Chapter 1

Is the Return of the Wolf, Wolverine, and Grizzly Bear to Oregon and California Biologically Feasible?

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Carnivores are indicators of ecosystem function and can serve as keystones in the top-down regulation of ecosystems (Terborgh et al. 1999). Although the strength of top-down processes varies widely among species and ecosystems (Noss et al. 1996), it is probably more prevalent than many ecologists have assumed (Terborgh et al. 1999; Crooks and Soulé 1999). Wide-ranging carnivores may serve as "bioassays" of emergent landscape characteristics such as connectivity and give us information on the optimal size and arrangement of reserves. Viability analysis of carnivore species may highlight potential reserve areas that are not targeted in other biodiversity assessments such as gap analysis (Scott et al. 1993).

The restoration of mammalian carnivore species to portions of their former range, either by restoration of habitat or through active reintroduction, presents new challenges. Besides the inevitable sociopolitical difficulties, large and medium-sized carnivores may be particularly sensitive to landscape configuration because of their low population densities and large area requirements. In these species, population processes operate on a regional scale. Thus, regional-scale habitat models can be useful management tools for prioritizing restoration efforts. Multispecies conservation strategies have

many advantages over single-species strategies (Noss et al. 1997). The extent to which restoration efforts for a particular species will enhance viability of the broader carnivore guild can be assessed by considering the major factors—such as topography, forest structure, and risk of human-induced mortality—that limit their distribution and abundance.

We used predictive habitat models to develop a carnivore restoration strategy for Oregon and northern California for three species: the gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), and wolverine (*Gulo gulo*)—species currently extirpated from most or all of the region. Natural range expansion from adjacent states or existing refugia may be possible for at least the wolf and wolverine, and reintroduction programs have been proposed for all three species. Knowledge of the current amount and configuration of habitat can help us to identify core habitat areas and dispersal routes for these species and predict the viability of restored populations.

The three carnivore species considered here differ in the degree to which they tolerate human-associated landscape change and direct persecution. Contrasts in behavior, demographic characteristics, and population or metapopulation structure result in differing levels of ecological resilience (Weaver et al. 1996). All three species avoid humans. The wolf is highly resilient demographically, but its social structure increases the area requirements for viable populations. In mountainous portions of the western United States, the wolf may be especially vulnerable because its avoidance of rugged terrain brings it into greater proximity to human settlements (Paquet et al. 1996). The wolverine has the lowest reproductive output despite its relatively small size. The grizzly bear's limited dispersal abilities make it the most vulnerable species at the metapopulation level (Weaver et al. 1996).

The three species differ as well in the ecological roles they have played in Pacific coastal ecosystems and the potential impact of their restoration on current ecosystem dynamics. Bears may be an important link between riparian and upland systems—especially in regions, such as the Pacific coast, with anadromous fish populations. Nutrient input from salmon may be a key factor in productivity of coastal forest ecosystems (Bilby et al. 1996). The grizzly bear in south-central Alaska redistributed 40 percent of the salmon entering a coastal stream and was the conduit for 20 percent of the nitrogen uptake in adjacent forests (Hilderbrand et al. 1999). Storer and Tevis (1955:17) comment: "Its numbers multiplied by its average daily metabolic requirement must have made the grizzly an outstanding factor in the total food consumption by mammals . . . [and] a dominant element in the original native biota of California." The historic ecological role of the wolf in the Pacific Northwest is unknown. Wolf reintroduction appears to have strongly affected ver-

tebrate communities in the Greater Yellowstone Ecosystem (Smith et al. 1999), and we might expect similar effects in portions of the Pacific states. The ecological influence of wolverine populations in the lower 48 states is almost entirely unknown.

The historical factors leading to range contraction and extirpation differ among the three species, but all three were affected by predator control programs during the late 1800s and early 1900s (Schullery and Whittlesey 1999). To the extent that today's land management agencies are more tolerant of predators, the absence of these species from much of their former range is not an inevitable consequence of current human population density and land use. In eastern Europe, Italy, and China, populations of large carnivores coexist with much higher levels of human population density (Mattson 1990). In this chapter we present an approach for evaluating the biological feasibility of restoring populations of wolf, grizzly bear, and wolverine to areas within their former range in Oregon and California. We adapt habitat suitability models developed for these species in the Rocky Mountains, show potential core areas in a combined study region, and estimate potential population size.

Wolf

The historical distribution and abundance of the wolf in the Pacific coastal states is uncertain. In California, wolves were probably most abundant on the northern coast, where elk (*Cervus elaphus*) were abundant, and in the northeastern corner of the state where they were found until 1922 (Grinnell et al. 1937; Schmidt 1991). Early extirpation from northern coastal California may have been due to human settlement patterns, including the gold rush of the 1850s, that briefly made the area one of the most densely populated in the western United States. Wolves were historically common in western Oregon (Bailey 1936), as well as east of the Cascades Range (Young and Goldman 1964). Most museum specimens were collected from the western foothills of the Cascades; the last wolf bounty in Oregon was awarded there in 1946 (Verts and Carraway 1998). Wolves reportedly persisted in the Oregon Cascades even after they were extirpated from the Rocky Mountain region (Young and Goldman 1964). While only scattered wolf reports exist from the latter half of the twentieth century, wolves have recently been documented dispersing into Oregon from the rapidly growing Idaho population (see chapter 6 in this volume).

Generally wolves locate their home ranges in areas where adequate prey are available and human interference is low (Mladenoff et al. 1995). The pri-

mary limiting factor for wolves has not been habitat degradation or prey depletion but direct persecution through hunting, trapping, and predator control programs. As human tolerance of large predators increases, however, wolves are well equipped to recolonize remaining areas of their former range. Because wolves reach sexual maturity at an early age and have large litters, the wolf has a high level of ecological resilience compared with other large carnivores (Weaver et al. 1996). The species' flexible social structure allows pack size, fecundity, and dispersal to respond to shifts in population density and prey abundance (Fuller 1989; Boyd et al. 1995; Weaver et al. 1996). Nonetheless, wolves were eliminated in areas of the western United States where grizzly bears persisted, suggesting that these compensatory mechanisms have limits. Population densities of wolves are usually far lower than population densities of sympatric grizzly bears. And as social animals, wolves are more susceptible to predator control than solitary animals.

Human activities affect wolf distribution and wolf survival (Thiel 1985; Fuller et al. 1992; Mladenoff et al. 1995; Paquet 1993; Paquet et al. 1996). In Wisconsin (Mladenoff et al. 1995) and Minnesota (Fuller et al. 1992), wolves selected areas with low human population density. The absence of wolves in human-dominated areas may reflect high levels of human-caused mortality, displacement resulting from behavioral avoidance, or some combination of both (Fuller et al. 1992; Mech and Goyal 1993). Roads, by increasing human access, negatively affect wolf populations at local, landscape, and regional scales (Fuller 1989; Thurber et al. 1994; Mladenoff et al. 1995). Wolves may avoid densely roaded areas because of traffic volume (Thurber et al. 1994), or their absence may be a direct result of mortality associated with roads (Van Ballenberghe et al. 1975). Even in areas where wolf harvest is prohibited, 80 to 95 percent of mortality is often anthropogenic (Fuller 1989; Mech 1989; Paquet 1993; Pletscher et al. 1997). Wolves in mountainous regions often concentrate their activities in forest valleys where snow conditions and prey availability are optimal (Paquet 1993; Paquet et al. 1996; Singleton 1995). Topography has not been incorporated in previous models (Mladenoff et al. 1995) developed in the north-central United States, due to the flatter terrain typical of that region.

Ungulates such as elk, deer (*Odocoileus virginianus* and *O. hemionus*), moose (*Alces alces*), 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 hare (*Lepus americanus*) and beaver (*Castor canadensis*). Ungulate biomass (Keith 1983; Fuller 1989), density, and species diversity (Corsi et al. 1999) are important habitat factors. In a review of studies from several regions, for example, prey density explained 72 percent of the varia-

tion in wolf density (Fuller 1989). A smaller core area can support a viable wolf population if prey biomass per unit area is high (Fritts and Carbyn 1995; Wydeven et al. 1995).

Grizzly Bear

The current distribution of the grizzly bear in the Pacific coastal states is confined to a small remnant population in the North Cascades of Washington, where 17 records have been confirmed in recent decades (Almack et al. 1993). Distribution was widespread in Oregon except in the arid east (Bailey 1936). The last grizzly bear in the state was killed in northeastern Oregon in 1931 (Verts and Carraway 1998). As many as 10,000 grizzly bears occurred throughout California except in the northeast and the Mojave Desert (Storer and Tevis 1955). Although the California grizzly may have been most common in chaparral rather than dense forest, it was also abundant in oak woodlands, river valleys, and mixed-hardwood forests (Storer and Tevis 1955). In the 1850s, a settler counted 40 bears feeding along the Mattole River in coastal northwestern California (Grinnell et al. 1937). Despite its initial abundance, the species was extirpated from northern California by 1902. The last known grizzly in the state was killed in the southern Sierra Nevada in 1924 (Storer and Tevis 1955).

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). Its low lifetime reproductive potential (as few as three female young per adult female) makes population viability sensitive to small declines in adult survivorship (Weaver et al. 1996). Although subadult males often disperse two home-range diameters (about 70 km), successful long-distance dispersal between subpopulations has not been recorded in the western United States.

The range of the grizzly has become increasingly fragmented (Craighead and Vyse 1996), exacerbating the demographic and genetic risks associated with small, isolated populations. Craighead and Vyse (1996) have compared the viability of bear populations on islands of varying size and conclude that isolated populations require at least 1000 bears for long-term persistence. Mattson and Reid (1991) found a similar size threshold for European brown bear populations. Roads and their traffic cause direct mortality, disrupt bear behavior, create barriers to movement (Archibald et al. 1987; McLellan and Shackleton 1988), and increase poaching and removal of habituated bears (Mattson et al. 1987; Weaver et al. 1996).

Although the grizzly is an omnivore, its resilience is limited by its

seasonally high caloric needs (Weaver et al. 1996). The species was widespread in western ecosystems, and its diet reflects this distribution. Key foods range from soft mast (drupes, berries) and hard mast (acorns, whitebark pine nuts) to fish, vertebrate carrion, and insects (Storer and Tevis 1955; Mattson and Reid 1991).

Wolverine

Because wolverines exist at low densities and inhabit remote areas, it is difficult to judge whether the Pacific Northwest supports reproducing populations or just dispersing individuals. In California, the last confirmed specimens were collected from the Sierra Nevada in the early 1900s (Grinnell et al. 1937). More recent unconfirmed reports originate from the southern Sierra Nevada (Barrett et al. 1994). In Oregon, specimens were confirmed in the Blue Mountains of eastern Oregon in 1986 and 1992 and from Steens Mountain in southeastern Oregon in 1973 (Verts and Carraway 1998). Specimens were collected from the central Oregon Cascades in 1965, 1969, and 1973 (Verts and Carraway 1998). The 1969 specimen was a female, suggesting the possibility of reproduction. It seems clear, however, based on the sparse evidence, that wolverines are scarce in Oregon and California relative to the Rocky Mountains. Although little is known about the wolverine's habitat needs and distribution in the Pacific Northwest, fragmentation of the landscape by roads and human development may hinder natural recovery there as in other regions (Carroll et al. 2001).

Because the wolverine's diet includes unpredictably distributed resources such as carrion, it has larger home-range requirements than equivalent-sized carnivores. Carrion use may link wolverines to other carnivores, such as wolves, that are much reduced in the western United States. Moreover, wolf poisoning campaigns have eradicated local wolverine populations as well in some regions (Banci 1994).

Female wolverines mature at three years of age and produce less than one kit per year until death at six to eight years (Copeland 1996). Large area requirements and low reproductive rates make the wolverine especially vulnerable to human-induced mortality and habitat alteration. Populations probably cannot sustain annual rates of human-induced mortality greater than 7 or 8 percent, a rate lower than that usually caused by trapping (Gardner 1985; Banci 1994; Weaver et al. 1996). Areas closed to trapping such as Yellowstone National Park and the Canadian mountain parks in Alberta and British Columbia appear to be wolverine refugia (Hatler 1989; Buskirk 1999).

Although the wolverine's long-range dispersal abilities (greater than 200 km in Idaho; Copeland 1996) may facilitate its persistence, females tend to settle closer to their place of birth (Banci 1994). The large home-range sizes of Idaho wolverine (a mean of 384 km² in females) relative to those in Canada and Alaska suggest more limited food or denning resources (Copeland 1996). Female wolverines must leave their kits for lengthy foraging trips. In the lower 48 states, they often select natal dens in alpine areas where snow tunnels in talus can provide thermoregulatory benefits and safety from predators (Magoun and Copeland 1998). Natal dens in Alaska, by contrast, appear less limited by topography or human settlement (Magoun and Copeland 1998).

Habitat Models

Using habitat quality to predict carnivore distribution is especially challenging because there is much to learn about the link between habitat and demography. Habitat models such as the habitat suitability index (HSI) system were developed primarily for site-level planning and may be poor templates for regional evaluations. Such conceptual models rely on qualitative relationships derived from expert opinion and published studies. Empirical models, in contrast, base predictions on statistical analyses of species occurrence data. Regional-scale empirical models have been used to predict range expansion of wolves in the north-central and northeastern United States (Mladenoff et al. 1995, 1999), as well as grizzly bear distribution in Idaho and Montana (Merrill et al. 1999; Mace et al. 1999; Boyce and MacDonald 1999).

For most carnivores, regional species occurrence data, primarily sighting and trapping records, are not systematically collected. If the biases are accounted for and the results checked against independent data, models built from occurrence data may be more reliable than conceptual models. When telemetry information is available for part of the region, mesoscale empirical models developed from these data may be adapted to predict distribution at the regional scale—although the reliability of the original data is offset by our ignorance of emergent regional-scale factors. When demographic data are available, spatial variation in survival and fecundity can be estimated and the results used to predict the distribution of regional sources and sinks—although such demographic data are rare.

Given the diversity of ecosystem types found within our analysis area, habitat models must be broad in order to be accurate across the region. Models that might have high predictive power in the east may extrapolate poorly

across the western United States. We used three approaches to predict habitat quality for wolf, grizzly bear, and wolverine: sighting and trapping records were used to develop an empirical model for the wolverine; grizzly bear habitat was predicted by adapting previously published models (Merrill et al. 1999; Mace et al. 1999); wolf habitat was predicted with a conceptual model in which individual elements were derived from statistical analysis of telemetry data (P. Paquet, unpublished data). All models used habitat data at a resolution of 1 km². Although our habitat maps are static models, they can form the basis for dynamic models that predict whether a patch of suitable habitat is large and connected enough to remain occupied by a species.

Wolf

We mapped predicted habitat value for gray wolf by combining an empirical model relating wolf distribution to topography (Paquet et al. 1996) with variables suggested by other studies. The three primary model components were prey density, prey accessibility, and security from human disturbances.

PREY DENSITY. Although ungulate population data are available for some areas (such as California and Idaho), comparable data are not available for the entire region. In order to build a seamless map of ungulate abundance, we developed a linear regression model using deer abundance data and forage availability based on "tasseled-cap greenness," a transformation of Landsat Thematic Mapper satellite imagery (Crist and Cicone 1984). We compared the regression results with deer harvest data from Oregon and ungulate abundance estimates from Idaho.

The deer regression model was developed from the average 1990–1996 deer population in northern and central California (CDFG 1998). Although a linear regression using data from all seven units was significant ($p = 0.02$; $R^2 = 0.69$; DF = 5), we chose a robust regression model that excluded the unit with highest deer density to avoid overestimating prey abundance ($p < 0.01$; $R^2 = 0.85$; DF = 4). The regression equation was deer/km² = 2.2789 + 0.0533 × greenness.

Deer harvest data for Oregon were correlated with greenness ($p < 0.01$; $R^2 = 0.4088$; DF = 65). Although elk population estimates were not available on a statewide level for California, elk abundance is low compared with deer. Oregon elk harvest was not correlated with greenness ($p > 0.10$). In Idaho, however, the only state where abundance estimates for all ungulate species were available, wolf population estimates derived from ungulate abundance data were within 6 percent of those derived using the deer/greenness model.

Although the greenness model may not accurately predict abundance of particular species as prey community composition changes in interior ecosystems, it may be more robust as an estimator of total prey biomass.

PREY ACCESSIBILITY. Rugged terrain may make prey less available to wolves (Paquet et al. 1996). The relationship between prey accessibility and slope was modeled as the power equation $Y = 28.18405 \times 0.931377^x$, where $x =$ slope in degrees. This equation was developed from wolf radiotelemetry data from four study areas with different topography (Riding Mountain National Park, Manitoba; Pukaskwa National Park, Ontario; Jasper National Park, Alberta; and the central Canadian Rockies) (Paquet et al. unpublished data).

SECURITY. We incorporated road and human population density into a composite habitat-effectiveness metric representing level of security or lack of human presence (Merrill et al. 1999). GIS data for roads, trails, and railroads at the 1:100,000 scale (USGS, unpublished data) were grouped into expected use classes, weighted, and examined at the 1-km^2 resolution. Paved highways were weighted two to three times more heavily than unpaved roads, and trails were weighted at 0.35 that of unpaved roads (Merrill et al. 1999).

Local human population density was derived from census blocks, which range in size from 1 to more than 100 km^2. The effects of population centers over distance were derived from population data interpolated by using an inverse distance weighting algorithm (Merrill et al. 1999).

COMBINING HABITAT FACTORS. To determine the likelihood that wolves or other wide-ranging carnivores will inhabit a region, we developed a GIS function (FOCALSEARCH) that sums total mortality risk within a variable-size moving window with a diameter based on habitat productivity. Wolf pack territories may range in size from 100 km^2 to more than 2000 km^2 depending on prey productivity (Wydeven et al. 1995; Paquet et al. 1996).

PREDICTING WOLF POPULATION SIZE. We used a two-step process for estimating potential wolf population size (Mladenoff and Sickley 1999). This method assumes that although regional wolf distribution is most limited by human-caused mortality, prey density determines abundance in otherwise suitable areas. Once mortality risk was approximated using a moving window, we delineated areas where survival rates would be high enough to permit wolf persistence. Although the habitat effectiveness values represent relative rather than absolute mortality risk, thresholds can be based on areas of known wolf

distribution. In our region, we used current wolf distribution in the Rocky Mountains (Houts 2000) to select the 25 percent of the region with lowest mortality risk as core habitat and the second most favorable quartile as peripheral habitat. These thresholds provide a means of ranking areas based on proportion of core habitat, which is known to influence population persistence (Haight et al. 1998).

Once areas of core and peripheral habitat were delineated, we could estimate the number of wolves expected to inhabit the area. Here we used an equation relating wolf density to prey density (Fuller 1989, 1995; Mladenoff et al. 1999):

$$\text{wolf density}/1000 \text{ km}^2 = 4.19 \times \text{DEPU/km}^2$$

where DEPU (deer-equivalent prey units) was estimated from our deer/greenness regression model. Besides evaluating the relative levels of mortality risk, we evaluated the proportion of an area in public ownership as a factor influencing the feasibility of wolf restoration.

Grizzly Bear

We mapped predicted habitat for grizzly bear by adapting a model previously developed from Idaho sighting data (Merrill et al. 1999) and incorporated tasseled-cap greenness in order to measure habitat productivity (Mace et al. 1999; Gibeau 2000). This model was similar to the wolf model but lacked the negative effect of rugged terrain. Mortality risk was summed within a variable-size moving window whose total productivity was similar to that of grizzly bear home ranges in the Rocky Mountains (Merrill et al. 1999). Because grizzly bears do not show a high ability to compensate demographically for increased mortality (Weaver et al. 1996), we used this scaled total mortality risk as the principal predictor of whether the species could persist. We did not attempt to incorporate greenness values further in predicting potential population size.

Wolverine

We combined wolverine occurrence records (Natural Heritage Database, unpublished data) with GIS data on vegetation, topography, climate, and human-use variables (Carroll et al. 2001). We used multiple logistic regression to compare habitat variables at sighting locations with those at random points (Hosmer and Lemershow 1989). A large set of alternative multivariate models was constructed and evaluated with the Bayesian information criterion (BIC) (Schwarz 1978). We used the coefficients from the final multi-

variate model to calculate a resource selection function (RSF) (Manly et al. 1993; Boyce and McDonald 1999) representing the relative probability of wolverine occurrence at a location. The final model incorporated annual snowfall (Daly et al. 1994), interpolated human population density (Merrill et al. 1999), road density, and cirque habitat for wolverine dens (Hart et al. 1997).

Results

Wolf

If wolves successfully disperse to the southern Cascades and Modoc Plateau, this region may well hold the largest subpopulation in the Pacific coastal states (190–470 wolves) (Figure 1.1). Northeastern Oregon could support a population of about 100. Although southeastern Oregon has low human use, it is arid and may only support a low-density population. Coastal areas may support small populations, but a lower proportion of core habitat may make persistence even less probable than in arid areas. The central and southern Sierra Nevada region, in contrast, has a high proportion of core habitat, but low prey densities, rugged terrain, and distance from existing wolf populations reduce the likelihood of occupation. Among the larger habitat areas, the southern Oregon Cascades and Modoc Plateau have a relatively high proportion of public land (Table 1.1), making these areas most feasible for restoration.

Table 1.1. GAP Land Management Classes in Potential Wolf Population Areas

Region	Area (km²)	Park/wilderness	Other public	Private
SE Oregon	18,100	14.4%	50.8%	34.8%
NE Oregon	7,800	18.1	31.6	50.3
N Oregon Cascades	6,700	28.8	48.4	22.8
S Cascades	14,600	13.6	58.2	28.2
Modoc Plateau	33,700	6.8	57.7	35.5
Sierra Nevada	15,400	54.2	42.2	3.6
North coast	7,300	0.6	9.7	89.7
Central coast	7,800	0.9	32.0	67.1
South coast	6,100	16.4	40.2	43.4
California coast	8,100	9.0	20.5	70.5

PREDICTED WOLF HABITAT
EFFECTIVENESS VALUE (QUANTILE)

☐ LOWEST (0-50)
▨ MEDIUM (50-75)
■ HIGH (75-100)
▨ NO DATA
N Study Area Boundary

POTENTIAL SUBPOPULATIONS
AND POPULATION SIZES IN
CORE AREA AND TOTAL REGION

A - CANADIAN ROCKIES (270/420)
B - NCDE (160/330)
C - GYE (380/580)
D - CENTRAL IDAHO (400/740)
E - SE OREGON (60/150)
F - NE OREGON (30/100)
G - N OREGON CASCADES (40/70)
H - S CASCADES (50/150)
I - MODOC PLATEAU (140/320)
J - SIERRA (70/140)
K - NORTH COAST (50/120)
L - CENTRAL COAST (20/110)
M - SOUTH COAST (20/90)
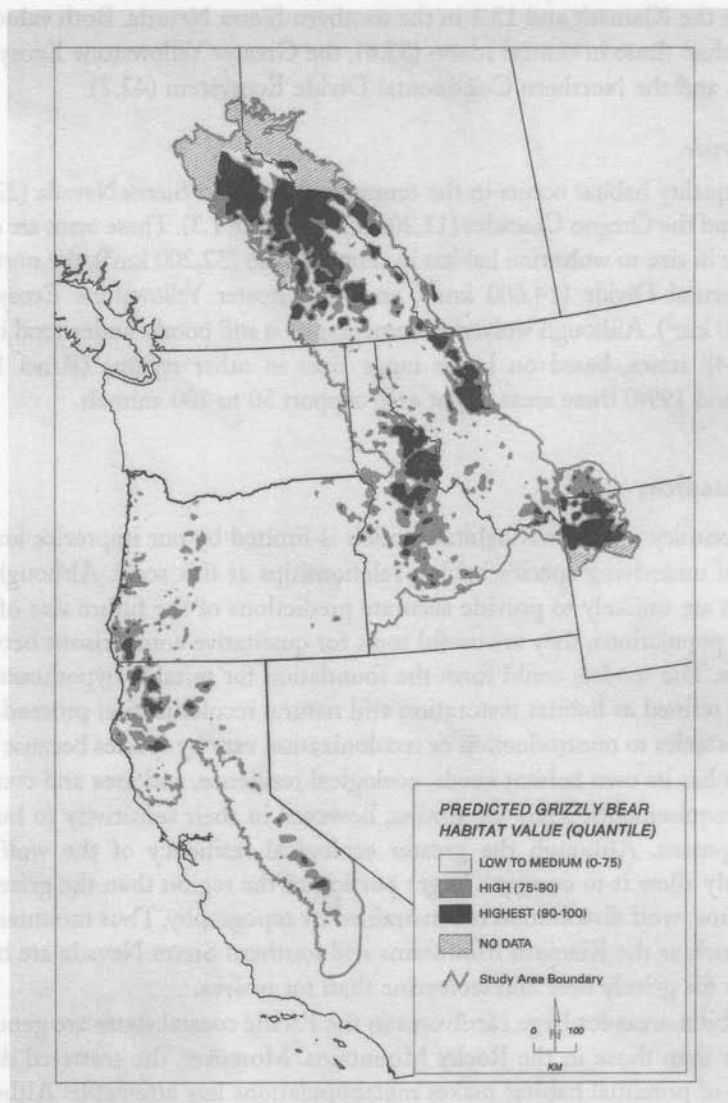N - CALIFORNIA COAST (30/100)

0   N   100

KM

Figure 1.1. Habitat for the gray wolf in the northwestern United States and Rocky Mountains as predicted by a regional-scale habitat model.

Grizzly Bear

Besides the large area of habitat in the proposed central Idaho reintroduction area, a smaller cluster of habitat patches is evident in the Klamath region (northwestern California and southwestern Oregon) and the southern Sierra Nevada (Figure 1.2). Based on population estimates from other areas in the

Figure 1.2. Habitat for the grizzly bear in the northwestern United States and Rocky Mountains as predicted by a regional-scale habitat model.

lower 48 states (USFWS 1993; Pease and Mattson 1999), the Klamath region could support 163 to 367 grizzly bears over 20,900 km^2 and the southern Sierra Nevada could support 48 to 108 bears over 6100 km^2. (Preliminary results of dynamic viability models [Carroll et al., unpublished data] suggest that this figure underestimates the potential size of the Sierra Nevada population.) The percentage of highest-security core habitat (90–100 decile) is 20.7 in the Klamath and 13.1 in the southern Sierra Nevada. Both values are lower than those in central Idaho (33.6), the Greater Yellowstone Ecosystem (43.3), and the Northern Continental Divide Ecosystem (42.7).
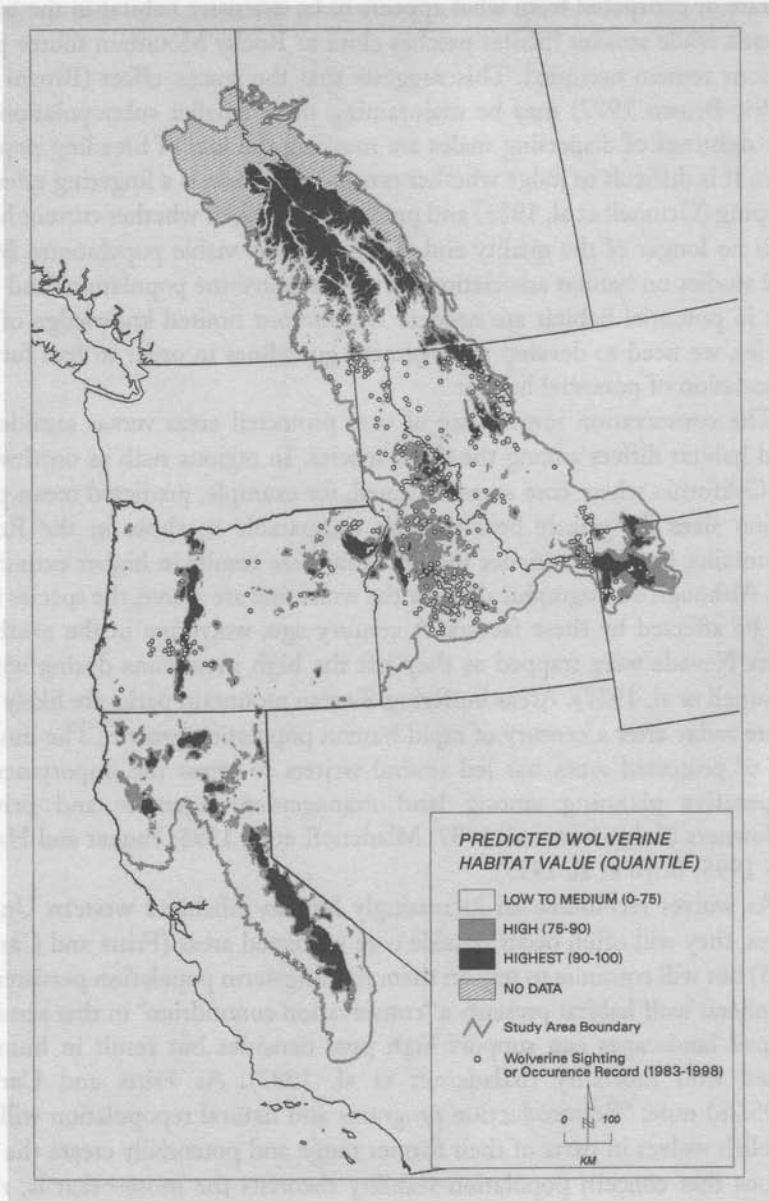
Wolverine

High-quality habitat occurs in the central and southern Sierra Nevada (22,000 km^2) and the Oregon Cascades (11,200 km^2) (Figure 1.3). These areas are comparable in size to wolverine habitat in central Idaho (32,200 km^2), the northern Continental Divide (14,600 km^2), and the Greater Yellowstone Ecosystem (20,200 km^2). Although wolverine demography is still poorly understood in the lower 48 states, based on home range sizes in other regions (Banci 1994; Copeland 1996) these areas might each support 50 to 100 animals.

Discussion

The accuracy of regional habitat models is limited by our imprecise knowledge of underlying species/habitat relationships at this scale. Although the models are unlikely to provide accurate predictions of the future size of carnivore populations, they are useful tools for qualitative comparisons between regions. The models could form the foundation for testable hypotheses that can be refined as habitat restoration and natural recolonization proceed.

Obstacles to reintroduction or recolonization vary by species because each species has its own habitat needs, ecological resilience, and area and connectivity requirements. They are similar, however, in their sensitivity to human development. Although the greater ecological resiliency of the wolf will probably allow it to occupy a larger portion of the region than the grizzly or wolverine, wolf distribution is constrained by topography. Thus mountainous areas such as the Klamath Mountains and southern Sierra Nevada are better habitat for grizzly bear and wolverine than for wolves.

Habitat areas for large carnivores in the Pacific coastal states are generally smaller than those in the Rocky Mountains. Moreover, the scattered distribution of potential habitat makes metapopulations less attainable. Although its extensive area requirements may help explain why the wolf was the first of the three species to be extirpated, its exceptionally high dispersal ability make its natural restoration more probable. Comparison of occupied and predicted

PREDICTED WOLVERINE
HABITAT VALUE (QUANTILE)

LOW TO MEDIUM (0-75)

HIGH (75-90)

HIGHEST (90-100)

NO DATA

Study Area Boundary

o   Wolverine Sighting
or Occurence Record (1983-1998)

0   100

KM

Figure 1.3. Habitat for the wolverine in the northwestern United States and Rocky Mountains as predicted by a regional-scale habitat model.

habitat for the wolverine suggests the importance of connectivity. Wolverines are rare or extirpated from what appears to be extensive habitat in the Sierra Nevada while smaller habitat patches close to Rocky Mountain source populations remain occupied. This suggests that the rescue effect (Brown and Kodric-Brown 1977) may be maintaining these smaller subpopulations or that sightings of dispersing males are masking the loss of breeding populations. It is difficult to judge whether range contraction is a lingering effect of trapping (Grinnell et al. 1937) and predator control, or whether current habitat is no longer of the quality and size to support viable populations. More field studies on habitat associations of extant wolverine populations and surveys in potential habitat are needed. Despite our limited knowledge of the species, we need to develop management guidelines in order to halt further degradation of potential habitat.

The conservation importance of core protected areas versus semideveloped habitat differs among the three species. In regions such as northwestern California where core areas are small, for example, predicted mean population sizes for grizzly bear may be comparable to those in the Rocky Mountains, but high variance in population size results in higher extinction risk. Although demographic data for the wolverine are scarce, the species may also be affected by these factors. A century ago, wolverine in the southern Sierra Nevada were trapped as they left the high mountains during winter (Grinnell et al. 1937). Areas buffering Sierran mountain parks are likely less secure today after a century of rapid human population growth. The limited size of protected areas has led several writers to stress the importance of cooperative planning among land management agencies and private landowners (Salwasser et al. 1987; Mladenoff et al. 1995; Paquet and Hackman 1995; Boyd et al. 1995).

As wolves recolonize an increasingly human-inhabited western United States, they will often occur outside core protected areas (Fritts and Carbyn 1995) but will continue to rely on them for long-term population persistence. Peripheral wolf habitat presents a "conservation conundrum" in that semideveloped landscapes can support high prey densities but result in human-caused wolf mortality (Mladenoff et al. 1997). As Fritts and Carbyn (1995:26) note: "Reintroduction programs and natural repopulation will reestablish wolves in parts of their former range and potentially create the situations that concern population-viability theorists the most—that is, relatively small populations that are isolated or semi-isolated from other populations."

The smaller size and greater isolation of high-quality core habitat in the Pacific states highlight the importance of metapopulation connectivity for

the survival of these semidisjunct populations. Simulation models suggest that connectivity can counteract the negative effects of small area, as wolves dispersing from protected areas strengthen peripheral populations (Haight et al. 1998). Regional planning that incorporates core, buffer, and dispersal habitat can increase the effective size of reserves and allow wolves to expand into the semideveloped landscape matrix (Fritts and Carbyn 1995). Translocation of animals may be necessary for some of the more isolated areas; others will benefit from the restoration of regional-scale linkages. Even if wolves successfully recolonize coastal Oregon and other areas with limited core habitat, they are likely to remain vulnerable to extirpation. A threat analysis that integrates information on the location of critical habitat with data on human population growth and landscape change can help in the prioritization of conservation efforts (Carroll et al., unpublished data). Although our results suggest a high potential for restoring large carnivores in the Pacific Northwest, current development trends may foreclose options for carnivore restoration unless steps are taken soon to protect critical habitat.

Acknowledgments

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