone. Although grizzly bear and wolverine share much priority habitat in our analysis, specific management guidelines may differ between the species, to accommodate factors such as winter habitat requirements that are encountered by wolverine and not by denning grizzly bear.

The association between carnivore distribution and patterns of habitat productivity, as measured by such variables as greenness, highlights a key conservation challenge that has been identified for other taxa. For example, bird species richness in the Greater Yellowstone region is correlated with net primary productivity (Hansen and Rotella 1999). In this predominantly montane region, productive habitats are also highly valued for human use and are increasingly threatened by development pressures. This problem is most serious in the central Canadian Rockies, where the proportional extent of productive habitat is lowest. Few areas in the study region combine high biological productivity and low human impact. The northern one-third of the region is generally of lower productivity, whereas the middle one-third, which straddles the United States–Canada border, has higher productivity and higher human use. This pattern has implications for species whose dispersal is limited by human development. For example, increasing development pressures in the border region could effectively isolate grizzly bear and wolverine populations in the United States because of a lack of large protected areas in southeastern British Columbia and southwestern Alberta. This area is generally in an earlier stage of forest fragmentation than industrial forest landscapes in the United States (Sachs et al. 1998), but is undergoing rapid development.

The fisher and lynx, although relatively more tolerant of human presence, may also be vulnerable to human-induced landscape change in areas where low-elevation or less rugged habitat is naturally fragmented. Lynx habitat in southern British Columbia appears to be highly fragmented by rugged terrain. Thus, the area is unlikely to be a good source of dispersers to rescue declining populations in the United States. Viability of fisher populations in the U.S. Rockies may be dependent on the large population found in north-central Idaho. Fisher habitat in the southern Canadian Rockies also appears to be fragmented by mountainous terrain. Areas that contain high-quality habitat for several or all of the four species, such as portions of southeastern British Columbia and northern Idaho, are obvious priority areas in a multispecies conservation strategy (Fig. 8). Because of the contrast in habitat associations within the carnivore guild, a comprehensive conservation strategy for carnivores in the region must be coordinated across multiple ownerships and must incorporate nonreserve lands through increased protected area designation, conservation management of nonreserved forest, and private-lands conservation agreements.

Regional-scale data on predicted habitat values may assist in the identification of potential reintroduction areas (Boyce and McDonald 1999). Area and configuration of habitat also must be evaluated at a regional scale to ensure sufficient habitat for long-term population viability. Our analysis does not directly incorporate differences in scale of habitat selection among the species. For example, the lower dispersal ability of the grizzly bear compared with the wolverine may create higher connectivity requirements for the bear. We are currently evaluating minimum area and connectivity requirements by incorporating the results of our static habitat models into an individual-based dynamic model.

Our results highlight both the potential and the difficulties involved in multispecies conservation planning. Regional land management and reserve allocation are highly inefficient if done on a species-by-species basis (Noss et al. 1997). Planning based on metrics of emergent ecosystem properties such as landscape fragmentation is unlikely to capture the complex viability thresholds of habitat area and connectivity evident in wide-ranging carnivores. Commonalities do exist among carnivore species that will simplify the design of multispecies strategies. These commonalities are not so large, however, that we can expect planning based on a single umbrella species to protect all threatened carnivores (Noss et al. 1996, 1997). Limiting factors and scales differ among species, as does the resolution of habitat data necessary for accurate predictive modeling.

In addition, integrating multiple single-species habitat models into a multispecies conservation plan requires understanding the nature of interactions among carnivores. Varying levels of tolerance of individual carnivore species for human disturbance suggest that species assemblages will not respond as units, given almost any scenario of anthropogenic change. Effects of anthropogenic climate change on vegetation patterns
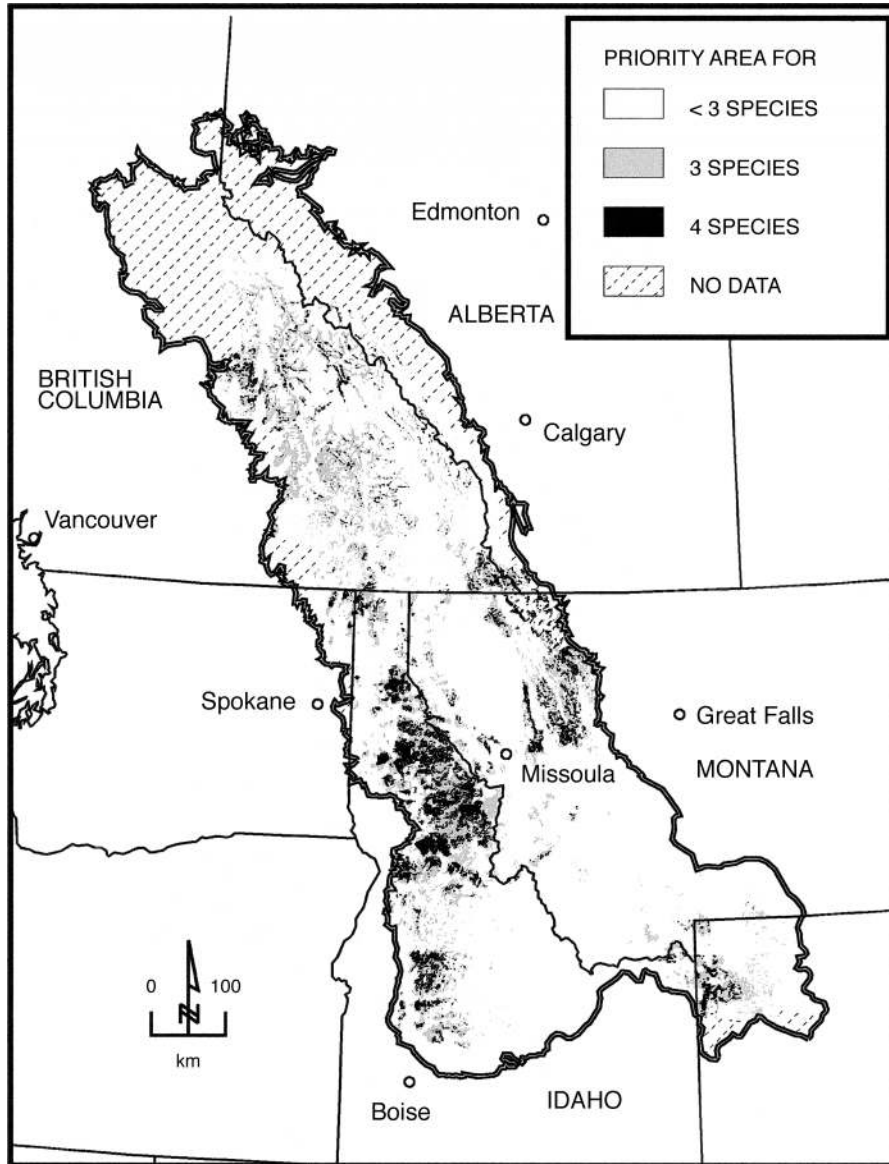
FIG. 8. Overlap among the four carnivore species in the areas with the highest one-third of RSF values (Fig. 5).

will increase this complexity. Critical areas for habitat generalists limited by direct human impacts are often distinct from critical areas for less affected species (e.g., fisher, lynx), whose distribution may reflect gradients in both productivity and human-induced landscape change.

### Future research needs

The lower fit of our models for wolverine and lynx highlights the need to collect systematic survey data that can be used to validate and iteratively refine initial empirical models. Other types of geographically extensive data sets, such as improved data on grizzly bear mortality, are also important for quantifying the effects of human impacts. New survey techniques that extract DNA from hair collected at survey stations or from scat allow the first geographically extensive estimates of abundance, and will be invaluable in improving habitat models (Foran et al. 1997, Wasser et al. 1997). Simultaneously, regional-scale data on important habitat attributes such as vegetation should be developed in areas where they do not presently exist. A new imagery source, the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor, combines the high spectral resolution of TM data with the high temporal resolution and low cost of AVHRR data, and should be ideal for regional-scale modeling (Huete et al. 1997).

Implementing a conservation strategy for mammalian carnivores in the Rocky Mountains requires an unprecedented effort involving international, national, regional, and local conservation groups, government agencies at several levels, industry, and local residents. Biological science must be at the heart of any strategy to conserve carnivores, but social science, economics, law, education, and many other disciplines must be involved in the process of finding politically acceptable solutions. The proximal threats to most species are related to habitat, but the ultimate threats are human population, behaviors, and attitudes.

### Literature Cited

Achuff, P. L. 1998. The vegetation of the Yellowstone to Yukon: a preliminary outline. Pages 19–31 *in* L. Willcox, B. Robinson, and A. Harvey, editors. A sense of place: issues, attitudes and resources in the Yellowstone to Yukon ecoregion. Y2Y Conservation Initiative, Canmore, Alberta, Canada.

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Apps, C. D. 2000. Space use, diet, demographics, and topographic associations of lynx in the southern Canadian rocky mountains: a study. *In* L. F. Ruggiero et al., editors. The scientific basis for lynx conservation. USDA Forest Service General Technical Report **RMRS-30**. USDA Forest Service Rocky Mountain Research Station, Missoula, Montana, USA.

Arthur, S. M., T. F. Paragi, and W. B. Krohn. 1993. Dispersal of juvenile fishers in Maine. Journal of Wildlife Management **57**:868–874.

Aubry, K. B., and D. B. Houston. 1992. Distribution and status of the fisher in Washington. Northwestern Naturalist **73**:69–79.

Bailey, T. C., and A. C. Gatrell. 1995. Interactive spatial data analysis. Addison-Wesley, New York, New York, USA.

Banci, V. 1987. Ecology and behavior of the wolverine in the Yukon. Thesis. Simon Fraser University, Burnaby, British Columbia, Canada.

Banci, V. 1994. Wolverine. Pages 99–127 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine. USDA Forest Service General Technical Report **RM-254**. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution **14**:268–272.

Brocke, R. H., K. A. Gustafson, and L. B. Fox. 1991. Restoration of large predators: potentials and problems. Pages 303–315 *in* D. J. Decker, M. E. Krasny, G. R. Goff, C. R. Smith, and D. W. Gross, editors. Challenges in the conservation of biological resources: a practitioner's guide. Westview Press, Boulder, Colorado, USA.

Buskirk, S. W. 1999. Mesocarnivores of Yellowstone. Pages 165–187 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Karieva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Carroll, C., R. F. Noss, N. H. Schumaker, and P. C. Paquet. 2001. Is the return of wolf, wolverine, and grizzly bear to Oregon and California biologically feasible?. *In* D. Maehr, R. F. Noss, and J. Larkin, editors. Large mammal restoration: ecological and sociological implications. Island Press, Washington, D.C., USA.

Carroll, C., W. J. Zielinski, and R. F. Noss. 1999. Using presence–absence data to build and test spatial habitat models for the fisher in the Klamath region, U.S.A. Conservation Biology **13**:1344–1359.

Cihlar, J., L. St.-Laurent, and J. A. Dyer. 1991. Relation between the normalized difference vegetation index and ecological variables. Remote Sensing of the Environment **35**:279–298.

Clark, T. W., P. C. Paquet, and A. P. Curlee. 1996. Introduction to special section: large carnivore conservation in the Rocky Mountains of the United States and Canada. Conservation Biology **10**:936–939.

Cliford, P., S. Richardson, and D. Hemon. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics **45**:123–134.

Cohen, W. B., T. A. Spies, and M. Fiorella. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. International Journal of Remote Sensing **16**:721–746.

Copeland, J. P. 1996. Biology of the wolverine in central Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.

Corsi, F., E. Dupre, and L. Boitani. 1999. A large-scale model of wolf distribution in Italy for conservation planning. Conservation Biology **13**:150–159.

Craighead, F. L., M. E. Gilpin, and E. R. Vyse. 1999. Genetic considerations for carnivore conservation in the greater Yellowstone ecosystem. Pages 285–321 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Karieva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Craighead, J. J., J. S. Sumner, and J. A. Mitchell. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992. Island Press, Washington, D.C., USA.

Craighead, L., and E. R. Vyse. 1996. Brown/grizzly bear metapopulations. Pages 325–351 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C., USA.

Crist, E. P., and R. C. Cicone. 1984. Application of the tasseled cap concept to simulated thematic mapper data. Photogrammetric Engineering and Remote Sensing **50**:343–352.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical–topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology **33**:140–158.

Demarchi, D. A. 1994. Ecoprovinces of the central North American cordillera and adjacent plains. Pages 153–167 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine. USDA Forest Service General Technical Report **RM-254**. USDA Forest Service Rocky Moun-

tain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Doak, D. 1995. Source–sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology **9**:1370–1379.

Eidenshink, J. C. 1992. The 1990 conterminous U.S. AVHRR data set. Photogrammetric Engineering and Remote Sensing **58**:809–813.

ERDAS. 1998. Imagine 8.3.1. Earth Resources Data Analysis Systems, Atlanta, Georgia, USA.

ESRI. 1998. Arc-Info Version 7.1. Environmental Systems Research Institute, Redlands, California, USA.

Foran, D. R., S. C. Minta, and K. S. Heinemeyer. 1997. DNA-based analysis of hair to identify species and individuals for population research and monitoring. Wildlife Society Bulletin **25**:840–847.

Forbes, S. H., and D. K. Boyd. 1996. Genetic variation of naturally colonizing wolves in the central Rocky Mountains. Conservation Biology **10**:1082–1090.

Gibeau, M. L. 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. Dissertation. University of Calgary, Alberta, Canada.

Groves, C. R., M. L. Klein, and T. F. Breden. 1995. Natural heritage programs: public–private partnerships for biodiversity conservation. Wildlife Society Bulletin **23**:784–790.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University Press, Cambridge, UK.

Hansen, A. J., and J. Rotella. 1999. Abiotic factors. Pages 161–209 *in* M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.

Harrell, F. E., K. L. Lee, and D. B. Mark. 1996. Multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. Statistics in Medicine **15**:361–387.

Hart, M. M., J. P. Copeland, and R. L. Redmond. 1997. Mapping wolverine habitat in the Northern rockies using a GIS. Poster presented at the Fourth Annual Conference of the Wildlife Society, Snowmass Village, Colorado, USA.

Hastie, T. J. 1993. Generalized additive models. Pages 249–308 *in* J. M. Chambers and T. J. Hastie, editors. Statistical models in S. Chapman and Hall, New York, New York, USA.

Hatler, D. F. 1988. A lynx management strategy for British Columbia. Wildlife Bulllletin **B-61**. Wildlife Branch, Ministry of Environment, Victoria, British Columbia, Canada.

Heinemeyer, K. S. 1993. Temporal dynamics in the movements, habitat use, activity, and spacing of reintroduced fishers in northwestern Montana. Thesis. University of Montana, Missoula, Montana, USA.

Heinemayer, K. S., and J. L. Jones. 1994. Fisher biology and management in the western United States: a literature review and adaptive management strategy. U.S. Forest Service Northern Region, Missoula, Montana, USA.

Heuvelink, G. B. M. 1998. Error propagation in environmental modelling with GIS. Taylor & Francis, London, UK.

Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology **59**:1286–1301.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley, New York, New York, USA.

Huete, A. R., H. Q. Liu, K. Batchily, and W. van Leeuwen. 1997. A comparison of vegetation indices over a global set of TM images for EOS-MODIS. Remote Sensing of the Environment **59**:440–451.

James, M. E., and S. Kalluri. 1993. The Pathfinder AVHRR land data set: an improved coarse resolution data set for terrestrial monitoring. International Journal of Remote Sensing **15**:3347–3364.

Keane, R. E., D. G. Long, J. P. Menakis, W. J. Hann, and C. D. Bevins. 1996. Simulating coarse-scale vegetation dynamics using the Columbia River Basin Succession Model—CRBSUM. USDA Forest Service General Technical Report **INT-GTR-340**. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.

Koehler, G. M., and K. B. Aubry. 1994. Lynx. Pages 74–98 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. USDA Forest Service General Technical Report **RM-254**. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Koehler, G. M., and J. D. Brittell. 1990. Managing spruce–fir habitat for lynx and snowshoe hares in north central Washington. Journal of Forestry **88**(10):10–14.

Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology **13**:367–377.

Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management **62**:1313–1320.

Maj, M., and E. O. Garton. 1994. Fisher, lynx, and wolverine: summary of distribution information. Pages 169–175 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. USDA Forest Service General Technical Report **RM-254**. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals. Chapman and Hall, New York, New York, USA.

Mattson, D. J., S. Herrero, R. G. Wright, and C. M. Pease. 1996. Designing and managing protected areas for grizzly bear: How much is enough? Pages 133–164 *in* R. G. Wright, editor. National parks and protected areas: their role in environmental protection. Blackwell Science, Cambridge, Massachusetts, USA.

McKelvey, K. S., J. J. Claar, G. W. McDaniel, and G. Harvey. 1999. National lynx detection protocol. USDA Forest Service Rocky Mountain Research Station, Missoula, Montana, USA.

McKelvey, K. S., Y. K. Ortega, G. Koehler, K. Aubry, and D. Brittell. 2000. Canada lynx habitat and topographic use patterns in north central Washington: a reanalysis. Pages 351–372 *in* L. F. Ruggiero et al., editors. The scientific basis for lynx conservation. USDA Forest Service General Technical Report **RMRS-30**. USDA Forest Service Rocky Mountain Research Station, Missoula, Montana, USA.

Merrill, E. H., M. K. Bramble-Brodahl, R. W. Marrs, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management **46**:151–157.

Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. Biological Conservation **87**:231–248.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology **9**:279–294.

Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: logistic re-

gression models vs. new field data. Ecological Applications **9**:37–44.

Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat planning: reserve design for Northern Spotted Owls. Ecological Applications **2**:3–17.

Nemani, R., L. Pierce, S. Running, and L. Band. 1993. Forest ecosystem processes at the watershed scale: sensitivity to remotely-sensed leaf-area index estimates. International Journal of Remote Sensing **14**:2519–2534.

Noss, R. F., M. A. O'Connell, and D. D. Murphy. 1997. The science of conservation planning: habitat conservation under the Endangered Species Act. Island Press, Washington, D.C., USA.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949–963.

Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, E. Vyse, R. Ward, and C. Strobeck. 1998. Variation in genetic diversity across the range of North American brown bears. Conservation Biology **12**:418–429.

Paquet, P. C., and A. Hackman. 1995. Large carnivore conservation in the Rocky Mountains. World Wildlife Fund-Canada, Toronto, Ontario, Canada, and World Wildlife Fund-U.S., Washington, D.C., USA.

Peterson, R. O. 1995. Wolves as interspecific competitors in canid ecology. Pages 315–323 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada.

Powell, R. A., and W. J. Zielinski. 1994. Fisher. Pages 38–73 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine. USDA Forest Service General Technical Report **RM-254**. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Redmond, R. L., M. M. Hart, J. C. Winne, W. A. Williams, P. C. Thornton, Z. Ma, C. M. Tobalske, M. M. Thornton, K. P. McLaughlin, T. P. Tady, F. B. Fisher, and S. W. Running. 1998. The Montana Gap Analysis Project: final report. Unpublished report, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.

Redmond, R. L., Z. Ma, T. P. Tady, and J. C. Winne. 1996. Mapping existing vegetation and land cover across western Montana and northern Idaho. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.

Redmond, R. L., T. P. Tady, F. B. Fisher, M. Thornton, and J. C. Winne. 1997. Landsat vegetation mapping of the southwest and central Idaho ecogroups. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.

Roy, K. D. 1991. Ecology of reintroduced fishers in the Cabinet Mountains of northwest Montana. Thesis. University of Montana, Missoula, Montana, USA.

Sachs, D. L., P. Sollins, and W. B. Cohen. 1998. Detecting landscape changes in the interior of British Columbia from 1975–1992 using satellite imagery. Canadian Journal of Forest Research **28**:23–36.

Schoener, T. 1971. The compression hypothesis and temporal resource partitioning. Proceedings of the National Academy of Sciences (USA) **71**:4169–4172.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics **6**:461–464.

Strittholt, J. R., and P. A. Frost. 1997. An enduring features gap analysis for the Canada–U.S. Rocky Mountains. A Technical Report to World Wildlife Fund-Canada. World Wildlife Fund, Ottawa, Canada.

Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. Ecology **77**:1698–1715.

USDA and USDI. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. U.S. Department of Agriculture and U.S. Department of Interior, Portland, Oregon, USA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893–901.

Wasser, S. K., C. S. Houston, G. M. Koehler, G. G. Cadd, and S. R. Fain. 1997. Techniques for application of faecal DNA methods to field studies of ursids. Molecular Ecology **6**:1091–1097.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964–976.

White, J. D., S. W. Running, R. Nemani, R. E. Keane, and K. C. Ryan. 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. Canadian Journal of Forest Research **27**:1714–1727.

Wisdom, M. J., R. S. Holthausen, B. C. Wales, D. C. Lee, C. D. Hargis, V. A. Saab, W. J. Haan, T. D. Rich, M. M. Rowland, W. J. Murphy, and M. R. Earnes. 1999. Source habitats for terrestrial vertebrates of focus in the interior Columbia basin: broad-scale trends and management implications. PNW [Pacific Northwest] Research Station, Portland, Oregon, USA.

Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs **50**:111–130.