MODELING CARNIVORE HABITAT IN THE ROCKY MOUNTAIN REGION:

A LITERATURE REVIEW AND SUGGESTED STRATEGY

Carlos Carroll, Paul C. Paquet, and Reed F. Noss

ACKNOWLEDGMENTS

This report was prepared by the
Conservation Biology Institute, 800 NW Starker Ave., Suite 31C, Corvallis, OR 97330 USA

The authors may be contacted at the following addresses:

C. Carroll, Klamath Center for Conservation Research, PO Box 104, Orleans, CA 95556 USA
email: carlos@pcweb.net
R. F. Noss, Conservation Science, Inc., 7310 NW Acorn Ridge, Corvallis, OR 97330 USA
email: nossr@ucs.orst.edu
P. C. Paquet, World Wildlife Fund Canada, Box 150, Meacham, SK S0K 2V0 CANADA
email: ppaquet@sk.sympatico.ca

Table of Contents

<u>Introduction</u>

In support of its carnivore conservation strategy (Paquet and Hackman 1995), World Wildlife Fund (WWF) has asked the Conservation Biology Institute to gather and map available information on carnivore habitat quality in the Rocky Mountains. Our study area is from the region surrounding Jasper National Park in Alberta and British Columbia to the Greater Yellowstone Ecosystem (GYE) in Montana, Idaho, and Wyoming. This literature review on carnivore habitat modeling is the first product of our study and the basis for development of new models and maps of habitat effectiveness. The report concludes with a suggested multi-species modeling strategy.

Ongoing declines in the distribution and abundance of carnivores in the Rocky Mountains suggest that common factors are affecting the viability of these species. Although the carnivore species considered here --- grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), gray wolf (*Canis lupus*), coyote (*Canis latrans*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), fisher (*Martes pennanti*), and marten (*Martes americana*) --- differ in their biology, they share some or all of a series of life history traits that make them vulnerable to human-associated disturbance. These include low population density, low fecundity, habitat specialization, limited dispersal ability across open or developed habitat, and other traits that lower ecological resilience (Weaver et al. 1996). The carnivore guild may be divided into three groups: large carnivores that are limited by direct human impact, mesocarnivores (medium-sized carnivores) that are most affected by habitat alteration, and more resilient habitat generalists such as the coyote and bobcat (Mattson et al. 1996b).

Deterministic pressures on the viability of carnivore populations may be due to human-associated disturbance and mortality factors, such as roads, or to habitat loss. Historical causes of endangerment may differ from current threats. Much suitable carnivore habitat in the U.S. remains unoccupied due to the legacy of predator-control programs. For example, in the central Canadian Rockies we have extirpated (and recovered) wolves three times since 1900. Recovery of wolves has always been associated with cessation of direct persecution (trapping or hunting) intended to eliminate the species. On each occasion wolves have had prey and habitat to return to. However, quality habitat has continued to decline, and the number of wolves that reoccupy the central Rockies is always less than before (Paquet et al. 1996). Although direct human-caused mortality remains important, human-associated landscape change is increasingly a critical factor limiting the persistence of the region's carnivore species.

Due to the small size and isolation of remnant carnivore populations in the U.S., stochastic factors are also of concern. The remaining distribution of these species often includes habitats with lower natural productivity that have escaped human settlement. High temporal variability in food resources often characterizes these areas, increasing chances of population extinction.

Despite these negative factors, the Rocky Mountain region from Jasper to Yellowstone may offer one of the best opportunities for carnivore conservation on the continent. The region currently retains a high diversity of carnivore species. Levels of human population density and intensive land use do not preclude human/carnivore coexistence, as similar regions in Europe and Asia currently support populations of large carnivores (Mattson 1990, Boitani 1995). Existing levels of core area protection, and the level of societal support for preserving the native

carnivores of the region, make this area of North America ideal for achieving the goals of carnivore conservation. These goals include ensuring the long-term viability of regional populations of focal carnivore species, and restoring well-distributed populations where we have extirpated them.

Because of the regional nature of population processes in wide-ranging carnivores, and the regional nature of human-associated threats, successful conservation planning efforts require a broad-scale approach. Our goal is to conduct a spatially-explicit multi-species evaluation that will identify the habitat necessary for the viability of carnivore populations. Although the ultimate factor determining population viability is human attitude, biological analysis has an important proximal role in facilitating human/carnivore coexistence.

Spatially-explicit habitat analysis can identify necessary spatial refugia or core areas that will have a level of protection sufficient to buffer populations against human-caused mortality. It can also identify optimal locations of buffer zones and corridors that will expand the effective size of core areas by allowing use of semi-developed lands while reducing the probability of human-caused mortality. The interaction between food resource availability, carnivore movement patterns, and consequent mortality risks implies that the requirements for viability are location-specific, requiring spatially-explicit analysis. Biological and societal factors interact complexly, and a comprehensive carnivore conservation strategy must address both aspects. Herein, we lay a foundation for biological analysis by reviewing existing habitat models for the focal carnivore species and outlining an integrated approach to habitat modeling that incorporates habitat requirements across multiple scales.

Summary of models by species

Grizzly bear (*Ursus arctos*)

      The grizzly bear is the flagship species of conservation planning in the Rockies, and has attracted more funding for research and population monitoring than any of the other carnivores. Despite this attention, its future presence in the region remains problematic. Planning efforts have lacked an integrated regional approach, treating each recovery zone as isolated from other zones and the intervening landscape matrix. Planning has relied on population indices that provide only delayed and ambiguous information on declining viability (Craighead et al. 1995, Doak 1995). Management and jurisdictional boundaries have fragmented habitat analysis. A spatially-explicit analysis of habitat capability at the biologically-appropriate scale has never been completed. These problems affect management of all of the region's carnivore species, but their effect is most dramatic for the grizzly. The ability to maintain and restore viable, well-distributed populations of the grizzly bear represents the litmus test for conservation planning in the Rocky Mountain region.

      In many landscapes the grizzly bear is the carnivore species extirpated first by human settlement, although it may be more resilient than the wolf in highly mountainous areas. However, extirpation of the grizzly from most of the western U.S. is a legacy of predator control programs rather than a necessary consequence of present human population density and land use (McLellan 1990). Brown bear populations coexist with much higher levels of human density in Eastern Europe, Italy, and China (Mattson 1990 and others). Retaining grizzlies in western ecosystems is not an impossible goal. Future conservation efforts, however, will require a more serious commitment to cross-jurisdictional planning and restriction of incompatible human activities than has been evident previously. Whether human attitudes toward the grizzly have improved enough to help population recovery remains to be seen.

      The grizzly bear has a combination of life history traits that contribute to its low resilience in the face of human encroachment (Bunnell and Tait 1981). The bear's low lifetime reproductive potential (three to four female young per adult female in many regions) makes population viability sensitive to small declines in adult survivorship (Weaver et al. 1996). Subadult males commonly disperse two home range diameters (about 70 km), a distance large enough to escape the protection of most western parks (Weaver et al. 1996). However, successful long-distance dispersal between subpopulations, although common for species such as the wolf, has not been recorded for the grizzly.

      The continuous bear distribution of the pre-settlement era has been fragmented into a "non-equilibrium" metapopulation (Craighead and Vyse 1996, Harrison and Taylor 1997). This makes the problems that conservation biologists associate with small, isolated populations (such as genetic isolation and demographic stochasticity) more relevant to grizzly bears than to most carnivores. The sex-biased dispersal pattern evident in ursids, in which females establish home ranges near the natal site, reduces the effective breeding size (N_e) of populations, and leads to potential genetic risks (Chepko-Sade et al. 1987). Craighead and Vyse (1996) compared the viability of bear populations on islands of varying size and concluded that while island populations of 100-300 bears have persisted with occasional immigration, isolated populations require at least 1000 bears to persist. Mattson and Reid (1991) found a similar size threshold for viability in

European brown bear populations, and placed the Yellowstone population below this threshold. If the definition of a recovery zone is an area of habitat large enough to support a self-sustaining population (Servheen 1993), this suggests that an effective grizzly conservation strategy must consider the status of the entire regional metapopulation.

The challenge of grizzly conservation in the Rockies is complicated because the areas occupied by bears often represent habitat where food resources vary greatly between years (Mattson et al. 1991a). East-slope ecosystems with continental climate are not generally as productive bear habitat as west-slope ecosystems with a maritime climate and high salmon abundance (B. McLellan, pers. comm., D. Mattson, pers. comm.). In addition, bears have been extirpated from the lowlands that once supported much of the population and they are now generally confined to higher-elevation regions in the Rocky Mountains. Within these regions, human development often converges with the critical lower elevations in spring habitat (Mattson et al. 1987, Mace et al. 1996, Gibeau et al. 1996). An example is recreational development near ungulate wintering areas or fish-spawning streams in Yellowstone and Banff National Parks (Knight et al. 1988 and others). The variability of food resources forces bears to increase their home range sizes (Blanchard and Knight 1991), resulting in increased mortality risk from humans. Knight et al. (1988) found that although most mortality sinks in Yellowstone were on the periphery of the park, most of the park's bears had such a mortality sink within their home range. The level of yearly mortality was inversely proportional to annual habitat productivity.

Although the grizzly is an omnivore, its resiliency is limited by seasonally high calorie needs (Weaver et al. 1996). The diet of bears in Yellowstone and the Canadian parks is notable for the absence or scarcity of berries and salmon (Mattson et al. 1991a). In other areas, these are the consistent high-quality food sources critical to the buildup of fall fat stores (hyperphagia) (Blanchard and Knight 1991). For example, berries are a large component of the bear diet in northwestern Montana and parts of southern Canada (Mealey et al. 1977, Mattson et al. 1991a). Several more variable food sources form substitutes in Yellowstone. Long-term studies are often required to identify key food resources, such as army worms (*Euxoa auxiliaris*), that are infrequently available (Mattson et al. 1991a). Whitebark pine (*Pinus albicaulis*) seeds are a critical, although inconsistent, food in autumn (Mattson et al. 1992). Poor years of pine seed production may limit Yellowstone bear populations by increasing movement and associated human-caused mortality (Knight et al. 1988). Ungulate calves and winter-killed carrion are important spring foods. Graminoids and forbs associated with wet meadows and riparian areas are also major components. *Hedysarum* roots are important, and other roots such as those of sweet cicely (*Osmorhiza* spp.) and pondweed (*Potamogeton* spp.) are important episodically (Mattson et al. 1991b). A variety of minor components such as rodents also contribute to the diet.

Mealey et al. (1977) surveyed vegetation in areas of grizzly activity in northwestern Montana and noted that berries associated with open areas (globe huckleberry (*Vaccinium globulare*), buffaloberry (*Shepherdia canadensis*), and *Sorbus* spp.) formed the bulk of the diet. Mesic meadows and riparian areas were second in importance as a source of graminoids and forbs. In contrast, Blanchard (1983) found that telemetry locations for Yellowstone bears were primarily in moderate to dense (26-75% cover) forest less than 100 m from the edge of an opening. Subalpine fir/whortleberry (*Abies lasiocarpa/Vaccinium scoparium*) was the most common plant community used. Regional variation in diet helps explain these contrasting results (Mattson et al. 1991a, Mattson 1997). In addition, although grizzlies are often associated with

open habitats, this may relate to their easier observability in the open. Landscapes with high levels of forest/meadow interspersion, such as subalpine parkland, seem important (Agee et al. 1989).

Mattson (1997) used a long-term data set to test grizzly bear selection for lodgepole pine (*Pinus contorta*) cover types, the major forest type in Yellowstone. Overall, this type was underused. However, high spatial and temporal variation in habitat selection made assigning habitat values to cover types problematic. Variation in security from humans, location relative to other bears, microscale feeding opportunities (e.g., berries, ungulates), and landscape context may have been more significant than stand type. The author concludes that extrapolation of results from intensive habitat studies is risky for wide-ranging carnivores and that geographically extensive studies are necessary. Craighead et al. (1995) also found high variability in cover type selection by bears in Montana. They concluded that subalpine fir was the most important forest type, followed by riparian areas and grassland/forest ecotones.

Habitat Models

Agee et al. (1989) analyzed historic sighting records of grizzly bears in the North Cascades to develop a map of predicted sighting potential for grizzly bears. A "moving-window" geographic information systems (GIS) function was used to measure interspersion of habitat types. They compared land-cover type and interspersion at sighting locations with those at random locations. Contingency table analysis showed that sightings were more common than expected in three cover types: whitebark pine-subalpine larch open canopy, subalpine fir open canopy, and subalpine herb. Bears also tended to be found in landscapes of moderate cover-type interspersion.

The second element of most grizzly bear habitat models attempts to quantify the effects of human-associated disturbance and mortality factors such as roads, development, or livestock grazing areas. This is complicated by the interaction between habitat type and disturbance or mortality. For example, the patch-level effect of a road may be influenced by adjacent forest cover, and the landscape-level effect by its position relative to seasonal food sources and migration routes. At the population level, behavioral effects such as avoidance of human development are often a secondary effect of selective killing of habituated bears by humans (Mattson et al. 1996).

In addition, the social structure of bear populations may cause disturbance effects to vary between sexes and age classes. For example, adult male bears generally avoid road corridors. However, recent research in Banff shows that male bears, but not females or cubs, will occasionally cross major highways (S. Herrero pers. comm.). Adult females with cubs use areas near roads as refuge from male aggression, especially during years of poor pine seed production (Mattson et al. 1992). This causes added risk of human-caused mortality to the females, which represent the most important demographic group for population viability.

Despite the variation caused by such interactions, researchers have documented consistent effects of human disturbance on bears, at least at the local level. Human-caused mortality comprises 86-91% of adult bear mortality in Yellowstone and Montana (Weaver et al. 1996). The sensitivity of bear populations to small increases in adult female mortality makes even incremental increases in mortality risk or disturbance a threat (Mattson and Reid 1991, Mattson and Craighead 1994). Using an analytical source-sink model, Doak (1995) showed that incremental

habitat degradation can have severe nonlinear effects on population viability. These threshold effects may take up to a decade to be detected by population indices currently used by agencies. Spatially-explicit modeling of habitat effects may be a more powerful monitoring tool (Mattson and Craighead 1994, Doak 1995).

Roads represent the most important human influence on grizzly habitat. Illegal killing and management control (removal of habituated bears), the two main sources of adult bear mortality in the GYE (Mattson et al. 1987, Weaver et al. 1996), are both associated with roads. Road use by humans may also disrupt bear behavior and social structure, reduce the availability of adjacent foraging habitats, and create barriers to movement (Archibald et al. 1987, McLellan and Shackleton 1988, McLellan 1990). The effect may extend up to three km from primary roads and one to 1.5 km from secondary roads (Kasworm and Manley 1990, Mattson and Knight 1991b). If these buffer areas represent 32.9% of the GYE, but account for 70.3% of bear mortalities (Mattson and Knight 1991b), mortality risk is almost five times higher near roads (Doak 1995). Craighead et al. (1995) conclude that road densities higher than $1km/6.4km^2$ (one third the threshold set by agencies) are suboptimal for bears.

Recreational development increases bear mortality risk and preempts biologically-productive habitats such as riparian areas. The effect of developments on mortality extends up to six km from the site (Mattson and Knight 1991b). Even non-motorized trails may be avoided to a distance of 300 m (Kasworm and Manley 1990, Mace et al. 1996). The impact of recreational development and associated roads reduces the ability of national parks to function as core areas (Gibeau et al. 1996). For example, Yellowstone National Park contains 867 km of roads and sees more than three million visitors a year (Craighead et al. 1995).

Bears inhabiting the "multiple-use" lands surrounding the parks face additional threats. The historical decline of the grizzly was associated with the expansion of livestock grazing, especially of sheep, and associated predator control (Peek et al. 1987, Mattson 1990). Livestock depredation-associated killing remains the second most important mortality source for bears in Canada (McLellan 1990). Recent movement of bears into the national forests northwest of Yellowstone may reflect a decline of sheep grazing on public land (Peek et al. 1987). Mineral and gas exploration forms another important disturbance source, primarily through associated road development (McLellan and Shackleton 1989, McLellan 1990).

Logging is the major extractive use of non-park lands in the region. Because grizzly bears use a variety of seral stages, the effects of logging on bears are not as evident as with forest mesocarnivores. The importance of open areas to bears in northwestern Montana led Mealey et al. (1977) to propose that timber cutting, at least in low elevation forest types, would improve berry production and habitat value by mimicking the effects of natural fires. Other researchers have challenged this interpretation (Peek et al. 1987, Mattson 1997). Berries are a minor resource to bears in the Yellowstone, and early seres have low value there (Mattson 1997). While the importance of early-seral stands for forage production varies by forest type and along regional gradients, the increased road access associated with logging is uniformly negative (Peek et al.1987). Low use of clearcuts, despite the presence of berries, may be due to avoidance of areas with high road density and associated mortality risk. If other vegetation types support a greater abundance of forage, and population densities are depressed due to access-related mortality, food resources in clearcuts may remain underused (McLellan 1990).

The primary method used by agencies to model bear habitat value is cumulative effects analysis (CEA) (Weaver et al. 1986). This is a theoretical modeling approach that assigns qualitative scores for each attribute, then sums scores for a composite index of habitat value. The approach is similar to that of the habitat suitability index (HSI) model, but is designed to incorporate changes in habitat effectiveness due to human disturbance in addition to habitat productivity. As with the HSI models, agencies generally developed the CEA out of a project-level planning and mitigation paradigm, rather than from studies designed to empirically estimate quantitative species/habitat relationships. However, recent versions of the CEA for the Yellowstone and Banff ecosystems incorporate parameters estimated from empirical data (Gibeau et al. 1996, D. J. Mattson, pers. comm.).

The CEA for the grizzly bear developed by Weaver et al. (1986) combines three types of effects of humans on bears: direct mortality, habitat alteration, and displacement from habitat. The mortality risk index is derived from a direct mortality component, which integrates habitat quality, type of activity, intensity, and sanitation practices. The habitat effectiveness value is derived from two elements: a habitat alteration component that integrates food/cover, diversity, and seasonal equity, and a habitat displacement component that integrates distance to cover, nature of activity, type of activity, and intensity of use. Habitat typing is based on such data as maps of forest timber types, ungulate seasonal ranges, and spawning streams.

The CEA approach has also been extended to modeling bear dispersal paths by means of a Linkage Zone Prediction (LZP) model (Ser12heen and Sandstrom 1993, Gibeau 1993b & 1996, Apps 1997). The LZP model predicts relative probability of movement by grizzly bears through an area by integrating four factors: human features, linear disturbance elements, visual cover, and riparian habitat. We are aware of no empirical validation of the LZP model to date.

Recently, models have appeared that we believe are superior to the CEA/LZP approach and other theoretical models. Mace et al. (1996) used logistic regression to estimate resource selection functions (Manly et al. 1993) from telemetry data in northwestern Montana. Analysis of road density effects shows the importance of their explicitly multi-scale approach. Selection against areas of higher road density was evident at the population-level but not at the individual-level. This suggests that bears establish home ranges in areas of lower road density, but will use habitat with higher road density that falls within their home range. Cover-type and elevation variables dominated within-home-range habitat associations. Lower-elevation forest represents important habitat made less available to bears due to higher levels of human access. Seasonal and individual variation in habitat associations were also significant. This type of multivariate empirical model to predict regional-scale distribution and would likely prove more statistically robust than HSI-derived predictions, although interpretability, for example, the separation of mortality and productivity factors, may be more difficult in some cases. Mace et al. (1999) present such a landscape-scale model for the Northern Continental Divide Ecosystem. Tasseled-cap greenness, a satellite imagery-derived metric (Crist and Cicone 1984), proved a useful surrogate for food resource availability in their multivariate model.

Merrill et al. (1999) developed a regional-scale habitat model using empirical relationships developed by themselves, Mace et al. (1996), and others. Habitat productivity values were created by assigning habitat values to macroscale vegetation types identified with satellite imagery. These values were reduced for areas of low vegetation density as measured by tasseled-cap (Crist and Cicone 1984), and increased in areas of higher topographic complexity. This combination of

information on finer-scale vegetation structure with coarse-level data on vegetation types is a useful approach. However, accuracy of coarse-scale vegetation cover type data may be too low in some cases even for regional-scale wildlife modeling, and finer-scale metrics such as tasseled-cap greenness may provide additional predictive power.

Habitat effectiveness values were derived from indices of road density and human presence. The relationship between road density and bear habitat use was derived from the resource selection function data in Mace et al. (1996). Human presence, or potential recreational visitor days, was modeled as a function of total human population within 80 km, interacting with the proportion of landscape that is roaded and with an inverse function of distance from population centers. This is a useful attempt to estimate road use, which is more biologically-relevant than simple road density.

In Merrill et al. (1999)'s conceptual model, habitat productivity and habitat effectiveness values are combined to produce a composite habitat suitability value. Habitat suitability is then averaged over a GIS "moving-window" equal in size to a female bear's lifetime home range (300 km^2). A cutpoint habitat suitability value for delineating core habitat was developed from field data on bear distribution in Idaho. The authors projected future habitat conditions by doubling the values of the human presence variable, but did not account for vegetation change. Although little regional-scale distribution data exist to validate model results, agreement with maps of grizzly bear distribution and abundance in Canada (Demarchi et al. 1993) was encouraging. Unlike many regional habitat analyses, Merrill et al. (1999) have sought to use empirical models [e.g., Mace et al. (1996)] to develop the relationships between component variables. As an alternative to somewhat arbitrary relationship between the productivity and effectiveness elements of their conceptual model, Merrill et al. (1999) also developed a multiple logistic regression model combining the two factors. Results of the two models were qualitatively similar, although the empirical model identified somewhat less area as suitable habitat. Models such as these can assist field research by identifying information gaps at regional scales. Data derived from directed field studies can then be used to build robust regional-scale models that allow assessment and monitoring of metapopulation status.

Empirical estimation of dispersal rates will remain difficult, however, and simulation models may provide the only solution. Boone and Hunter (1996) used a simulation model to predict dispersal routes between grizzly subpopulations in northern Montana and Yellowstone. They assigned "permeability" values to coarse-scale habitat types (one km^2 cell size) based on a literature review. They judged that the whitebark pine/lodgepole pine type had highest permeability, followed by older stands of other forest types and riparian areas. Clearcuts and sapling stages were judged to be relative barriers. Walker and Craighead (1997) created a similar model for a larger portion of the Rockies. They assigned cells permeabilities based on vegetation type, length of forest edge, and road density. Forest edge was treated as a positive factor. This may be realistic in subalpine parkland types (Craighead et al. 1995), but is questionable in landscapes of anthropogenic high-contrast edges (e.g., clearcuts).

Model attributes

        As Craighead et al. (1995) state, the grizzly bear's habitat needs are "a mosaic of diverse plant communities recurring over an entire ecosystem, not enclaves within them." Patch-level habitat quality may be a poor predictor of the actual value of an area to bear populations. A habitat model is necessary that incorporates the interspersion of seasonal food sources and the interaction between habitat quality, movement patterns, and consequent human-caused mortality risk. Landscape and regional-scale factors can be analyzed using data on road density, human land use, and landscape pattern. These can be expected to form the coarse-scale constraints within which patch-level resource value becomes important (Mace et al. 1996).

        The large body of research on the diet of grizzly bears may allow us to assign resource values to habitat patches based on detailed ground-based vegetation survey data. Assignment of habitat values to the more generalized vegetation types available from remotely-sensed data is more difficult. Bears use microscale resources within many macroscale vegetation types, and the power of vegetation data to predict their distribution is weaker than with forest carnivores such as marten and fisher. Prediction of population-level distribution and performance over decadal time scales may be possible without data on microscale resources. The reality of bear conservation in marginal habitats such as Yellowstone requires an ecosystem-level approach to a greater extent than is necessary where concentrated food sources such as salmon are available.

        Although researchers have attempted habitat mapping for smaller areas (e.g., Craighead et al. 1982), they have yet to develop a standardized habitat mapping system that would allow habitat comparisons among recovery zones. This has been identified as the major research need for the species, as it would allow objective evaluation of impacts on habitat quality and of the ability of unoccupied areas to support bears (Craighead et al. 1995).

        Remotely-sensed vegetation data may be useful in mapping of resources such as whitebark pine stands, a key food resource in Yellowstone (Mattson et al. 1992). Data on climate variation might also help in mapping areas of high variability in pine seed crops, which are associated with temperature and precipitation in preceding years (Blanchard and Knight 1991, D. J. Mattson pers. comm.). Similarly, if a reliable correlation between berry abundance and specific cover types was evident, this would be important in the many areas where berries are the key plant food. Linking minor prey such as ground squirrels and voles to specific cover types may be possible (Craighead et al. 1995). Graminoids and sedges could be mapped as a function of distance from streams. Although these form an important food component by volume, it is unlikely that they are a limiting resource for bears (Mattson 1997). Mapping of avalanche chutes, which are important sources of forbs (Mace et al. 1996), may be possible using digital elevation models (DEM). Mapping of trout spawning areas and wintering and rutting ranges and calving areas for elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and bison (*Bison bison*) would locate key resources for Yellowstone bear populations, and to a lesser extent, those in other regions (Mattson et al. 1991a). The expert knowledge required for mapping these types of resources would make creation of a regional data layer difficult. Surrogates for ungulate abundance such as tasseled-cap greenness (Crist and Cicone 1984) may be useful. Cover-type diversity or interspersion is another potential model component (Agee et al. 1989, Walker and Craighead 1997).

A recently completed five-year study at Lake Ohara in Yoho National Park used an approach similar to that outlined above (Donelon and Paquet 1998, McCrory et al. 1999). Spatial data layers included avalanche chutes, rub trees, vegetation types, berry distribution, ground squirrel distribution, sheep distribution, and goat distribution. Bear data were collected by ground tracking, remote still and video cameras, and radio telemetry. Attributes included use of trails, proximity to development, understory density, slope, and use of rub trees. Human use data were collected simultaneously. The composite grizzly habitat model and human use model was used for trail risk analysis and decision support. Scaling-up of these model attributes to regional analysis will prove challenging, however.

Correlations between bear distribution and sources of human-caused mortality are likely to be more consistent across the region. The effects will, of course, vary by management category and jurisdiction based on hunting regulations. Nevertheless, attributes such as roads are negative factors even within protected areas (Knight et al. 1988). Data on road-density thresholds or buffer widths are available from field studies (McLellan and Shackleton 1988, Mattson and Knight 1991b).

In addition to road data, information on levels of stock production or grazing allotments would form an important model input for assessing mortality risk. The role of disturbance factors such as road density, human population density, or land use in constraining bear distribution at a regional level is clear (Mattson 1990), but development of empirical predictive models, similar to those for the wolf (e.g., Mladenoff et al. 1995, L. Biotani pers. comm., Paquet et al. 1996), has only recently begun. If regional-scale models based on data scaled up from fine-scale field studies are substituted, predictions should be validated against coarse-scale distribution patterns.

Black bear (*Ursus americanus*)

The black bear has higher ecological resilience than other ursids due to factors such as its higher natality rate and earlier age of first reproduction (Bunnell and Tait 1981). Black bears also show more tolerance of human-associated disturbances such as roads than do grizzly bears (Tietje and Ruff 1983, Kasworm and Manley 1990). However, in portions of the central Canadian Rockies black bears appear more threatened than grizzly bears, perhaps due to competition with grizzlies, the marginal quality of higher elevation habitats, and greater susceptibility to management-caused mortality. Transect data from Yellowstone National Park also shows low black bear abundance, and strong interspecific interaction leading to avoidance of grizzly bear through use of lower elevations (D. J. Mattson, pers. comm.).

Although black bear populations have persisted in most of the west, they are threatened or extirpated in much of the eastern U.S. (Mattson 1990). As a result, biologists have developed most conservation strategies and habitat models for eastern populations (e.g., Clark et al. 1993, Powell et al. 1997). Powell et al. (1997) developed and validated an HSI model for black bear in the southern Appalachian mountains of the U.S.. Although their work shares the weaknesses of theoretical models, the validation effort and the incorporation of several innovative measures of habitat quality justify review as the most biologically-realistic HSI model we have encountered.

The model incorporated three elements: food, escape cover, and denning habitats. A fourth component quantified the interspersion of these elements. Because humans are the primary source of mortality for black bears in the southeastern U.S., and most human-caused mortality occurs within one km of a road (including 4WD routes)(Powell et al. 1997), the escape cover element incorporated distance from roads. Area of conterminous forest without roads was also determined from aerial photos. Roadless areas less than four km^2 in size (the minimum size of a black bear home range) had zero escape cover value. Understory density and slope also were incorporated, as steep and brushy areas limit human access.

The denning element incorporated availability of dens (as density of large trees > 90cm diameter at breast height (dbh)), and security from human disturbance. Security was modeled as dependent on slope, understory density, and conterminous roadless forest area.

The food resource element was modeled as combining individual indices for abundance of spring, summer, fall, and non-seasonal foods, as well as interspersion of food resources. Most black bear food habit studies show seasonal changes in diet. Typically, emerging green vegetation near riparian areas, catkins, and insects are important in early spring and summer. The diet then shifts to berries and increasing amounts of animal protein such as small rodents and carrion. Scavenging can be important on emergence from dens where winter die-off of ungulates is common. Usually, mast, berries, and animal matter constitute the bulk of the fall diet. Multi-species models will need to incorporate the effects of apex predators such as wolves on availability of winter-kill.

In Powell et al.'s (1997) model, spring food was green forbs and grasses, modeled as distance from water. Summer food depends on the cover of berry-producing plants as extrapolated from ground-surveyed data. Fall food, the most important resource element, is dependent on the abundance and diversity of hard-mast producing trees (large oaks).

The interspersion element evaluates whether all critical resources are within the range of the average seasonal movements of adult female bears. It is modeled as dependent on the maximum, over the three resource elements, of the distance between the focal cell and the nearest cell with non-zero resource value. Distances between seasonal activity centers for this area's bears average one to five km, with a maximum of about 19 km. Therefore habitat value is modeled as decreasing after an interspersion distance of five km, to reach zero at 19 km. We may expect interspersion values to become more important as human development fragments formerly contiguous habitat.

This critical-distance method can also be applied to define seasonal security zones. If a buffer from human disturbance is required, habitat polygons whose geometry does not provide adequate distance from humans will be excluded. A similar 'core area analyis' has been conducted for grizzly bears in the Rockies. However, although this approach may identify the best remaining core security habitat, it does not identify which areas of highly-productive habitat may need restoration in order to sustain regional bear populations. Therefore, it is important to iterate the model both with and without human-induced landscape changes.

Powell et al. (1997) validated the model predictions with telemetry data. The HSI value was correlated ($p < 0.0001$, $r^2 = 0.42$) with the distribution of activity of the bear population as a whole, although not with the distribution of individual bears within their home ranges. The authors suggest that bears choose where to locate their home ranges on a landscape scale, but use all parts of their home range. This reinforces the importance of a multi-scale analysis, and offers support for the utility of regional-scale habitat modeling efforts, even where fine-scale data are lacking. Powell et al.(1997)'s work shows why theoretical models are attractive, as the researcher's field knowledge can be incorporated in an intuitive and interpretable manner. Although this approach proves useful in identifying critical habitat elements, development of an empirical, multi-scale model using telemetry and survey data would further strengthen the analysis.

Clark et al. (1993) took such an empirical approach to model development in their analysis of habitat use by black bears in the Ozark Mountains of Arkansas. They overlaid telemetry locations on GIS data layers of forest cover, elevation, aspect, slope, distance to roads, distance to streams, and cover-type diversity. A "moving-window" equal in size to the mean daily movement area of an adult female bear ($3 km^2$) was used for the diversity analysis. Habitat selection was analyzed using a discriminant analysis incorporating Mahalanobis distance, a multivariate distance metric.

Arkansas bears were found to select hardwood and hardwood-pine forest types over pine types. Bears avoided areas within 240 m of roads, and selected steeper terrain, as well as areas less than 600 m from streams and areas with high cover-type diversity. They avoided north and northeasterly aspects, and varied elevation use seasonally. The researchers created a predictive map but attempted no model validation.

Summary of models

The models discussed above were developed for black bears in the eastern and central U.S., and some model attributes may not generalize well to western ecosystems. Though few models have been developed for the Rockies, several studies of black bear diet have been completed (Pelchat and Ruff 1986, Young and Beecham 1986, Raine and Kansas 1990).

Although the role of mast-producing hardwoods may be limited in the Rockies, seeds of conifers such as whitebark pine are important but variable food resources (Raine and Kansas 1990). Aspen (*Populus* spp.) cover types in eastern Alberta were preferred by bears (Pelchat and Ruff 1986). This may be due to the consistent availability of forage in all seasons in this forest type. Aspen catkins are a spring food resource for black bear in the Rockies. Pine cover types also had high forage abundances in this study and in the Banff area (Pelchat and Ruff 1986, Raine and Kansas 1990).

Spring forbs and summer berries, important resources in the southern U.S., retain their importance in the Rockies. Graminoids and forbs associated with mesic and upland cover types were important in eastern Alberta (Pelchat and Ruff 1986). Blueberry (*Vaccinium myrtiloides*) was the most important food overall in that area, and between-year variations in berry production affected bear movements and survival. Black bears in Idaho and Banff showed a similar dependence on globe huckleberry (*Vaccinium globulare*) and buffaloberry (*Shepherdia* spp.) respectively (Young and Beecham 1986, Raine and Kansas 1990).

We could derive many attributes in Powell et al.(1997)'s HSI model from currently available extensive GIS data sets. These include road and stream data and forest type data. We could model forb production as a function of distance from streams. Other elements that depend on ground surveys (such as berry abundance) are impractical for incorporation in regional models unless they can be correlated with vegetation type. Data on cover-type diversity or interspersion is available from remotely-sensed vegetation layers. Interspersion of openings and closed forest may provide the escape cover that allows bears to use forage in open areas (Young and Beecham 1986). The appropriate scale for such interspersion analysis would need to be determined.

A habitat model based on food resource abundance has been developed for the Banff area (Kansas and Raine 1990). Model predictions showed qualitative agreement with data derived from telemetry locations and scat analysis. Food resource values were assigned to major cover types based on data from ground-based surveys. Although abundance of buffaloberry could be assessed, the relative abundance of ants associated with CWD was difficult to estimate. Graminoids were of uniformly high abundance, and tended to mask variation in other food resources.

Powell et al.'s (1996, 1997) conclusions as to the importance of roadless areas to black bear populations may be generalized to other areas. Road density explained 69% of variation in black bear density in New York state, outperforming attributes such as human population density or forest cover (Brocke et al. 1991), although this may reflect mortality and not behavioral avoidance. Black bears in Idaho foraged extensively in selectively-logged stands, but were found to avoid roads and clearcuts (Young and Beecham 1986). In Montana, black bears avoided areas within 300 m of roads, but were more tolerant of roads than were grizzly bears (Kasworm and Manley 1990).

Recreational hunting and market hunting for gall bladders and paws have been important sources of mortality for black bears in the western U.S. and Canada (Hummel et al. 1992), but it is unclear if this currently represents a threat to species persistence. The status of the species may vary from relatively secure in parts of the U.S. Rockies to declining in portions of the central Canadian Rockies. Constraints such as roads or other sources of human-caused mortality, if analyzed at a fine scale, may only become important as regional-scale suitability becomes marginal (Lenihan 1993). The fragmented distribution of bears in the eastern U.S. results from this effect (Mattson 1990). We could expect similar range fragmentation in the Rockies with increases in human population density. Until that time, source-sink dynamics (Pulliam 1988) and other coarse-scale processes may weaken correlations between black bear distribution and roadless areas.

Gray wolf (*Canis lupus*)

The wolf as a species shows a high level of ecological resilience compared with other large carnivores due to exceptional vagility and favorable life history traits (Weaver et al. 1996). The species' flexible social structure allows pack structure, fecundity, dispersal, and level of intraspecific tolerance to respond as population density shifts with changes in mortality rates and prey abundance (Fritts and Mech 1981, Fuller 1989, Boyd et al. 1995, Weaver et al. 1996). In many areas of the Rocky Mountains, however, wolves were eliminated whereas grizzly bears persisted, suggesting that these compensatory mechanisms have limits. In the rugged landscapes of high elevation or northern mountains, wolves depend primarily on secure valley bottoms for survival. Humans prefer these same areas, which usually results in displacement of wolves.

Wolves have a high capacity to replace numbers because they reach sexual maturity at an early age and have large litters. Thus, in comparison with grizzly bears, they are able to withstand relatively high levels of mortality. On the other hand, population densities of wolves are usually far lower than population densities of bears occupying the same areas. Wolves do not easily habituate to humans and because their diet is less diverse than bears wolves are less likely to become problem animals and thus casualties of management. However, livestock depredation is a problem in some areas. Wolves appear to be more easily displaced by human activities. In addition, social animals are more susceptible to removal than solitary animals and the large size of pack territories increases mortality risks (Woodruffe and Ginsberg 1998).

The wolves occurring in the Rocky Mountains have low population densities and require large home ranges compared with wolves elsewhere (Paquet 1993). Known home ranges (adaptive kernal method) vary from 500 km^2 to greater than 2,000 km^2 (Noss et al 1996, Paquet et al. 1996). Mean dispersal distance for males and females is 148 km, and a dispersal of 840 km has been recorded (Boyd et al. 1995). In expanding populations, many wolves may become dispersers. Forty percent of wolves in the Banff area were either dispersers or long-distance transients (Boyd et al. 1995). Genetic threats associated with small populations are of less concern in wolves due to their long-distance dispersal ability (Chepko-Sade et al. 1987, Fritts and Carbyn 1995, Boyd et al. 1995, Forbes and Boyd 1996). Unlike ursids, both sexes disperse, resulting in higher effective population size (N_e) (Chepko-Sade et al. 1987, Forbes and Boyd 1996). Dispersal dynamics are important at within-population and metapopulation scales (Haight et al. 1998).

Historically, the primary limiting factor for wolves has not been habitat degradation, but direct persecution through hunting, trapping, and predator control programs. As public anti-predator sentiment and the economic importance of the livestock industry diminishes in the west, wolves are well equipped biologically to recolonize what remains of their former range. The role of core versus buffer habitat in ensuring population persistence will differ between wolves and species such as the grizzly (Noss et al. 1996, Craighead et al. 1997). As in the north-central U.S., most of the wolf population in the Rockies will probably be found outside core protected areas (Fritts and Carbyn 1995). Map-based regional conservation planning can help facilitate human-wolf coexistence by identifying areas where human development trends create potential conflicts (Mladenoff et al. 1995, Boitani et al. 1997, Mladenoff et al. 1997).

<u>Modeling approaches</u>

Several modeling methods have been used to analyze species/habitat relationships in wolves. A static predictive model of potential wolf distribution in the north-central U.S. used multiple logistic regression to analyze correlations between pack distribution and such landscape-level attributes as road density and fractal dimension (Mladenoff et al. 1995, 1997). The analysis scale, a moving window of 150 km^2, was based on mean pack territory size. Boitani et al. (1997) used a similar approach to predict the potential distribution of wolves in Italy. They conducted discriminant function analysis (DFA), using a Mahalanobis distance metric, with a moving window of 100 km^2 (the mean pack territory size in Italy). The significant variables included: number of ungulate species, landscape diversity, human population density, road density, land use (percentage farmland, forest, and urban settlement), and dump site density. Elevation and sheep population density were non-significant.

Boyd-Heger (1997) analysed landscape attributes selected by six colonizing wolves that dispersed from protected refugia into northwestern Montana, southeastern British Columbia, and southwestern Alberta. Wolves selected for landscapes with relatively lower elevation, flatter terrain, and closer to water and roads than expected based on availability inside and outside their new home ranges. A logistic regression model was derived using elevation, slope, and distance to roads to predict wolf presence in areas of potential colonization.

A modified "least-cost path" model of landscape connectivity has been used to identify critical barriers to movement in Banff National Park (Paquet et al. 1996, 1997). The least-cost path can be modeled in GIS as a combination of the attraction to preferred habitats minus energetic costs (due to topography, etc.), security costs (exposure to humans or roads), and impediments to movement (Paquet et al. 1996, 1997). The Banff study used a time-series analysis to project effects of increased development and road creation on habitat quality and landscape connectivity. The habitat model was tested using an independent telemetry data set and found to have high predictive power (Alexander et al. 1996). Dynamic diffusion models based on road density and vegetation type have also been used to model wolf dispersal in U.S. Rockies (Walker and Craighead 1997).

Boyce (1992, 1995a) developed a simulation model based on stochastic difference equations to explore wolf-prey interactions in GYE. This was a "pseudospatial" model in that separate submodels for three areas in the GYE were created and linked by dispersal. The main prey species for wolves in the GYE are elk, mule deer, moose (*Alces alces*) and bison. In the model, both hunter harvest and climate influenced prey populations. When human-caused mortality was held constant in the model, the effect of elk population dynamics dominated wolf population dynamics. Elk population dynamics were in turn dominated by the density-independent effects of winter severity, although summer forage production was also important. Although not directly applicable to map-based conservation planning, this type of model affords qualitative insights concerning predator-prey interactions.

Haight et al. (1998) used a simulation model to analyze wolf population dynamics in a semi-developed landscape. They found that low levels of immigration allowed the persistence of isolated wolf populations inhabiting the landscape matrix. Wolves can inhabit areas with high levels of mortality risk (40%) if either spatial refugia (protected populations) exist or if dispersal is possible between buffer populations. This suggests that regional planning incorporating core,

buffer, and dispersal habitat can increase the effective size of reserves and allow the distribution of wolves to expand to include much of the landscape matrix (Fritts and Carbyn 1995, Craighead et al. 1997). This message, and the limited size of existing protected areas, have led several authors to stress the importance of cross-jurisdictional planning (Salwasser et al. 1987, Bath et al. 1988, Mladenoff et al. 1995, Paquet and Hackman 1995, Boyd et al. 1995).

Model attributes

Habitat selection by wolves is a complex interaction of physiography, security from harassment, positive reinforcement (e.g., easily obtained food), population density, available choice, and disturbance history. Seasonal feeding habitat, thermal and security needs, travel, denning, and the bearing and raising of young are all essential life requirements. Generally, wolves locate their home ranges in areas where adequate prey are available and human interference minimized (Mladenoff et al.1995). Wolves use areas within those home ranges in ways that maximize encounters with prey (Huggard 1993a,b). Topographic position influences selection of home ranges and travel routes (Paquet et al.1996).

As with bears, we can divide components of wolf habitat models into biological attributes and human-associated disturbance factors. Because of the wolf's inherent behavioral variability, it is unlikely that all wolves react equally to human induced change. Moreover, many extraneous factors contribute to variance in behavior of individual wolves. Because we have developed no reasonable expression of those differences, assessment should be applied at the pack and population levels. Solitary individuals (i.e., lone wolves) may show different habitat associations than packs.

Land use attributes

We can extract various land use attributes from census data and records of land management agencies. We can acquire data on livestock grazing from allotment maps (Fritts 1990) or records of state/provincial (Henshaw 1982) or national agricultural agencies (Boitani et al. 1997). For example, Henshaw (1982) mapped areas with a density of farms with cattle greater than $0.1/km^2$ to examine wolf reintroduction feasibility in New York state. We can map private inholdings as a potential conflict source. Human-caused mortality in response to wolf depredation on livestock in non-core areas (national forests, private lands) could limit recolonization potential. Sheep are more vulnerable than cattle, especially because the latter are released onto allotments after calving. However, herders often accompany sheep, reducing predation risk (Fritts 1990). The low levels of depredation in B.C., Alberta, and Minnesota (Fritts and Mech 1981, Fritts 1990) where wolves and livestock live in close proximity suggest that exaggerated perceptions of depredation risks, rather than wolf/livestock incompatibility, have limited wolf distribution. However, improved sanitation and use of guardian dogs has been important in reducing livestock depredation in southern British Columbia (V. Banci, pers. comm.).

Land use and ownership data may either be incorporated into the model (Boitani et al. 1997) or analyzed at a later stage to evaluate the role of various management classes in species conservation (Mladenoff et al. 1995, Carroll et al. 1999).

Human population density

Human activities have been shown to influence the distribution (Thiel 1985, Fuller et al.1992, Paquet 1993, Mladenoff et al.1995) and survival of wolves (Mech et al.1995, Mladenoff et al. 1995, Paquet 1993. Paquet et al. 1996). Although human-caused mortality is consistently cited as a major cause of displacement (Fuller et al. 1992, Mech and Goyal 1993, and others), we have limited empirical information on tolerance to indirect human disturbance.

We are aware of only three studies that have systematically and explicitly examined human population density and wolf distribution. In all studies, the absence of wolves in human dominated areas may have reflected high levels of human caused mortality, displacement resulting from behavioral avoidance, or some combination of both. All were conducted at a landscape scale and assessed population or pack level responses of wolves to humans. In Wisconsin, human population density was much lower in pack territories than in non pack areas. Wolf pack territories also had more public land, forested areas with at least some evergreens, and lower proportions of agricultural land. Overall, wolves selected those areas that were most remote from human influence (Mladenoff et al.1995) using areas with fewer than 1.54 humans/km^2. Most wolves in Minnesota (88%) were in townships with <4 humans/km^2 or with <8 humans/km^2. High human densities likely precluded the presence of wolf packs in several localities within contiguous, occupied wolf range (Fuller et al. 1992). However, road density, a highly correlated variable, may provide greater predictive power in a multivariate model (Mladenoff et al. 1995), especially in regions of the west characterized by high levels of recreational hunting mediated by road access.

Boitani (1995) analyzed the record of human/wolf coexistence in southern Europe versus that of wolf extirpation in northern Europe and the U.S. Human population density was only one of several factors determining the ability of the two species to coexist. A settled agricultural, rather than pastoral culture, lack of organized governmental eradication efforts, and high topographic heterogeneity contributed to the survival of wolves in southern Europe. In Italy, wolf absence was related to human density, road density, urban areas, cultivated areas, and cattle and pig density. However, because human density, road density, and urbanized areas were highly inter correlated no specific human effect was established (Duprè et al. in press).

In the Bow River Valley, Alberta the selection or avoidance of particular habitat types was related to human use levels and habitat potential (Paquet et al. 1996). Wolves used disturbed habitats less than expected, which suggests the presence of humans altered their behavior. Very low intensity disturbance (<100 people/month) did not have a significant influence on wolves, nor did it seriously affect the ecological relationships between wolves and their prey. At low to intermediate levels of human activity (100-1,000 people/month) wolves were dislocated from suboptimal habitats. Higher levels of activity resulted in partial displacement but not complete abandonment of preferred habitats. As disturbance increased, wolves avoided using some most favorable habitats. In portions of the Valley where high elk abundance was associated with high road and/or human population density, wolves were completely absent. Overall, habitat alienation resulted in altered predator/prey relationships.

The degree of human influence probably varies according to the environmental context. If a particular habitat is highly attractive, wolves appear willing to risk exposure to humans, at least within some limits (Chapman 1977). The presence of artificial food sources (e.g., carrion pits,

garbage dumps) also attracts wolves and reduces avoidance of human activity (Chapman 1977, L.D. Mech pers. comm., Paquet 1996).

Road density

Roads, by increasing human access, have been documented to negatively affect wolf populations at local, landscape (Fuller 1989, Thurber et al. 1994, Paquet et al. 1997) and regional (Mladenoff et al. 1995, Boitani et al. 1997) scales. Although researchers have documented infrequent dispersal across major highways for wolves in Minnesota (Mech et al. 1995), Montana (D. Boyd, pers. comm.), and Wisconsin (D. Shelley pers. comm.), major roads such as the Trans-Canada Highway may function as partial barriers or filters (Paquet et al. 1997). Roads may also function as disturbance factors. Road data can be incorporated into a model as distance from road, size of contiguous roadless area, or road density (using moving windows of varying scales). The "distance from road" metric may be more appropriate at finer scales. An avoidance zone of 500 m was documented in Banff (Paquet et al. 1997). Thurber et al. (1994) showed a negative response up to five km from roads in Alaska. In winter, wolves are also attracted to roads for ease of travel (P. Paquet, unpublished data).

Road density becomes the more relevant metric at landscape and regional scales (Mladenoff et al. 1995, Boitani et al. 1997). Studies in Wisconsin, Michigan, Ontario, and Minnesota have shown a strong relationship between road density and the absence of wolves (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989). Wolves generally are not present where the density of roads exceeds 0.58 km/km^2 (Thiel 1985, Jensen et al. 1986, Fuller 1989). Landscape level analysis in Wisconsin, Minnesota, and Michigan found mean road density was much lower in pack territories (0.23 km/km^2 in 80% use area) than in random nonpack areas (0.74) or the region overall (0.71). Road density was the strongest predictor of wolf habitat favorability out of five habitat characteristics and six indices of landscape complexity (Mladenoff et al. 1995). Few areas of use exceeded a road density of >0.45 km/km^2 (Mladenoff et al. 1995). Notably, radio collared packs were not bisected by any major federal or state highway. In Minnesota, densities of roads for the primary range, peripheral range, and disjunct range of wolves were all below a threshold of 0.58 km/km^2.

These results, however, probably do not apply to areas on which public access is restricted. Mech (1989), for example, reported wolves using an area with a road density of 0.76 km/km^2, but it was next to a large, roadless area. He speculated that excessive mortality experienced by wolves in the roaded area was compensated for by individuals that dispersed from the adjacent roadless area. Wolves on Prince of Wales Island, Alaska currently use areas with road densities greater than 0.58 km/km^2. This may reflect the limited options wolves have to relocate when they live on islands or insularized and naturally fragmented landscapes. Road density thresholds in the more open landscapes of the Rockies may differ from those reported in the above studies (Weaver et al. 1996). Topographic effects also influence how road densities influence wolves. For example, in mountainous landscapes roads and usable wolf habitats converge in low elevation valley bottoms. Effective road densities calculated only for valley bottoms differ dramatically from densities calculated using the full areal extent of a wolf pack's home range.

There are several plausible explanations for the absence of wolves in densely roaded areas. Wolves may behaviorally avoid densely roaded areas depending on the type of use the road receives (Thurber et al. 1994). In other instances, their absence may be a direct result of mortality associated with roads (Van Ballenberhe et al. 1975, Mech 1977b, Berg and Kuehn 1982). Wolves are still hunted with minimal regulation in the Rocky Mountains of Canada. Refugia from hunting and trapping constitute less than 10% of B.C. and 5% of Alberta (Hayes and Gunson 1995), and wolf packs in these areas often use adjacent non-refugia lands (Paquet et al. 1996). The effects of road density may therefore vary between the U.S. and Canada due to restrictions on hunting in the U.S..

However, even in areas where killing of wolves is generally prohibited, 90% of mortality is human-caused (Pletscher et al. 1997). Despite legal protection, 80% of known wolf mortality in a Minnesota study was human-caused (30% shot, 12% snared, 11% hit by vehicles, 6% killed by government trappers, and 21% killed by humans in some undetermined manner) (Fuller 1989). Mech (1989) reported 60% of human-caused mortality in a roaded area (even after full protection), whereas human-caused mortality was absent in an adjoining region without roads. On the east side of the central Rockies between 1986 and 1993, human caused mortality was 95% of known wolf death. Thirty-six percent (36%) of mortality was related to roads (Paquet 1993). Though offering only partial protection, parks such as Banff and Glacier have historically played a critical role as sources for recolonization (Boyd et al. 1995).

Wolves in Minnesota are now occupying ranges formerly assumed to be marginal because of prohibitive road densities and high human populations (Mech 1993, Mech 1995). Legal protection and changing human attitudes are cited as the critical factor in the wolf's ability to use areas that have not been wolf habitat for decades. Nonetheless, wolves in Minnesota continue to avoid populated areas, occurring most often where road density and human population are low (Fuller et al. 1992). Dispersers or marginalized individuals may be pushed into suboptimal habitat as more suitable and safe habitat becomes saturated by dominant animals or packs.

Elevation and Topography

Although ecosystem and prey generalists, wolves in the Rocky Mountain region concentrate activities in forested valley bottoms due to the effects of physiography, weather, prey distribution, and prey abundance (Paquet 1993, Paquet et al. 1996, Singleton 1995, and others). The dendritic pattern of forests separated by intervening rock and ice, creates a high degree of natural fragmentation. Steep rock, ice-covered slopes, and deep snow, which are associated with higher elevations, are avoided by wolves and their prey. Wolves respond to movements of their prey, using montane valleys during winter, and increasing their range to subalpine and alpine habitats during summer. Travel routes are usually composed of adjoining habitats or patches of habitat linked by natural linear features (e.g., mountain passes).

Though travel and habitat selection are influenced by availability of prey and location and connectivity of optimal inter-patch travel routes, rugged topography severely limits the number of landscape linkages in the Rocky Mountains. Although wolves are highly vagile, they cannot reach all areas of potential habitat if landscape connectivity is limited. Dispersal also is critical to the persistence of populations in marginal habitat. Data on characteristics of dispersal habitat is limited, but studies in the Rockies have identified topographic "funnels," prey patches, distance

from centers of human development, and low human population density as factors favoring north-south dispersal along the Rockies from Banff to Montana (Boyd et al. 1995). Slope, aspect and elevation were finer-scale constraints on wolf movement within the Banff area (Paquet et al. 1997). In areas such as Minnesota, where larger source populations are found in gentler terrain, effective dispersal may be possible through semi-developed habitat (Mech et al. 1995).

Prey Density

Biological factors relating to food resource availability are the second important group of model attributes. Several studies suggest the main factor limiting wolves where they are present and tolerated by humans is adequate prey density (Fuller et al. 1992). Ungulates such as elk, deer (*O. virginianus and O. hemionus*), moose, and bighorn sheep (*Ovis canadensis*) make up the bulk of the wolf diet (Mech 1970, Fuller 1989), although they may take smaller prey such as snowshoe hares (*Lepus americanus*) and beaver (*Castor canadensis*). Ungulate biomass index (Keith 1983, Fuller 1989), ungulate density, and ungulate species diversity (Boitani et al. 1997) have been significantly correlated with wolf density in some regions. For example, in a review of wolf demographics, prey density was shown to explain 72% of the variation in wolf density (Fuller 1989). A smaller core area, such as Riding Mountain NP (Manitoba), can support a viable wolf population if prey biomass per unit area is high (Fritts and Carbyn 1995). Observed correlations between prey density and wolf distribution may be compared with data from analysis of scat and kill samples.

Although wolves are the most abundant and rapidly-reproducing of the large carnivores in the Rocky Mountains of Alberta, population densities are low in comparison with other carnivore species that use the same range, reflecting the wolf's dependency on ungulate prey species (Keith 1983). Though the diversity of ungulate species within the study region is unparalleled, numbers are limited by the low productivity and rugged topography of the mountainous environment.

Maintaining viable, well-distributed wolf populations for the next 100 years will ultimately depend on maintaining an abundant, stable ungulate population. In southeast Alaska, biologists generally recognize that clear-cut logging of old-growth forest results in reduced populations of Sitka black-tailed deer. Clear-cut logging replaces productive old-growth forest, which is an important deer winter habitat, with even-aged second-growth stands of much lower habitat value (Walmo and Schoen 1980). Although young clearcuts may produce forage that is abundant, typically, it is of poorer nutritional quality and is not available to deer during periods of deep snow.

Within 30 years of clear cutting, regenerating conifers shade out most understory vegetation (Alaback 1982), creating poor habitat conditions for deer (Walmo and Schoen 1980). These stands represent a serious problem for deer because the habitat is very poor in all season, and these poor conditions persist for a very long time (150-200 years) (Alaback 1982, Wallmo and Schoen 1980). Contrasts in vegetation succession between this coastal ecoregion and the Rocky Mountains may limit the generality of these conclusions, however.

Forest fragmentation due to logging may focus wolf predation on specific sites where deer are concentrated and vulnerable, causing declines in deer abundance and population viability (Nelson and Mech 1986, Hebert et al. 1982, Janz 1989, McNay and Voller 1995). Activities such as cross-country skiing or keeping roads snow-free may provide wolves access to refugia

traditionally used by ungulates to avoid predators (Paquet 1993, Paquet et al. 1996). Conversely, wolves may be deprived access to ungulate prey because of human created impediments to movement (e.g., town sites, highways), which results in artificial predator-free zones (Paquet 1993, Paquet et al. 1996).

High prey biomass in biologically-productive matrix lands could compensate for higher rates of human-caused mortality if connectivity is maintained with core areas (Fritts and Carbyn 1995, Haight et al. 1998). However, excessive mortality can cause these prey patches to become wolf population sinks. For example, in areas such as the Banff/Jasper park complex, ungulates concentrate on winter range near human development, leading to high levels of mortality for wolves (Paquet et al. 1997). In the GYE, most ungulate winter range lies outside of core protected areas, with seven of nine elk herds wintering outside the park (Fritts 1990, Fritts and Carbyn 1995). In Glacier National Park (U.S.), the scarcity of ungulate winter range limits wolves to the western edge of the park (Fritts and Carbyn 1995). These wintering areas may play the role of "keystone" habitats if their seasonal availability limits wolf population density (Fritts and Carbyn 1995).

Prey (deer) density was not significant in a model predicting wolf distribution in Michigan and Wisconsin. Recolonizing wolves there may still be at too low a population density to be affected by prey limitations (Mladenoff et al. 1997). This supports the conclusion that limiting resource factors operate in a hierarchical framework and will not correlate well with distribution under all conditions. Data on ungulate prey density can be assembled from records of state and provincial game agencies (e.g. Mladenoff et al. 1995). If unavailable, we can assess ungulate species diversity from range maps and species lists or by the use of surrogates such as tasseled-cap greenness (Crist and Cicone 1984), a metric derived from satellite imagery. As with prey density, sources of data on wolf density and distribution vary between jurisdictions, making regional analysis difficult (Hayes and Gunson 1995).

Vegetation attributes are not strongly correlated with wolf distribution in most studies, except as they relate to prey density. Wolves and elk in the Banff area showed a 90% similarity in cover-type use in both summer and winter (Paquet et al. 1996). Percentage forest was a significant positive factor for Italian wolves (Boitani et al. 1997). Petersen (1995) reviewed data on interspecific interactions for canids in the north-central U.S. and concluded that relative abundance varied in relation to human population density, prey density, and forest cover. Wolves were abundant in forested regions with low human population density, whereas coyotes were abundant in more open landscapes. This regional-scale correlation would not necessarily be evident at finer scales. For example, Yellowstone wolves may be associated with open range favored by elk (Fritts 1990). In Canada, forest cover may reduce mortality from hunting, but trapping mortality remains high (Hayes and Gunson 1995).

Coyote (*Canis latrans*)

The coyote has the highest ecological resilience of any large carnivore (Voight 1987). Although persecuted throughout its range, the species has persisted and expanded its distribution. Despite its relatively secure status, it merits conservation interest due to its effect on prey populations and its interactions with other carnivores (Crooks and Soulé 1999). The species' resilience stems from life history characteristics that were evident but less pronounced in its congeneric the wolf. The expanded distribution of the coyote in the Rockies may be linked to the decline of the wolf and the expansion of livestock industry. The coyote's behavioral plasticity allows it to respond to variation in prey size, distribution, and seasonal availability through variation in pack structure and other social characteristics (Bekoff and Wells 1986).

Coyote social structure may vary from predominantly pairs to packs of varying size. Percentage of the diet composed of larger prey such as mule deer varies with pack size in Jasper NP (Bowen 1982) and the GYE (Bekoff and Wells 1986). Large coyote packs may be more common in protected areas due to greater density of large ungulates such as elk, particularly in the absence of wolves. Social structure may vary seasonally to exploit spatially concentrated (ungulate winter carrion) or dispersed (rodents) resources (Bekoff and Wells 1986). Snow depth can also influence pack size (Gese 1988). As in the wolf, fecundity and other life history characteristics vary in response to human-caused mortality. High dispersal ability increases resiliency. Mean dispersal distances are close to 30 km (Nellis and Keith 1976), but maximum distances are greater than 500 km (Carbyn and Paquet 1986). Dispersal is primarily by juveniles, but is not sex-biased (Bekoff 1982).

Population density of coyotes in the Rocky Mountain region is relatively low when compared with that in the southwestern U.S. (Dixon 1982). This has been attributed to greater snow depth and lower small mammal densities in northern latitudes (Bekoff 1982). Lagomorph species form the bulk of the coyote diet in many areas, with rodents and ungulates (often primarily carrion) also important. Lagomorph species that experience population cycles, such as the snowshoe hare in the boreal forest and the black-tailed jackrabbit (*Lepus californicus*) in the Great Basin, may cause cyclic variation in coyote density (Clark 1972, Todd and Keith 1983). During hare lows, carrion and mice dominate coyote diet in the agricultural/forest transition zone of Alberta (Nellis and Keith 1976)

Habitat attributes likely to be associated with coyote density include predictors of lagomorph habitat quality such as stem density, and data on ungulate abundance, especially ungulate wintering areas. Data on type and abundance of livestock, available from census and agricultural databases, may also be useful.

Snow depth has been shown to have a negative correlation with coyote density (Pyrah 1984, Carbyn 1982). Elevation data may be used as a surrogate, for example in Jasper NP where coyotes are found most often below 1,200 m elevation (Bowen 1982). In landscapes of intermixed forest and open areas, forest cover is positively correlated with coyote distribution (Roy and Dorrance 1985, Gese 1988), and high interspersion of forest and open areas may be optimal (Nellis and Keith 1976). Forest and areas of high topographic complexity provide secure den sites that lessen impacts of human persecution.

Density of other carnivores, particularly wolves, may influence coyote abundance and distribution (Paquet 1991a, 1991b, Paquet 1992). The decline in coyote abundance following wolf reintroduction has illustrated this in Yellowstone (Crabtree and Sheldon 1998). Competition with non-canid carnivores such as the bobcat is less apparent despite dietary overlap. This may be due to differences in hunting strategies between canid searching predators and felid ambush predators (Witmer and DeCalesta 1986). Strength of competitive interactions with wolves may vary with prey density, forest cover, and human population density (Petersen 1995). Humans create coyote habitat at regional and local scales through persecution of wolves (Petersen 1995, Crabtree and Sheldon 1998), and through creation of forest openings such as clearcuts (Witmer and DeCalesta 1986). In the northern U.S. and southern Canada, the wolf often dominates in forested areas and the coyote in the forest/agricultural transition zone. The Canadian part of our study area is thus a transition zone between the two species due to vegetation type and snow depth (Carbyn 1982).

Distribution of coyotes relative to wolves may range from regionally parapatric, such as in the northern boreal forest and in the eastern U.S. (Harrison et al. 1989, Petersen 1995), to regionally sympatric and locally parapatric (Carbyn 1982, Petersen 1995), to locally sympatric (Paquet 1991a). A good predictor of sympatry may be the prey species used by wolves. In western North America wolves and coyotes overlap when the primary prey of wolves is large enough to support scavenging by coyotes. In Riding Mountain NP and Yellowstone NP, wolves are an important source of coyote mortality, but also benefit coyotes who scavenge from wolf kills (Paquet 1991a, Crabtree and Sheldon 1998). In Yellowstone National Park, where coyote abundance has dropped nearly half since wolf reintroduction, coyotes establish territories in areas near roads that wolves avoid (Crabtree and Sheldon 1998). This resembles the use of such areas by black bears to avoid grizzly bears (Kasworm and Manley 1990). Smaller carnivore species such as mustelids and foxes may increase as wolves limit coyote numbers and rodent prey becomes more readily available.

Coyote mortality rates are high in most populations due to human exploitation (Pyrah 1984). Mortality rates of 40-50% for adults and 70-80% for pups are common (Nellis and Keith 1976, Pyrah 1984). Nellis and Keith (1976) estimate that a stable population requires pup mortality rates of less than 65%. As in grizzly bears, human-caused mortality varies with habitat as lower habitat quality increases foraging movement requirements and vulnerability (Nellis and Keith 1976).

Although extensive research on coyotes has occurred in connection with predator-control efforts, little work has been devoted to developing habitat models. A study in the Bow Valley of Banff NP used radio telemetry data to analyze coyote habitat selection (Gibeau 1993a). Nonspatial simulation models developed for assessing predator-control strategies have been criticized for not incorporating habitat quality or dispersal dynamics (Connolly 1978). Although the habitat breadth of the species may reduce the strength of habitat correlations, simple approaches incorporating landscape-level metrics of forest cover may be useful (Gese 1988). Incorporating coyote abundance into multispecies models is necessary due to the strength of interactions with other carnivore species (Crooks and Soulé 1999).

<u>Mountain lion (*Puma concolor*)</u>

The mountain lion has relatively high ecological resilience due to its behavioral plasticity and generalist habitat associations (Weaver et al. 1996). Although still widely distributed throughout the Rocky Mountain region, its status is not secure in all areas. Southern Alberta is near the northern limit of the species' range (Dixon 1982). Mountain lions can occur at all elevations but prefer mixed wood and coniferous vegetation. Mountain lions are closely tied to cervids as their main prey so that conserving mountain lions often amounts to conserving cervid populations and habitats. Overall, the protection, management, and enhancement of prey habitat and populations are a major sustaining factors for mountain lion populations.

Limiting factors may include changes in climate, prey composition and abundance, vegetation or terrain that lessen the competitive advantages of a stalking predator (Ross and Jalkotzy 1992). In telemetry studies in Arizona and Utah, where home range sizes are similar to those in Alberta, mountain lions consistently concentrated their activities in areas where road densities were lower than average for the region. They crossed improved dirt roads and hard-surfaced roads less frequently than unimproved roads. "Established residents and young mountain lion that ultimately became residents selected home areas with road densities lower than the study area average, no recent timber sales, and few or no sites of human residence." (Van Dyke et al. 1986:95). Annual mortality in southern Alberta in 1992, primarily from hunting, was low compared with historical levels and the population was reported to be increasing (Ross and Jalkotzy 1992)**.** However, hunting regulations in Alberta have since been liberalized, and current population trajectory is unknown (I. Ross, pers. comm.). Populations in southeastern B.C. were reported to be declining in 1982 (Dixon 1982), but consistently high harvest levels in the East Kootenay region may contradict this conclusion. Weaver et al. (1996) estimated a lifetime reproductive output for the cougar of three to four female offspring per adult female, and concluded that populations often cannot sustain levels of adult mortality much above 10%, lower than that occurring in many jurisdictions in the region (Weaver et al. 1996). Data from southwestern Alberta suggest a somewhat higher average lifetime reproductive output of five to six offspring per adult female (I. Ross, pers. comm.).

Mule deer and elk are usually the most available, and hence the most important prey species for cougar in the Rocky Mountain region (Hornocker 1970, Seidensticker et al. 1973, Koehler and Hornocker 1991), although moose may be important for males (I. Ross, pers. comm.). Prey habitat is primarily open woodland and forest, so interspersion and forest edge may be positively correlated with mountain lion abundance (Dixon 1982). Correlation between cervid biomass and mountain lion density is evident in some areas (e.g., Lindzey et al. 1994), but is less well-documented than in the wolf (Keith 1983, Fuller 1989). Estimates of suitable habitat derived from coarse-scale vegetation types have been weakly correlated with levels of livestock depredation by mountain lions in California (Torres et al. 1996).

The "vegetation-topography/prey numbers-vulnerability" hypothesis predicts optimal habitat to depend on vegetation and terrain (Seidensticker et al. 1973). Mixed conifer types in steep areas may be ideal in that they provide both forage for prey and vegetative or topographic stalking cover (Hornocker 1970, Logan and Irwin 1985). A strong seasonal component to habitat selection is evident in the Rocky Mountain region. In Idaho, mountain lions preferred rocky, open, southwest aspects and drier Douglas-fir (*Pseudotsuga menziesii*) forest types in winter,

while selecting for mesic Engelmann spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*) forest without rocky areas in summer (Dixon 1982, Koehler and Hornocker 1991). A habitat suitability model is currently being developed for cougars in southwestern Alberta. Terrain ruggedness, a function of aspect variability and slope, was found to be a more significant predictor of cougar habitat than were vegetation variables (I. Ross, pers. comm.).

Logging may lower habitat value by decreasing stalking cover and increasing human access. Although resident animals avoid semi-developed areas, transient lions may use them, especially nocturnally (Van Dyke et al. 1986, Beier 1993, 1995). Mortality rates from roadkill and other sources may be high, however (Beier 1993, 1995). Degradation of habitat resulting from residential developments, recreational developments, and road building for access to residential, recreational and industrial activities is a serious threat to western mountain lions (M. Jalkotzy pers. comm.).

The mountain lion's high mobility increases ecological resilience. Dispersal averages 80 km, or five to seven home range diameters (HRD) (Weaver et al. 1996). Dispersal is primarily by males, but barriers to juvenile dispersal affect females indirectly by disrupting population dynamics and skewing sex ratios (Van Dyke et al. 1986, Beier 1995). Demographic trends are most sensitive to levels of adult female mortality (Weaver et al. 1996).

 Beier (1993) developed a pseudospatial model to predict the viability of mountain lion populations inhabiting fragmented habitat in coastal southern California. He used habitat maps and telemetry data to estimate the population size residing in each of the semi-disjunct islands of undeveloped habitat and potential immigration rates between them. This information was used to parameterize an age-structured Leslie matrix to derive estimates of population viability. The model showed that immigration increases persistence times of small populations.

Mountain lion habitat was relatively easy to identify in the urbanizing landscape of Beier's study area. Evaluating the relative habitat value of different natural vegetation types in the Rocky Mountain region may be more difficult. An approach that combines estimates of ungulate biomass with topographic roughness and snow depth may be useful. Dynamic modeling that incorporates data on dispersal and human-associated mortality will be useful in areas where these factors may be limiting: the fragmented habitat of the forest/agricultural fringe and areas of high road density.

As the largest extant carnivore in many areas of the region, the mountain lion may interact strongly with other predators and prey species. Densities of large ungulate prey are more likely to be controlled by forage and weather than by mountain lion predation, so exploitation competition may be less important than interference competition (Hornocker 1970). In Yellowstone National Park and Glacier National Park (Montana), black and grizzly bears often displace cougars from cougar-killed ungulate carcasses (Murphy et al. 1998)

Mountain lions compete directly with wolves and are occasionally killed by wolves and coyotes (Paquet 1993, D. Boyd pers. comm., M. Hornocker pers. comm., I. Ross pers. comm.). Some mountain lion population increases may be related to wolf extirpations (I. Ross pers. comm., M. Hornocker pers. comm.). Similarly, wolf recovery may be reflected in suppressed mountain lion numbers. Researchers have also documented usurpation of mountain lion kills by wolves, although the distinct hunting strategies of the two species may reduce competition (Weaver et al. 1996). Mountain lion populations in good habitat may demonstrate moderately rapid recovery from depression owing largely to high juvenile survival (Ross and Jalkotzy 1992).

Sweitzer et al. (1997) attributed the near-extirpation of porcupines from a study area in Nevada to mountain lion predation. Their hypothesis links historic livestock grazing to an increased population of primary prey (mule deer). The resulting increase in mountain lion depressed secondary prey populations. The generality of this conclusion may be limited, however, because regional-scale studies of mountain lion population trends in other areas of the west (e.g., Torres et al. 1996) have been inconclusive.

Lynx (*Felis lynx*)

Of the three wild felids that inhabit the U.S. Rockies, the lynx has aroused the most conservation concern. In contrast, the bobcat is at the edge of its range in the Canadian Rockies and attracts more attention there. In the U.S., the lynx has been the focus of a protracted legal battle that has recently led to a listing as threatened under the Endangered Species Act (National Wildlife Federation 1991). In Canada, lynx form a major part of trapping harvest, generally ranking second only to martens in B.C. depending on pelt price and demand (Hatler 1988). Lynx populations in northern B.C. are considered relatively secure, but trapping harvest is low and declining near the U.S. border (B.C. Wildlife Branch, unpublished data). Conservation assessments in the U.S. that base population persistence on dispersal from Canada may thus untenable due to increasing human settlement, roads, and habitat alteration in the transborder region.

The vulnerable status of lynx populations in the southern part of their range (southern Canada and the northern U.S.) is due to their obligate association with their major prey, the snowshoe hare. Although they take other small prey such as grouse and squirrels, hares make up the bulk of the diet. For example, hares constituted 91% of prey biomass in Alberta (Brand et al. 1976). Hare populations undergo cyclical fluctuations in the northern part of their range, the extensive boreal forest of northern Canada and Alaska. Populations in the south do not show such dramatic cycles, instead remaining stable at densities typical of the low point of the northern cycle (Koehler and Aubry 1994). This may be due to the fragmented distribution of boreal forest types in the south, and the greater diversity of lagomorph species and hare predators (Wolff 1980). Facultative predators on hares such as coyotes, red fox, bobcat, and raptors may indirectly keep populations of the lynx, an obligate hare predator, at low levels (Wolff 1980).

A gradient of decreasing habitat suitability with decreasing latitude is established as areas of high-elevation forest become smaller and more fragmented and prey density declines. Although the species ranges into Colorado, the U.S. lynx populations with the greatest prospects for viability are in Montana, Idaho, and Washington (Koehler and Aubry 1994). These populations show densities of 2.3 adults/100km^2, equivalent to those at the low point of the northern cycle (Koehler 1990, Koehler and Aubry 1994). The naturally low density of southern lynx populations makes them more vulnerable to the effects of trapping and forest management (Koehler and Aubry 1994).

The periodic irruptions associated with the high points of cycles in the boreal forest may be important as a source of dispersers for augmenting southern populations (Mech 1980, Koehler and Aubry 1994). This would make maintenance of regional connectivity important. During these irruptions, long-distance dispersal of 300-500 km has been recorded (Mech 1977a, Brainerd 1985).

The strong association of lynx with a single prey species might be expected to simplify the development of habitat models. However, 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. While optimal foraging habitat is found in early-seral stands, mature forest is required for denning (Koehler and Britell 1990). Lynx thus depend on two forest age classes lying at opposite ends of the sere. Intermediate-age stands are used for traveling, but are of lesser importance (Koehler and Aubry 1994).

Several studies have shown that snowshoe hare densities peak in stands that provide dense cover and large quantities of browse that is accessible above the snow pack (Koehler and Britell 1990). These qualities are found in 15-30 year old conifer stands in the U.S., and in stands up to 40 years old in the north (Koehler and Aubry 1994). Hares occur at low densities in the southern part of their range. Predation may restrict them to the highest quality habitat, and hares typically occupy only 10% of suitable habitat (Koehler and Aubry 1994). However, habitat attributes associated with hare density explain only part of lynx foraging success. Prey vulnerability is mediated by factors such as stalking cover.

High quality denning habitat is limited to mature forest, which provides the coarse woody debris (CWD) needed for thermal cover and protection for the young (Koehler and Aubry 1994). Lynx show high variability in home range size and may concentrate winter use in activity centers (Nellis et al. 1972, Koehler 1990). These "keystone habitats" may be a limiting resource, and habitat models focusing on their distribution may be useful.

In moving between denning and foraging habitats, lynx select areas of high canopy closure and avoid open areas (Koehler 1990). Openings greater than 100 m in width may disrupt movement patterns (Koehler and Britell 1990). Coarse-scale connectivity may be especially important for southern populations that inhabit fragmented patches of boreal habitat. At the landscape level, we might expect lynx habitat requirements to include optimal interspersion of foraging and denning habitat. This could be created by an uneven-aged mosaic of early-seral and mature forest (Koehler and Britell 1990). The patchy fire regimes of certain high-elevation forest types creates such a mosaic, while retaining high levels of coarse woody debris (CWD) (Agee 1993).

Timber harvest techniques have been proposed as an alternate method of creating such a mosaic (Koehler and Britell 1990). However, the effects of logging on lynx habitat remains a subject of debate. The recommended methods, such as dispersed cutblocks, contradict recommendations for maintaining area-sensitive interior-habitat specialists such as the marten (Hargis and Bissonette 1997). In addition, mature forest denning habitat may already be limiting in western forests subject to timber harvest. Further harvest of older stands, even if it led to increasing prey densities, might have negative effects on lynx populations.

The continuing decline in lynx distribution in the western U.S. and southern Canada, despite the presence of early-seral prey habitat, suggests that higher-level constraints may be limiting population viability. Conservation organizations cite the increase in road access into high-elevation areas due to logging and other development as a problem (National Wildlife Federation 1991). Direct mortality from roadkill was the major cause of low survival for reintroduced lynx in New York state (Brocke et al. 1991). Trapping mortality can be high, especially for males and during irruptions when much of the population is nomadic (Carbyn and Patriquin 1983, Koehler and Aubry 1994). High pelt prices in the 1970's and 1980's reportedly resulted in increased trapping activity in the U.S. (Skatrud 1997). The higher viability of lynx populations in B.C. compared with Alberta may be due to the spatial refugia from trapping provided by mountainous areas (Hatler 1988). Refugia areas must be of relatively large size, and it has been suggested that an area the size of Riding Mountain NP (3000 km^2) is insufficient to maintain long-term viability (Carbyn and Patriquin 1983). Roads may increase interspecific competition in winter by allowing coyotes and bobcats to access areas of deep snow (Koehler and Aubry 1994).

Summary of models

Vegetation attributes available from remotely-sensed imagery may be useful in predicting lynx distribution. At a minimum, we can delineate the extent of coniferous forest, and more detailed information on forest type would be useful. For example, Engelmann spruce, subalpine fir, lodgepole pine, and aspen forest types were associated with lynx in Washington (Koehler 1990). Aspen forests may be marginal habitat in winter, however, due to low cover values (Wolfe et al. 1982).

Stand age or size class will also be a major attribute where data are available. Foraging habitat is associated with 15-40 year old stands in the Rocky Mountains (Koehler and Aubry 1994), but density and shrub cover are also important variables, as sparse stands rank as poor hare habitat (Wolfe et al. 1982). Denning habitat is associated with stands greater than 200 years old in eastern Washington (Koehler 1990). Data on structural attributes such as CWD are difficult to obtain from remotely-sensed imagery. The most likely surrogate is stand age/size, in interaction with forest type.

The level of human disturbance can be modeled as distance from road or road density (Brocke et al. 1991). We can measure proximity to foraging habitat as distance to young sere or as cover-type interspersion. However, the appropriate scale of analysis for deriving landscape-level metrics is unclear. Minimum usable size for mature forest stands is at least one ha (Koehler and Britell 1990).

Other coarse-scale variables may also be useful. Lynx have strong association with high elevation areas (more than 1463 m in Washington) (Koehler 1990). High-elevation areas of low topographic relief (e.g., plateaus) may be especially important (Koehler and Aubry 1994). Land use data, such as the distribution of private lands, may aid in mapping mortality risks (Brocke et al. 1991).

Legal battles over ESA listing have helped prompt the development of several habitat management strategies by private companies (Roloff 1998) and agencies (Washington Department of Natural Resources (DNR) 1996). Plans for reintroduction of lynx into Idaho and Colorado have also highlighted the lack of good habitat models for the species (Seidel et al. 1997). The controversy surrounding habitat management for the lynx highlights the complex interaction of limiting factors at multiple scales. ESA listing is likely to focus further attention on these issues.

Bobcat (*Felis rufus*)

The status of the bobcat is generally considered more secure than that of its congeneric, the lynx. However, in recent years increased levels of exploitation due to restrictions on trade in other spotted cat furs have led to population declines in some areas of the western U.S. (Rolley 1987). Requirements for population monitoring under the Convention on International Trade in Endangered Species (CITES) have led to more research on the species, but uncertainty remains as to the reliability of current population estimates based on trapping data (Gluesing et al. 1986). Incidental and illegal trapping mortality are often high, and the bobcat's relatively low reproductive output makes the species vulnerable to overexploitation (Rolley 1987, Knick 1990).

The species distribution has expanded northward in Canada, while contracting in parts of eastern and midwestern U.S. due to intensive land clearing (McCord and Cardoza 1982). Like the coyote, the bobcat does well in the forest/agricultural transition zone and may benefit during the initial stages of forest fragmentation at the expense of more area-sensitive carnivores. Anthropogenic landscape change may be helping the expansion of the bobcat's range at the expense of lynx. However, the bobcat may be near the climatic limit of its range in the Canadian Rockies due to its poor morphological adaptations to hunting in snow and a higher lower-critical temperature than the lynx (Major and Sherburne 1987).

Although well distributed in the Rocky Mountain region, bobcat population density is lower there than in the more productive habitats of the southeastern U.S. and California. Home range size averaged 200 km in males and 65 km in females in southeastern B.C. (Apps 1996). Northern boreal forest generally has lower prey densities than do landscapes with interspersed cover and openings (Fuller et al. 1985). For these reasons, the ability of northern bobcat populations to recover from trapping may be lower than in the southern U.S. (Rolley 1987). The species therefore merits attention in its own right and for its influence on more threatened carnivores. In addition, populations inhabiting the edge of a species range, such as bobcat in Canada and lynx in the U.S., are important for the maintenance of genetic diversity.

Lagomorphs, such as the black-tailed jackrabbit, cottontail (*Sylvilagus* spp.), and snowshoe hare, often form the bulk of the bobcat's diet. As was true with the lynx, bobcat populations may cycle with lagomorph densities (Knick 1990). During prey lows, habitats associated with lagomorph aggregations are key areas (Knick 1990).

However, the bobcat's diet is more diverse than that of the lynx, limiting the influence of prey cycles. In southeastern B.C., red squirrels (*Tamiasciurus hudsonicus*) were the most important prey, followed by ungulates, microtine rodents, and snowshoe hares (Apps 1996). Although their lagomorph prey prefers early-seral habitats, alternate prey such as deer and microtines are found in a variety of habitats. Deer are generally a more important resource in montane forest (Koehler and Hornocker 1991) than in lower-elevation Great Basin habitats (Knick 1990).

As in the lynx, bobcat demographics are most sensitive to adult survival, whereas juvenile survival may vary widely (Crowe 1975, Gluesing et al. 1986). Trapping mortality on juveniles may not be additive, however, and populations may be unable to compensate with increased reproductive output (Knick 1990). Adult survival in unexploited populations is high, but may be as low as 20% where trapping is intensive (Fuller et al. 1985). Trapped populations may be primarily composed of non-reproductive yearlings and may be sustained by immigration from

unexploited areas (Knick 1990).

Bobcats, like lynx, become increasingly nomadic during periods of prey scarcity, and are exposed to increased human-associated mortality. Dispersal during these prey lows may dominate population dynamics in sink habitats (Knick 1990). Dispersal distances average 20-30 km (seven HRD's)(Knick 1990), but may reach 100 km during prey lows. Dispersal is primarily by juvenile males (Apps 1996).

Habitat components

Because the bobcat is a habitat generalist, the explanatory power of habitat variables may be low (Litvaitis et al. 1986). As in the lynx, we can identify the three elements of foraging, denning, and travel habitat. Foraging habitat is often associated with dense understory. Lagomorph habitat, in particular, can be correlated with stem density (Litvaitis et al. 1986). Overstory cover is also important. Canopy cover greater than 52%, associated with Douglas-fir, juniper, and riparian forest types, was selected for in Montana (Knowles 1985). In southeastern B.C., bobcats selected mature, multi-storied forest stands of Douglas-fir in winter (Apps 1996).

Stalking cover is associated with rocky or shrubby areas (Knowles 1985, Witmer and DeCalesta 1986). Snow condition limits winter foraging, leading to strong seasonality in habitat selection in northern regions. In winter, rocky open areas with south to southwesterly aspect are selected for their low snow accumulation (Apps 1996). Conifer and mixed stands are preferred over deciduous stands (Fuller et al. 1985). In contrast, summer selection is often for deciduous areas (Fuller et al. 1985, Knowles 1985). Dense, lowland conifer sites may be important throughout the year for their high lagomorph density, stalking cover, and high snow-intercept values (Fuller et al. 1985, Koehler and Hornocker 1991)

Requirements for denning habitat are less well known than for lynx. Rocky outcrops and other areas with high topographic diversity are important and coarse woody debris (CWD) may also be associated with dens. Unlike canids, bobcats are "single prey loaders," and they do not regurgitate food for their young. Interspersion of denning and foraging habitat is therefore important for females with young, especially when they are forced to switch to smaller prey during lagomorph population lows (Knowles 1985). We could assess amount and interspersion of forest versus open habitats in GIS with a "moving-window" analysis of canopy closure. In a similar approach, Apps (1996) used discriminant function analysis of winter habitat selection to develop a landscape-level predictive model with a landscape size of 75 km^2.

Knick (1990) developed a spatial model to predict the persistence of bobcat populations in Idaho. The model, like early models for the northern spotted owl (Lamberson et al. 1992), was not habitat based, but could be used to estimate general reserve design criteria such as the critical size of habitat clusters. Model results suggested a viability threshold at trapping mortality levels of 35%. No-trapping refugia needed to contain at least 3-5 core territories and 11-13 buffer territories to protect populations. This would be equivalent to about 1000 km^2 in the Rocky Mountain region (Knick 1990). Buffer areas are particularly important during prey lows, when animals forage over greater areas. The species' relatively short dispersal distances suggest the need for multiple refugia (Knick 1990). In our analysis, we will use the size of contiguous roadless areas or areas with low road density to assess the adequacy and distribution of current refugia.

Interspecific interactions with other felid species may be important. Although mountain lion kills may serve as a food source (Gashwiler et al. 1960), mortality at food caches from mountain lions is also evident (Koehler and Hornocker 1991). Winter access along roads may increase competition with lynx in human-altered habitats (Koehler and Aubry 1994). Interspecific interaction with non-felid carnivores is generally weaker (Witmer and DeCalesta 1986), although coyotes may be a predator (Knick 1990). The greatest potential for interspecific competition occurs in winter, due to increased overlap of foraging areas (Major and Sherburne 1987, Koehler and Hornocker 1991).

Wolverine (*Gulo gulo*)

The wolverine is often characterized as a wilderness species whose persistence is linked to the presence of large areas of low human population density. However, until recently almost no data were available on more specific habitat requirements. The current knowledge base derives in a large part from five field studies (Banci 1987, Copeland 1996, Gardner 1985, Hornocker and Hash 1981, and Magoun 1987), two of which were conducted in the Rockies (Hornocker and Hash 1981, Copeland 1996).

As a result of the dependence of the wolverine on temporally variable and unpredictable food resources such as ungulate carrion, it has home ranges which are much larger than those of other carnivores of similar size. Average home range size for male wolverine in Idaho was found to exceed 1500 km^2 (Copeland 1996). Dependence on carrion may link the viability of wolverine populations to that of other carnivores such as wolves, which we have extirpated from large areas of the west. Wolf poisoning campaigns in some areas have eradicated wolverine (Banci 1994). However, wolverine have persisted in the lower 48 states in the absence of wolves.

Demographic potential is low, with females first producing offspring at around three years of age and producing less than one kit per year until death at six to eight years (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 seven to eight percent, a rate lower than that documented in most studies of trapping mortality (Gardner 1985, Banci 1994, Weaver et al. 1996).

Long-range dispersal abilities (more than 200 km in Idaho (Copeland 1996)) may promote the persistence of wolverine populations. Wolverine populations in southern British Columbia may be connected by dispersal with those in Montana and Wyoming (Weaver et al. 1996).

The wolverine shows more generalized use of open areas and a wider variety of vegetation types than the marten and fisher (Banci 1994, Copeland 1996). The fossil record shows that pre-settlement distribution included lowland environments (Copeland 1996), and extended as far south as Arizona and New Mexico (Banci 1994). Present distribution of the wolverine, like that of the grizzly bear, may therefore be primarily related to which regions escaped human settlement. Conservation requirements for this species may show more parallels with those of the grizzly bear than with those of more closely related mesocarnivores. However, our low level of knowledge about the species makes ruling out more specific habitat requirements difficult. Extrapolation of results from a few study areas to the regional scale may be difficult.

Hornocker and Hash (1981) found that most of their telemetry locations for wolverine were from large areas of medium or scattered mature timber. Rocky areas were used less, and young, dense timber least. Subalpine fir forest types and higher elevation areas were selected for in summer. Wolverine may select coniferous forest in winter (Banci 1987), while avoiding these types in summer (Whitman et al. 1986). Differential seasonal use of elevation zones and forest types may be due to availability of carrion in ungulate wintering areas, summer availability of rodent prey in alpine habitats, avoidance of thermal extremes, or avoidance of humans (Copeland 1996). Large and diverse ungulate populations (elk, mule deer, white-tailed deer, moose, mountain goat (*Oreamnos americanus*), and mountain sheep in this area) are thought to benefit wolverine populations (Van Zyll de Jong 1975, Hornocker and Hash 1981).

A five-year field study of wolverine in central Idaho provides the best data on habitat associations in our region (Copeland 1996). Wolverine strongly preferred rocky alpine habitats in summer, but avoided them in winter. They selected montane forest, especially Douglas-fir, in winter, whereas lodgepole pine stands were the most heavily used forest type in summer. Ponderosa pine (*Pinus ponderosa*) and shrub/grass types saw little use in all seasons.

Natal denning sites were found in remote alpine cirques where deep snow lingered into spring. We could characterize these as rocky sites less than 100 m in width containing large boulder talus (greater than two m in size) on north to northeasterly aspects at elevations greater than 2,500 m. Since females must leave their kits for lengthy foraging trips, natal den sites secure from disturbance by predators or humans are chosen. Maternal dens were placed in talus or woody debris. Adult rest sites, unlike those of martens and fishers, were not associated with specific habitats or structural elements.

Long-distance movements to revisit scattered foraging sites (such as ungulate calving areas and rodent habitations) suggest that individual wolverine hold a "cognitive map" or spatial memory of an extensive gleaning network (Copeland 1996). In contrast to the wolverine's reputation as a solitary animal, the Idaho study found that offspring commonly forage with parents and siblings for extended periods, which may familiarize them with gleaning networks. Wolverine are likely to encounter other carnivores while feeding on carrion, and predation by larger carnivores accounted for at least 42% of mortalities for wolverine in Idaho (Boles 1977, Copeland 1996). Although rodents (marmots [*Marmota* spp.] and sciurids) were seasonally important, carrion of elk and mule deer was the most important food resource (Copeland 1996). It is estimated that one ungulate is wounded for every four taken by hunters, and carrion associated with the fall hunt is a seasonally important food resource.

Unlike in previous studies (Hornocker and Hash 1981), wolverine in Idaho readily crossed open areas. Sex-biased dispersal was evident, with all long-range dispersers being males of at least two years of age. The large home range sizes of Idaho wolverine (mean of 384 km^2 in females, 1522 km^2 in males) may indicate that food resources are more widely dispersed there than in Canada and Alaska, or that a critical resource, such as natal den sites, is limited. Regional-scale population processes may explain why much apparently suitable habitat in Canada and the western U.S. is unoccupied and other areas with relatively high levels of human disturbance (such as central B.C.) retain wolverine (Banci 1994). In areas where wolverine are legally killed, trapping is often over half the annual mortality. Although trapping is prohibited in the U.S. outside of Montana and Alaska, incidental trapping mortality is important there, as well as in southern B.C.. It is possible that U.S. populations are dependent on immigration from Canada, and the low or declining populations in southern B.C. and Alberta are thus of regional importance (V. Banci, pers. comm.). These trends are occurring despite a decline in trapping, and could also be related to logging, oil and gas exploration, and other human development. The southern interior of B.C. is the fastest growing area in the province, with large increases in human settlement, recreational facilities, and backcountry use.

Loss of ungulate winter range to development and reduction in numbers of spawning salmon have affected wolverine food resources in some regions. Landscape level diversity, such as between dry and wet forest types in the Canadian Rockies, allows the wolverine to survive on temporally variable food resources. However, as with the grizzly bear, seasonal movements to use variable resources make wolverine vulnerable to human-caused landscape fragmentation.

The importance of spatial refugia is demonstrated by the role of the Canadian parks in sustaining wolverine populations in southern Alberta, a similar role to that of Yellowstone National Park (Buskirk in press). Connectivity between the GYE and remnant Colorado wolverine populations, as well as between the Canadian Rockies and U.S. populations in Idaho and the Cascades may be lost if current trends continue. Although male wolverine may successfully cross developed habitat, dispersal requirements for females with young are more habitat-specific. In addition, subadult females rarely disperse because, unlike male offspring, they are tolerated near their natal home ranges (Banci 1994).

Summary of models

As the above studies show, conservation planning for wolverine populations requires a regional-scale perspective. We can use data on road density, human population density and land use to define core areas with minimal human disturbance. Alpine areas and subalpine spruce/fir forest types with low road density that may be too small to function as core areas can be delineated as potential landscape linkages between populations. Areas of high interspersion of alpine cirques with montane forest may have enhanced habitat value.

Data on ungulate prey diversity and abundance may be available from state and provincial game agencies, and can be used to predict carrion availability. Distribution of large carnivores, especially wolves, is a factor promoting carrion availability, but also increasing competition. Little overlap was evident between home ranges of cougar and wolverine in Idaho, suggesting interspecific competition (J. Copeland, pers. comm.) or partitioning due to topography. Ungulate wintering areas that are remote from human settlement may be rare, especially in the U.S.

Potential natal denning habitat can be identified in GIS by delineating areas of the appropriate elevation (> 2,500 m), soil type (large boulder talus), and aspect (north to northeast) as potential denning habitat (Hart et al. 1997). These areas may be at risk from disturbance by winter recreation such as heli-skiing (Copeland 1996). However, extrapolation of these requirements to other areas may be problematic.

A spatially-explicit conservation plan for the wolverine is likely to show a high degree of overlap with that designed for the grizzly bear due to similar large-area requirements and low tolerance for human development. The greater dispersal abilities of the wolverine, and its lower risk of mortality from humans during dispersal, may allow it to remain more broadly distributed than the grizzly. Substantial uncertainties remain about which habitat and mortality factors are responsible for the decline of the wolverine in the Rockies. However, it should be possible to identify critical areas where steps such as the creation of refugia from trapping, the reintroduction of wolves, and protection of roadless areas from development will have the greatest long-term benefit for the species.

Fisher (*Martes pennanti*)

Although not as extreme as with the wolverine, the scarcity of field data from fisher populations in the west has until recently slowed the development of habitat models. The HSI model for the fisher (Allen 1983) is based on the rationale that the limiting habitat resource for fishers is overhead cover during winter and early spring, as it affects prey availability and foraging efficiency. The maximum HSI index value occurs when tree canopy closure is above 75%, mean dbh of overstory trees is more than 40 cm, three or more species compose the tree canopy, and 10-50% of the overstory is deciduous.

Thomasma et al. (1991, 1994) tested the fisher HSI model with snow tracking data from Michigan. They found that although the composite HSI score was a significant predictor of fisher habitat use, only two of the four component variables (mean dbh of overstory trees and percentage of overstory deciduous) were significant in the multivariate model. In addition, the shape of the response function was not monotonically increasing, but multimodal.

Although the availability of coniferous forest for winter cover may be a limiting factor in areas of deep snow, optimal habitat for fisher, in contrast to marten, may be found in the transitional mixed deciduous/conifer forest types rather than in coniferous boreal forest (Arthur et al. 1989). Berg and Kuehn (1994) offer evidence from trapping records that succession of Minnesota landscapes from mixed conifer/aspen to predominantly conifer has favored marten over fisher. This may weaken the validity of the HSI model. Conifer-dominated (> 75%) forest types were sub-optimal in a study area in Maine (Arthur et al. 1989). Mature aspen were important for den sites. High diversity and interspersion of stand types may increase habitat value by promoting a diverse prey base. In Maine, fishers often rested in conifer stands and foraged in mixed stands during summer. However, they showed the opposite pattern during winter, reflecting increased foraging for snowshoe hare found in conifer stands. They avoided open areas on the stand level, but landscapes containing small openings associated with human settlement supported fishers, as forested areas still predominated as the landscape matrix. The finer grain and lower intensity of human disturbance in these forests, and characteristics of regenerating mixed forests in the eastern U.S., may explain the greater tolerance of eastern fisher populations to human-caused landscape change.

Although most fisher research has occurred in the northeastern U.S., several studies have been completed in the Rockies. In Montana, reintroduced fishers were found to prefer low-elevation mesic forests, especially riparian areas, and dense young mixed-conifer stands (Roy 1991, Heinemeyer 1993). Fishers in Idaho also preferred riparian areas in all seasons (Jones and Garton 1994). Habitat selection by forest age class, however, varied with season. Mature and old-growth stands were selected in summer, whereas young and old-growth stands were used in winter (Jones and Garton 1994**).**

A recent study in B.C. found no consistent landscape-level selection for forest type by fishers, either seasonally or throughout the year (Weir and Harestad 1997). This study was conducted on transplanted fishers, and resident populations may show different habitat associations. Dispersing fishers showed avoidance of early-seral stands, perhaps reflecting selection for high levels of canopy closure. Cavities in large cottonwoods were important for maternal dens, and rest sites were often found in large spruce (> 50cm dbh).

Fishers in Manitoba preferred to travel on coniferous ridges during winter, but they preferred areas of consolidated snow (hare and other trails) during heavy snow conditions (Raine 1983). Fisher distribution in California was correlated with elevation (Krohn et al. 1997), but changes in forest composition that covary with elevation may be more robust predictors than elevation itself (Carroll et al. 1999).

In northwestern California, fisher detection rates were correlated with dbh of hardwoods at the patch level, canopy closure, percent conifer, and tree dbh at the landscape level, and precipitation at the regional level (Carroll et al. 1999). Fisher detection rates were highest at sites with large hardwoods in landscapes of dense, mixed hardwood/conifer forests. New survey data were collected and used to validate the model.

Dark (1997) also found that canopy closure showed a significant positive correlation with fisher distribution in a study area in interior northern California. High canopy closure is associated with riparian areas in these more xeric interior forests. Relationships between fisher detections and road density and landscape pattern attributes were difficult to interpret. For example, fishers were positively correlated with low-use road density, perhaps due to the placement of logging roads in more heavily-forested areas.

Klug (1996), also in northern California, found positive stand level correlations between fisher detection rates and stand-level attributes such as hardwood dbh, percent basal area in hardwoods, canopy closure, and volume of logs, and a negative correlation with basal area of conifers between 52 and 90 cm. The strongest correlations, however, were with regional-scale factors such as elevation and distance to the ocean. This strong regional-scale component, which was also evident in the model of Carroll et al. (1999), may limit the predictive power of such models when applied to other regions. Fisher detections were also correlated with increasing stand size (up to 100 ha) and decreasing insularity in forests of northwestern California (Rosenberg and Raphael 1986).

The evidence for low or declining fisher populations in the Rockies has prompted several efforts at devising a regional conservation strategy for the species. Banci (1989) summarized the existing data in B.C.. Habitat diversity, as represented by riparian areas, small openings and other ecotones, was judged important to fishers. She advocated untrapped reserves or spatial refugia in areas open to trapping. Because extensive salvage logging and pulping of aspen stands may be linked to the decline of fishers in southern B.C., we should preserve areas of mixed coniferous and deciduous stands as important habitat.

Heinemeyer and Jones (1994) performed a management assessment for the western U.S., and advocated a multi-scale approach to designing a conservation strategy for the species. Boundaries of suitable forest habitat would be mapped at the scale of the physiographic province (for example, the northern Rockies) using cover type maps developed by the gap analysis program (GAP). As a finer scale, they would identify barriers to dispersal (such as major road or development corridors). By overlaying data on land management categories (e.g., the distribution of protected areas) and maps of historic and current fisher distribution, core and peripheral populations could be identified and metapopulation viability assessed.

Summary of models

The limited amount of data on habitat use and distribution of fishers in the Rockies is evident. Three studies have been conducted in the region (Roy 1991, Heinemayer 1993, and Jones and Garton 1994). Several factors may confound attempts to analyze habitat correlations. The effect of trapping mortality may complicate comparisons between the various states and provinces with their different trapping regulations. Even where fishers are legally protected, incidental trapping may be a threat to low density populations (Lewis and Zielinski 1997). One hundred sixty three (163) fishers were killed by incidental trapping during a five-year period in Idaho (Luque 1983 cited in Weaver 1993) and incidental trapping mortality remained high in British Columbia after the season was closed there in 1991.

Powell (1979) used a simple population model to show that even low levels of trapping could result in extirpation. If road access mediates trapping mortality, and we preferentially target productive forest lands for logging and associated road building, a complex interaction of road density and "natural" habitat quality may be evident. Road density was not significant in some studies (Carroll et al. 1999), but is likely to affect viability where trapping harvest is high, and may need to be modeled as an interaction with management status and trapping regulations.

The medium-range dispersal ability of fishers results in coarse-scale population-level processes (e.g., source-sink processes [Pulliam 1988]) that may confound analysis of the effects of local habitat selection. Fishers in Massachusetts dispersed an average of 33 km (range 10-107 km)(York 1996). Dispersal distances were similar for both sexes. Although rivers and large highways were not absolute dispersal barriers, dispersers avoided areas of high human population or road density.

A review of published demographic data suggested that most studies are conducted on sink populations, perhaps because most are in areas subject to trapping (York 1996). In a heavily-trapped population in Maine, 94% of mortality was human-related (Krohn et al. 1994). In contrast, natural mortality from coyote predation and drowning was as important as human-related causes (roadkill, trapping) for Massachusetts fishers (York 1996). Dispersal rates dominated the demographics of this population. A high rate of emigration (40%) was partially compensated by immigration, leaving the area a net source. Fishers have innate dispersal tendencies even when density and fecundity are low (York 1996). If this leads to dispersal into sink habitat, it would lower population viability in fragmented habitat (Doak 1995).

Although dispersal evidently contributes to fisher demographics on a subregional scale, evidence of effective long-range dispersal is more limited. Although Powell and Zielinski (1994) review studies documenting dispersal distances up to100 km, average distances are closer to 10 km. Fishers in Maine dispersed distances averaging 10 to 20 km, or one to three home range diameters (Arthur et al. 1993). This may limit recolonization ability and reduce regional viability in regions such as the intermountain west where habitat areas are small and isolated.

These coarse-scale population dynamics suggest that development of robust predictive models will require a multi-scale analysis. Regional or landscape-level thresholds of habitat value, area, or connectivity may exist below which population viability is compromised (Lande 1987, Noon and McKelvey 1996b).

Commonalities among the models reviewed above suggest that canopy closure is a consistently important attribute. Selection for size and age class is not as consistent, except the avoidance of open early-seral stands, which is likely due to their low canopy closure. Selection for forest type is also inconsistent. Mixed conifer and mixed conifer/hardwood types are generally favored. Resolution of floristics is difficult with regional-scale satellite imagery, although information on the relative proportion of hardwood versus conifer cover may be available. The gap analysis project (GAP) database (Scott et al. 1993) offers increased thematic resolution of forest types at the expense of low spatial resolution. Polygons are typically greater than 100 ha in size (Edwards et al. 1996). GAP data layers and similar forest type maps for Canada might best be used as a regional-scale constraint, possibly combined with elevation, to exclude areas of unsuitable vegetation. However, these relationships are difficult to validate without geographically extensive distributional data sets that are presently unavailable.

If floristic, as opposed to structural, attributes are important in determining fisher distribution, generalizing information from studies conducted outside the region may be difficult. For example, the positive correlation with hardwoods evident in California (Carroll et al. 1999, Klug 1996) may be due to increased prey densities stimulated by mast production or to the presence of cavities. The dominant hardwood in the Rockies is aspen, which is not mast-producing. Aspen does, however, retain importance as a source of denning cavities (Weir and Harestad 1997).

Although regional-scale attributes are highly significant, their use in habitat models limits the ability to generalize results to other regions. Recent development of improved spatial modeling techniques may help overcome this problem (Augustin et al. 1996, Wu and Huffer 1997). Alternatively, regional effects can be analyzed post hoc using distributional data sets. Extensive distributional surveys for the fisher and other poorly-studied mesocarnivores are a research priority and a necessary but often neglected complement to intensive telemetry studies. Once regional-scale constraints are identified, canopy closure becomes the best candidate for landscape or mesoscale analysis. A "moving-window" index of landscape-level canopy closure is possible using satellite imagery. Stand-level or microsite attributes such as coarse woody debris or hardwood dbh are probably not practical to incorporate in this type of regional analysis. However, the predictive power of coarser-scale models that lack such information is encouraging.

Marten (*Martes americana*)

A much larger body of field research is available for marten than for fisher in the Rocky Mountain region. This is due to the greater abundance of marten in the region and to greater awareness of the potential effects of human-induced habitat change such as logging on marten populations.

Thompson and Harestad (1994) summarized the conclusions of nine studies of marten habitat selection and found preference for mature or overmature stands and avoidance of shrub and pole stages. Although only one of these studies was from regions next to the Rockies (Kelly 1982), the association between martens and closed-canopy, older forest has proved consistent across North America. Martens in Montana were associated with mature stands of mesic, closed-canopy forest, and avoided open areas in winter (Koehler and Hornocker 1977). Martens in the GYE also avoided regenerating clearcuts (Campbell 1979). In southern Wyoming, marten selected older spruce/fir stands during winter (Wilbert 1992). This association was weaker in other seasons. High levels of coarse woody debris (CWD) characterized these stands. Winter use of these stands may thus be due to high canopy closure and/or the use for denning or foraging of the subnivean openings associated with CWD.

The HSI model for marten (Allen 1984) is similar to that for fisher in that winter cover is considered the limiting resource for the species in the boreal coniferous forests of the western U.S.. Percent tree canopy closure, percent spruce/fir in the overstory, stand age, and surface cover of downfall (woody debris) determine cover value. The model predicts optimal habitat value for mature or old-growth stands of greater than 50% canopy closure, of which more than 50% is spruce/fir, and that have 20-50% cover of downfall.

Spencer (unpublished) developed a similar HSI model for the Sierra Nevada. Besides the habitat elements for canopy closure, proportion of fir, and size class, this model assigned values to mesic non-fir cover types, and incorporated an attribute measuring habitat interspersion. When tested against new track plate data from the same region, the model showed significant predictive power (r^2=0.59, $p < 0.05$). A revised model that doubled the importance of canopy closure relative to other attributes provided a significantly better fit to the data. Inclusion of data on woody debris marginally improved the correlation.

Stand-level habitat models developed for other boreal forest regions may also be relevant to the Rockies. Bowman and Robitaille (1997) found that martens in Ontario, although not limited to old-growth, preferred closed canopy spruce/fir forest with abundant downed logs. They developed a model incorporating percentage spruce/fir, canopy closure, and number of logs. It was only weakly validated by an independent snow tracking data set, which the authors attributed to relative homogeneity of their study area.

To examine the effect of landscape-level factors, Hargis and Bissonette (1997) compared marten abundance in 18 landscapes of nine km^2 in size in the mountains of northern Utah. The landscapes were composed primarily of mature conifer forests, and varied in the portion of the landscape in openings (both natural and due to logging) and the fragmentation associated with habitat loss. Landscape-level habitat loss was negatively correlated with marten abundance, and landscape pattern (fragmentation) had a secondary additive negative effect.

Their final model included as variables the percentage of each landscape unforested and the percent overstory in snags. Both correlations were negative, perhaps because both are associated with decreasing canopy closure. Although small mammal density was highest in open areas, the forest vole preferred by martens in Utah was associated with closed stands. Differences in the prey community between the Rockies and eastern North America may explain the lack of a positive association between martens and snags in this study. The effects of logging may be most pronounced in high-elevation boreal forests such as these, where canopy closure remains low for extended periods following disturbance. The low threshold of about 25% openings at which martens disappeared from the landscape raises concerns over the viability of populations in areas subject to extensive timber harvest.

Chapin (1998) found similar correlations between marten distribution and landscape pattern in Maine. Martens were absent from smaller and more isolated patches, and all marten home ranges contained at least 60% forest cover. Coarse-scale dynamics driven by adjacency to a large unlogged forest preserve were also significant. However, the lack of trapping in the preserve, and heavy trapping pressure in the logged forest, complicate analysis of habitat effects (Hodgman et al. 1997). Although logging and trapping mortality are correlated through increased road density, removal of trapping pressure may permit marten to colonize areas with lower levels of forest cover, at least in eastern forests (D. Harrison, pers. comm.).

A spatially-explicit model developed for Newfoundland martens may provide a means of incorporating such landscape-level factors. Schneider and Yodzis (1994) developed a pseudospatial model that used the concept of "Optimum Territory Size" to address the influence of spatial dynamics (i.e., habitat quality and heterogeneity) on energy balance and reproductive output. As prey abundance and/or habitat area decreased, marten in the model increased territory size and associated energy cost, resulting in lower fecundity. Population extinction scenarios were due to deterministic factors such as negative growth rate or habitat loss or stochastic risks to marginally viable populations. This confirmed the results of earlier nonspatial models (Lacy and Clark 1993) and provided a means of linking changes in habitat area and pattern to demographic parameters. A subsequent spatially-explicit model allowed marten distribution and viability to be predicted under varying habitat scenarios (Schneider 1997).

The effect of increasing habitat fragmentation on dispersal and predation risk was identified as a missing parameter in this study. Unfortunately, accurate parameter estimation in these types of spatially-explicit models often requires long-term data on difficult to measure quantities such as prey abundance or dispersal distance. A weakness of the Newfoundland model is that habitat quality is derived from data on forest timber strata (stand age class). The author suggests that marten HSI values would provide a better base layer. In our opinion, values derived from an empirical model would provide an even stronger foundation. The output of complex dynamic models will have only heuristic value unless the model inputs accurately characterize species/environment relationships.

Summary of Models

Unlike fishers, which seem to show variable responses to forest structure across their range, marten show a consistently strong association with closed-canopy coniferous forest throughout North America. This will likely make regional-scale predictive habitat modeling more successful for this species. The general approach, however, follows that outlined for the fisher. A coarse-scale evaluation of forest type can be derived from the GAP databases where available or from a model based on elevation and climate. The strong association of marten with spruce/fir forest types is evident in numerous studies.

Once these types of areas have been identified, a finer-scale analysis of canopy closure should be performed. Canopy closure or its correlates are consistently among the most significant predictors of marten distribution and abundance in the studies reviewed above. A "moving-window" analysis of this attribute in GIS will identify areas of contiguous forest. Incorporation of data on stand structure (e.g., CWD) will be more difficult. Although regional data layers of CWD volume are not available, correlation between CWD and forest type may allow limited incorporation of this factor. Several studies found good predictive power even when such fine-scale structural data were not incorporated.

Levels of trapping mortality can be expected to vary among the states and provinces in the study area. Martens have historically constituted the bulk of the fur harvest in the region, and continue to be legally trapped at varying levels throughout the region. Trapping may lead to negative correlations between road density and marten abundance in some areas. The importance of spatial refugia has been shown in Maine (Hodgman et al. 1997) and Yellowstone National Park (Buskirk in press). Incorporation of road density into the habitat model will be more complex than for other attributes and will benefit from validation data from a variety of areas with different trapping levels.

In the long-term, development of regional-scale SEPM's will provide a more mechanistic understanding of the processes responsible for coarse-scale patterns of marten distribution. However, static habitat modeling is a necessary first step given the current imperfect understanding of the association between martens and coarse-scale habitat attributes.

Critique of current modeling approaches

Habitat suitability index (HSI) models are the models most commonly used by agencies, especially the US Fish and Wildlife Service, to assess habitat "take" in project-level planning and mitigation analyses. They are theoretical mathematical models (Morrison et al. 1992) in that they are based on "expert opinion" of relationships between habitat and species abundance.

Several examples of HSI models have been reviewed above. Thomasma et al. (1991, 1994) tested the fisher HSI model and found varying degrees of significance for the model elements. Powell et al. (1997) used telemetry data to validate an HSI model for the black bear in the southeastern U.S.. A marten HSI model has also been tested in California (W. D. Spencer, unpublished report).

These HSI's are an improvement on univariate models in that they offer a method of integrating multiple habitat attributes in an explicit manner (usually the geometric mean).Although based on qualitative review of the literature, HSI models are rarely validated with field data, and are usually less robust and of lower predictive power than empirical models. The CEA and LZP approaches also produce descriptive, qualitative models, although the Yellowstone CEA is more empirical than those in other areas (D. J. Mattson, pers. comm.).

Unfortunately, managers unaware of the qualitative judgements involved in model development may misinterpret their numeric output as similar to that of quantitative and empirical models. Even if we can assign qualitative rankings to individual factors, little consideration is given to which factors will dominate the final composite score. To analyze this problem, Apps (1997) performed a sensitivity analysis on the grizzly bear LZP model. He found that the human features and linear disturbance elements dominated over the visual cover and riparian attributes, but this was not obvious from the original model. Although it is possible to incorporate non-linearities and interactions (e.g., visual cover may only be important near roads), more complex interactions are difficult to model based on expert opinion.

The biologically-appropriate scale of analysis is often unclear in habitat studies, and we can criticize CEA models for choosing an arbitrary scale. For example, in grizzly bear LZP analysis, modelers analyze the linear features component with a "moving-window" 2.25 km^2 in size (Serveen and Sandstrom 1993, Apps 1997). Apps (1997) employs this scale to be consistent with previous applications of the model, but suggests that a coarser-scale analysis may be more biologically realistic.

In the grizzly bear CEA (Weaver et al. 1986), factors such as "seasonal equity" are assessed at the scale of a Bear Management Unit (BMU) of 250-1000 km^2. Although appropriate for many resident females, this scale may not incorporate ecosystem-level effects on bears that commonly make long distance seasonal movements between areas encompassed by several BMU's (Craighead et al. 1995). Weaver et al. (1986) propose that their habitat effectiveness value integrates spatial and temporal aspects of perturbations. However, they acknowledge the need for more information on spatial and temporal lags in responses to disturbance, termed by them "spatial ripple" and "refractory period." In particular, road development may trigger long-term development pressures that are not adequately addressed in the CEA model (McLellan 1990).

By not incorporating the effects of coarser-scale population processes, analysis of connectivity using the LZP approach may fail to identify the most biologically important landscape linkages. We may conceive of patch boundaries and dispersal barriers as membranes or filters (Doak 1995, Wiens et al. 1993). The "rate of flow" or functional connectivity through these areas will depend on characteristics of the membrane and on dispersal "pressure" from source habitat. If the spatial distribution of source habitat creates pressure for dispersal through already degraded habitat with associated high risk of human-caused mortality, restoration of these areas may be more important to functional connectivity than protection of other more pristine linkages.

Verification of the model assumptions of CEA/LZP models is difficult and validation of model predictions is rarely attempted. Field studies have given qualitative support to some model assumptions (e.g., Mattson et al.1987). However, successful prediction of distribution and abundance patterns, much less relative levels of population performance (survival, fecundity) has proved elusive. Comparisons of radiotelemetry data with predictions from CEA/LZP models have often shown poor correlation.

In summary, CEA/LZP analysis may be useful for local planning purposes. However, using the model for regional-scale analysis is likely to be non-informative or misleading. Telemetry studies are generally located where the species is abundant, and are less helpful in modeling species presence and absence. Incorporating variation in habitat relations across the region and exploring the fit between alternate models and empirical data are difficult. We agree with Craighead et al. (1995) that CEA is not sufficient for ecosystem-scale conservation planning, and that regional-scale empirically-based multivariate analysis of carnivore/habitat relationships based on remotely-sensed imagery, road density and land use data is a necessary next step.

The gap analysis program (GAP) is an approach explicitly designed to address these regional-scale planning questions (Scott et al. 1993). State-level gap analysis projects have used predicted distributions of vertebrates to assess the adequacy of existing protected area designations. The GAP vertebrate models are developed from expert opinion and published descriptions of wildlife/habitat associations. The occurrence of the species is predicted based on vegetation data layers developed from satellite imagery, in combination with elevation data and range boundary information (Edwards et al. 1996).

Cover-type/vertebrate species associations are often crude (e.g., birds may be associated with "coniferous forest" [Edwards et al. 1996]), due in part to the mismatch between regional cover type classification systems and the finer scale habitat attributes measured in many wildlife studies (Bolger et al. 1997, *contra* Jennings et al. 1997). We might expect this to lead to over prediction of species occurrence. In a review of validation studies of GAP-type wildlife/habitat models, Flather et al. (1997) found that commission error rates were generally high. GAP models also do not incorporate human disturbance factors.

Edwards et al. (1996), who evaluated the accuracy of GAP vertebrate models in predicting species occurrence in Utah parks, provided a more positive appraisal. Predictive power varied among taxa. Bird models had the highest accuracy (90.6%), followed by mammals (83.6%), reptiles (78.4%), and amphibians (69.4%). Although these figures are encouraging, the strength of this validation exercise may be limited. The authors did not compute correlations between a species and the cover type they classed as suitable habitat, but between species lists and all cover types contained within a park. If a park contained many cover types, and therefore most of the species were predicted to occur there, or if species were predicted to be associated with

many cover types, evaluation of model accuracy is difficult without a comparison of model error rate against the error rate of a random model.

These types of thematically-coarse, theoretical models may be necessary when evaluating representation in protected areas of large assemblages of species. Similar approaches in Canada have used ecosection maps to predict grizzly bear distribution and abundance (Banci et al. 1994). However, when evaluating the distribution of habitat for one or a few focal species, especially those such as large carnivores that we expect to have complex spatial dynamics due to large area requirements, GAP models may have limited value and should be supplemented with finer-scale data where available (Bolger et al. 1997).

In summary, most existing modeling approaches for carnivores in the Rocky Mountains have evolved out of a site-level planning paradigm. Even when given qualitative support by field data, researchers have rarely validated them when applied in different areas. Usually, they have uncritically assumed that patch-level associations between habitat attributes and species abundance were possible to scale up to the ecosystem or regional level. Although some validation studies have demonstrated correlation between HSI predictions and field data (Thomasma et al. 1994, Powell et al. 1997), the relative contribution of different scales of habitat selection is rarely evaluated. Even with good patch-level models, it is likely that a further increase in predictive power can be achieved by incorporating coarser-scale habitat attributes.

An increased focus on these coarser-scale factors may arise from an analysis of the spatial population dynamics of carnivore species. There are several reasons why species distribution may not match the distribution of "suitable" patch-level habitat. A species may be absent in suitable habitat due to factors such as lack of connectivity or lack of sufficient habitat to meet minimum area requirements. On the other hand, a species may be present in unsuitable habitat due to population-level processes such as source-sink dynamics. Failure to explicitly analyze landscape and regional-scale correlations may lead to misleading conclusions concerning patch-level habitat selection. This may be especially true in the case of wide-ranging carnivores, which integrate perceptions of landscape quality over large areas.

New modeling approaches

In recent years, several new approaches have been developed for modeling wildlife/habitat interactions. These can be divided into several types. Analytical models can be distinguished from approaches using computer simulation. Dynamic models, which describe change over time, can be distinguished from static models depicting species distribution at "equilibrium" with the environment. The models can be purely deterministic, or can be designed to incorporate stochastic or random factors. The types described below include several approaches that appear promising for modeling habitat selection or spatial population dynamics at multiple scales. These include analytical diffusion models, percolation-theory based models, dynamic pseudospatial models, dynamic individual-based simulation models, and static spatial statistical models.

Analytical models have been used extensively in population viability analysis. Well-known examples include age-structured matrices and simple metapopulation models (Leslie 1945, Levins 1970, Lande 1987). Incorporating spatial heterogeneity into these models usually increases model complexity so they become analytically intractable. However, analytical diffusion models (Turchin 1991) may allow movement data collected from foraging carnivores (e.g,. through snow tracking

[Foran et al. 1997]) to be modeled with partial differential equations. These models produce a "residence index" value that characterizes the relative abundance of the animals in different types of habitat. This approach has to date been applied only in studies of fine-scale habitat selection. However, the underlying hypothesis that fine-scale individual movements can be scaled up to produce coarser-scale distribution patterns forms the basis for other approaches such as individual-based simulation models.

An alternative approach applies percolation theory (Stauffer and Aharony 1985) to model the functional connectivity of landscapes based on the interaction between a species dispersal capability and patch geometry (Keitt et al. 1997). Percolation theory proposes that in a landscape of randomly distributed habitat, nonlinear increases in connectivity will occur when 59% of the area is suitable habitat. At this critical threshold, habitat specialists will be able to "percolate" across the landscape. In real landscapes, the threshold level will depend on the actual arrangement of patches. The distance a particular species can disperse interacts with landscape pattern to produce critical thresholds of functional connectivity. Species with dispersal capabilities below the critical distance will experience the landscape as fragmented. This allows connectivity to be compared among different species in a landscape and between different landscapes. Patch removal simulations document the effect on connectivity of removing individual patches, and allow identification of critical landscape linkages. Keitt et al. (1997) apply this technique to assess the impacts of habitat fragmentation on the Mexican spotted owl (*Strix occidentalis lucida*) in the southwestern U.S.. The high level of contrast between suitable montane forest habitat and the matrix of lower-elevation arid non-forested areas makes a binary habitat classification more realistic there than in most regions.

This approach may be useful for regional-scale analyses of carnivores that are strong habitat specialists, such as some mustelids, especially in regions where contrast between protected and human-altered habitat is strong. However, the extreme simplification inherent in a binary habitat classification may obscure the effects on connectivity of the landscape mosaic as a whole (Wiens 1997). This would be a particular problem for species such as wolves that make use of the semi-developed landscape matrix.

Evolving out of earlier nonspatial models for population viability analysis is a class of "pseudospatial" models. These incorporate information derived from the mapped distribution of habitat, but lack the topological information such as patch shape that is present in spatially-explicit population models. This approach has been used to model the viability of mountain lion populations in California (Beier 1993) and of endangered marsupials inhabiting old-growth eucalypt patches in southern Australia (Lindenmayer and Possingham 1996a). The latter study used a Monte Carlo simulation model called ALEX (Possingham and Davies 1995). In this model, they treat each patch as internally uniform, but retain derived information on inter patch distance. ALEX allows individual patches to be ranked as to their contribution to long-term metapopulation viability. Other widely available simulation models such as VORTEX and RAMAS use a similar pseudospatial approach (Lacy 1993, Akcakaya 1994).

As with percolation-theory-based analysis, these pseudospatial models work best in situations where we can clearly divide habitat into suitable and non-suitable. Examples are mountain lions inhabiting the wildland-urban interface in southern California or forest habitat specialists isolated in a matrix of agricultural lands. These models have the advantage of incorporating the effects of demographic and environmental stochasticity on long-term population

viability. These threats to viability are the concern of the "small-population paradigm," and represent a different focus than "declining-population paradigm" factors such as habitat loss (Caughley 1994). This approach may be particularly valuable for a species such as the grizzly bear whose low fecundity and large home range size make it vulnerable to the stochastic effects accompanying small population size.

In contrast to pseudospatial models, individual-based simulation models retain spatially-explicit information on habitat distribution (DeAngelis and Gross 1992). These models track the fates of many individuals through time as they move across a grid of cells. Each cell can be assigned different levels of habitat quality. The attributes of the cells surrounding an individual interact with movement rules to govern the behavior of the organism. The behavior of large numbers of individuals collectively determine the aggregate characteristics that form the model output.

Individual-based models span a range of complexity, depending on the degree of biological realism and number of demographic parameters they incorporate. One of the simpler applications involves the simulation of dispersal behavior with diffusion models. Individuals disperse from their starting point across a landscape of habitat types with different levels of permeability or dispersal mortality risk. The individuals are "correlated random walkers" (CRW) because their direction of movement is based on a combination of the relative habitat values of the neighboring cells, previous direction of travel, and a random component. Although real organisms use cognitive maps in more complex ways than portrayed in a CRW, these models are useful in mapping the spatial distribution of potential dispersal paths across a landscape. For example, this method has been used to map regional-scale dispersal routes for grizzly bears in the northern Rockies (Boone and Hunter 1996, Walker and Craighead 1997).

Because field data on dispersal is notoriously difficult to gather, many CRW models base movement rules and relative habitat permeability on qualitative rankings. A more promising approach is to derive movement rules from parameters such as turning angle, mean move length and duration that we can estimate for different habitats from field data (Turchin 1991, 1996). A study of marten in the Yellowstone area is currently exploring this approach (Minta 1996). Validation of these models may be possible with species such as wolves for which dispersal data are available. The grizzly bear, however, has never been recorded to move between regional subpopulations in the lower 48 states (Weaver et al. 1996), although linkages have been proposed (Picton 1986). Validation of grizzly bear dispersal models may require genetic analysis (Craighead and Vyse 1996).

We can develop static dispersal models using the "least-cost path" functions found in several GIS software packages (e.g., ESRI, Inc. 1996). The least-cost path can be modeled in GIS as a combination of the attraction to preferred habitats minus energetic costs (due to topography, etc.) and security costs (exposure to humans or roads). As with CRW, individuals disperse from their starting point across a landscape surface of cells (pixels) with different levels of permeability. Direction of movement is based on a combination of the relative habitat values of the neighboring cells, differentially permeable impediments such as roads and fences, previous direction of travel, and a random component. Multiple iterations delineate a hierarchy of probable pathways based on the cumulative cost of travel. This approach is currently being used to study barriers to wolf movement in the parks of the Canadian Rockies (Paquet et al. 1996, 1997). Landscapes such as these, where topography constrains movement options, may be good

candidates for least-cost path analysis. One drawback to the standard least-cost path function is that the single path it identifies may have the least total cost but be biologically unrealistic if segments of it traverse developed areas. Modification of the function to derive a movement probability surface may increase realism by including exposure to development as an added cost (Paquet et al. 1996, 1997). The resistance value of habitats in human dominated landscapes is increased according to the distance from development, and type and intensity of human activity that predominates.

Spatially-explicit population models (SEPM) are a class of individual-based simulation models that incorporate additional biological realism as habitat-specific demographic parameters. Individuals not only move between cells, but grow, reproduce and die. Model output from SEPM's may include the mean population size, mean time to extinction, or the percentage of suitable habitat occupied. The development of SEPM's has allowed data gathered from intensive demographic studies to be combined with GIS maps of landscape composition and pattern in dynamic models (Murphy and Noon 1992, McKelvey et al. 1993).

Spatial statistical models are similar to traditional wildlife habitat models. However, they incorporate the effects of habitat selection at multiple scales through "moving-window" functions in GIS or through more complex spatial statistical functions such as autoregressive models (Augustin et al. 1996, Wu and Huffer 1997) or trend surface analysis (Periera and Itami 1991). Spatial statistical models have been used to predict potential habitat for the gray wolf (Mladenoff et al. 1995) and the fisher (Carroll et al. 1999). Although the effects of landscape pattern (as opposed to landscape composition) can be incorporated through metrics derived from programs such as FRAGSTATS (McGarigal and Marks 1995), usually these static models deal poorly with connectivity. This suggests that a hybrid approach incorporating static and dynamic modeling may be appropriate.

Problems with complex models

Although the modeling approaches described above are more biologically realistic than current methods, their complexity may limit applicability in some situations. Although rapidly developing technology allows analyses that would not have been practicable a few years ago, regional-scale spatial analysis still imposes high data storage and processing requirements. Added to this is the challenge of integrating data from many states and provinces into a seamless whole. To some extent, analysis is constrained to a least common denominator of attributes available for the entire region. This often requires the use of attributes that are surrogates for the biological variables controlling species distribution. For example, we may substitute forest type for more detailed data on available forage. Many variables that have proved significant in fine-scale habitat analyses would not be possible to compile on a regional level, even if their effects were thought to scale up to that level. Besides limitations in habitat data availability, lack of data on the carnivore species of interest constrains the analysis.

Approaches that take into account the limitations of existing knowledge may be preferable to more complex models such as SEPM's (Karieva et al. 1996). Output from SEPM's may be especially sensitive to errors in difficult-to-estimate parameters such as dispersal-mortality rates, highlighting the need for sensitivity analysis (Ruckelshaus et al. 1997). After reviewing several examples of how complex models can lead to incorrect results, Karieva et al. (1996) conclude that

although "advocacy of habitat description and analysis spurns many of the more modern ideas in conservation biology ... practical concerns-that is, what data are available and an appreciation for multiple explanations of species loss-need to play a larger role in conservation research."

Potential modeling approaches

Integrating multiple single species habitat models into a multi-species conservation plan requires additional data as to the nature of interspecific interactions. The information is important because interspecific interactions of carnivores have been shown to change the distribution and abundance of sympatric competitors and cause "ripple effects" in populations of other species. Tolerances of individual carnivore species for human disruption suggest that present day species assemblages will not move as units given almost any scenario of anthropogenic change. Rather than simply overlaying single species habitat quality maps to create a map of multi-species habitat value, evaluating commonalities among the species in limiting factors to viability may be more productive. For example, critical areas for habitat generalists that direct human persecution limits (such as wolves) may be distinct from critical areas for less-persecuted species that suffer from loss of particular habitat types (such as the fisher). However, the biological productivity of an area, through its effect on carnivore movement patterns, may interact complexly with the potential for human/carnivore conflict, making interactions among individual limiting factors important.

The most productive modeling approach will vary depending on the type of threat facing the species. If loss of habitat is important, vegetation data will be most useful. If human-associated mortality is significant, data on roads and land use may be more important. The degree of habitat specialization shown by the species will affect the role of landscape pattern metrics. If it is a habitat specialist, and habitat patches are isolated, landscape pattern may be important. If it is a generalist, or patches are clumped, habitat area may be more critical (Wiens 1997).

Although species within each of the four carnivore families considered here (canids, felids, ursids, and mustelids) vary in their level of ecological resilience, they share common life history characteristics that form a starting point for analysis. Canids have high demographic potential and resiliency. Although habitat generalists and good dispersers, high levels of human persecution may make them area-limited. Felids have generally low demographic potential but are fairly good dispersers. Their food and denning resources may be associated with different seral stages, making landscape interspersion important. Ursids have generally low demographic potential and are dispersal-limited. They are energetically constrained by seasonally high food requirements. As dietary and habitat generalists, they respond to landscape interspersion. Mustelids have low demographic potential and may be dispersal-limited. They are habitat specialists, with the possible exception of the wolverine, which shows similarities to larger carnivores.

The species' social structure is another important variable affecting resilience (Weaver et al. 1996). The social characteristics of wolf packs enhance resiliency, as the proportion of females breeding and subadults dispersing can adjust to compensate for changes in human-caused mortality and prey density. In contrast, martens and fishers maintain intrasexually-exclusive territories, but territoriality changes as habitat quality shifts (Powell 1994).
Learned foraging behavior is important in the grizzly bear and wolverine and allows the use of widely-dispersed and temporally variable food resources. This may increase site fidelity and make recolonization more difficult. It would also increase the long-term effects of habitat disturbance

and the potential of human-caused mortality to disrupt social structure (Craighead et al. 1995).

Commonalities are evident between species in demographic parameters such as home range size, fecundity, and degree of sex-biased dispersal (Weaver et al. 1996). A large home range size suggests that small-population issues such as inbreeding and Allee effects may be important. Low fecundity increases risks from human persecution. Dispersal characteristics interact with landscape pattern to affect functional connectivity. Wolves and mountain lions have a strongly long-tailed (leptokurtic) distribution of dispersal distances and have been documented crossing semi-developed areas. This suggests that a relatively higher proportion of the population of these species can exist in buffer areas, with core areas forming a smaller but still critical component.

Grizzly bears, however, although capable of large seasonal movements within ecosystems, have never been documented moving between ecosystems (Weaver et al. 1996). Their high rate of mortality in non-core areas suggests that ensuring regional connectivity will be problematic and viability will depend on core areas large enough to support most of the population (Weaver et al. 1996, Craighead et al. 1997).

A robust regional-scale modeling approach must explicitly examine cross-scale linkages in the factors limiting distribution and population viability. This represents a departure from the fine-scale focus of traditional wildlife models. Aspects of these models that we can expect to scale-up must be separated from those that we can ignore for the purposes of model simplification. Hierarchy theory provides a framework for analyzing the links between processes operating at multiple scales (Allen et al. 1984). Models representing a particular focal scale will have dynamics generated by integrating events occurring at finer scales and will have constraints imposed by processes operating at coarser scales (Wiens 1989b, Johnson et al. 1992). For example, constraints imposed on grizzly bear distribution by areas of high road density may be most evident at coarse-scales, while vegetation attributes dominate at finer scales (Mace et al. 1996).

This suggests that the first stage of development of regional models will be analysis of regional-scale constraints, followed by incorporation of progressively finer-scale factors. These finer-scale factors may increase in importance as regional-scale suitability becomes marginal. An example would be tree species' that occupy a variety of microsite types at the center of their distribution, but are restricted to the most favorable microsites at the margins of their range (Lenihan 1993).

The hierarchy of scales developed by Delcourt et al. (1983) provides a conceptual framework for regional modeling (Walker and Walker 1991). Micro-, meso-, and megascale processes are identified and data are collected through a nested study design that links intensive study sites with spatially-extensive regional data.

Existing modeling approaches such as the HSI and CEA rely on qualitative generalizations on species/habitat relationships derived from a review of the literature. This approach may be attractive in that it summarizes qualitative field knowledge intuitively. However, such theoretical models are evidently poor at predicting the regional-scale distribution of wide-ranging carnivores. Prospective monitoring and management of carnivore species assemblages require the development of empirical models that can reliably predict the status of multiple species over regional scales. Until recently, collecting the extensive survey data sets that form the basis for these types of models was a low research priority. However, new agency monitoring mandates have led to increasing availability of such data, and regional-scale data on habitat attributes are also increasingly available through sources such as remotely-sensed vegetation layers. However,

integrating these two types of data into regional-scale models is just beginning.

Where such standardized survey data on species distribution are unavailable, alternative information such as trapline records may be useful if spatially-referenced. Alternately, if fine-scale telemetry data are available from several study areas distributed across the region, comparisons of occupied and unoccupied habitat may allow a general model incorporating regional variation to be developed. If insufficient data are available and a theoretical model must be used, we should compare model predictions with coarse-scale range boundaries for a weak validation.

Static spatial statistical modeling can be used to analyze correlations between species distribution data and the coarsest level of constraints. These might include road density, human population density, and land use categories. The second level of habitat factors might include vegetation type or ungulate biomass indexes. Climatic and topographic variables, including slope, aspect, elevation, precipitation, and snow depth, will be important at coarser scales and may also contribute to fine-scale selection (Paquet et al. 1996, 1997). Trend surface variables, derived from geographic coordinates, are potential "place-holders" for regional trends that cannot be associated with other attributes, but the development of autoregressive models may make their use unnecessary (Augustin et al. 1996, Wu and Huffer 1997).

Such static models predict the distribution of species at "equilibrium" with the distribution of habitat. Hybrid approaches are necessary to combine static habitat analysis with the effects of connectivity and landscape pattern. Because functional connectivity depends on habitat permeability and on dispersal "pressure" from source habitats, modeling of more complex dynamics such as source-sink effects may require integration of the habitat quality of the landscape mosaic as a whole (Wiens 1996, 1997).

Because spatially-explicit dispersal data are only rarely available, analyzing correlations between the above habitat factors and dispersal directly is usually not possible. Genetic analyses may allow this in future (Craighead and Vyse 1996). The existing distribution of carnivores in the Rockies may not provide data on present levels of connectivity due to lag effects from factors such as past predator control. Data from wolf recolonization may be one of the few sources of data on connectivity. For most species and for areas more distant from source populations, modeling of dispersal paths is the only option.

Results of nonspatial PVA's have been highly sensitive to subtle variations in model structure, leading to the suggestion that multiple models be considered (Doak and Mills 1994, Mills et al. 1996, Pascual et al. 1997) and integrated using Bayesian approaches (Milne 1989, Aspinall and Veitch 1993). Static spatial modeling techniques that can use coarser-resolution data such as presence/absence records may complement analytical or simulation modeling, especially in 'data-poor' situations (e.g. with most mustelids) (Hanski 1996, Karieva et al. 1996).

Because validation data are scarce, modeling of dispersal should use multiple approaches. Modified least-cost path modeling is the most practical approach (Paquet et al. 1997), but we should also explore dynamic models (Walker and Craighead 1997) and hybrids. We could create a CRW diffusion model where the number of starting dispersers is based on the area and habitat quality of a core area, as defined through a previous static modeling stage, or use the habitat values derived from a static model as input to a pseudospatial model (Akcakaya and Atwood 1997). CRW models could also be used to parameterize interpatch dispersal rates for pseudospatial models (Gustafson and Gardner 1996).

A potential opportunity for use of a hybrid approach can be found in two studies that model the regional viability of wolves in the north-central U.S.. Mladenoff et al. (1995) used a static model based on road density to predict "equilibrium" wolf distribution. Haight et al. (1998) used a nonspatial simulation model to analyze the effects of dispersal and human-induced mortality on wolf occupation of semi-developed lands surrounding core areas. These two approaches could be integrated by basing a pseudospatial model or a SEPM on habitat values provided by the static model. This would allow conclusions about the differential suitability of "islands" of low road density that varied in size and degree of isolation from other habitat, due to distance and character of the intervening landscape matrix.

To apply these models to an area such as the Rocky Mountains where topographic barriers limit connectivity would require further adaptations. However, the general approach of integrating multiple models at multiple scales is likely to have wide applicability. Recent studies have resulted in models that are more biologically- and spatially-realistic than those in current use by agencies. Development of new techniques such as outlined above should allow researchers to improve upon this work further. Regional-scale predictive models that allow objective habitat-based status assessment and monitoring will be critical tools for insuring the survival of carnivores in the Rocky Mountain region.

Literature cited and additional references

Adair, W. A., and J. A. Bissonette. 1995. Individual-based models as a forest management tool: the Newfoundland marten as a case study. Trans. N. Amer. Wildl. Nat. Resour. Conf. 60: 251-57.

Agee, J. K. 1993. Fire ecology of Pacific northwest forests. Island Press, Washington, D.C.

Agee, J. K., S. C. F. Stitt, M. Nyquist, and R. Root. 1989. A geographic analysis of historical grizzly bear sightings in the North Cascades. Photogrammetric Engineering and Remote Sensing 55:1637-1642.

Akcakaya, H. R. 1994. RAMAS/GIS: Linking landscape data with population viability analysis (version 1.0). Applied Biomathematics, Setauket, NY.

Akcakaya, H. R., and J. L. Atwood. 1997. A habitat-based metapopulation model of the California gnatcatcher. Conservation Biology 11:422-434.

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. Ecology 63:1932-1948.

Alexander, S., C. Callaghan, P. Paquet, and N. Waters. 1996. GIS predictive model for habitat use by wolves (Canis lupus). GIS '96 --- 10 Years of Excellence, March 19-23. CD Conference Proceedings. GIS World Inc. Fort Collins, Colorado.

Alexander, S., P. Paquet, and N. Waters. 1997. Playing god with GIS: uncertainty in wolf habitat suitability models. Pages 449-453 in Conference Proceedings, Eleventh annual symposium on geographic information systems. GIS World Inc. Fort Collins, Colorado.

Allen, A. W. 1983. Habitat suitability index models: fisher. FWS/OBS-82/10.45(rev.). USDI Fish and Wildlife Service.

Allen, A. W. 1984. Habitat suitability index models: marten. FWS/OBS-82/10.11(rev.). USDI Fish and Wildlife Service. 13 pp.

Allen, A. W. 1987. The relationship between habitat and furbearers. Pages 164-179 in M. Novak, J. A. Baker, and M. E. Obbard, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario.

Allen, T. F. H., R. V. O'Neill, and T. W. Hoekstra. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110, Rocky Mtn. Forest and Range Experiment station, Fort Collins, CO. 11 pp.

Andersen, M. C., and D. Mahato. 1995. Demographic models and reserve designs for the California Spotted Owl. Ecological Applications 5: 639-47.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355-66.

Apps, C. D. 1996. Bobcat (*Lynx rufus*) habitat selection and suitability assessment in Southeast British Columbia. MS Thesis. University of Calgary, Calgary, AB. 145 pp.

Apps, C. D. 1997. Identification of grizzly bear linkage zone along the highway 3 corridor of Southeast British Columbia and Southwest Alberta. Prepared for B.C. MELP and WWF-Canada. Aspen Wildlife Research, Calgary, AB. 45pp.

Apps, C. D. In press. Space use, diet, demographics, and topographic associations of lynx in the southern Canadian rocky mountains: a study. In L. F. Ruggiero, et al., eds. The scientific basis for lynx conservation. Gen. Tech. Rep. RMRS-30. USDA Forest Service Rocky Mtn. Research Station, Missoula, MT.

Archibald, W. R., R. Ellis, and A. N. Hamilton. 1987. Responses of grizzly bears to logging truck traffic in the Kimsquit river valley, British Columbia. Int. Conf. Bear Res. and Mgmt. 7:251-257.

Armbruster, P., and R. Lande. 1993. A population viability analysis for African elephant (Loxodonta africana): how big should reserves be? Conservation Biology 7: 602-10.

Arthur, S. M., W. B. Krohn, and J. R. Gilbert. 1989. Home range characteristics of adult fishers. Journal of Wildlife Management 53:674-679.

Arthur, S. M., W. B. Krohn, and J. R. Gilbert. 1989. Habitat and diet use of fishers. Journal of Wildlife Management 53:680-688.

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

Aspinall, R., and N. Veitch. 1993. Habitat mapping from satellite imagery and wildlife survey data using a Bayesian modeling procedure in a GIS. Photogrammetric Engineering and Remote Sensing 59:537-543.

Augustin, N. H., M. A. Mugglestone, and S. T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology. 33:339-347.

Austin, M., and J. A. Meyers. 1996. Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. Forest Ecology and Management 85:95-106.

Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. Ecological Monographs 60: 161-77.

Bailey, T. C. 1993. A review of statistical spatial analysis in geographic information systems. Pages 13-44 in S. Fotheringham and P. Rogerson, editors. Spatial analysis and GIS. Taylor and Francis, Bristol, PA.

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

Bailey, T. N. 1981. Factors of bobcat social organization and some management implications. Pages 984-1000 in J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf. Frostburg, MD.

Baker, B. W., B. S. Cade, W. L. Mangus, and J. L. McMillen. 1995. Spatial analysis of sandhill crane nesting habitat. Journal of Wildlife Management 59: 752-58.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98:1-54.

Banci, V. 1987. Ecology and behavior of the wolverine in Yukon. M.S. thesis. Simon Fraser University, Burnaby, B.C.

Banci, V. 1989. A fisher management strategy for British Columbia. Wildlife Bulletin No. B-63. B.C. Ministry of the Environment, Lands and Parks, Wildlife Branch. Victoria, B.C.

Banci, V. 1992. Status of lynx, wolverine, and fisher in western Canada. Unpublished report.

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. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mtn. Forest and Range Experiment Station, Ft. Collins, CO.

Banci, V., and A. Harestad. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. Ann. Zool. Fenn. 25:265-270.

Banci, V., D. A. DeMarchi, and W. R. Archibald. 1994. Evaluation of the status of grizzly bears in Canada. Int. Conf. Bear Res. and Mgmt. 9:129-142.

Bart, J., D. R. Petit, and G. Linscombe. 1984. Field evaluation of two models developed following the habitat evaluation procedures. Trans. N. Amer. Wildl. Nat. Resour. Conf. 49: 489-99.

Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. Ecological Applications 5: 411-20.

Bath, A. J., H. A. Dueck, and S. Herrero. 1988. Carnivore conservation areas: a potential for comprehensive, integrated management. Unpublished report, World Wildlife Fund-Canada, Ottawa, Ontario.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94-108.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228-237.

Beier, P. 1996. Metapopulation models, tenacious tracking, and cougar conservation. Pages 293-323 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Beissinger, S. R., E. C. Steadman, T. Wohlgenant, G. Blate, and S. Zack. 1996. Null models for assessing ecosystem conservation priorities: threatened birds as titers of threatened ecosystems in South America. Conservation Biology 10: 1343-52.

Bekoff, M., ed. 1978. Coyotes: biology, behavior, and management. Academic Press, New York, NY.

Bekoff, M. 1982. Coyote (*Canis latrans*). Pages 447-459 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

Bekoff, M., and M. C. Wells. 1986. Social ecology of coyotes. Scientific American 242:130-148.

Beldon, R. C., and B. W. Hagedorn. 1993. Feasibility of translocating panthers into northern Florida. Journal of Wildlife Management 57:388-397.

Bender, L. C., G. J. Roloff, and J. B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildl. Soc. Bull. 24: 347-52.

Berg, W. E., and R. E. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pages 229-247 in M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, NY.

Berg, W. E., and D. W. Kuehn. 1982. Ecology of wolves in north-central Minnesota. Pages 4-11 in F. H. Harrington and P.C. Paquet, eds. Wolves of the world. Noyes Publ., Park Ridge, N.J.

Berg, W. E., and D. W. Kuehn. 1994. Return of two natives: fisher and marten demographics in a changing Minnesota landscape. Pages 262-271 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R.A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Bissonette, J. A., R. J. Frederickson, and B. J. Tucker. 1989. American marten: a case for landscape level management. Transactions of the North American Wildlife and Natural Resources Conference 54:89-101.

Bissonette, J. A., D. J. Harrison, C. D. Hargis, and T. G. Chapin. 1997. The influence of spatial scale and scale-sensitive properties on habitat selection by American marten. Pages 368-385 in J. A. Bissonette, ed. Wildlife and landscape ecology: effects of pattern and scale. Springer, New York, NY.

Blanchard, B. M. 1983. Grizzly bear-habitat relationships in the Yellowstone area. Int. Conf. Bear Res. and Mgmt. 5: 118-123.

Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41-67.

Blanchard, B. M., and R. R. Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal of Wildlife Management 59:560-565.

Boitani, L. 1995. Ecological and cultural diversities in the evolution of wolf-human relationships. Pages 3-11 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Boitani, L., F. Corsi, and E. Dupre. 1997. Large scale approach to distribution mapping: the wolf in the Italian peninsula. Oral presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada. ,

Bojórquez-Tapia, L. A., I. Azuara, E. Ezcurra, and O. Flores-Villela. 1995. Identifying conservation priorities in Mexico through geographic information systems and modeling. Ecological Applications 5:215-31.

Boles, B. K. 1977. Predation by wolves on wolverines. Canadian Field-Naturalist 91:68-69.

Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. Conservation Biology 11:406-421.

Boone, R. B., and M. L. Hunter, Jr. 1996. Using diffusion models to simulate the effects of landuse on grizzly bear dispersal in the Rocky Mountains. Landscape Ecology 11:51-64.

Bowen, W. D. 1982. Home range and spatial organization of coyotes in Jasper National Park, Alberta. Journal of Wildlife Management 46:201-216.

Bowman, J. C., and J.-F. Robitaille. 1997. Winter habitat use of American martens *Martes americana* within second-growth forest in Ontario, Canada. Wildlife Biology 3:97-105.

Boyce, M.S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23: 481-506.

Boyce, M. S. 1992. Wolf recovery for Yellowstone: a simulation model. Pages 123-138 in D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier, Essex, U.K.

Boyce, M. S. 1995a. Anticipating consequences of wolves in Yellowstone: model validation. Pages 199-210 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Boyce, M. S. 1995b. Population viability for grizzly bears (*Ursus arctos horribilis*): a critical review. Report to the Interagency Grizzly Bear Committee, Missoula, MT.

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

Boyd, D. K., P. C. Paquet, S. Donelon, R. R. Ream, D. H. Pletscher, and C. C. White. 1995. Transboundary movements of a recolonizing wolf population in the Rocky Mountains. Pages 135-140 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Boyd-Heger, D. K. 1997. Dispersal, genetic relationships, and landscape use by colonizing wolves in the Central Rocky Mountains. Ph.D. Thesis. University of Montana, Missoula, Mt. 184pp.

Brainerd, S. M. 1985. Reproductive ecology of bobcats and lynx in western Montana. M.S. thesis. University of Montana, Missoula, MT.

Brainerd, S.M. 1990. The pine marten and forest fragmentation: a review and general hypothesis. Pages 421-434 in Transactions of the 19th IUGB Congress, Trondheim, Norway.

Brand, C.J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. Journal of Wildlife Management 40:416-428**.**

Breininger, D. R., V. L. Larson, B. W. Duncan, R. B. Smith, D. M. Oddy, and M. F. Goodchild. 1995. Landscape patterns of Florida Scrub Jay habitat use and demographic success. Conservation Biology 9: 1442-53.

Brewster, W. G., and S. H. Fritts. 1995. Taxonomy and genetics of the gray wolf in North America: a review. Pages 353-373 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

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, eds. Challenges in the conservation of biological resources: a practitioner's guide. Westview Press, Boulder, CO.

Brody, A. J., and J. N. Stone. 1987. Timber harvest and black bear population dynamics in a southern Appalachian forest. Int. Conf. Bear Res. and Mgmt. 7: 243-250.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.

Buckland, S. T. 1994. The principles and practice of large-scale wildlife surveys. Trans. N. Amer. Wildl. Nat. Resour. Conf. 59: 149-58.

Buckland, S. T., D. A. Elston, S. J. Beaney. 1996. Predicting distributional change, with application to bird distributions in northeast Scotland. Global Ecology and Biogeography Letters. 5:66-xx.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears- implications. Pages 75-98 in C. W. Fowler and F. D. Smith, eds. Dynamics of large mammal populations. Wiley, New York, NY.

Burgman, M.A., S. Ferson, and H.R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman and Hall. London, England.

Buskirk, S. W. 1983. The ecology of marten in southcentral Alaska. Ph.D. thesis. University of Alaska, Fairbanks, AK.

Buskirk, S. W. 1992. Conserving circumboreal forests for martens and fishers. Conservation Biology 6:318-320.

Buskirk, S. W. 1995. The refugium concept and the conservation of forest carnivores. Pages 242-245 in Transactions of the 21st IUGB Congress, Halifax, Canada.

Buskirk, S.W. 1998. Mesocarnivores of Yellowstone. In T. W. Clark, S. C. Minta, P. K. Karieva, and A. P. Curlee, eds. Carnivores in Ecosystems. Yale University Press, New Haven, CT.

Buskirk, S.W., A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. 1994. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283-296 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Buskirk, S.W. and L.F. Ruggiero. 1994. American Marten. Pages 7-37 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. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. 184 pp.

Buskirk, S. W., M. Yiqing, X. Li, and J. Zhaowen. 1996. Winter habitat ecology of sables (Martes zibellina) in relation to forest management in China. Ecological Applications 6: 318-25.

Butts, T. W. 1992. Lynx (*Felis lynx*) biology and management, a literature review and annotated bibliography. USDA Forest Service Northern Region Threatened and Endangered Species Program, Missoula, MT. Unpublished.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, NY.

Campbell, T. M. 1979. Short-term effects of timber harvests on pine marten ecology. M.S. thesis, Colorado State University, Ft. Collins, CO.

Carbyn, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. Canadian Field-Naturalist 96:176-183.

Carbyn, L. N., and P. C. Paquet. 1986. Long distance movement of a coyote from Riding Mountain National Park. Journal of Wildlife Management 50:89.

Carbyn, L. N., and D. Patriquin. 1983. Observations on home range sizes, movements, and social organization of lynx, *Lynx canadensis*, in Riding Mountain National Park, Manitoba. Canadian Field-Naturalist 97:262-267.

Carreker, R. G. 1985. Habitat suitability index models: snowshoe hare. USDI Fish and Wildlife Service Biol. Rep. 82/10.101. 21 pp.

Carroll, C. 1997. Predicting the distribution of the fisher in northwestern California, U.S.A. using GIS modeling and survey data. M.S. thesis, Oregon State University, Corvallis, OR.

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 13:00-00.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Chapin, T. G. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. Conservation Biology 12:1327-1337.

Chapin, T. G., D. M. Phillips, D. J. Harrison, and E. C. York. 1997. Seasonal selection of habitats by resting martens in Maine. Pages 166-181 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes*: taxonomy, ecology, techniques, and management. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.

Chapman, R. C. 1977. The effects of human disturbance on wolves (Canis lupus). M.S. Thesis, Univ. Alaska, Fairbanks. 209pp.

Chepko-Sade, B. D., and W. M. Shields. 1987. The effects of dispersal and social structure on effective population size. Pages 287-321 in B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, IL.

Ciucci, P. and L. Boitani. 1991. Viability assessment of the Italian wolf and guidelines for the management of the wild and a captive population. Ricerche di Biologia dela Selvaggina No. 89.

Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343-356.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519-26.

Clark, T. W., E. Anderson, C. Douglas, and M. Strickland. 1987. *Martes americana*. Mammalian Species Number 289. American Society of Mammalogists. 8 pp.

Clevenger, A. P., F. J. Purroy, and M. A. Campos. 1997. Habitat assessment of a relict brown bear *Ursos arctos* population in northern Spain. Biological Conservation 80:17-22.

Cole, C. A., and R. L. Smith. 1983. Habitat suitability indices for monitoring wildlife populations - an evaluation. Trans. N. Amer. Wildl. Nat. Resour. Conf. 48: 367-75.

Connolly, G. E. 1978. Predator control and coyote populations: a review of simulation models. Pages 327-345 in M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, NY.

Conroy, M. J. 1993. The use of models in natural resource management: prediction, not prescription. Trans. N. Amer. Wildl. Nat. Resour. Conf. 58: 509-19.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications 5: 17-19.

Conroy, M. J., and B. R. Noon. 1996. Mapping of species richness for conservation of biological diversity: conceptual and methodological issues. Ecological Applications 6: 763-73.

Conroy, M. J., and D. R. Smith. 1994. Designing large-scale surveys of wildlife abundance and diversity using statistical sampling principles. Trans. N. Amer. Wildl. Nat. Resour. Conf. 59: 159-69.

Contreras, G. P., and K. E. Evans, eds. 1986. Proceedings- grizzly bear habitat symposium. Gen. Tech. Rep. INT-207. USDA Forest Service Intermountain Research Station, Missoula, MT. 252 pp.

Copeland, J. P. 1996. Biology of the wolverine in central Idaho. M.S. thesis, University of Idaho, Moscow, ID.

Costello, C. M., and R. W. Sage, Jr. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems.

Crabtree, R. L., and J. W. Sheldon. 1998. Coyotes and canid coexistence in Yellowstone National Park. In T. W. Clark, S. C. Minta, P. K. Karieva, and A. P. Curlee, eds. Carnivores in Ecosystems. Yale University Press, New Haven, CT.

Craighead, J. J., J. R. Varney, and F. C. Craighead, Jr. 1974. A population analysis of Yellowstone grizzly bears. Bulletin 40. Montana Forestry and Conservation Experiment Station, Missoula, MT.

Craighead, J. J., and J. A. Mitchell. 1982. Grizzly bear (*Ursus arctos*). Pages 515-556 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

Craighead, J. J., J. S. Summer, and G. B. Skaggs. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Monograph no. 1. Western Wildlands Institute, University of Montana, Missoula, MT.

Craighead, J. J., F. L. Craighead, and D. J. Craighead. 1986. Using satellites to evaluate ecosystems as grizzly bear habitat. Pages 101-112 in G. P. Contreras and K. E. Evans, eds. Proceedings- grizzly bear habitat symposium. Gen. Tech. Rep. INT-207. USDA Forest Service Intermountain Research Station, Missoula, MT.

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.

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.

Craighead, L., R. Walker, R. Noss, and K. Aune. 1997. Applying conceptual models to landscapes: using habitat suitability models of selected species to define core areas and buffer zones for wildlife corridors. Oral presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada.

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.

Crooks, K. R., and M.E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

Crowe, D. M. 1975. A model for exploited bobcat populations in Wyoming. Journal of Wildlife Management 39:408.

Dagg, A. I., and C. A. Campbell. 1974. Historic changes in the distribution and numbers of wolverine in Canada and the northern United States. Canadian Wildlife Service, Ottawa, Ontario. 21 pp.

Dark, S. J. 1997. A landscape-scale analysis of mammalian carnivore distribution and habitat use by fisher. M.S. thesis, Humboldt State University, Arcata, CA.

DeAngelis, D. L., and L. J. Gross, eds. 1992. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Chapman and Hall, New York, NY.

Delcourt, H. R., P. A. Delcourt, and T. Webb. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. Quaternary Science Review 1:153-175.

DeMarchi, R., D. Demarchi, and D. Blower. 1993. Wildlife distribution mapping: grizzly bear. Province of British Columbia Ministry of Environment, Lands, and Parks, Wildlife and Integrated Management Branch, Victoria, B.C. (map)

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115-143.

Dixon, K. R. 1982. Mountain lion (*Felis concolor*). Pages 711-727 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

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.

Doak, D. F. 1997. Using spatial models to address the monitoring and management of rare species. Oral presentation, Annual Meeting of the ESA, August 10-14, Albuquerque, NM.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation biology. Ecology 75:615-626.

Dolbeer, R. A., and W. C. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. Journal of Wildlife Management 39:535-549.

Donelon, S. and P.C. Paquet. 1998. Technical report on development of a decision support model for the Lake O'Hara socio-ecological study. Report prepared by Ptarmigan Designs for Parks Canada, Yoho National Park, B.C..

Donovan, M. L., D. L. Rabe, and C. E. Olson, Jr. 1987. Use of geographic information systems to develop habitat suitability models. Wildl. Soc. Bull. 15: 574-79.

Donovan, T. M., R. H. Lamberson, A. Kimber, F. R. Thompson, III, and J. Faaborg. 1995. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. Conservation Biology 9: 1396-407.

Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9: 1380-1395.

Dorrance, M. J., and L. D. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. Journal of Wildlife Management 49:307.

Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications 5: 3-11.

Duprè, E., F. Corsi, and L. Boitani. In press. Potential distribution of the wolf in Italy: a multivariate GIS based model.

Eberhardt, L. L. 1990. Survival rates required to sustain bear populations. Journal of Wildlife Management 54:587-590.

Eberhardt, L. L., B. M. Blanchard, and R. R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72:360-363.

Edge, W. D., C. L. Marcum, S. L. Olson-Edge. 1990. Distribution and grizzly bear, Ursus arctos, use of yellow sweetvetch, Hedysarum sulphurescens, in northwestern Montana and southeastern British Columbia. Can. Field-Nat. 104:435.

Edwards Jr., T. C., E. T. Deshler, D. Foster, and G. G. Moisen. 1996. Adequacy of wildlife habitat relation models for estimating spatial distributions of terrestrial vertebrates. Conservation Biology 10: 263-270.

Elston, D. A., S. T. Buckland. 1993. Statistical modelling of regional GIS data: an overview. Ecological Modelling. 67:81-102.

ESRI, Inc. 1996. Arc-Info Version 7.0. Environmental Systems Research Institute, Inc. Redlands, CA.

Fager, C. W. 1991. Harvest dynamics and winter habitat use of the pine marten in southwest Montana. M.S. thesis, Montana State University, Bozeman, MT.

Farmer, A. H., M. J. Armbruster, J. W. Terrell, and R. L. Schroeder. 1982. Habitat models for land-use planning: assumptions and strategies for development. Trans. N. Amer. Wildl. Nat. Resour. Conf. 47: 47-56.

Fielding, A. H., and P. F. Haworth. Testing the generality of bird-habitat models. Conservation Biology 9:1466-1481.

Flather, C. H., and S. J. Brady. 1991. Use of geographically extensive databases in regional planning models for wildlife resources. Trans. N. Amer. Wildl. Nat. Resour. Conf. 56: 123-30.

Flather, C. H., and T. W. Hoekstra. 1985. Evaluating population-habitat models using ecological theory. Wildl. Soc. Bull. 13: 121-30.

Flather, C. H., K. R. Wilson, D. J. Dean, and W. C. McComb. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. Ecological Applications 7:531-542.

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.

Foresman, K. R., and D. E. Pearson. 1995. Testing of proposed survey methods for the detection of wolverine, lynx, fisher, and American marten in Bitterroot National Forest. INT-94918 Final Report. USDA Forest Service Intermountain Research Station, Missoula, MT.

France, T. 1994. Politics, forest management, and bears. Int. Conf. Bear Res. Mgmt. 9:523-528.

Fritts, S. H. 1990. Management of wolves inside and outside Yellowstone National Park and possibilities for wolf management zones in the greater Yellowstone area. Pages 1.3-1.88 in J. D. Varley and W. G. Brewster, eds. Wolves for Yellowstone?: a report to the United States Congress. Volume II: Research and analysis. National Park Service, Yellowstone National Park, WY.

Fritts, S. H. 1992. Reintroductions and translocations of wolves in North America: an analysis. Pages 3.3-3.31 in J. D. Varley and W. G. Brewster, eds. Wolves for Yellowstone?: a report to the United States Congress. Volume IV: Research and analysis. National Park Service, Yellowstone National Park, WY.

Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly-protected wolf population in northwestern Minnesota. Wildlife Monographs 80. 79 pp.

Fritts, S. H., E. E. Bangs, and J. F. Gore. 1994. The relationship of wolf recovery to habitat conservation and biodiversity in the Northwestern United States. Landscape and Urban Planning 28:23-32.

Fritts, S. H. and L. N. Carbyn. 1995. Population viability, nature reserves, and the outlook for gray wolf conservation in North America. Restoration Ecology 3:26-38.

Fritts, S. H., E. E. Bangs, J. A. Fontaine, W. G. Brewster, and J. F. Gore. 1995. Restoring wolves to the northern Rocky Mountains of the United States. Pages 107-126 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105:1-41.

Fuller, T. K. 1995. Comparative population dynamics of North American wolves and African wild dogs. Pages 325-328 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Fuller, T. K. 1996. The case of the missing fishers: searching for a source. Oral presentation, Annual conference of the Ecological Society of America, Providence, RI. August 10-14, 1996.

Fuller, T. K., W. E. Berg, and D. W. Kuehn. 1985. Bobcat home range size and daytime cover-type use in northcentral Minnesota. Journal of Mammalogy 66:568-571.

Fuller, T. K., and L. B. Keith. 1980. Summer ranges, cover-type use, and denning of black bears near Fort McMurray, Alberta. Canadian Field-Naturalist 94:80-83.

Fuller, T. K., and D. M. Heisey. 1986. Density-related changes in winter distribution of snowshoe hares in northcentral Minnesota. Journal of Wildlife Management 50:261-264.

Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and G. B. Joselyn. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildl. Soc. Bull. 20:42-55.

Gardner , C . L. 1985. The ecology of wolverines in southcentral Alaska. M.S. thesis. University of Alaska, Fairbanks, AK.

Gardner, C. L., W. B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. Journal of Mammalogy 67:603.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs no. 84.

Gashwiler, J. S., W. L. Robinette, and O. W. Morris. 1960. Foods of bobcats in Utah and eastern Nevada. Journal of Wildlife Management 24:226-229.

Gates, S., D. W. Gibbons, P. C. Lack, and R. J. Fuller. 1994. Declining farmland bird species: modelling geographical patterns of abundance in Britain. Pages 153-177 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Science, Cambridge, UK.

Gese, E. M. 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management 52:640-646. check authorship

Gese, E.M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. Amer. Midl. Nat. 133:36-43.

Gese, E.M., R. L. Ruff, and R. L. Crabtree 1996. Foraging ecology of coyotes (Canis latrans): the influence of extrinsic factors and a dominance hierarchy. Can. J. Zool. 74:769-783.

Gibeau, M. L. 1993a. Use of urban habitats by coyotes in the vicinity of Banff, Alberta. M.S. Thesis. University of Montana, Missoula, MT. 66pp.coyote

Gibeau, M. L. 1993b. Grizzly bear habitat effectiveness model for Banff, Yoho, and Kootenay National Parks. Parks Canada Rep. Banff National Park, Banff, AL.

Gibeau, M. L. 1996. Chapter 7 in: Green, J., C. Pacas, S. Bayley and L. Cornwell, eds. A Cumulative Effects Assessment and Futures Outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, ON.

Gibilisco, C. J. 1994. Distributional dynamics of modern *Martes* in North America. Pages 59-71 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, Sables, and Fishers: Biology and Conservation. Cornell Press, Ithaca. 484 pp.

Gluesing, E. A., S. D. Miller, and R. M. Mitchell. 1986. Management of the North American bobcat: information needs for nondetriment findings. Trans. N. Amer. Wildl. Nat. Resour. Conf. 51: 183-92.

Goodchild, M. F. 1994. Integrating GIS and remote sensing for vegetation analysis and modeling: methodological issues. Journal of Vegetation Science 5: 615-26.

Goss-Custard, J. D., R. W. G. Caldow, R. T. Clarke, S. E. A. le V. dit Durell, J. Urfi, and A. D. West. 1995. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. Ibis 137(Suppl.): 56-66.

Green, G. I., D. J. Mattson, and J. M. Peek. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. Journal of Wildlife Management 61:1040-1055.

Gunther, K. A. 1994. Bear management in Yellowstone National Park, 1960-93. Int. Conf. Bear Res. Mgmt. 9:549-560.

Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94-107.

Hadden, D. A., W. J. Hann, and C. J. Jonkel. 1986. An ecological taxonomy for evaluating grizzly bear habitat in the Whitefish range of Montana. Pages 67-77 in G. P. Contreras and K. E. Evans, eds. Proceedings- grizzly bear habitat symposium. Gen. Tech. Rep. INT-207. USDA Forest Service Intermountain Research Station, Missoula, MT.

Haight, R. G., D. J. Mladenoff, and A. P. Wydeven. 1998. Modeling disjunct gray wolf populations in semi-wild landscapes. Conservation Biology in press.

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

Hall, F. G., D. E. Strebel, and P. J. Sellers. 1988. Linking knowledge among spatial and temporal scales: Vegetation, atmosphere, climate and remote sensing. Landscape Ecology 2: 3-22.

Hamer, D., and S. Herrero. 1987. Grizzly bear food and habitat in the front ranges of Banff National Park. Int. Conf. Bear Res. Mgmt. 7:199-214.

Hamer, D., S. Herrero, and K. Brady. 1991. Food and habitat used by grizzly bears, Ursus arctos, along the continental divide in Waterton Lakes National Park, Alberta. Can. Field-Nat. 105:325.

Hansen, A. J., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications 3: 481-96.

Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. TREE 9:131-135.

Hanski, I. 1996. Metapopulation ecology. Pages 13-44 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, IL.

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10, no. 2: 578-90.

Hanski, I., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Hargis, C. D., and J. A. Bissonette. 1997. Effects of forest fragmentation on populations of American marten in the intermountain west. Pages 437-451 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes*: taxonomy, ecology, techniques, and management. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.

Harrington, F. H., and P. C. Paquet. 1982. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ.

Harrison, D. J., J. A. Bissonette, and J. A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. Journal of Wildlife Management 53:181-185.

Harrison, S. 1994. Metapopulations and conservation. Pages 111-128 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-Scale Ecology and Conservation Biology. Blackwell Scientific Publications, Cambridge, MA.

Harrison, S., A. Stahl, and D. Doak. 1993. Spatial models and spotted owls: exploring some biological issues behind recent events. Conservation Biology 7:950-953.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27-42 in I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Hart, M. M., J. P. Copeland, and R. L. Redmond. 1997. Mapping wolverine habitat in the Northern Rockies using GIS. Poster presentation, Annual conference of the Wildlife Society, snow mass Village, CO.

Hash, H. S. 1987. Wolverine. Pages 575-585 in M. Novak, J. A. Baker, and M. E. Obbard, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario.

Hastie, T. J. 1993. Generalized additive models. Pages 249-308 in J. M. Chambers and T. J. Hastie. Statistical Models in S. Chapman and Hall, New York, NY.

Hastie, T. J., and D. Pregibon. 1993. Generalized linear models. Pages 195-248 in J. M. Chambers and T. J. Hastie. Statistical Models in S. Chapman and Hall, New York, NY.

Hastings, A. and S. Harrison. 1994. Metapopulation dynamics and genetics. Annual Review of Ecology and Systematics 25:167-188.

Hatler, D. F. 1988. A lynx management strategy for British Columbia. Wildlife Bulletin B-61. Wildlife Branch, Ministry of Environment, Victoria, B.C. 122 pp.

Hatler, D. F. 1989. A wolverine management strategy for British Columbia. Wildlife Bulletin B-60. Wildlife Branch, Ministry of Environment, Victoria, B.C. 124 pp.

Haufler, J. B., C. A. Mehl, and G. J. Roloff. 1996. Using a coarse-filter approach with species assessment for ecosystem management. Wildl. Soc. Bull. 24: 200-208.

Hayes, R. D., and J. R. Gunson. 1995. Status and management of wolves in Canada. Pages 21-33 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Hebert, D., J. Youds, R. Davies, H. Langin, D. Janz, and G. W. Smith. 1982. Preliminary investigations of the Vancouver Island wolf (C. lupus crassodon). Pages 54-68 in F. H. Harrington and P.C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publ., Parkridge, N.J.

Hecnar, S. J., and R. T. M'Closkey. 1996. Regional dynamics and the status of amphibians. Ecology 77: 2091-97.

Heinemeyer, K. S. 1993. Temporal dynamics in the movements, habitat use, activity, and spacing of reintroduced fishers in northwestern Montana. University of Montana, Missoula, MT. M.S. thesis. 158 pp.

Heinemayer, K. S., and J. L. Jones. 1994. Fisher biology and management in the western United States: a literature review and adaptive management strategy. USDA Forest Service Northern Region, Missoula, MT. 108 pp.

Henshaw, R. E. 1982. Can the wolf be returned to New York? Pages 395-422 in F. H. Harrington and P. C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. Journal of Wildlife Management 58: 479-87.

Herrero, S., W. McCrory, and B. Pelchat. 1986. Using grizzly bear habitat evaluations to locate trails and campsites in Kananaskis Provincial Park. Int. Conf. Bear Res. and Mgmt. 6: 187-194.

Herrero, S., and J. Herrero. 1996. Cheviot Mine Project: Specific and Cumulative Environmental Effects Analysis for Mammalian Carnivores. 122 pp.

Hoak, J. H., J. L. Weaver, and T. W. Clark. 1982. Wolverines in western Wyoming. Northwest Science 56:159-161.

Hobbs, N. T., M. W. Miller, J. A. Bailey, D. F. Reed, and R. B. Gill. 1990. Biological criteria for introductions of large mammals: using simulation models to predict impacts of competition. Trans. N. Amer. Wildl. Nat. Resour. Conf. 55: 620-632.

Hodgman, T. P., D. J. Harrison, D. D. Katnik, and K. D. Elowe. 1994. Survival in an intensively trapped marten population in Maine. Journal of Wildlife Management 58:593-600.

Hodgman, T. P., D. J. Harrison, D. M. Phillips, and K. D. Elowe. 1997. Survival of American marten in an untrapped forest preserve in Maine. Pages 86-99 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes*: taxonomy, ecology, techniques, and management. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.

Hogmander, H., and J. Moller. 1995. Estimating distribution maps from atlas data using methods of statistical image analysis. Biometrics 51:393-404.

Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. Ecology 75: 17-29.

Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecological Applications 5: 20-27.

Horejsi, B. L. 1986. Industrial and agricultural incursion into grizzly bear habitat: the Alberta story. Pages 116-123 in G. P. Contreras and K. E. Evans, eds. Proceedings- grizzly bear habitat symposium. Gen. Tech. Rep. INT-207. USDA Forest Service Intermountain Research Station, Missoula, MT.

Horejsi, B. L., 1995. Habitat fragmentation by the oil and gas industry in Alberta and British Columbia: Its impact on wildlife. Western Wildlife Environments Consulting Ltd., Calgary, AB,. 10 p.

Hornocker, M. 1970. An analysis of mountain lion predation on mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1-39.

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

Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65: 155-92.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, NY. 307 pp.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. Biological Conservation 57:239-255.

Huggard, D. J. 1991. Prey selectivity of wolves in Banff National Park. M.S. Thesis. Univ. B.C., Vancouver, B.C. 119pp.

Huggard, D. J. 1993a. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management 57:382-388.

Huggard, D.J. 1993b. Prey selectivity of wolves in Banff National Park, I. Age, sex, and condition of elk. Canadian Journal of Zoology 71:130-139.

Huggard, D.J. 1993c. Prey selectivity of wolves in Banff National Park, II. Age, sex, and condition of elk. Canadian Journal of Zoology 71:140-147.

Hummel, M., and S. Pettigrew, and J. Murray. 1992. Wild hunters: predators in peril. Rinehart, Boulder, CO.

Irwin, L. L., and F. M. Hammond. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin 13:477-483.

Jalkotzy, M. G., P. I. Ross, and M. D. Nasserden. 1997. The effects of linear developments on wildlife: a review of selected scientific literature. Prep. for Canadian Association of Petroleum Producers. Arc Wildlife Services Ltd., Calgary. 115pp.

Jalkotzy, M. G., P. I. Ross, and J. Wierzchowski. 1999. Cougar habitat use in southwestern Alberta. Unpublished report prepared for the Alberta Conservation Association. Arc Wildlife Services Ltd., Calgary, AB. 32pp. + app.

James, F. C., C. A. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecological Applications 7:118-129.

Janz, D. W. 1989. Wolf-deer interactions on Vancouver Island --- a review. Pages 26-42 in Wolf-prey dynamics and management --- proceedings. Wild. Working Rep. No. WR-40. B.C. Ministry of Environment, Victoria, B.C.

Jennings, M. D., B. Csuti, and J. M.. Scott. 1997. Wildlife habitat relationship models: distribution and abundance. Conservation Biology 11:1271-1272.

Jensen, W. F.; Fuller, T. K.; Robinson, W. L. 1986. Wolf, Canis lupus , distribution on the Ontario-Michigan border near Sault Ste. Marie. Can. Field Nat.??

Johnson, A. R. 1996. Spatiotemporal hierarchies in ecological theory and modeling. Pages 451-456 in M. F. Goodchild, L. T. Steyaert, B. O. Parks, C. Johnston, D. Maidment, M. Crane, and S. Glendinning, editors. GIS and environmental modeling: progress and research issues. GIS World Books, Fort Collins, CO., editors. GIS and Environmental Modeling.

Johnson, A. R., J. A. Wiens, B. T. Milne, and T. O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7:63-75.

Jones, J. L., and E. O. Garton. 1994. Selection of successional stages by fishers in northcentral Idaho. Pages 377-387 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Jones, L. L. C., and M. G. Raphael. 1991. Ecology and management of marten in fragmented habitats of the Pacific Northwest. USDA PNW Research Station, Portland, OR. Unpublished. 26 pp.

Kansas, J., M. Raine, and M. Gibeau. 1989. Ecological studies of black bears in Banff National Park 1986-1988. Final Report. 135 pp. Prepared for Canadian Parks Service, Banff National Park.

Kansas, J. L., and R. M. Raine. 1990. Methodologies used to assess the relative importance of ecological land classification units to black bears in Banff National Park, Alberta. Int. Conf. Bear Res. and Mgmt. 8: 155-160.

Kansas, J. L., P. L. Achuff, and R. M. Raine. 1989. A food habits model for grizzly bear habitat evaluation in Banff, Jasper, Kootenay, and Yoho National Parks. Beak Assoc. Consulting, Ltd. Unpublished report. 118 pp.

Kansas, J. L., and R. N. Riddell. 1995. Grizzly bear habitat model for the four contiguous mountain parks: second iteration. Report AB 2702A39(DW) prepared for Parks Canada Alberta region by Ursus Ecosystem Management, Ltd. and Riddell Environmental Resources Ltd., Calgary, AB. 95 pages + appendices.

Katnik, D. D., D. J. Harrison, and T. P. Hodgman. 1994. Spatial relations in a harvested population of marten in Maine. Journal of Wildlife Management 58:600-607.

Karieva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299-302.

Karieva, P., D. Skelly, and M. Ruckelshaus. 1996. Reevaluating the use of models to predict the consequences of habitat loss and fragmentation. Pages 156-166 in S. T. A. Pickett, R.S. Ostfeld, M. Schachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York, NY.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Kasworm, W. F., and T. L. Manley. 1990. Road and trail influences on grizzly bears and black bears in northwest Montana. Int. Conf. Bear Res. and Mgmt. 8: 79-84.

Kasworm, W. F., and T. J. Thier. 1994. Adult black bear reproduction, survival, and mortality sources in northwest Montana. Int. Conf. Bear Res. Mgmt. 9:223-230.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66-77 in L. N. Carbyn, ed., Wolves in Canada and Alaska. Can. Wildl. Rpt. Series No. 45., Ottawa.

Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology [online]1:4.

Kelly, J. P. 1982. Impacts of forest harvesting on the pine marten in the central interior of British Columbia. M.S. thesis, University of Alberta, Edmonton, Alberta.

Kenney, J. S., J. L. D. Smith, A. M. Starfield, and C. W. McDougal. 1995. The long-term effects of tiger poaching on population viability. Conservation Biology 9: 1127-33.

Klug, Jr., R. R. 1996. Occurrence of Pacific fisher (*Martes pennanti*) in the redwood zone of northern California and the habitat attributes associated with their detections. M.S. thesis, Humboldt State University, Arcata, CA.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monograph No. 108. 42 pp.

Knight, R. R., and L. L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323-334.

Knight, R. R., and L. L. Eberhardt. 1987. Prospects for Yellowstone grizzly bears. Int. Conf. Bear Res. and Mgmt. 7: 45-50.

Knight, R. R., B. M. Blanchard, and L. L. Eberhardt. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973-1985. Wildlife Society Bulletin 16:121-125.

Knowles, P. R. 1985. Home range size and habitat selection of bobcats, Lynx rufus, in north-central Montana. Can Field-Nat. 99:6.

Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in northcentral Washington. Canadian Journal of Zoology 68:845-851.

Koehler, G. M. 1991. Snowshoe hare, Lepus americanus, use of forest successional stages and population changes during in north-central Washington. Can. Field-Nat. 105:291-293.

Koehler, G. M., and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. Journal of Wildlife Management 41:500-505.

Koehler, G. M., M. G. Hornocker, and H. S. Hash. 1979. Lynx movements and habitat use in Montana. Canadian Field-Naturalist 93:441-442.

Koehler, G. M., and M. G. Hornocker. 1989. Influence of seasons on bobcats in Idaho. Journal of Wildlife Management 53:197-202.

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

Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy 72:391-396.

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. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. 184 pp.

Koth, B., D. W. Lime, and J. Vlaming. 1990. Effects of restoring wolves on Yellowstone area big game and grizzly bears: opinions of fifteen North American experts. Pages 4.51-4.81 in J. D. Varley and W. G. Brewster, eds. Wolves for Yellowstone?: a report to the United States Congress. Volume II: Research and analysis. National Park Service, Yellowstone National Park, WY.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications 2: 203-216.

Krohn, W. B. 1992. Sequence of habitat occupancy and abandonment: potential standards for testing habitat models. Wildl. Soc. Bull. 20: 441-44.

Krohn, W. B., S. M. Arthur, and T. F. Paragi. 1994. Mortality and vulnerability of a heavily trapped fisher population. Pages 137-145 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Krohn, W. B., W. J. Zielinski, and R. B. Boone. 1997. Relations among fishers, snow, and martens in California: results from small-scale spatial comparisons. Pages 211-232 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes*: taxonomy, ecology, techniques, and management. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.

Kujala, Q. J. 1993. Winter habitat selection and population status of pine marten in southwest Montana. M.S. thesis, Montana State University, Bozeman, MT.

Lacy, R. C. 1993. VORTEX: a computer simulation model for population viability analysis. Wildlife Research 20:45-65.

Lacy, R. C., and T. W. Clark. 1993. Simulation modeling of American marten (*Martes americana*) populations: vulnerability to extinction. Great Basin Naturalist 53:282-292.

Laing, S. P. 1988. Cougar habitat selection and spatial use patterns in southern Utah. M.S. thesis, University of Wyoming, Laramie. 68 pp.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 11:849-856.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conservation Biology 6: 505-12.

Lamberson, R. H., B. R. Noon, C. Voss, and R. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. Conservation Biology 8:185-195.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130:624-635.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2:316-328.

Lawton, J. H., and G. L. Woodroffe. 1991. Habitat and the distribution of water voles: why are there gaps in a species' range? Journal of Animal Ecology 60:79-91.

Lebreton, J.-D. 1996. Demographic models for subdivided populations: the renewal equation approach.. Theoretical Population Biology 49:291-313.

Lenihan, J. M. 1993. Ecological response surfaces for North American boreal tree species and their use in forest classification. Journal of Vegetation Science 4:667-680.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Levins, R. 1970. Extinction. Pages 77-107 in M. Gerstenhaber, ed. Some mathematical questions in biology. Am. Math. Soc., Providence, RI.

Lewis, J. and W. J. Zielinski. 1997. Historical harvest and incidental capture of fisher in California. Northwest Science 70:291-297.

Lindenmayer, D. B., and R. C. Lacy. 1995. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. Ecological Applications 5: 183-99.

Lindenmayer, D. B., and H. P. Possingham. 1996a. Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. Landscape Ecology 11:79-105.

Lindenmayer, D. B., and H. P. Possingham. 1996b. Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using population viability analysis. Conservation Biology 10:235-251.

Lindenmayer, D. B., M. A. Burgman, H. R. Akcakaya, R. C. Lacy, and H. P. Possingham. 1995.. A review of the generic computer programs ALEX, RAMAS/Space, and VORTEX for modeling the viability of wildlife metapopulations. Ecological Modelling 82:161-174.

Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics inn southern Utah. Journal of Wildlife Management 58:619-624.

Litvaitis, J. A., J. A. Shelburne, and J. A. Bissonette. 1985. Bobcat-coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180-1188.

Litvaitis, J. A., J. A. Shelburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110-117.

Liu, J., J. B. Dunning, Jr., and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's Sparrows (Aimophila aestivalis): linking a spatially explicit model with GIS. Conservation Biology 9: 62-75.

Logan, K., and L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. Wildlife Society Bulletin 13:257-262.

Lomolino, M. V., and R. Channell. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. Journal of Mammalogy 76: 335-47.

Lovallo, M. J., and E. M. Anderson. 1996. Bobcat (Lynx rufus) home range size and habitat use in northwest Wisconsin. Am Mid Nat 135:241.

Luque, M. H. 1983. Report on 1983 fisher survey for the Idaho Dept. Fish and Game. Idaho Coop. Wildlife Research Unit, Moscow, ID. Unpublished report.

Mace, R. D. 1986. Analysis of grizzly bear habitat in the Bob Marshall Wilderness, Montana. Pages 136-149 in G. P. Contreras and K. E. Evans, eds. Proceedings- grizzly bear habitat symposium. Gen. Tech. Rep. INT-207. USDA Forest Service Intermountain Research Station, Missoula, MT.

Mace, R. D., and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. Wildl. Soc. Bull. 24, no. 3: 461-67.

Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana Journal of Applied Ecology 33:1395-1404.

Mace, R. D., and J. S. Waller. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. Journal of Wildlife Management 61:39-52.

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.

Maehr, D. S., C. T. Moore. 1992. Models of mass growth for 3 North American cougar populations. Journal of Wildlife Management 56:700.

Maehr, D. S., and J. A. Cox. 1995. Landscape features and panthers in Florida. Conservation Biology 9: 1008-19.

Magoun, A. J. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. PhD. thesis. University of Alaska, Fairbanks, AK. 197 pp.

Magoun, A. J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. Canadian Field-Naturalist 101:392-397.

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

Major, J. T., and J. A. Sherburne. 1987. Interspecific relationships among coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51:606-616.

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, NJ.

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

Marcot, B. G., M. G. Raphael, and K. H. Berry. 1983. Monitoring wildlife habitat and validation of wildlife-habitat relationships models. Trans. N. Amer. Wildl. Nat. Resour. Conf. 48: 315-29.

Massolo, A., and A. Meriggi. 1998. Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. Ecography 21:97-107.

Mattson, D. J. 1987. Habitat dynamics and their relationship to biological parameters for he Yellowstone grizzly bear, 1977-1983: progress report. U.S. National Park Service, Interagency Grizzly Bear Study Team, Bozeman, MT.

Mattson, D. J. 1990. Human impacts on bear habitat use. Int. Conf. Bear Res. and Mgmt. 8:35-56.

Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biological Conservation 81:161-177.

Mattson, D. J. 1997. Use of lodgepole pine cover types by Yellowstone grizzly bears. Journal of Wildlife Management 61:480-496.

Mattson, D. J. 1998. Changes in mortality of Yellowstone grizzly bears. Int. Conf. Bear Res. Mgmt. 10:129-138.

Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1986. Derivation of habitat component values for the Yellowstone grizzly bear. Pages 222-229 in G. P. Contreras and K. E. Evans, eds. Proceedings --- grizzly bear habitat symposium. Gen. Tech. Rep. INT-207, USDA Forest Service Intermountain Research Station, Missoula, MT.

Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of development and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. Int. Conf. Bear Res. and Mgmt. 7:259-273.

Mattson, D. J., and R. R. Knight. 1989. Evaluation of grizzly bear habitat using habitat type and cover type classifications. Pages 135-143 in D. E. Ferguson, P. Morgan, and F. D. Johnson, eds. Proceedings-land classifications based on vegetation: applications for resource management. USDA Forest Service Gen. Tech. Rep. INT-257, USDA Forest Service Intermountain Research Station, Missoula, MT.

Mattson, D. J., and R. R. Knight. 1991a. Implications of short-rotation (70-120 year) timber management to Yellowstone grizzly bears. U.S. National Park Service, Bozeman, MT.

Mattson, D. J., and R. R. Knight. 1991b. Effects of access on human-caused mortality of Yellowstone grizzly bears. U.S. National Park Service, Bozeman, MT.

Mattson, D. J., and M. M. Reid. 1991. Conservation of the Yellowstone grizzly bear. Conservation Biology 5:364-372.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991a. Food habits of Yellowstone grizzly bears, 1977-1987. Canadian Journal of Zoology 69:1619-1629.

Mattson, D. J., C. M. Benson, and R. R. Knight. 1991b. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. Canadian Journal of Zoology 69:2430-2435.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56:432-442.

Mattson, D. J., and J. J. Craighead. 1994. The Yellowstone grizzly bear recovery program: uncertain information, uncertain policy. Pages 101-130 in T. W. Clark, R. P. Reading, and A. L. Clarke, eds. Endangered species recovery: finding the lessons, improving the process. Island Press, Washington, D.C.

Mattson, D. J., D. P. Reinhart, and B. M. Blanchard. 1994. Variation in production and bear use of whitebark pine seeds in the Yellowstone area. Pages 205-220 in D. G. Despain, ed. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. USDI National Park Service Tech. Rep. NPS/NRYELL/NRTR-93/XX.

Mattson, D. J., S. Herrero, R. G. Wright, and C. M. Pease. 1996. Designing and managing protected areas for bears: how much is enough? Pages 133-164 in R. G. wright, ed. National parks and protected areas: their role in environmental protection. Blackwell Science, Cambridge, MA.

Mattson, D. J., and D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34:926-940.

May, R. 1994. The effects of spatial scale on ecological questions and answers. Pages 1-18 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Science, Cambridge, MA.

McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. Biological Conservation 73:93-100.

McCord, C. M., and J. E. Cardoza. 1982. Bobcat and lynx (*Felis rufus* and *F. lynx*). Pages 728-768 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

McCrory, W., McTavish, C, and P.C. Paquet. 1999. Grizzly bear background research document 1993-1996 for GIS bear encounter risk model, Yoho National Park, B.C.. Report prepared for Parks Canada, Yoho National Park, B.C. McCrory Wildlife Services Ltd., Box 146, New Denver, BC V0G 1S0.

McCulloch, C. E., and M. L. Cain. 1989. Analyzing discrete movement data as a correlated random walk. Ecology 70: 383-88.

McGarigal, K., and B.J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. USDA Forest Service Pacific Northwest Research Station, Portland, OR. 122 pp.

McGarigal, K. 1993. Relationships between landscape structure and breeding birds in the Oregon coast range. Doctoral thesis, Oregon State University, Corvallis, OR.

McGarigal, K., and W.C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs 65: 235-260.

McKelvey, K., B. R. Noon, and R.H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. pp. 424-450 in P.M. Kareiva, J. G. King solver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA.

McKelvey, K. S., Y. K. Ortega, G. Koehler, K. Aubry, and D. Brittell. In press. Canada lynx habitat and topographic use patterns in north central Washington: a reanalysis. In L. F. Ruggiero, et al., eds. The scientific basis for lynx conservation. Gen. Tech. Rep. RMRS-30. USDA Forest Service Rocky Mtn. Research Station, Missoula, MT.

McKelvey, K. S., K. Aubry, and Y. K. Ortega. In press. History and distribution of lynx in the contiguous United States. In L. F. Ruggiero, et al., eds. The scientific basis for lynx conservation. Gen. Tech. Rep. RMRS-30. USDA Forest Service Rocky Mtn. Research Station, Missoula, MT.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555-1558.

McLellan, B. N. 1990. Relationships between human industrial activity and grizzly bears. Int. Conf. Bear Res. and Mgmt. 8: 57-64.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource extraction industries: effects of roads on behaviour, habitat use, and demography. Journal of Applied Ecology 25:451-460.

McLellan, B. N., and D. M. Shackleton. 1989. Grizzly bears and resource extraction industries: habitat displacement in response to seismic exploration, timber harvesting, and road maintenance. Journal of Applied Ecology 26:371-380.

McNay, R. S. and J. M. Moller. 1995. Mortality causes and survival estimates for adult female columbian black-tailed deer. Journal of Wildlife Management 59:138-146.

Meagher, M., and J. R. Phillips. 1983. Restoration of natural populations of grizzly and black bears in Yellowstone National Park. Int. Conf. Bear Res. and Mgmt. 5:152-158.

Mealey, S. P., C. J. Jonkel, and R. DeMarchi. 1977. Habitat criteria for grizzly bear management. Int. Cong. Game Biol. 13: 276-288.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, NY.

Mech, L. D. 1977a. Record movement of a Canada lynx. Journal of Mammalogy 58:676-677.

Mech, L. D. 1977b. Productivity, mortality, and population trends of wolves in northeastern Minnesota. J. Mammal. 58:559-574.

Mech, L. D. 1977c. Wolf pack buffer zones as prey reservoirs. Science 198:320-321.

Mech, L. D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnesota. Journal of Mammalogy 61:261-267.

Mech, L. D. 1987. Age, season, distance, direction, and social aspects of wolf dispersal from a Minnesota pack. Pages 55-74 in B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, IL.

Mech, L. D. 1989. Wolf population survival in an area of high road density. Am. Midl. Nat. 121:387-389.

Mech, L. D. 1993. Updating our thinking on the role of human activity in wolf recovery. Research Information Bulletin 57. U.S. Fish and Wildlife Service. St. Paul, Minnesota.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology 9:270-278.

Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin 16:85-87.

Mech, L. D. and S.M. Goyal. 1993. Canine parvovirus effect on wolf population change and pup survival. Journal of Wildlife Diseases. 22:104-106.

Mech, L. D., S. H. Fritts, and D. Wagner. 1995. Minnesota wolf dispersal to Wisconsin and Michigan. American Midland Naturalist 133:368-370.

Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. Unpublished. Analysis of the current and future availability and distribution of suitable habitat for grizzly bears in the transboundary Selkirk and Cabinet-Yaak ecosystem.

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63:1068-1077.

Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. Pages 187-197 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Metzgar, L. H., and M. Baker. 1992. Large mammal predators in the northern Rockies: grizzly bears and their habitat. Northwest Environmental Journal 8:231-233.

Miller, R. I., S. N. Stuart, and K. M. Howell. 1989. A methodology for analyzing rare species distribution patterns utilizing GIS technology: the rare birds of Tanzania. Landscape Ecology 2:173-190.

Mills, L. S., S. G. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology 10:863-873.

Mills, L. S., and F. F. Knowlton. 1990. Coyote space use in relation to prey abundance. Canadian Journal of Zoology 69:1516-1521.

Milne, B. T., K. M. Johnston, and R. T. T. Forman. 1989. Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. Landscape Ecology 2:101-110.

Minta, S.C., and P.M. Kareiva. 1994. A conservation science perspective: conceptual and experimental improvements. Pages 275-304 in T. W. Clark, R. P. Reading, and A. Clarke, editors. Endangered Species Recovery. Island Press, Washington, DC.

Minta, S. C. 1996. Summary of progress to date: Western Yellowstone Forest Carnivore Project. Unpublished report. 56 pp. with appendices.

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

Mladenoff, D. J., R. G. Haight, T. A. Sickley, and A. P. Wydeven. 1997. Causes and implications of species restoration in altered ecosystems: a spatial landscape projection of wolf population recovery. Bioscience 47:21-31.

Monthey, R. W. 1986. Responses of snowshoe hares, Lepus americanus, to timber harvesting in northern Maine. Can. Field-Nat. 100:568-570.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68: 362-69. 1106.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. University of Wisconsin Press, Madison, WI.

Mowat, G., B. G. Slough, and S. Boutin. 1996. Lynx recruitment during a snowshoe hare population peak and decline in southwest Yukon. Journal of Wildlife Management 60:441-52.

Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Conservation Biology 4:41-51.

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.

Murphy, K. M., G. S. Felzien, M. G. Hornocker, T. K. Ruth. 1998. Encounter competition between bears and cougars: some ecological implications. Int. Conf. Bear Res. and Mgmt. 10:55-60.

Murray, D. L., and S. Boutin. 1991. The influence of snow on lynx and coyote movements: does morphology affect behaviour? Ecologia 88:463-469.

National Wildlife Federation. 1991. Draft petition for a rule to list the lynx as endangered in Colorado, Idaho, Montana, and Wyoming. Unpublished. 20 pp.

Nead, D. M., J. C. Halfpenny, and S. Bissell. 1985. The status of wolverines in Colorado. Northwest Science 58:286-289.

Neave, H. M., R. B. Cunningham, T. W. Norton, and H. A. Nix. 1996. Biological inventory for conservation evaluation III. Relationships between birds, vegetation and environmental attributes in southern Australia. Forest Ecology and Management 85:197-218.

Nellis, C. H., and L. B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964-68. Journal of Wildlife Management 40:389-399.

Nellis, C. H., S. P. Wetmore, and L. B. Keith. 1972. Lynx-prey interactions in central Alberta. Journal of Wildlife Management 38:541-545.

Nelson, M.E. and L. D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. J. Wildl. Mange. 50:471-474.

Newmark, W. D. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology 9: 512-26.

Noon, B. R. and K. S. McKelvey. 1996a. A common framework for conservation planning: linking individual and metapopulation models. Pages 139-165 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Noon, B. R. and K. S. McKelvey. 1996b. Management of the spotted owl: a case history in conservation biology. Annual Review of Ecology and Systematics 27:135-62.

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 10:949-63.

O'Connor, R. M., D. J. Reed, and R. O. Stephenson. 1987. Lynx population dynamics and harvest: insight from a computer model. In B. Townsend, ed. Fourth Northern Furbearer Conf., Alaska Dept. Fish and Game, Juneau, AK.

Okarma, H., Jedrzejewska, B., Jedrzejewski, W., Milkowski L. and Krasinski, Z. 1995. The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. Acta Theriologica 40: 335-386.

Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer, New York, NY.

Opdam, P., R. Foppen, R. Reijnen, and A. Schotman. 1995. The landscape ecological approach in bird conservation: integrating the metapopulation concept into spatial planning. Ibis 137(Suppl.): 139-46.

Pacas, C. J., and P. C. Paquet. 1994. Analysis of black bear home range using a geographic information system. Int. Conf. Bear Res. Mgmt. 9:419-426.

Paquet, P.C. 1991a. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy. 72:397-401.

Paquet, P.C. 1991b. Scent marking behavior of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park. Canadian Journal of Zoology. 69:1721-1727.

Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy. 73:337-343.

Paquet, P.C. 1993. Summary reference document --- ecological studies of recolonizing wolves in the Central Canadian Rocky Mountains. Unpublished report by John/Paul and Assoc. for Canadian Parks Service, Banff, AB. 176pp.

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

Paquet, P. C, J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in: Green, J., C. Pacas, S. Bayley and L. Cornwell, eds. A Cumulative Effects Assessment and Futures Outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, ON.

Paquet, P. C., J. Wierzchowski, and C. Callaghan. 1997. Assessing reserve designs using a predictive habitat suitability and movement model. Oral presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada.

Paradiso, J. L., and R. M. Nowak. 1982. Wolves (*Canis lupus*). Pages 460-474 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

Parker, G. R., J. W. Maxwell, L. D. Morton, and G. E. J. Smith. 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. Canadian Journal of Zoology 61:770-786.

Pascual, M. A., P. Karieva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology 11:966-976.

Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. Ecology 80:957-975.

Peek, J. M., M. R. Pelton, H. D. Picton, J. W. Schoen, and P. Zager. 1987. Grizzly bear conservation and management: a review. Wildlife Society Bulletin 15: 160-169.

Peek, J. M., D. E. Brown, L. D. Mech, J. H. Shaw, and V. Van Ballenberghe. 1991. Restoration of wolves in North America. Wildlife Society Technical Review 91-1.

Pelchat, B. O.., and R. L. Ruff. 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. Int. Conf. Bear Res. and Mgmt. 6: 81-92.

Pelton, M. R. 1982. Black bear (*Ursus americanus*). Pages 504-514 in J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, MD.

Periera, J. M., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression --- a study of the Mt. Graham red squirrel. Photogrammetric Engineering and Remote Sensing 57: 1475-1486.

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, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Picton, H. D. 1986. A possible link between Yellowstone and Glacier grizzly bear populations. Int. Conf. Bear Res. and Mgmt. 6:7-10.

Pletscher, D. H., R. R. Ream, D. K. Boyd, M. W. Fairchild, and K. E. Kunkel. 1997. Population dynamics of a recolonizing wolf population. Journal of Wildlife Management 61:459-465.

Poole, K. G., L. A. Wakelyn, and P. N. Nicklen. 1994. Habitat selection by lynx in the Northwest Territories. Can. J. Zool. 74:845-850.

Possingham, H. P., and I. Davies. 1995. ALEX: a model for the viability analysis of spatial structured populations. Biological Conservation 73:143-150.

Powell, R. A. 1979. Fishers, population models, and trapping. Wildlife Society Bulletin 7:149-154.

Powell, R. A. 1993. The fisher: life history, ecology, and behavior. 2nd ed. University of Minnesota Press, Minneapolis, MN.

Powell, R.A. 1994. Structure and spacing of *Martes* populations. Pages 101-121 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Powell, R. A., J. W. Zimmerman, and D. E. Seaman. 1997. Ecology and behaviour of North American black bears: home ranges, habitat, and social organization. Chapman and Hall, New York, NY.

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. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mtn. Forest and Range Experiment Station, Ft. Collins, CO.

Powell, R. A., J. W. Zimmerman, D. E. Seaman, and J. F. Gilliam. 1996. Demographic analysis of a hunted back bear population with access to a refuge. Conservation Biology 10:224-234.

Pulliam, R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652- 661.

Pulliam, R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45-69 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, IL.

Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications 2:165-77.

Pulliam, H. R., J. Liu, J. B. Dunning, Jr., D. J. Stewart, and T. D. Bishop. 1995. Modelling animal populations in changing landscapes. Ibis 137(Suppl.): 120-126.

Pullianen, E. 1968. Breeding biology of the wolverine (*Gulo gulo*) in Finland. Ann. Zool. Fenn. 5:338-344.

Purves, H. D., White, C.A., and Paquet, P.C. 1992. Wolf and grizzly bear habitat use and displacement by human use in Banff, Yoho, and Kootenay National Parks: a preliminary analysis. Canadian Parks Service Rept. Banff, Alta. 54pp.

Pyrah, D. 1984. Social distribution and population estimates of coyotes in north-central Montana. Journal of Wildlife Management 48:679-690.

Quinn, N. W. S., and G. Parker. 1987. Lynx. Pages 683-694 in M. Novak, J. A. Baker, and M. E. Obbard, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario.

Quinn, N. W. S., and J. E. Thompson. 1987. Dynamics of an exploited Canada lynx population in Ontario. Journal of Wildlife Management 51:297-305.

Raine, R. M. 1983. Winter habitat use and response to snow cover of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. Canadian Journal of Zoology 61:25-34.

Raine, R. M., and J. L. Kansas. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. Int. Conf. Bear Res. and Mgmt. 297-304.

Ralls, K., and A. M. Starfield. 1995. Choosing a management strategy: two structured decision-making methods for evaluating the predictions of stochastic simulation models. Conservation Biology 9:175-81.

Ramsey, F. L., M. McCracken, J. A. Crawford, M. S. Drut, and W. J. Ripple. 1994. Habitat association studies of the northern spotted owl, sage grouse, and flammulated owl. Pages 189-209 in N. Lange, L. Ryan, and L. Billard, D. Brillinger, L. Conquest, and J. Greenhouse, editors. Case studies in Biometry. John Wiley & Sons, New York, NY.

Rastetter, E. B., A. W. King, B. J. Cosby, G. M. Hornberger, R. V. O'Neill, and J. E. Hobbie. 1992. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. Ecological Applications 2: 55-70.

Reading, R. P., and T. W. Clark. 1996. Carnivore reintroductions: an interdisciplinary examination. Pages 296-336 in J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution, Volume 2. Cornell University Press, Ithaca, NY.

Ream, R. R., M. W. Fairchild, D. K. Boyd, and D. H. Pletscher. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349-366 in R. B. Keiter and M. S. Boyce, eds. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, CT.

Reinhart, D. P., and D. J. Mattson. 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. Int. Conf. Bear Res. Mgmt. 8:343-350.

Rogers, L. L. 1987. Factors influencing dispersal in the black bear. Pages 75-84 in B. D. Chepko-Sade and Z. T. Halpin, eds. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, IL.

Rolley, R. E. 1987. Bobcat. In M. Novak, J. A. Baker, and M. E. Obbard, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario.

Roloff, G. J., and J. B. Haufler. 1998. Establishing population viability planning objectives based on habitat potentials. Wildlife Society Bulletin in press.

Rosenberg, K.V. and R.G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263-272 in J. Verner, M. L. Morrison, and C.J. Ralph, editors. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417-426.

Ross, P. I., and M. G. Jalkotzy. 1997. Cougar predation on moose in southwestern Alberta. Alces 32:1-8.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24:490-494.

Roy, L. D., and M. J. Dorrance. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. Journal of Wildlife Management 49:307-313.

Roy, K. D. 1991. Ecology of reintroduced fishers in the Cabinet Mountains of northwest Montana. M.S. thesis. University of Montana, Bozeman, MT.

Ruckelshaus, M., C. Hartway, and P. Karieva. 1997. Assessing the data requirements of spatially explicit models. Conservation Biology 11:1298-1306.

Rudis, V. A., and J. B. Tansey. 1995. Regional assessment of remote forests and black bear habitat from forest resource surveys. Journal of Wildlife Management 59:170-180.

Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. 1994. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mtn. Forest and Range Experiment Station, Ft. Collins, CO. 184 pp.

Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. Conservation Biology 8:364-72.

Ruggiero, L. F. et al. 1999. The scientific basis for lynx conservation. Gen. Tech. Rep. RMRS-30. USDA Forest Service Rocky Mtn. Research Station, Missoula, MT.

Ruth, T. K., K. A. Logan, L. L. Sweanor, M. G. Hornocker, and L. J. Temple. 1998. Evaluating cougar translocations in New Mexico. Journal of Wildlife Management 62:1264-1275.

Salwasser, H., C. Sconewald-Cox, and R. Baker. 1987. The role of interagency cooperation in managing for viable populations. Pages 159-173 in M. Soulé, ed. Viable populations for conservation. Cambridge University Press, New York, NY.

Sawyer, M., D. Mayhood, P. Paquet, C. Wallis, R. Thomas and W. Haskins. 1997. Cumulative Effect Assessment On Alberta's Southern Eastern Slopes. Report to Morrison Petroleums, Ltd. by Hayduke and Associates, Ltd., Calgary, Alberta.

Schneider, R. 1997. Simulated spatial dynamics of martens in response to habitat succession in the Western Newfoundland Model Forest. Pages 419-436 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes*: taxonomy, ecology, techniques, and management. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.

Schneider, R.R. and P. Yodzis. 1994. Extinction dynamics in the american marten (*Martes americana*). Conservation Biology 8:1058-1068.

Schoen, J. W. 1990. Bear habitat management: a review and future perspective. Int. Conf. Bear Res. and Mgmt. 8: 143-154.

Schoen, J. W., R. W. Flynn, L. H. Suring, K. Titus, and L. R. Beier. 1994. Habitat-capability model for brown bear in southeast Alaska. Int. Conf. Bear Res. and Mgmt. 9:327-337.

Schulz, T. T., and L. A. Joyce. 1992. A spatial application of a marten habitat model. Wildlife Society Bulletin 20:74-83.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. Ecology 77:1210-1225.

Scott, J. M.., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, Jr., J. Ulliman, and R. G. Wright. 1993. Gap analysis: a geographic approach to the protection of biological diversity. Wildlife Monographs 123.

Seidel, J., B. Andree, S. Berlinger, K. Buell, G. Byrne, B. Gill, D. Kenvin, and D. Reed. 1997. Draft strategy for the conservation and reestablishment of lynx and wolverine in the southern Rocky Mountains. Colorado Division of Wildlife, Fort Collins, CO. 116 pp.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:1-60.

Seip, D. R. 1995. Introduction to wolf-prey interactions. Pages 179-186 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Seitz, W. K., C. L. Kling, and A. H. Farmer. 1982. Habitat evaluation: a comparison of three approaches on the Northern Great Plains. Trans. N. Amer. Wildl. Nat. Resour. Conf. 47: 82-95.

Servheen, C. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. Journal of Wildlife Management 47:1026-1035.

Servheen, C. 1990. The status and conservation of bears of the world. Eighth Int. Conf. Bear Res. and Mgmt. Monograph Series no. 2, Victoria, B.C.

Servheen, C. ed. 1993. Grizzly bear recovery plan. USDI Fish and Wildlife Service, Missoula, MT.

Servheen, C., W. Kasworm, and A. Christensen. 1987. Approaches to augmenting grizzly bear populations in the Cabinet Mountains of Montana. Int. Conf. Bear res. and Mgmt. 7: 363-368.

Servheen, C. W., and R. R. Knight. 1990. Possible effects of a restored wolf population on grizzly bears in the Yellowstone area. Pages 4.35-4.49 in J. D. Varley and W. G. Brewster, eds. Wolves for Yellowstone?: a report to the United States Congress. Volume II: Research and analysis. National Park Service, Yellowstone National Park, WY.

Servheen, C., and P. Sandstrom. 1993. Human activities and linkage zones for grizzly bears in the Swan-Clearwater Valleys, Montana. University of Montana, Missoula, MT. **models**

Servheen, C., P. Sandstrom, and S. Meitz. 1996. Habitat fragmentation factors and linkage considerations for the maintenance of global bear populations. Int. Conf. Bear Res. and Mgmt. 10:xx.

Shaffer, M. L. 1983. Determining minimum population sizes for the grizzly bear. Int. Conf. Bear Res. and Mgmt. 5:133-139.

Shaffer, M. L. 1992. Keeping the grizzly bear in the American West: a strategy for real recovery. The Wilderness Society, Washington, D.C.

Shaffer, M. L., and F. B. Samson. 1985. Population size and extinction: a note on determining critical population sizes. American Naturalist 125:144-152.

Simberloff, D. 1995. Habitat fragmentation and population extinction of birds. Ibis 137(Suppl.): 105-11.

Singer, F. J. 1991. The ungulate prey base for wolves in Yellowstone National Park. Pages 323-348 in R. B. Keiter and M. S. Boyce, eds. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, CT.

Singer, F. J. 1992. Some predictions concerning a wolf recovery in Yellowstone National Park: how wolf recovery may affect park visitors, ungulates, and other predators. Pages 4.3-4.34 in J. D. Varley and W. G. Brewster, eds. Wolves for Yellowstone?: a report to the United States Congress. Volume II: Research and analysis. National Park Service, Yellowstone National Park, WY.

Singleton, P.H. 1995. Winter habitat selection by wolves in the North Fork of the Flathead River Basin, Montana and British Columbia. M.S. Thesis. Univ. Of Montana, Missoula. 116pp.

Skatrud, M. 1997. Logging threatens lynx in northern WA. Home Range 7:6-7.

Slough, B. G., and G. Mowat. 1996a. Population dynamics of lynx in a refuge and interactions between harvested and unharvested sub-populations. Journal of Wildlife Management 60:441-452.

Slough, B. G., and G. Mowat. 1996b. Lynx population dynamics in an untrapped refugium. Journal of Wildlife Management 60:946-961.

Smith, J. N. M., M. J. Taitt, C. M. Rogers, P. Arcese, L. F. Keller, A. L. E. V. Cassidy, and W. M. Hochachka. 1996. A metapopulation approach to the population biology of the Song Sparrow Melospiza melodia. Ibis 138: 120-128.

Smith, D. S. 1984. Habitat use, home range, and movements of bobcats in western Montana. M.S. thesis, University of Montana, Missoula, MT.

Species Analysis Team. 1994. Results of additional species analysis: appendix J2 to the FSEIS on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. Government Printing Office, Washington, DC. 486 pp.

Spencer, W. D. Unpublished. A test of a pine marten habitat suitability model for the northern Sierra Nevada. 43 pp.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1181-1186.

Staples, W. R. 1995. Lynx and coyote diet and habitat relationships during a low hare population on the Kenai peninsula. M.S. thesis, University of Alaska, Fairbanks, AK. 150 pp.

Starfield, A. M., J. D. Roth, and K. Ralls. 1995. 'Mobbing' in Hawaiian monk seals (Monachus schauinslani): the value of simulation modeling in the absence of apparently crucial data. Conservation Biology 9: 166-74.

Stauffer, C. E., and A. Aharony. 1985. Introduction to percolation theory. Taylor and Francis, London, U.K.

Stelfox, J. G. 1971. Wolves in Alberta: a history 1800-1969. Alberta Lands, Forests, Parks, and Wildlife 12:18-27.

Stephenson, R. O., and P. Karczmarczyk. 1989. Development of techniques for evaluating lynx population status in Alaska. P-R Report W-23-1, job 7.13. Alaska Dept. Fish and Game, Juneau, AK.

Stith, B. M., J. W. Fitzpatrick, G. E. Woolfenden, and B. Pranty. 1996. Classification and conservation of metapopulations: a case study of the Florida scrub jay. Pages 187-215 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Stoms, D. M., F. W. Davis, C. B. Cogan, M. O. Painho, B. W. Duncan, J. Scepan, and J. M. Scott. 1993. Geographic analysis of California condor sighting data. Conservation Biology 7: 148-59.

Strickland, M. A., and C. W. Douglas. Marten. Pages 530-546 in M. Novak, J. A. Baker, and M. E. Obbard, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario.

Strickland, M. D. 1990. Grizzly bear recovery in the contiguous United States. Int. Conf. Bear Res. and Mgmt. 8: 5-10.

Strong, P. I. V. 1994. Viability analysis in biological evaluations. Conservation Biology 8: 927-28.

Stuart, T. W. 1978. Management models for human use of grizzly bear habitat. Trans. N. Amer. Wildl. Nat. Resour. Conf. 43: 434-41.

Sturtevant, B. R., J. A. Bissonette, and J. N. Long. 1996. Temporal and spatial dynamics of boreal forest structure in western Newfoundland: silvicultural implications for marten habitat management Forest Ecology and Management 87(1-3):13.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin desert. Conservation Biology 11:1407-1417.

Taylor, B. L., P. R. Wade, R. A. Stehn, and J. F. Cochrane. 1996. A Bayesian approach to classification criteria for Spectacled Eiders. Ecological Applications 6: 1077-89.

Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biology 9: 551-58.

Taylor, M. K., D. P. DeMaster, F. L. Bunnell, and R. E. Schweinsburg. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management 51: 811-20.

Taylor, M. K., F. Bunnell, D. DeMaster, R. Schweinsburg, and J. Smith. 1987. ANURSUS: a population analysis system for polar bears. Int. Conf. Bear Res. and Mgmt. 7: 117-125.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2: 340-347.

Theberge, J. B., and D. A. Gauthier. 1985. Models of wolf-ungulate relationships: when is wolf control justified? Wildl. Soc. Bull. 13: 449-58.

Theberge, J. B. 1991. Ecological classification, status, and management of the gray wolf, *Canis lupus*, in Canada. Canadian Field-Naturalist 105:459-463.

Thiel, R. P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. Am Mid Nat. 113:404.

Thiel, R. P., and R. R. Ream. 1995. Status of the gray wolf in the lower 48 United States to 1992. Pages 59-62 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Thomasma, L. E., T. D. Drummer, and R. O. Peterson. 1994. Modeling habitat selection by the fisher. Pages 316-325 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Thomasma, L. E., T. D. Drummer, and R. O. Peterson. 1991. Testing the habitat suitability model for the fisher. Wildlife Society Bulletin 19:291-297.

Thompson, I.D. 1991. Could marten become the spotted owl of Canada? Forestry Chronicle 67:136-140.

Thompson, I.D. and A.S. Harestad. 1994. Effects of logging on American martens with models for habitat management. Pages 355-367 in S. W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, Sables, and Fishers: Biology and Conservation. Cornell Press, Ithaca, NY. 484 pp.

Thurber, J. M., R. O. Peterson, T. R. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin 22:61-68.

Tietje, W. D., and R. L. Ruff. 1983. Responses of black bears to oil development in Alberta. Wildlife Society Bulletin 11:99-112.

Tilman, D., and P. M. Kareiva, editors. 1997. Spatial ecology : the role of space in population dynamics and interspecific interactions. Princeton Univ. Press, Princeton, NJ.

Todd, A. W., and L. B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 47:394-404.

Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildl. Soc. Bull. 24: 451-60.

Tumlinson, R. 1987. Felis lynx. Mammalian Species. American Society of Mammalogists. 269:1-8.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72:1253-66.

Turchin, Peter. 1996. Fractal analyses of animal movement: a critique. Ecology 77:2086-90.

USDI Fish and Wildlife Service. 1992. Recovery plan for the eastern timber wolf. St. Paul, MN.

USDI Fish and Wildlife Service. 1994. 12 month finding for a petition to list as endangered or threatened the contiguous United States population of the Canada lynx. Federal Register 59:66507-66509.

USDI Fish and Wildlife Service. 1996. 90-day finding for a petition to list the fisher in the western United States as threatened. Federal Register 61:8016.

USDI Fish and Wildlife Service. 1997. Grizzly bear recovery in the Bitterroot ecosystem: draft environmental impact statement. Missoula, MT. 23 pp.

Vales, D. J., and J. M. Peek. 1995. Projecting the potential effects of wolf predation on elk and mule deer in the east front portion of the northwest Montana wolf recovery area. Pages 211-222 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Van Ballenberghe, V., W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildlife Monographs 43. 43pp.

Van Dyke, F. G., R. H. Brocke, H. G. Shaw, B. B. Ackerman, T. P. Hemker, and F. G. Lindzey. 1986. Reactions of mountain lions to logging and human activity. Journal of Wildlife Management 50:95-102.

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

Van Zyll de Jong, C. G. 1975. The distribution and abundance of the wolverine (*Gulo gulo*) in Canada. Canadian Field-Naturalist 89:431-437.

Villard, M.-A., G. Merriam, and B. A. Maurer. 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. Ecology 76: 27-40.

Voight, D. R., and W. E. Berg. 1987. Coyote. Pages 345-356 in M. Novak, J. A. Baker, and M. E. Obbard, eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Ontario.

Vroom, G. W., S. Herrero, and R. T. Ogilvie. 1980. The ecology of winter den sites of grizzly bears in Banff National Park, Alberta. Int. Conf. Bear Res. and Mgmt. 4: 321-330.

Walker, D. A., and M. D. Walker. 1991. History and pattern of disturbance in Alaskan arctic terrestrial ecosystems: a hierarchical approach to analyzing landscape change. Journal of Applied Ecology 28:244-276.

Walker, R., and L. Craighead. 1997. Monte Carlo simulation of wildlife movements through a GIS model landscape: defining potential wildlife corridors, bottlenecks, and critical areas. Oral presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada.

Walmo, O. C. and J. W. Schoen. 1980. Response of deer to secondary forest succession in Southeast Alaska. For. Sci. 26:448-462.

Walsh, P. D., H. R. Akcakaya, and M. Burgman. 1995. PVA in theory and practice. Conservation Biology 9: 704-8.

Washington State Department of Wildlife. 1993. Status of the North American lynx (*Lynx canadensis*) in Washington. Unpublished report, Washington Department of Wildlife, Olympia, WA. 101 pp.

Washington State Department of Natural Resources. 1994. Lynx habitat management plan for DNR managed lands, November, 14, 1996. 180 pp.

Weaver, J. 1993. Lynx, wolverine, and fisher in the western United States: research assessment and agenda. USDA Forest Service Intermountain Research Station, Missoula, MT. 132 pp.

Weaver, J., R. E. F. Escano,, and D. S. Winn. 1986. A framework for assessing cumulative effects on grizzly bears. North American Wildlife and Natural Resources Conference 52:364-376.

Weaver, J., R. Escano, D. Mattson, T. Puchlerz, and D. Despain. 1986. A cumulative effects model for grizzly bear management in the Yellowstone ecosystem. Pages 234-246 inn G. P. Contreras and K. E. Evans, eds. Proceedings-grizzly bear habitat symposium. USDA Forrest Service Gen. Tech. Rep. INT-207, USDA Forest Service Intermountain Research Station, Missoula, MT.

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.

Weir, R. D. 1995. Diet, spatial organization, and habitat relationships of fishers in south-central British Columbia. M.S. thesis. Simon Fraser University, Burnaby, B.C.

Weir, R. D., and A. S. Harestad. 1997. Landscape-level selection by fishers in south-central British Columbia. Pages 252-264 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes*: taxonomy, ecology, techniques, and management. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.

Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. Journal of Wildlife Management 50:460-463.

Wielgus, R. B., and F. L. Bunnell. 1993. Dynamics of a small, hunted brown bear population in southwestern Alberta, Canada. Biological Conservation 67:298-305.

Wielgus, R. B., F. L. Bunnell, W. L. Wakkinen, and P. E. Zager. 1994. Population dynamics of Selkirk Mountain grizzly bears. Journal of Wildlife Management 58:266-272.

Wiens, J. A. 1989a. The ecology of bird communities. Vol. II. Processes and Variations. Cambridge University Press, New York, NY.

Wiens, J. A. 1989b. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wiens, J.A. 1995. Habitat fragmentation: island vs. landscape perspectives on bird conservation. Ibis 137: S97-S104.

Wiens, J. A.. 1996. The emerging role of patchiness in conservation biology. Pages 93-107 in S. T. A. Pickett, R.S. Ostfeld, M. Schachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York.

Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43-62 in I. Hanski and M. E. Gilpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Wilbert, C. J. 1992. Spatial scale and seasonality of habitat selection by martens in southeastern Wyoming. M. S. thesis, University of Wyoming, Laramie, WY. 91 pp.

Williams, J. S., J. J. McCarthy, and H. D. Picton. 1995. Cougar habitat use and food habits on the Montana Rocky Mountain Front. Intermountain Journal of Sciences 1:16-28.

With, K. A. 1997. The application of neutral landscape models in conservation biology. Conservation Biology 11:1069-1080.

With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

Witmer, G. W., and D. S. DeCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian Journal of Zoology 64:2333-2338.

Wolfe, M. L., N. V. Debyle, and C. S. Winchell. 1982. Snowshoe hare cover relationships in northern Utah. Journal of Wildlife Management 46:662-670.

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

Woodruffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.

Wu, H., and F. W. Huffer. 1997. Modelling the distribution of plant species using the autologistic regression model. Environmental and Ecological Statistics 4:49-64.

Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring of a recovering gray wolf population in Wisconsin, 1979-1991. Pages 147-156 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

York, E. C. 1996. Fisher population dynamics in north-central Massachusetts. M.S. thesis. University of Massachusetts, Amherst, MA.

Young, D. D., and J. J. Beechum. 1986. Black bear habitat use at Priest Lake, Idaho. Int. Conf. Bear Res. and Mgmt. 6:73-80.

Zager, P. E., and C. J. Jonkel. 1983. Managing grizzly bear habitat in the northern Rocky Mountains. Journal of Forestry 8:524-526.

Zager, P. E., C. J. Jonkel, and J. Habeck. 1983. Logging and wildfire influence on grizzly bear habitat in northwestern Montana. Int. Conf. Bear Res. and Mgmt. 5: 124-132.

Zielinski, W. J. and T. E. Kucera. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. Gen. Tech. Rep. PSW-GTR-157. USDA Forest Service Pacific Southwest Research Station, Albany, CA. 163 pp.

Zielinski, W.J. and H. B. Stauffer. 1996. Monitoring *Martes* populations in California: survey design and power analysis. Ecological Applications 6:1254-1267.