Defining Recovery Goals and Strategies for Endangered Species: The Wolf as a Case Study

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*We used a spatially explicit population model of wolves (*Canis lupus*) to propose a framework for defining rangewide recovery priorities and finer-scale strategies for regional reintroductions. The model predicts that Yellowstone and central Idaho, where wolves have recently been successfully reintroduced, hold the most secure core areas for wolves in the western United States, implying that future reintroductions will face greater challenges. However, these currently occupied sites, along with dispersal or reintroduction to several unoccupied but suitable core areas, could facilitate recovery of wolves to 49% of the area in the western United States that holds sufficient prey to support wolves. That percentage of the range with recovery potential could drop to 23% over the next few decades owing to landscape change, or increase to 61% owing to habitat restoration efforts such as the removal of some roads on public lands. Comprehensive habitat and viability assessments such as those presented here, by more rigorously defining the Endangered Species Act's concept of "significant portion of range," can clarify debate over goals for recovery of large carnivores that may conflict with human land uses.*

Keywords: Canis lupus, *conservation planning, Endangered Species Act, reintroduction, spatially explicit population model*

As human impacts on the biosphere increase, conservation biology must increasingly focus not only on preserving the current distribution of biodiversity but also on restoring species to areas from which they have been extirpated (figure 1). The success of restoration efforts depends in part on clarification of both the normative and the technical components of recovery goals (Breitenmoser et al. 2001). For example, the level of extinction risk tolerated or the extent of historic range to which recovery is desired are normative decisions guided by laws such as the US Endangered Species Act (ESA; 16 USC 1531–1540 [1988]). Once these normative aspects are resolved, conservation science can help identify which restoration strategy is most likely to ensure the desired level of recovery. Many of the species listed under the ESA are narrowly distributed endemics that can be protected by preserving a limited number of sites (Dobson et al. 1997). It is more difficult to define recovery goals for species such as the gray wolf (*Canis lupus*), which have large area requirements for viable populations, and whose protection may conflict with existing land uses such as livestock production. The scientific methodology used to define recovery goals and strategies for endangered species has not fully integrated recent technical advances in conservation biology, such as spatially explicit population models (SEPMs; Dunning et al. 1995). We present an example of such an analysis applied to the wolf, a high-profile endangered species whose proposed recovery goals (68 Federal Register 15804–15875) have recently been the subject of litigation (*Defenders of Wildlife v. Norton,* Civ. 03-1348-JO [2005]; *National Wildlife Federation v. Norton,* 03-CV-340 [2005]), to demonstrate how these methods can introduce key scientific knowledge into the debate over recovery goals and facilitate the decisionmaking process by illustrating the efficacy of alternate management scenarios.

Although the ESA of 1973 was the third in a series of laws aimed at protecting imperiled species, it was the first to offer protection to any species in danger of extinction throughout all or a significant portion of its range. By including the phrase "significant portion of its range," Congress signaled its intent that listed species should not simply be saved from extinction, but rather recovered so that populations inhabit relatively large areas (i.e., significant portions) of suitable habitat within historic ranges. Case law (*Defenders of Wildlife v. Norton,* 258 F.3d 1136 [2001], 239 F. Supp. 2d 9 [2002], Civ. 03-1348-JO [2005]; *National Wildlife Federation v. Norton,* 03-CV-340 [2005]) and previous delisting actions by the US Fish and Wildlife Service (USFWS) are consistent with this intent, as the 15 taxa that have been declared recovered since passage of the ESA were generally widely distributed at the time of delisting. This expectation was buttressed when Con-

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Figure 1. In 1995, M. K. P. (the second author) and others released the first wolves to inhabit Yellowstone National Park in 70 years. Endangered species recovery efforts often involve reintroduction of animals to unoccupied but potentially suitable habitat. However, the extent of historic range to which reintroduction is needed is a controversial issue for formerly widespread species such as the wolf whose restoration may conflict with human land uses, such as livestock grazing on public lands. Photograph: National Park Service/Jim Peaco.

gress defined the term "species" to include "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature" (ESA section 3[15]). The policy of recognizing distinct population segments (DPSs) allows for protective measures before the occurrence of large-scale declines that would necessitate listing a species or subspecies throughout its entire range (61 Federal Register 4722).

In the late 1950s, the number of gray wolves inhabiting the conterminous United States reached an all-time low, with fewer than 1000 wolves occupying less than 1% of the species' historic range in northeastern Minnesota and the adjacent Isle Royale National Park (Phillips et al. 2004). Three decades after passage of the ESA, owing to the expansion of populations in Minnesota and Canada and to reintroduction efforts in the northern Rocky Mountains (USFWS 1994) and the southwestern United States (USFWS 1996), about 4500 wolves occupy about 5% of the species' historic range in the conterminous United States (figure 2). In response to this improved conservation status, in April 2003 the USFWS published a reclassification rule that divided the lower 48 states into three DPSs (figure 2), retaining the experimental–nonessential population areas in the northern Rocky Mountains (USFWS 1994), but elsewhere downlisting the eastern and western gray wolf DPSs from endangered to threatened and indicating that recovery objectives for both had been met (68 Federal Register 15804–15875). However, in 2005, two federal court rulings vacated and enjoined the rule on the basis, in part, that it lacked comprehensive consideration of the phrase "significant portion of range" and misapplied the DPS policy (*Defenders of Wildlife v. Norton,* Civ. 03-1348-JO [2005]; *National Wildlife Federation v. Norton,* 03-CV-340 [2005]). When considered with the two earlier rulings cited above, this indicates that future recovery plans for wolves and other listed species should be guided by a rangewide determination of habitat suitability and relevant principles of conservation planning. The three principles of representation (establishing populations across the full array of potential habitats), resiliency (protecting populations large enough to remain viable), and redundancy (saving enough different populations that some can be lost without a loss of the species) are widely invoked guidelines for ensuring conservation of threatened species, even in the face of geographically widespread threats such as climate change (Shaffer and Stein 2000). By broadening recovery criteria to encompass representation, these principles recognize that a single population may not represent species recovery, even if it is large enough to be significantly resilient to extinction. For wide-ranging species such as the wolf, the importance of connectivity (protecting linkage areas, especially those that enhance viability by connecting larger with smaller populations) may justify its addition as a fourth principle for defining recovery goals (Soulé and Terborgh 1999).

In the 2003 proposed rule, the USFWS conflated the concepts of population viability and recovery. The claim that the ESA mandates only maintaining a species' viability (preventing extinction) rather than effecting recovery was first made in a 1986 revision to the regulations governing ESA enforcement (50 CFR 402), but has been repeatedly rejected by the courts (Suckling and Taylor 2005). This distinction is especially important for species such as the wolf or grizzly bear (*Ursus arctos*) that currently occupy a small portion of their historic range, because ESA mechanisms for maintaining viability restrict only "take" of individuals or occupied habitat, whereas ESA mechanisms for effecting recovery may restrict the destruction of unoccupied but suitable habitat and call for proactive measures to promote population reestablishment (Suckling and Taylor 2005). Although the bulk of the ESA's language addresses recovering individual species, Congress also included language that mandates the conservation of ecosystems on which listed species depend. Because of this, some researchers have proposed an additional guideline for recovery planning, the principle of ecological effectiveness (Soulé et al. 2005). An ecologically effective population contains enough individuals with a wide enough geographic distribution to reestablish the species' role in ecosystems. The argument for reestablishing ecologically effective populations is most persuasive in the case of the wolf and other "keystone" species that strongly influence ecosystem function through interspecific interactions such as predation (figure 3). For example, the return of wolves to Yellowstone has triggered a cascade of top-down effects on that ecosystem (Smith et al. 2003). Wolf predation has reduced the ability of elk to concentrate browsing on preferred species such as aspen (*Populus tremuloides*), leading to the recovery of riparian vegetation and associated species (Ripple and Beschta 2004). Because the wolf is a keystone species that was historically widespread throughout the western United States, yet whose recovery may conflict with current land-use practices such as livestock grazing on public lands, it provides an ideal case study of the role of conservation science in clarifying species recovery goals. We first present an example of a rangewide analysis for the wolf in the western contiguous United States, and then describe the use of an SEPM to help define recovery goals and strategies at a finer scale for the southwestern DPS (SWDPS) for the gray wolf (figure 2).

Rangewide analysis for the western United States

We analyzed potential wolf habitat and population viability across the western contiguous United States, from the western edge of the Great Plains to the Pacific Ocean, an area of about 2,800,000 square kilometers (km^2) (figure 2). The structure of the SEPM (PATCH, or program to assist in tracking critical habitat) and input habitat models used in this study are described in detail elsewhere (Schumaker 1998, Carroll et al. 2001a, 2001b, 2003a, 2003b) and summarized here (box 1). We calibrated habitat rankings to specific demographic values based on field studies from areas that showed similar habitat quality to the habitat classes in the SEPM input layers (Ballard et al. 1987, Fuller 1989, Hayes and Harestad 2000, Fuller et al. 2003, Smith et al. 2004). Because the analysis covers a large and ecologically diverse region, the geographic information system, or GIS, models for fecundity and survival must use general habitat data that are available in every state. This is a lesser problem for the survival input layer, because roads and human population have a similar negative effect on large carnivore survival in diverse habitats (Thiel 1985, Fuller et al. 2003). A metric combining road density, local human population density, and interpolated human population density (Merrill et al. 1999) predicted survival in the spatially explicit population modeling (figure 4b).

Estimating wolf fecundity (reproductive rates) across the western United States is more difficult. Abundance estimates of ungulate prey are not collected in some areas of the western United States, and where they do exist, they show strong

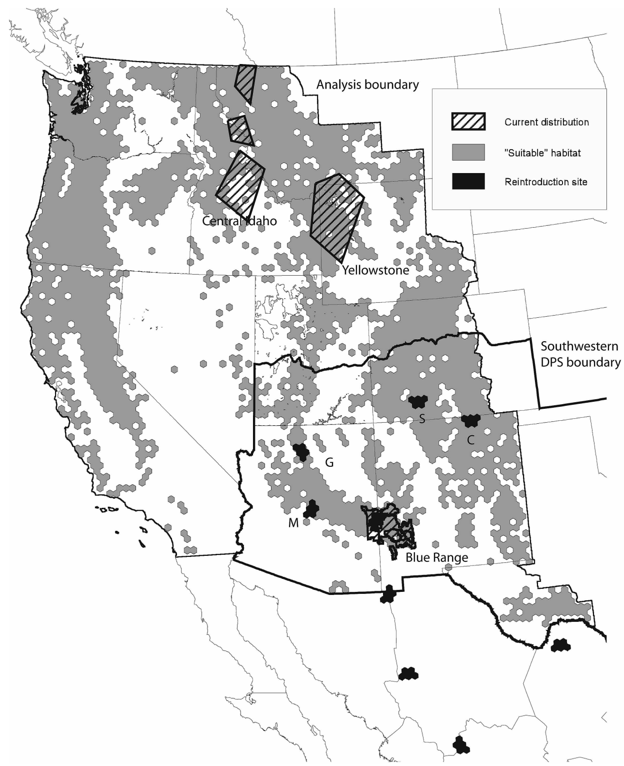

*Figure 2. Map of the analysis area and the approximate location of wolf (*Canis lupus*) populations in the western United States, including the existing Yellowstone, central Idaho, and Blue Range reintroduction sites and the population in northwestern Montana established by dispersal from Canada. Nearly all of the area within the analysis boundary is within the historic geographic range boundary of the gray wolf, although more arid areas typically held few wolves. The extent of habitat defined as "suitable" in this analysis (meeting the productivity threshold that allows breeding in the PATCH model) is shown in gray. The boundaries of the southwestern distinct population segment, or DPS (as proposed by the US Fish and Wildlife Service [68 Federal Register 15804–15875]), are shown. Locations within the southwestern DPS evaluated as potential reintroduction sites in this study are shown in black. Abbreviations: C, Carson; G, Grand Canyon; M, Mogollon; S, San Juan Mountains.*

Figure 3. Wolves in Yellowstone have reduced the ability of elk to concentrate foraging on aspen, cottonwood, and other favored species, thus allowing the recovery of key riparian vegetation and its associated biota. Restoring such top-down ecosystem processes involving wolves and other keystone species may require ecologically effective populations (i.e., populations that are larger and more widespread than would be necessary to ensure viability of the species itself). Photograph: Bob Landis.

Box 1. Spatially explicit population models.

Conservation planners assess the distribution of wildlife habitat (including potentially suitable but currently unoccupied areas) with the aid of computer models of varying complexity. Broadly speaking, large carnivores such as the wolf can persist in areas where there is sufficient food and where persecution by humans is low (Fuller et al. 2003). A simple model of recovery potential could therefore highlight large roadless areas with sufficient productivity or extensive forest habitat. More complex spatially explicit population models (SEPMs) might also begin with data on road density and productivity, but would then integrate additional information on species characteristics such as demographic rates and dispersal behavior. For example, social carnivores, such as the wolf, often require larger territories than solitary species of similar size, and may thus be more vulnerable to landscape fragmentation (Carroll et al. 2003a). Unlike the simpler model, an SEPM can provide insights on the effects of population size and connectivity on viability and can help identify the locations of population sources and the degree of threat to those areas from landscape change (figure 4a; Carroll et al. 2003b).

PATCH (program to assist in tracking critical habitat), the SEPM used here, is designed for studying territorial vertebrates. It links the survival and fecundity of individual animals to geographic information system (GIS) data on mortality risk and habitat productivity at the scale of an individual or pack territory (Schumaker 1998). Territories are allocated by intersecting the GIS data with an array of hexagonal cells (figure 4c). The different habitat types in the GIS maps are assigned weights based on the relative levels of fecundity and survival expected in those habitat classes. Base survival and reproductive rates, derived from published field studies, are then supplied to the model as a population projection matrix (box 2; Caswell 2001). The model scales these base matrix values using the mean of the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output (figure 4c). Each individual in the population is tracked through a yearly cycle of survival, fecundity, and dispersal events (figure 4a). Environmental stochasticity is incorporated by drawing each year's base population matrix from a randomized set of matrices whose elements were drawn from a beta (survival) or normal (fecundity) distribution (coefficients of variation given in box 2). Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a parameter for site fidelity, but floaters must always search for available breeding sites. As pack size increases, pack members in the model have a greater tendency to disperse and search for new available breeding sites (Carroll et al. 2003a). Movement decisions use a directed random walk that combines varying proportions of randomness, correlation, and attraction to higher-quality habitat (Schumaker 1998).

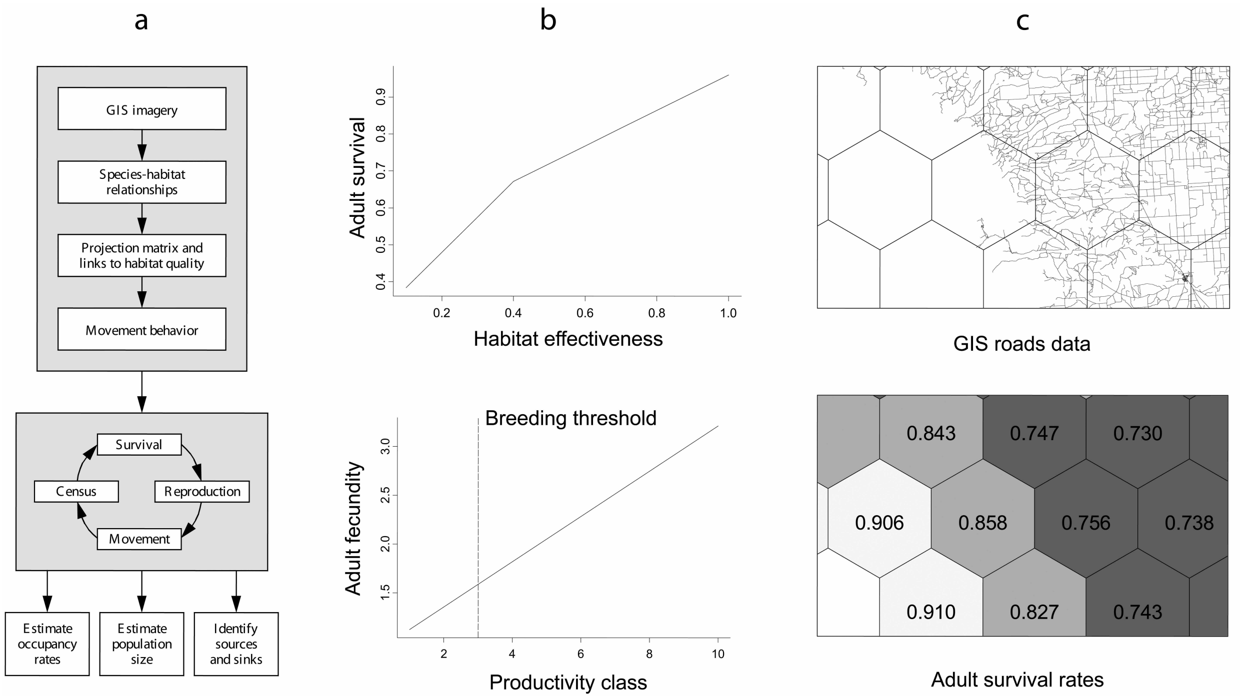

Figure 4. Spatially explicit population models (SEPMs) represent population processes by tracking the spatial location of individuals and landscape features. (a) A flowchart of the simulation process in PATCH, the SEPM used in this study. (b) Graphs of the relationship between GIS-based habitat values and demographic values for fecundity (given as females produced per pack) and survival for wolves. (c) Territories are allocated by overlaying an array of hexagonal cells on GIS habitat data. For the wolf, data on roads are used in combination with human population data to calculate the metric of habitat effectiveness used to scale wolf survival rates. Abbreviation: GIS, geographic information system.

inconsistencies across state boundaries. Therefore, as a surrogate for fecundity, we used tasseled-cap greenness (Crist and Cicone 1984), a metric derived from MODIS (Moderate Resolution Imaging Spectroradiometer) satellite imagery from mid-July 2003 and 2004 (Wharton and Myers 1997). "Pseudohabitat" variables such as greenness that are derived directly from unclassified satellite imagery are correlated to varying degrees with ecological factors such as net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997), and thus with abundance of ungulate prey species, although this relationship is weakened by phenological variation between years and by spatial variation in the percentages of bare ground and of dry biomass (Merrill et al. 1993). Summer greenness values are strongly correlated with ungulate density in the northern Rocky Mountains and Pacific Northwest (Carroll et al. 2001b, 2003a), and with carnivore habitat in other regions (Mace et al. 1999, Carroll et al. 2001a). However, the link between greenness and prey abundance may be less general across the larger and more ecologically varied region addressed in this study than is the well-established link between prey abundance and wolf density (Fuller et al. 2003). Therefore, to avoid overestimation of prey abundance in nonforest habitats, we used data on vegetation type to rate forest habitat higher than shrubland habitat with similar greenness values. Nonnatural (agricul-

Box 2. Parameters used in the PATCH model of wolf population dynamics in the western United States.

Territory size: 504 square kilometers (km^2)
Maximum dispersal distance: 750–1500 km
Survival rates (maximum):

- Young, year 0: 0.46
- Subadult, year 1: 0.86
- Adult, > 2 years: 0.96
- At senescence (year 8): 0.69

Fecundity rates (maximum number of female offspring per adult female or pack):

- Subadult, year 1: 0
- Adult, year 2: 2.29
- Adult, > 3 years: 3.21

Coefficient of variation in demographic rates:

- Fecundity: 30%
- Pup (year 0) mortality: 40%
- Adult mortality: 30%

tural and urban) habitat was given zero habitat value. Because wolves are coursing predators that avoid steep terrain, the wolf fecundity model also incorporated the negative effect of slope on prey vulnerability (Paquet et al. 1996, Carroll et al. 2001b).

The results of the PATCH model are generally more sensitive to the demographic parameters used, and to how these parameters were assigned to habitat classes, than to variation in other parameters, such as dispersal distance (Carroll et al. 2003b). The large body of published research on relationships between wolf demographics and habitat (e.g., as reviewed in Fuller et al. 2003) strengthens the power of conceptual models such as those used here. In previous studies, SEPM predictions of wolf distribution were strongly correlated with wolf distributions as recorded in regional-scale field surveys (Carroll et al. 2003a). This is most likely because large carnivore distribution is strongly limited by human influences, for which easily mapped attributes such as road density are good surrogates (Carroll et al. 2001a). Such "pattern-oriented" calibration of complex spatial models may in some cases reduce uncertainty due to poorly known demographic parameters (Wiegand et al. 2004).

The landscape-change scenarios we used estimated potential change in human-associated impact factors (e.g., roads and human population) by proportionately increasing road density and by increasing human population on the basis of current trends derived from a time series of human census data. Census data were available for the period 1990–2000 (USCB 1991). We predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 2000, but adjusted the predicted 2025 population to match state-level predictions based on more complex socioeconomic models. Human population in the area of our analysis is predicted to grow 42%, from 62 million to 88 million, in the period 2000–2025. Because available road data are of varying dates, it is not possible to assemble a regional chronosequence of road distribution and determine county-level rates of increase in roads. Therefore, the road density parameters incorporate an increase of 1% per year (proportional to the current road density at the 1-km^2 scale) across the study area. We chose to use a rate (1% per year) that is half of that seen in the most rapidly growing portions of our study region (e.g., western Colorado; Theobald et al. 1996). Similarly, we used a simplified habitat restoration scenario that assessed the effects of removing 1% of the roads on public lands per year.

We treated human impacts within strictly protected areas (parks with no hunting or trapping) as less lethal than in other areas, because of the lack of incidental mortality from hunters in those areas. In the landscape-change analysis, we also treated all protected areas (including those with hunting) differently from unprotected habitat in that we assumed no increase in road density over time. The simulations began with animals inhabiting all suitable habitat. We define "suitable habitat" as the areas with sufficient food resources to support reproduction (i.e., fecundity values above the threshold value for breeding; figure 2). The threshold determining the extent of suitable habitat was based on the historic distribution and abundance of wolves and their prey, which was low in semiarid, nonforested regions of the Great Basin and Sonoran Desert (Young and Goldman 1944). By the end of the 200-year simulations, animals persisted only in "occupiable" habitat, which we define as the areas with greater than 50% potential for long-term occupation despite the presence of human impacts (figure 5). Thus "current" predictions depict, not the number of animals now inhabiting an area, but the capacity of current habitat conditions to support a resident wolf population over the long term (200 years).

The five landscape scenarios examined (table 1) were as follows:

1. Scenario A: Current conditions (i.e, potential long-term viability given current habitat conditions).
2. Scenario B: Future conditions (with human population as of 2025), with increased road development on private lands only.
3. Scenario C: Future conditions (with human population as of 2025), with increased road development on both private and unprotected public lands.
4. Scenario D: Current conditions (with human population as of 2000), with decreased road development on public lands.
5. Scenario E: Future conditions (with human population as of 2025), with decreased road development on public lands and increased road development on private lands.

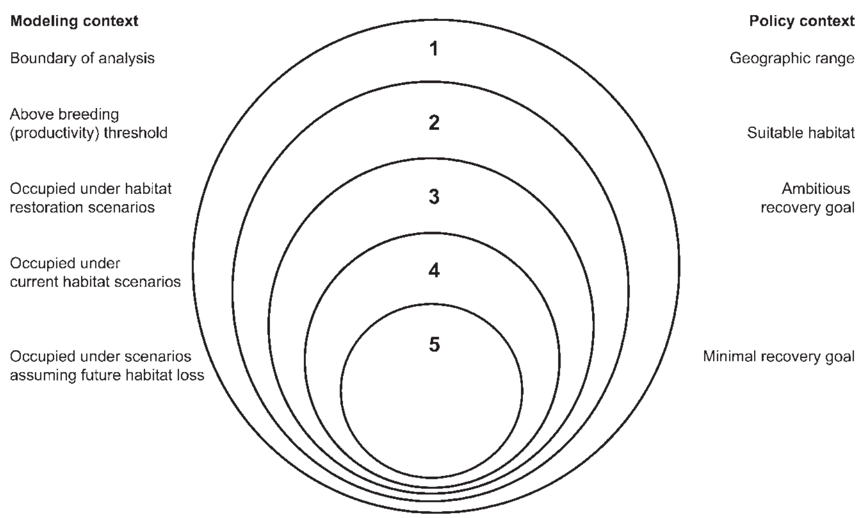

Figure 5. Conceptual diagram of the relationship between the various geographic levels of range occupancy as defined by the application of spatially explicit population models to evaluate recovery thresholds.

Table 1. Levels of human impacts used to parameterize wolf survival in alternate scenarios using the PATCH (program to assist in tracking critical habitat) model.

Scenario	Parameter: Human population	Roads on public land	Roads on private land
A	Current level (2000)	Current level (2000)	Current level (2000)
B	Predicted level (2025)	Current level (2000)	Predicted level (2025)
C	Predicted level (2025)	Predicted level (2025)	Predicted level (2025)
D	Current level (2000)	Potential level given road closure/removal on public lands[a]	Current level (2000)
E	Predicted level (2025)	Potential level given road closure/removal on public lands[a]	Predicted level (2025)

Note: Wolf survival was parameterized to vary inversely to levels of human population and road density.

a. Assumes closure or removal on 1% of public lands per year for 25 years.

Although any restoration of public lands would take place over time, we included scenario D to help separate the contrasting effects of this restoration of public lands and the continued degradation of private lands. Scenario E depicts a high-contrast landscape with restored core areas of public lands embedded in a generally unfavorable environment of heavily roaded private lands.

Analysis at the scale of a distinct population segment

We next evaluated restoration strategies at the scale of a DPS. The SWDPS encompasses the states of Arizona, New Mexico, southern Utah, southern Colorado, and western Texas and Oklahoma, as well as adjacent areas in northern Mexico that were part of the historic range of the Mexican wolf (*C. lupus baileyi;* figure 2). The Mexican wolf has been the focus of conservation concern due to its high level of genetic distinctiveness and the fact that it is extinct in the wild, with the exception of a small population reintroduced to the Blue Range of Arizona and New Mexico in 1998 (Brown and Parsons 2001). We used the SEPM to evaluate the adequacy of a recovery goal similar to that established for the gray wolf in the northern Rocky Mountains: the creation of three wolf populations of at least 100 individuals each (USFWS 1987). We compared the wolf distribution achieved by this goal with the extent of suitable habitat and ecoregions in the DPS. Ecoregions are commonly used as surrogates for biogeographic gradients (Groves 2003). These analyses, as in the earlier rangewide assessment, were based on the long-term potential of an area to support wolf populations, as predicted by the PATCH simulations. Because management actions to remove wolves often arise from livestock depredation, we added a scenario that incorporated data on levels of cattle grazing into the mortality risk metric for wolves. We also modeled specific reintroduction options to assess transient dynamics such as the probability of extinction and the probability of an area being colonized by dispersers from a specific reintroduction site (Carroll et al. 2003a). We evaluated the sensitivity of results to varying assumptions as to maximum dispersal distance. We performed 1000 simulations of 200 years each for each reintroduction scenario.

We identified eight potential reintroduction sites, four in the United States and four in Mexico, based on the results of initial SEPM simulations. Here we discuss only the results for the US sites: Carson (northern New Mexico), the Grand Canyon (northern Arizona), the Mogollon Rim (central Arizona), and the San Juan Mountains (southwestern Colorado; figure 2). A fifth site in the Blue Range Wolf Recovery Area (BRWRA; Arizona and New Mexico) was also included to provide comparability with current recovery program results. Each of these sites was evaluated in detail by simulating the effects of releasing wolves at that site alone. Each reintroduction site comprised five adjacent potential wolf territories, totaling 2500 km^2. We approximated the standard reintroduction protocol (Bangs and Fritts 1996) by introducing five breeding-age females in the first year and setting survival for the first 5 years at close to 100% under the assumption that new animals would be released to replace mortality among the initial releases.

Results of rangewide analysis

The habitat quality threshold used in the SEPM simulations resulted in 44% of the western United States being judged suitable for breeding (i.e., having sufficient prey to support territorial wolves). The proportion of that "suitable" habitat likely (> 50% probability) to be occupied by wolves was 49% under current conditions (scenario A; figure 6a), 32% under future conditions without new roads on public lands (scenario B; a decrease of 35%), 23% under future conditions with development on public lands (scenario C; figure 6b; a decrease of 53%), 61% under current conditions with road closure or removal on some public lands (scenario D; figure 6c; an increase of 25%), and 45% under future conditions with road removal on public lands (scenario E; a decrease of 8%). The potential size of the wolf population in the western United States was predicted to be close to 7000 under current conditions, with a decrease of 29% under scenario B, a decrease of 44% under scenario C, an increase of 24% under scenario D, and a decrease of 6% under scenario E.

Under current conditions, the states of Montana, Colorado, Wyoming, and Idaho have the largest potential wolf populations, followed by Arizona, Utah, and New Mexico (figure 7). Rather than artificially dividing habitat by state lines, one can also identify distinct population centers from the SEPM results (figure 6a). The largest wolf populations could inhabit the Greater Yellowstone ecosystem (GYE) and central Idaho (figure 6), both areas in which wolf reintroduction has already achieved notable success (Phillips et al. 2004). Population centers of the second rank (smaller size) are found in north-

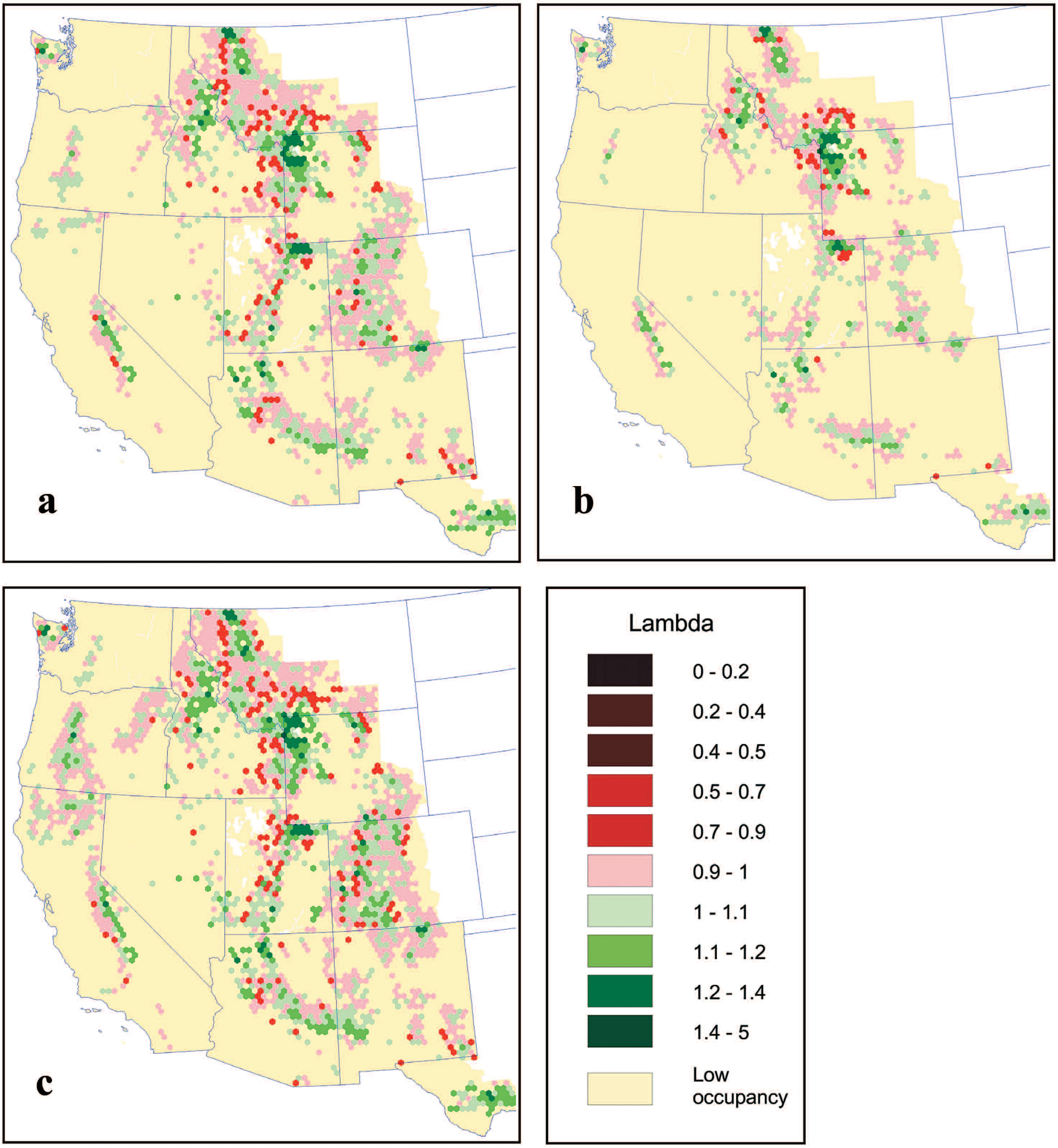

Figure 6. Potential distribution and demography of wolves as predicted by the PATCH model in the western United States under three landscape scenarios: (a) scenario A, current conditions (i.e., potential long-term viability given current habitat conditions); (b) scenario C, future conditions, with human population as of 2025, with increased road development on both private and unprotected public lands; and (c) scenario D, current conditions, with human population as of 2000, with restoration (reduction in roads) on public lands. Those areas with a predicted probability of occupancy of less than 25% are shown as "low occupancy." Some of these areas are infrequently occupied (i.e., between 25% and 50% of the simulations) but are shown to illustrate potential landscape linkages.

western Montana and western Colorado, of the third rank in the Blue Range and Utah's high plateaus region, and of the fourth rank in Oregon's Cascades. The populations most vulnerable to landscape change (as reflected by percentage decline from scenario A to scenario C) are those in Colorado and Oregon (figure 6). The New Mexico wolf population also declines dramatically under landscape change (figure 6b) but is supported by its connections to Colorado and Arizona populations. The populations that most benefit from road removal on public lands (scenarios D and E) are those in (a) western Oregon and northern California, (b) Colorado and New Mexico, and (c) western Montana (figures 6c, 7).

Results of analysis at the scale of a distinct population segment

In addition to the current reintroduced population in the Blue Range, the Grand Canyon reintroduction site showed a high probability of success (low extinction rates) and rapid geographic expansion (table 2). Several other reintroduction sites showed higher, but still relatively low, extinction rates. If we assumed that two additional reintroduction projects, in addition to the current Blue Range program, were conducted in the Grand Canyon and Carson sites, then three populations of 100 wolves each would occupy 5.24% of the SWDPS's suitable habitat, and 7.86% of its occupiable habitat (as defined above and in figure 5). Moreover, 5, or 38.5%, of the SWDPS's 13 ecoregions (Bailey 1995) would contain wolves (as a result of two reintroduction sites lying in more than one ecoregion). The probability that a reintroduction at a single site will fail (extinction probability) under scenario A ranges from near zero (0 of 1000 simulations) for the Blue Range and Grand Canyon sites to near 10% for the Mogollon Rim and San Juan Mountains sites (table 2). Under scenario C, the extinction probability for the Mogollon and San Juan Mountains sites increases to 16%–20%. The probability of extinction for the Blue Range, Grand Canyon, and Carson sites increases slightly but remains low (< 3%; table 2). Occupancy of the larger (10,000-km^2) restoration zone surrounding each 2500-km^2 reintroduction site gives a sense of the extent of suitable habitat that might be important in the early stages of population establishment. The Blue Range restoration zone has the highest occupancy, at 72.5%, followed closely by the Carson and Grand Canyon zones (table 2). The Grand Canyon zone is more resilient to landscape change than the Blue Range or Carson; thus, it shows the highest wolf population density among US restoration zones under scenario C (table 2). A scenario that incorporated cattle density as an additional mortality risk factor resulted in a similar ranking of restoration zones, except that the San Juan Mountains zone appeared less vulnerable, and thus only the Mogollon zone showed high relative extinction risk.

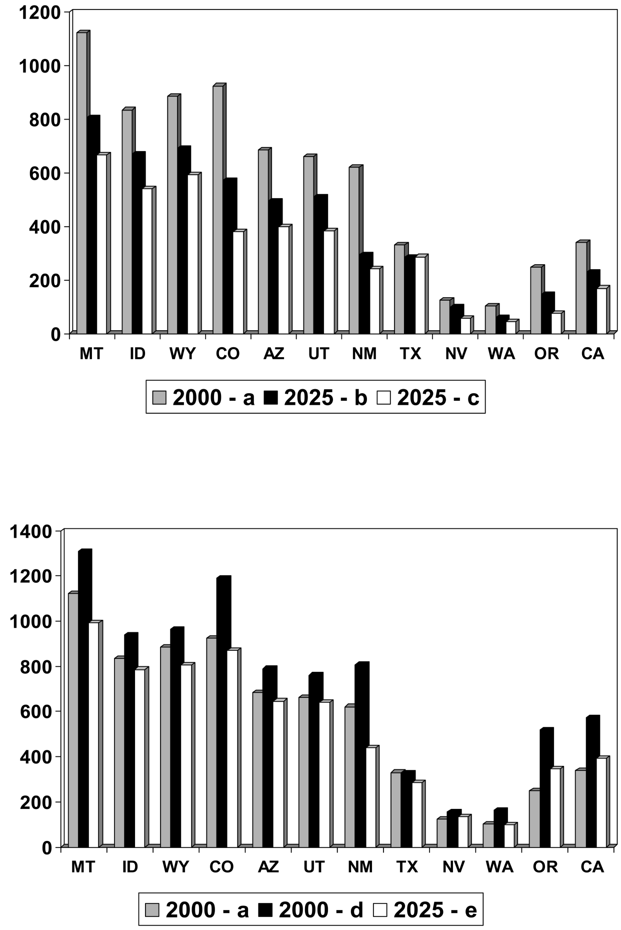

Figure 7. Potential wolf population size, by state, under one scenario for current conditions (2000a), two habitat degradation scenarios (above; 2025b, 2025c), and two habitat restoration scenarios (below; 2000d, 2025e) of the PATCH model, as shown in table 1.

Table 2. Comparative summary of results of analysis of potential wolf restoration zones (areas of 10,000 square kilometers in size surrounding initial reintroduction sites) in the southwestern distinct population segment for the gray wolf.

Reintroduction site	Population: Scenario A	Population: Scenario C	Occupancy (%), scenario A	Lambda, scenario A	Extinction risk (%): Scenario A	Extinction risk (%): Scenario C	Vulnerability, scenarios A–C/scenario A
Blue Range	92	67	72.5	1.04	0	1.4	27.2
Carson	84	66	68.2	1.04	0.8	2.7	21.4
Grand Canyon	91	79	68.5	1.06	0	0.4	13.2
Mogollon Rim	71	45	60.3	1.00	8.6	15.8	36.6
San Juan Mountains	79	51	63.6	1.04	10.5	19.6	35.4

Note: See the text for a definition of PATCH (program to assist in tracking critical habitat) scenarios A through C.

The regional population size achieved at the end of the SEPM reintroduction simulations (year 200) gives an indication of the ability of a particular reintroduction site to enhance the broader regional population, an ability that is due to factors such as ease of dispersal to other suitable habitat. The Grand Canyon site achieves the highest regional population within the US SWDPS. As a result of sink habitat and other barriers to population spread, the largest regional US population achieved from a single reintroduction is only 59.9% of the maximum population size achieved in the equilibrium scenario (scenario A) that began with all habitat occupied. However, a regional population of 89.3% of the maximum population size is eventually achieved by using three reintroduction sites (Blue Range, Grand Canyon, and Carson). At the end of the 200-year simulations, this reintroduced population occupied 54.3% to 57.5% (depending on assumptions about dispersal distance) of the US SWDPS's suitable habitat under scenario A, 26.3% to 26.6% under scenario C, and 100% of the region's ecoregions under both scenarios. Population predictions in peripheral areas with fragmented habitat were most sensitive to alternate assumptions about maximum dispersal distance (e.g., New Mexico, with 13% relative change), with most other areas showing less than 5% relative change. Extinction probability at individual reintroduction sites was not sensitive to dispersal parameterization, with a doubling of maximum dispersal distance from 750 to 1500 km generally producing changes in extinction risk of less than 0.5% (absolute percentage), with a maximum of 1.6% change.

Using model results to inform policy

Advances in conservation science since the passage of the ESA have provided scientists and managers with a better understanding of the factors, such as interpopulation connectivity, necessary for successful reintroductions and for the long-term viability of reintroduced populations (Breitenmoser et al. 2001). For example, a key element of the Northwest Forest Plan, designed to facilitate recovery of the northern spotted owl (*Strix occidentalis caurina*), was the recognition that the viability of any particular owl subpopulation was dependent on the successful establishment of territories by dispersing individuals, and hence on the size and connectivity of habitat patches across the landscape (Noon and McKelvey 1996). Such a regional-scale perspective on processes such as loss of connectivity has been difficult to achieve with simpler models of habitat suitability, but is now possible with SEPMs that combine spatial data such as satellite imagery with information from the field on how well animals survive and reproduce in different habitats. Because SEPMs such as the PATCH model (Schumaker 1998) can incorporate changes in landscapes over time, they are also more useful than simpler models in forecasting how species' populations might respond to alternative futures in which current trends either continue or instead are slowed or reversed through habitat protection and restoration.

Complex spatial viability models such as SEPMs may be more biologically realistic than simpler tools, but their realism has a cost: SEPM results may suffer from increased sensitivity to a lack of detailed demographic, habitat, and movement data (Kareiva et al. 1996). We found that population predictions in peripheral areas were most sensitive to alternate assumptions about maximum dispersal distance, and that extinction probability at individual reintroduction sites was not sensitive to dispersal parameterization. Nonetheless, it is important to assess which conservation questions can or cannot be answered with relative confidence in the face of model uncertainty. For example, the minimum threshold of food (prey) availability at which wolves can persist is poorly known (Fuller at al. 2003). Therefore, especially in semiarid areas of the West, the exact population estimates from PATCH, which are strongly affected by where this threshold is set, should be viewed with caution (Carroll et al. 2005). However, because we know more about habitat security thresholds for large carnivores, the proportion of this "suitable" habitat that the model predicts as occupied is more informative (figure 6). In general, population viability analysis tools such as SEPMs are more suitable for comparing alternative management options and suggesting qualitative insights about population structure and threat processes than for providing exact population estimates (McCarthy et al. 2003). As knowledge of wolf–habitat relationships is gathered through long-term field studies in areas such as Yellowstone (Smith et al. 2004), SEPM results can be updated to predict future population distribution more accurately.

For species for which demographic data are too sparse to parameterize SEPMs, simpler, static models of habitat suitability may still be useful for guiding recovery planning. Even for these species, SEPMs may be valuable as heuristic tools to generate hypotheses concerning limiting factors and regional population structure. Emergent characteristics of the regional landscape, such as interpopulation connectivity, are likely to be significant for wide-ranging species and poorly addressed by static models. Connectivity in SEPMs depends on both the strength of the source habitat and the permeability of the intervening landscape (Carroll forthcoming), and thus SEPMs more realistically portray factors fragmenting carnivore populations in the western United States. Wolves in threatened habitat patches, unlike those in the boreal "mainland" of their distribution, cannot expect a large rescue effect (Brown and Kodric-Brown 1977) from surrounding regions. Landscape change in the western United States thus can quickly result in a loss of connectivity. In our SEPM results, semi-isolated (e.g., Oregon) and fragmented (e.g., Colorado) wolf populations show greater threats than they would in a static model of habitat suitability (figure 6). Counterintuitively, landscape change has a greater negative impact on wolves (a 35% to 53% decrease in occupied habitat) than on grizzly bears (a 24% to 40% decrease) in the SEPM simulations. Although currently wolves can occupy a broader spectrum of the landscape than grizzly bears, more of this matrix is threatened by landscape change than are the core areas used by grizzlies. The loss of such high proportions of potential wolf habitat as a result of landscape change in the western United States over the next quarter-century suggests that absent the protection of important habitat, many western landscapes will become unsuitable for the species, and possibly for other large carnivores as well.

The SEPM results can help planners evaluate the extent of currently "occupiable" and potentially restorable habitat across a species' range. They reveal a potential wolf population structure that combines two highly resilient core areas (the GYE and central Idaho) and several smaller cores, with many peripheral areas that may be dependent on dispersal from core areas for their initial colonization, their continued demographic rescue, or both (Brown and Kodric-Brown 1977). An optimal strategy for establishing representative wolf populations might therefore be based on initial reintroductions to a geographically well-distributed set of core areas (e.g., the current reintroduction areas in the GYE, Idaho, and the Blue Range [figure 2], plus the Grand Canyon and western Colorado). This would seek to maximize the area of peripheral habitat affected by dispersal from the core reintroductions. Secondary targets for reintroductions, to achieve representation and buttress redundancy, would be regions that lack large core areas, but might be unlikely to be rapidly recolonized because of their distance from initial reintroduction sites (e.g., the Oregon Cascades). The high relative vulnerability to future threats and high potential benefit from restoration actions would justify more aggressive habitat protection in Colorado and Oregon, where protected public lands are fragmented and embedded in a rapidly developing matrix of private lands.

Because wolf habitat, as depicted in the SEPM results, is not distributed uniformly across the western United States, it makes sense to break the region into several subareas, each of which might support tightly interacting populations and be linked loosely with the other subareas by infrequent dispersal. Such areas include (a) the northern Rockies, (b) Colorado, (c) the Southwest (Arizona, New Mexico, and portions of Utah), and (d) the Pacific states (figures 2, 6a). These regions could serve as the basis for DPSs or multistate management coordination areas. Ecological barriers, such as expanses of unsuitable habitat, are more appropriate for delineating DPSs than geographic divisions, such as state boundaries (*National Wildlife Federation v. Norton,* 03-CV-340 [2005]). However, management decisions such as delisting proposals that affect a particular DPS should also take into account the broader rangewide context for recovery. For example, even infrequent dispersal between DPSs may be important for initial recolonization and subsequent genetic interchange. The SEPM results suggest that important areas for maintaining population connectivity, both within and among DPSs, include (a) linkages between the three northern Rockies populations (central Idaho, the GYE, and northwestern Montana), (b) linkages along an arc of mountainous habitat extending southward from the GYE to the Blue Range (Arizona and New Mexico) and southward into Mexico, and (c) a linkage between Colorado and the Uintas of northern Utah (figure 6a). Connectivity between central Idaho and the Oregon Cascades is more tenuous but is strongly enhanced by road removal on public lands (figure 6c). Our results suggest that the potential still exists to recreate a metapopulation of wolves stretching from Canada to Mexico. Similar habitat analyses for adjacent regions of Mexico will allow binational coordination of recovery efforts (Carroll et al. 2005). Expanding analyses beyond the United States is difficult because of inconsistencies in habitat data. However, planners should be aware that truncating analysis at the US border may affect results for areas dependent on dispersal from source habitat outside the United States. For example, inclusion of Mexico and western Canada in the wolf analysis increases predicted occupancy in southern Arizona and northeastern Washington.

SEPM results such as those reported here are also relevant to planners at the DPS scale, in that they make it possible to consider recovery throughout the DPS, rather than constrained within artificially defined recovery areas. For example, current regulations require that wolves dispersing outside of the 17,546 km^2 BRWRA (figure 2) be recaptured, a policy that has severely impeded the success of the recovery program (Oakleaf et al. 2004). The inadequacy of the BRWRA alone to support a self-sustaining population, and the likelihood of high dispersal rates, could have been anticipated on the basis of SEPM results showing fragmented source habitat within the BRWRA but sufficient additional habitat northwest of the area (figure 6a). Our results suggest that at least two more reintroduction sites will be necessary to achieve recovery within the SWDPS, because of the more fragmented nature of regional wolf habitat there when compared with the northern Rockies. This fragmentation is due to the natural isolation of forest habitat on mountain ranges in this semiarid region, as well as other anthropogenic barriers to dispersal. Although all four candidate reintroduction sites have low enough extinction risk that they can be included in further planning for wolf recovery, the vulnerability to landscape change of the Mogollon Rim and San Juan Mountains sites, and the relative isolation of the Carson site from the bulk of wolf habitat in the region, may make it advisable to pair any of these three sites with a second site to ensure the establishment of a well-distributed, viable population.

Although it achieves viability (resiliency and redundancy) goals, the potential recovery goal of three populations of 100 wolves each achieves a relatively low level of representation in the short term. However, the eventual wolf distribution achieved from a three-site reintroduction approach appears adequate, at least under the assumption that current habitat conditions do not deteriorate. The central issue then becomes the role of federal versus state management of wildlife during the recovery process, and the appropriate stage for transfer of regulatory authority from the federal to the state level, given the ESA mandate to ensure that a recovered species occupies a significant portion of range. A state plan sufficient to ensure this mandate would most likely be more precautionary than those approved by the USFWS to date.

In their efforts to restore imperiled species and ecosystems, planners must be both ambitious and realistic. Inadequacy and lack of rigor in current ESA recovery plan goals (Gerber and Hatch 2002) are due in part to a shifting-baseline effect (Jackson et al. 2001) that limits the "realistic" range of goals from considering the historic extent of suitable habitat. As Leonard and colleagues (2005) concluded on the basis of genetic analysis, "restoration goals for grey wolves in the western contiguous US include far less area and target vastly lower population sizes than existed historically." The population estimates from the SEPM scenarios reported here are far more ambitious than current recovery goals but at least an order of magnitude lower than historic population estimates (Leonard et al. 2005), and should thus fall within the range of options considered in recovery planning.

To clarify the debate over wolf recovery goals, suitable habitat might be divided into three categories: (1) areas that can be occupied by wolves despite current human impacts and anticipated habitat loss (figure 5, zone 5), (2) areas that are unlikely to support wolves even with substantial habitat restoration or policy change (figure 5, zone 2), and (3) intermediate areas where long-term wolf recovery might require proactive conservation measures (e.g., road removal and restriction of lethal control in response to livestock depredation) (figure 5, zones 3 and 4). While recovery goals must incorporate the ESA mandate concerning significant portion of range, beyond this threshold a normative decision must be made as to what level of biologically suitable habitat should be made occupiable by mitigating human impacts. Our results suggest that more ambitious recovery goals (up to about two-thirds of suitable habitat occupied) may be feasible. Closure or removal of roads on public lands greatly enhances wolf recovery in regions such as Colorado and Oregon that have high ecosystem productivity but currently lack large core areas. Although wolves could inhabit portions of these states without habitat restoration, their distribution might be too restricted to fulfill ESA mandates.

Ecological effectiveness is the most ambitious of the five guiding principles for recovery, as it speaks to abundance as well as distribution (Soulé et al. 2005). Unlike the concept of "significant portion of range," ecological effectiveness is only implicitly mandated by the ESA's charge to conserve the ecosystems on which endangered species depend. Although the role of wolves as keystone species presents a particularly strong argument for restoration of ecologically effective populations, conservation science has increasingly highlighted the high proportion of threatened species that may strongly influence ecosystem function (Soulé et al. 2005), and the high value to humankind of the services arising from functioning ecosystems (Daily 1997). The normative debate over recovery goals for wolves, although tied to the specific legal context of the ESA, thus illuminates a larger debate over the necessity for "rewilding," a reversal of the trend toward increasing human domination of Earth's natural ecosystems (Vitousek et al. 1997, Soulé and Noss 1998).

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