Impacts of Landscape Change on Wolf Restoration Success: Planning a Reintroduction Program Based on Static and Dynamic Spatial Models

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Abstract: *Mammalian carnivores are increasingly the focus of reintroduction attempts in areas from which they have been extirpated by historic persecution. We used static and dynamic spatial models to evaluate whether a proposed wolf reintroduction to the southern Rocky Mountain region (U.S.A) would advance recovery by increasing species distribution beyond what might be expected through natural range expansion. We used multiple logistic regression to develop a resource-selection function relating wolf distribution in the Greater Yellowstone region with regional-scale habitat variables. We also used a spatially explicit population model to predict wolf distribution and viability at several potential reintroduction sites within the region under current conditions and under two contrasting predictions of future landscape change. Areas of the southern Rocky Mountains with resource-selection-function values similar to those of currently inhabited areas in Yellowstone could potentially support >1000 wolves, 40% within protected areas and 47% on unprotected public lands. The dynamic model predicted similar distribution under current conditions but suggested that development trends over 25 years may result in the loss of one of four potential regional subpopulations and increased isolation of the remaining areas. The reduction in carrying capacity due to landscape change ranged from 49% to 66%, depending on assumptions about road development on public lands. Although much of the wolf population occurs outside core protected areas, these areas remain the key to the persistence of subpopulations. Although the dynamic model's sensitivity to dispersal parameters made it difficult to predict the probability of natural recolonization from distant sources, it suggested that an active reintroduction to two sites within the region may be necessary to ensure low extinction probability. Social carnivores such as the wolf, which often require larger territories than solitary species of similar size, may be more vulnerable to environmental stochasticity and landscape fragmentation than their vagility and fecundity would suggest.*

Impacto del Cambio de Paisaje sobre el Exito de Restauración de Lobos: Planeación de Programas de Reintroducción Utilizando Modelos Espaciales Estáticos y Dinámicos

Resumen: *Con mayor frecuencia, los mamíferos carnívoros son el foco de intentos de reintroducción en áreas de las que han sido extirpados por persecución histórica. Utilizamos modelos espaciales estáticos y dinámicos para evaluar si la propuesta de reintroducción de lobos a la región sur de las Montañas Rocallosas (E.U.A.) haría progresar la recuperación al incrementar la distribución de la especie más allá de lo que pudiera esperarse por su expansión natural. Usamos regresión logística múltiple para desarrollar una función recurso-selección que relacionó la distribución de lobos en la región de Greater Yellowstone con variables de hábitat a escala regional. También utilizamos un modelo poblacional espacialmente explícito para predecir la distribución y viabilidad de lobos en varios sitios potenciales de reintroducción dentro de la región bajo condiciones actuales y bajo dos predicciones contrastantes de cambios futuros en el paisaje. Las*

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áreas del sur de las Montañas Rocallosas con valores recurso-selección similares a los de áreas actualmente habitadas en Yellowstone potencialmente podrían albergar >1000 lobos, con 40% en áreas protegidas y 47% en tierras públicas no protegidas. El modelo dinámico predijo una distribución similar bajo condiciones actuales pero sugirió que las tendencias de desarrollo a 25 años pudieran resultar en la pérdida de una de cuatro potenciales subpoblaciones regionales y en el incremento en el aislamiento de las áreas remanentes. La reducción en la capacidad de carga debido a cambios en el paisaje varió de 49 a 66% dependiendo de la construcción proyectada de caminos en tierras públicas. Aunque buena parte de la población de lobos ocurre fuera de las áreas protegidas núcleo, estas áreas siguen siendo la clave para la persistencia de las subpoblaciones. Aunque la sensibilidad a los parámetros de dispersión del modelo dinámico dificultó la predicción de la probabilidad de recolonización a partir de fuentes lejanas, sugirió que puede ser necesaria una reintroducción activa en dos sitios dentro de la región para asegurar una baja probabilidad de extinción. Carnívoros sociales, tales como los lobos, que a menudo requieren territorios mayores que especies solitarias de similar tamaño, pueden ser más vulnerables a la estocacidad ambiental y a la fragmentación del paisaje de lo que pudieran sugerir su vagilidad y fecundidad.

Introduction

Mammalian carnivores such as the gray wolf (*Canis lupus*) have increasingly been the focus of restoration efforts in North America and several other continents (Breitenmoser et al. 2001). Large carnivores merit conservation attention in their own right (Gittleman et al. 2001). Because they may also be particularly sensitive to fragmentation effects that will eventually influence a larger suite of species (Woodroffe & Ginsberg 1998), examining the effects of human-induced landscape change on carnivores may also provide more general guidelines for regional-scale conservation. The wolf was extirpated from the Rocky Mountains of the United States during the early to middle 1900s (Young & Goldman 1944). In the 1980s, wolves reoccupied portions of the northern Rocky Mountain region (U.S.A) through natural recolonization from Canada (Ream et al. 1991). In the 1990s, wolves were re-introduced to the Greater Yellowstone Ecosystem (GYE), central Idaho, and Arizona (Bangs et al. 1998; Brown & Parsons 2001).

Wolves locate their home ranges in areas with adequate prey and low levels of human interference (Mladenoff et al.1995). Human-caused mortality often comprises 80–95% of total mortality (Fuller 1989). Roads, by increasing human access, negatively affect wolf populations at local, landscape, and regional scales (Fuller 1989; Mladenoff et al. 1995). Ungulates such as elk (*Cervus elaphus*), deer (*Odocoileus virginianus* and *O. hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) make up the bulk of the wolf's diet (Fuller 1989). Prey density explains up to 72% of the variation in wolf density in areas where anthropogenic mortality is low (Fuller 1989). Because wolves in mountainous regions such as the western United States often concentrate activities in forested valley bottoms where snow condition and prey availability are optimal (Singleton 1995), topographic and snowfall data may be correlated with habitat productivity.

Wolves reach sexual maturity at an early age and have large litters. The species' flexible social structure allows pack structure, fecundity, and dispersal to respond to shifts in population density and prey abundance (Fuller 1989; Weaver et al. 1996). However, wolves, like many other large carnivores, require large areas to support viable populations, and the social structure of the wolf may make limits to habitat area even more important because social animals require larger territories than solitary animals of similar size (Woodroffe & Ginsberg 1998). Social structure may also increase the effects of demographic stochasticity by limiting reproduction to the dominant pair within a breeding group (Vucetich et al. 1997).

Regional habitat suitability can be predicted in a geographic information system (GIS) by combining data on different components of wolf habitat quality, such as prey availability and human-associated mortality risk (Mladenoff et al. 1995; Harrison & Chapin 1998). These static habitat models provide a snapshot of habitat quality and potential population distribution. Alternately, nonspatial dynamic viability models (Lacy 1993) use summary information on habitat characteristics to predict carrying capacity and other habitat-related parameters over time. Combining both spatial habitat information and demographic data in a dynamic model results in a spatially explicit population model (SEPM) (Karieva & Wennergren 1995; Schumaker 1998). Such models can be used to evaluate area and connectivity factors and predict source-sink behavior, but they can be sensitive to errors in poorly known parameters such as dispersal rate (Karieva et al. 1996). Nevertheless, they provide qualitative insights into factors, such as variance in population size, that are difficult to explore using static spatial models. In contrast, static habitat models and nonspatial demographic viability models can provide robust results even when data on a species' demography and habitat associations are limited.

We used two types of spatial models to help evaluate whether a wolf reintroduction to the southern Rocky Mountain region (U.S.A.) would advance recovery goals by increasing species distribution and viability beyond what might be expected through natural range expansion. We also compared the viability of reintroduced populations at several potential reintroduction sites within the region under two contrasting predictions of future landscape change.

Species-reintroduction efforts generally require large investments of time and resources. If spatial models such as those evaluated here can provide robust predictions of reintroduction success, they may become important tools in planning the recovery of endangered species. In addition, model results may provide more-general insights into the vulnerability of wide-ranging species to human-associated landscape change.

Methods

Study Area

The study area covered 280,000 km^2 in the Rocky Mountains of the western United States and included the Southern Rocky Mountain (SRM) ecoregion (Shinneman et al. 2000) and adjacent areas (Fig. 1). Areas to the northwest that link the study area with current wolf range in the GYE were also analyzed but were not included in the summary statistics. Mean elevation is 2300 m, ranging from approximately 1200 m in the Colorado River canyon to approximately 4200 m in the mountains of central Colorado. The climate ranges from semiarid in the southwestern portion of the region to continental on the eastern margin. Mean annual precipitation is 1500 mm, and mean annual snowfall is 2700 mm (Daly et al. 1994). Major vegetation types include evergreen needleleaf forests, aspen (*Populus* spp.) parklands, sagebrush (*Artemisia* spp.) shrublands, and grasslands (Shinneman et al. 2000).

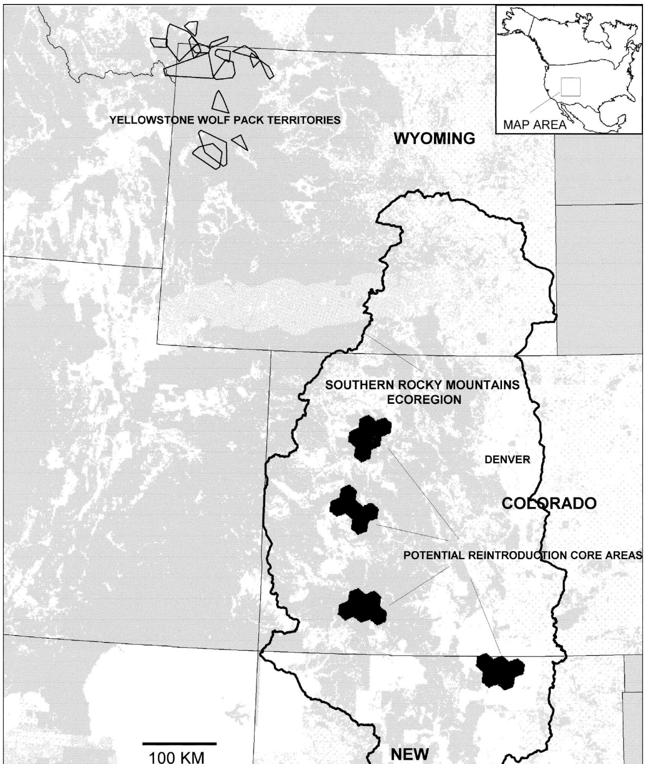


Figure 1. Study area in the U.S. southern Rocky Mountains, with public lands shown in gray and candidate wolf reintroduction sites in black.

Public lands make up 53% of the region (Fig. 1). Designated protected areas, which comprise 20% of public lands, are primarily located in higher elevations along the continental divide (Gap Analysis Program, unpublished data), which also hold most other unprotected areas with few roads. Prey such as elk and deer are most abundant on lower-elevation public lands to the west of these areas.

Historically important economic activities such as mining, livestock production, and agriculture remain significant but are increasingly eclipsed by other employment categories such as the service industry and the retail trade (Shinneman et al. 2000; Theobald 2000). Livestock production, a land use which potentially conflicts with large-carnivore restoration, is concentrated in west-central and especially northwest Colorado. Grazing is permitted on the majority of public lands, including those designated as wilderness. Public lands and adjacent private lands also may experience high levels of recreational use.

Mean population density in the SRM region is approximately 9 persons/km^2 (Shinneman et al. 2000). Portions of the study area, such as western Colorado, have among the highest rates of human population growth in the United States, resulting in conversion of forest and large agricultural holdings to low-density residential development (Theobald 2000). Although private lands form less than half of the landscape, their rapid development may disproportionately affect key areas, such as productive riparian corridors, and geographically fragment public lands (Theobald 2000).

Static Model

We compared spatial data on the boundaries of wolf pack territories (Fig. 1) in the GYE (annual minimum convex polygon, 2000 data) with habitat characteristics to predict wolf distribution in the SRM region. Habitat variables, which are reviewed in detail in Carroll et al. (2001*a*), included vegetation, satellite imagery metrics derived from the MODIS sensor (Huete et al. 1997), topography, climate, and human-impact variables. The MODIS data were used to derive the "tasseled-cap" indices of brightness, greenness, and wetness (Crist & Cicone 1984), which are correlated to varying degrees with ecological factors such as net primary productivity and which have proved useful in modeling wildlife distributions (Mace et al. 1999; Carroll et al. 2001*a*). We used MODIS data from both midsummer and early winter to incorporate seasonal changes in resource availability and phenology. All GIS layers were generalized to a 1-km^2 resolution for the analysis. Multiple logistic regression was used to compare habitat variables at points within territories with those at points outside territories within the GYE. We selected an optimal multivariable model using the Bayesian information criterion (BIC), a diagnostic statistic that penalizes for overfitting (Schwarz 1978). We used the coefficients from the final model to calculate a resource-selection function (RSF) $w(x)$ for used (occurrences) and unused resources (Manly et al. 1993; Boyce & McDonald 1999), which is referred to subsequently as the static model. Although the resulting RSF predictions were produced at the resolution of the input data (1 km^2), we used these predictions to compare the relative capacity of larger landscapes of over 500 km^2 to support wolves. This larger scale, which approximates the average size of wolf pack territories in the region (D. Smith, unpublished data), was also the scale of the predictions produced by the dynamic model described below.

We used a two-step process for estimating potential wolf population size that first delineated potential wolf distribution and then estimated wolf abundance within those areas based on auxiliary data on prey density (Mladenoff & Sickley 1999). We predicted the potential size of wolf populations that might inhabit areas with high habitat suitability as predicted by the static model, based on an equation relating wolf density to prey density (Fuller 1989; Mladenoff & Sickley 1999): wolf density/1000 km^2 = 4.19*DEPU/km^2, where DEPU, or deer-equivalent prey units, were derived from elk and deer abundance data (Colorado Division of Wildlife Resources 1997; New Mexico Game and Fish, unpublished data; Wyoming Game and Fish, unpublished data).

Dynamic Model

We performed population viability analyses by using a modified version of the program PATCH (Schumaker 1998), which links the survival and fecundity of female territorial animals to GIS data on mortality risk and habitat productivity measured at the scale of the individual territory. The model tracks the population through time as individuals are born, disperse, reproduce, and die, predicting population size, time to extinction, and migration and colonization rates. Territories are allocated by intersecting the GIS data with an array of hexagonal cells. We modified the model to associate each hexagon with a single wolf pack rather than with an individual territory holder. The GIS maps were assigned weights based on the relative fecundity and survival rates expected in the various habitat classes, as described below. Survival and reproductive rates are then supplied to the model as a population projection matrix. The model scales the matrix values based on the hexagon scores, with poorer habitat translating into lower scores and thus higher mortality rates and lower reproductive output. Each hexagon can then be assigned a value for lambda, the finite rate of increase, indicating its expected source-sink properties.

Conceptual models were used to estimate relative fecundity and survival. The fecundity model was based on tasseled-cap greenness (Mace et al. 1999), which has been shown to be correlated with ungulate density (Carroll et al. 2001*b*). The fecundity metric incorporated the negative effect of terrain (slope) on prey availability (Carroll et al. 2001*b*). We used a habitat model rather than directly using prey data because we could obtain relatively consistent prey data for the SRM region but not for the larger region analyzed in the PATCH model simulations. A metric combining road density, local human population density, and interpolated human population density (Merrill et al. 1999) predicted mortality risk. Survival was also proportionately increased in parks as a result of lack of hunting and a consequent lower lethality of humans.

We were able to build a strong link between the GIS habitat data and demographic parameters because a large number of published field studies with estimates of fecundity and survival are available (e.g., Ballard et al. 1987; Fuller 1989; Pletscher et al. 1997). We calibrated the demographic rates assigned in PATCH so that, for example, wolves in an area showing levels of habitat productivity and human impacts similar to those of Yellowstone National Park would be assigned fecundity and mortality values near those actually recorded there. Even for a well-studied species such as the wolf, however, generalizing local demographic data to a regional scale based on habitat models requires assumptions that strongly affect resulting model predictions. Because the dynamic model, unlike the static model, was developed without the use of the GYE pack-territory data, we validated the wolf distribution predicted by PATCH with that pack-territory data.

Mean and maximum demographic rates are shown in Table 1. Fecundity is given as the number of female offspring per pack. Expected rates (Table 1) are given as averaged over the entire region, including areas with low suitability for wolves. Because most areas assigned rates at the lower end of the scale remain unoccupied in the simulations, packs actually show higher mean rates and a smaller range of rates than are shown in Table 1. The expected lambda values were predicted by scaling the Leslie matrix based on the hexagon scores. These values (Fig. 2a) show that most of the region is expected to be at least weak source habitat. Mean expected lambda was 1.062 and maximum expected lambda was 1.274.

We modified PATCH to better reflect wolf demography by allowing territory holders to be social rather than solitary. This social structure added demographic resilience because individuals from the same pack could rapidly replace territory holders (alpha females) that die, and it strongly influenced movement rates and patterns. We assumed fecundity to be independent of pack size because no general relationship between the two factors has been

Table 1. Demographic values used in the PATCH simulations of wolf population dynamics in the southern Rocky Mountains.*

	Age									
	0	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Maximum fecundity	0.00	0.00	2.29	3.21	3.21	3.21	3.21	3.21	3.21	1.15
Mean fecundity	0.00	0.00	1.20	1.68	1.68	1.68	1.68	1.68	1.68	0.60
Maximum survival	0.46	0.86	0.96	0.96	0.96	0.96	0.96	0.96	0.69	0.46
Mean survival	0.37	0.69	0.77	0.77	0.77	0.77	0.77	0.77	0.55	0.37

** Fecundity is given as number of female offspring per pack. Mean values are averaged over the entire region, including areas that did not support wolves in the subsequent simulations. Maximum values are before adjustment for environmental stochasticity.*

documented (Ballard et al. 1987). As pack size increases, individual wolves in PATCH have a greater tendency to disperse and search for new available breeding sites. The probability of leaving a pack is a quadratically increasing function, with high dispersal probabilities as pack size approaches the theoretical maximum. Setting the maximum at 24 adults resulted in observed maximum pack sizes of 8–11 adults. C. C., unpublished data). Packs in the GYE currently average 5.9 adults (D. W. S., unpublished data). The size of hexagons or pack territories used in the PATCH model was 500 km^2. The mean territory size of GYE packs in 2000 was 545.6 km^2 (n = 16, range = 154-1675 km^2, SD = 504.0) (D. Smith, unpublished data).

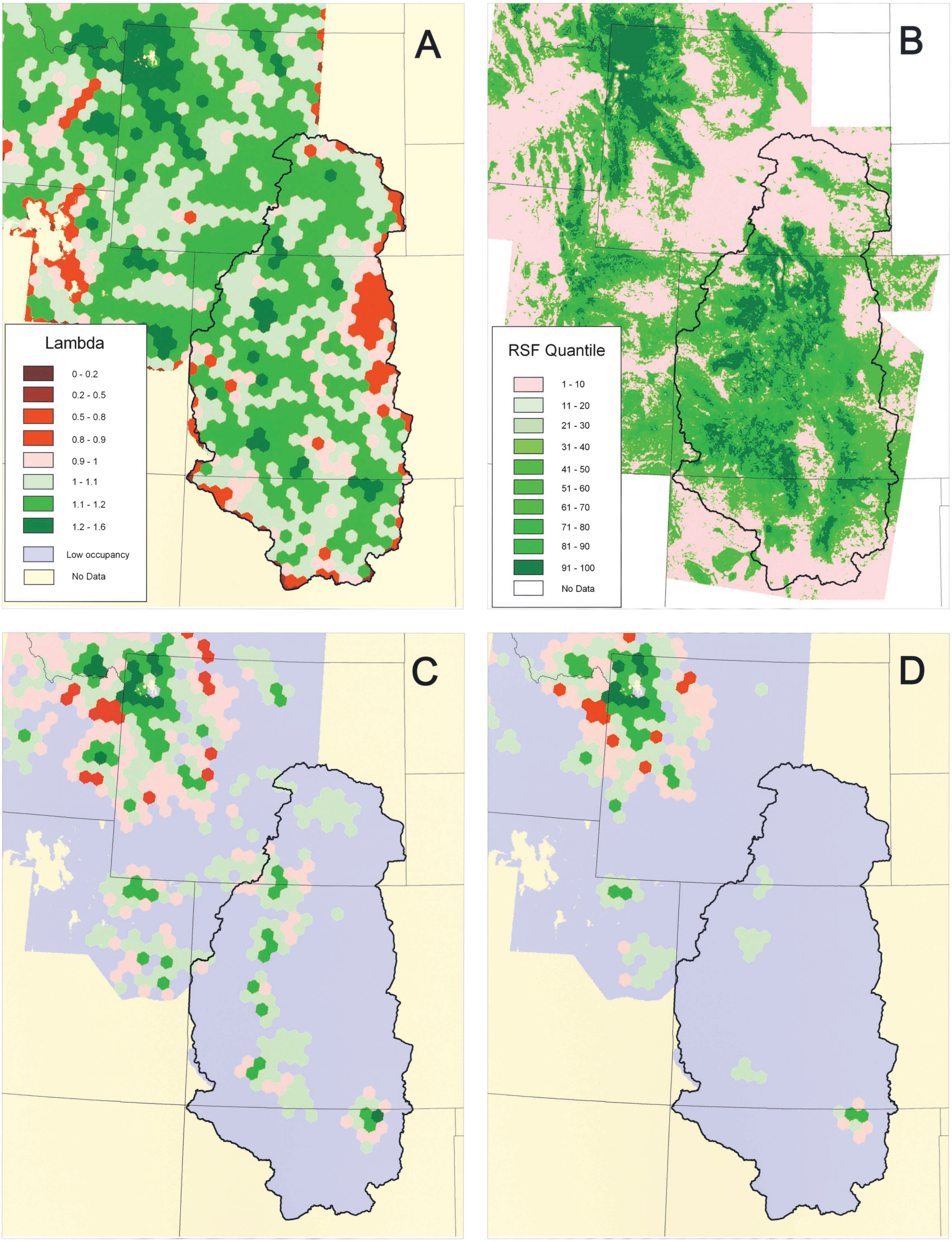
We simulated dispersal by using a directed random walk with a maximum dispersal distance of 250 km. Movement decisions in a directed random walk combine varying proportions of randomness, correlation (tendency to continue in the direction of the last step), and attraction to higher quality habitat, but without knowledge of habitat quality beyond the immediately adjacent territories.

We modeled environmental stochasticity by drawing the maximum Leslie matrix values (Table 1) from a truncated normal distribution with coefficients of variation of 30% for fecundity, 40% for pup mortality, and 30% for adult mortality (Ballard et al. 1987; Fuller 1989). We compared those outcomes to results from simulations conducted without environmental stochasticity. One thousand replicate simulations of 200 years were conducted per scenario. In addition to assessing model sensitivity to environmental stochasticity, we explored the plausibility of the model's predicted wolf distributions by comparing them with known distribution in other areas of the Rocky Mountains (C.C., unpublished data).

The PATCH model allows the landscape to change through time. Hence, the user can quantify the consequences of landscape change for population viability and examine changes in vital rates and occupancy patterns that result from habitat loss or fragmentation. We used this feature to explore the consequences for wolves of road development and human population growth during the period 2000–2025. Census data were available for the period 1990–2000. We predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 2000, but we adjusted the predicted 2025 population to match state-level Census Bureau predictions (U.S. Census Bureau, unpublished data). Road density was predicted to increase at 1% per year (Theobald et al. 1996). The landscape scenarios we evaluated included: (A) current conditions, (B) human population as of 2025, with increased road development on private lands only, and (C) human population as of 2025, with increased road development on private and unprotected public lands. A new map including all landscape change over the period 2000–2025 was introduced into the simulation at year 25, rather than incrementally over 25 yearly time steps.

In addition to using PATCH to assess the overall potential of the region to support wolf populations (carrying capacity), we modeled specific reintroduction options to assess transient dynamics such as the probability of extinction and the probability of an area being colonized by wolves from a specific reintroduction site. Based on a review of the literature (Bennett 1994; Martin et al. 1999), field knowledge, and preliminary modeling results, we chose to compare reintroduction areas in southwestern, west-central, and northwestern Colorado and northern New Mexico (Fig. 1). Within each of these general regions, the 2500-km^2 area exhibiting the highest long-term potential occupancy rates in PATCH was selected as the candidate reintroduction core sites (Fig. 1). We also combined the individual core sites to construct four composite

Figure 2. Predicted distribution and demography of wolves in the southern Rocky Mountain region under the differing models used in this study: (a) expected demographic potential for wolves as predicted by the scaled Leslie matrix used as input to the PATCH simulations; (b) relative probability of occupancy by wolves as predicted by a resource-selection function (RSF) developed from wolf distribution data in the Greater Yellowstone Ecosystem; (c) potential distribution and demography of wolves as observed in the PATCH simulations under current landscape conditions; and (d) potential distribution and demography of wolves as observed in the PATCH simulations under future scenario C (development on both public and private lands through 2025). Only those areas with a predicted probability of occupancy of >50% are shown in (c) and (d).


A
Lambda
0 - 0.2
0.2 - 0.5
0.5 - 0.8
0.8 - 0.9
0.9 - 1
1 - 1.1
1.1 - 1.2
1.2 - 1.6
Low occupancy
No Data
B
RSF Quantile
1 - 10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
71 - 80
81 - 90
91 - 100
No Data
C
D

reintroduction options: (1) natural recovery from northern Rocky Mountain populations, (2) reintroduction to northern New Mexico, (3) option 2 plus reintroduction to southwestern Colorado, and (4) option 3 plus reintroduction to northwestern Colorado. We approximated the standard reintroduction protocol (Bangs & Fritts 1996) by introducing five breeding-age females in the first year and setting survival for the first five years at close to 100%, under the assumption that new animals would be released to compensate for mortality among the initial releases.

Results

Static Model

We selected an optimal RSF model ($-2\text{LL} = 2034$, $\chi^2 = 3897$, df $= 11$, $p < 0.001$) of the form

$$\begin{aligned} w(x) = {} & \exp(0.1369949\text{GREEN} - 0.07082755\text{WET} + \\ & 1.286847\text{ELK} + 0.004094865\text{SNOW} - \\ & 5.523428 * 10^{-7}\text{SNOW}^2 + 0.2073694\text{SLOPE} - \\ & 0.0117322\text{SLOPE}^2 + 0.3847016\text{PUBLIC} + \\ & 0.4901291\text{WILD} + 2.877422\text{PARK}), \end{aligned}$$

where GREEN is MODIS July greenness, WET is MODIS November wetness, ELK is elk winter range, SNOW is annual snowfall, SLOPE is slope in degrees, and PUBLIC, WILD, and PARK are the general public, wilderness, and park management classes.

Extrapolating the model southward from the GYE into Colorado produces a predicted distribution map (Fig. 2b) showing that wolf habitat similar to that occupied within the GYE is found in a band running across northwestern Colorado and also within southwestern Colorado. Based on this model, 46.7% of the region's wolves would be found within general public lands, followed by 40.0% within parks and wilderness areas, and 13.3% on private, unprotected land. The overall number of wolves potentially supported within habitat in the SRM region with RSF values similar to currently inhabited habitat in the GYE (the upper 10% areal quantile of RSF values) is 1305, according to the estimation method based on the model of Fuller (1989), which makes use of the auxiliary data on prey abundance for the SRM region. For comparison, the number of wolves potentially supported within the three Colorado reintroduction core areas of 2500 km^2 in size, according to the Fuller (1989) model, ranges from 97 individuals for northern New Mexico to 75 wolves for southwestern Colorado, 102 for west-central Colorado, and 155 for northwestern Colorado.

Dynamic Model

CURRENT CARRYING CAPACITY: LANDSCAPE SCENARIO A

Under current conditions, strong source areas are present in all of the potential reintroduction sites and on the Wyoming-Colorado border (Fig. 2c). Weaker source habitat between the three western Colorado sites facilitates their connectivity, whereas the northern New Mexico site is more isolated. Based on this model, 41.8% of the region's wolf packs would be found within general public lands, followed by 38.8% on private unprotected land, and 18.7% within parks and wilderness areas. The mean number of packs predicted by the PATCH simulations for the larger subregions surrounding the core reintroduction sites ranged from 21.6 for northern New Mexico to 23.1 for west-central Colorado, 32.2 for southwestern Colorado, and 42.6 for northwestern Colorado. Adjusting the PATCH estimate to account for both sexes of adults and for the percentage of packs composed of pups (range 35–67%, $\bar{x} = 46\%$; Fuller 1989) resulted in a total population estimate of 1486. This figure may be high because mean percentage of pups in packs is based on both autumn and winter data, whereas the wolf density model is based on late winter data (Fuller 1989). The mean lambda observed in the simulations is 0.999, which is lower than the mean expected lambda of 1.062 as a result of the influence of infrequently occupied territories, which tend to show a lambda of near 1.000. Weighting the estimate by the probability that a pack territory is occupied in a particular year gives a mean lambda of 1.017. The maximum lambda observed in the simulations is 1.215, which is also lower than the maximum expected lambda of 1.274. Wolf distribution predicted by the dynamic model is significantly correlated with the observed location of the wolf pack territories in the GYE ($R_s = 0.35$, $p < 0.001$).

FUTURE CARRYING CAPACITY: LANDSCAPE SCENARIO B

Human population growth, coupled with road development on private lands only, reduced the carrying capacity of the region by 49.2% to a total wolf population estimate of 755. Mean number of packs predicted by the PATCH simulations was 9.7 for northern New Mexico, 9.2 for west-central Colorado, 18.9 for southwestern Colorado, and 14.3 for northwestern Colorado. Although we report these as point estimates, we emphasize that model predictions are best used in a relative sense to rank potential sites and management options. Based on this model, 43.8% of the region's wolf packs would be found within general public lands, followed by 32.3% on private, unprotected land, and 23.9% within parks and wilderness areas.

FUTURE CARRYING CAPACITY: LANDSCAPE SCENARIO C

Human population growth, coupled with road development on both private and unprotected public lands, reduced the wolf carrying capacity of the region by 66.3% to a total wolf population estimate of 501. Areas with a >50% likelihood of occupancy remained in all potential reintroduction areas except in west-central Colorado (Fig. 2d). Connectivity, in the form of permanently occupied "stepping-stone" areas, no longer existed between reintroduction areas, although long-distance dispersal by floaters could still occur. Due to the high proportion of private lands in northern New Mexico, the results from both future landscape scenarios were similar in that region. Mean number of packs predicted by the PATCH simulations was 10.7 for northern New Mexico, 4.3 for west-central Colorado, 9.8 for southwestern Colorado, and 9.7 for northwestern Colorado. Based on this model, 38.8% of the region's wolf packs would be found within general public lands, followed by 34.5% on private, unprotected land, and 26.7% within parks and wilderness areas.

A comparison of predicted wolf distribution between simulations using identical mean demographic rates with or without incorporating environmental stochasticity (Fig. 3) showed that year-to-year variation in demographic rates had a strong effect on the likelihood that wolves would occupy habitat areas with higher edge-to-area ratios (i.e., smaller core areas and linear linkages connecting major core areas).

Reintroduction Options

Under current habitat conditions (landscape scenario A), most options show a low probability of extinction. Excluding the natural recolonization option, option 2 has the highest extinction probability at 6.4% (Table 2). Under future landscape scenario B, extinction probability is 16.6% for option 2, 4.5% for option 3, and 1.7% for option 4. Under future landscape scenario C, extinction probability is 13.7% for option 2, 5.3% for option 3, and 2.2% for option 4.

Mean number of packs within the southern Rocky Mountains at year 200 is estimated at 1.7 for the natural recolonization option, 21.6 for option 2, 51.4 for option 3, and 93.1 for option 4 (Fig. 4), given current landscape scenario A. Increasing the maximum dispersal distance parameter from 250 to 500 or 1500 km resulted in estimates of 3.3 or 6.1 packs, respectively, for the natural recolonization option. Under future landscape scenario B, mean number of packs within the southern Rocky Mountains at year 200 is estimated at <1 for the natural recolonization option, 9.7 for option 2, 28.0 for option 3, and 41.1 for option 4 (Fig. 4). Under future landscape scenario C, mean number of packs within the southern Rocky Mountains at year 200 is estimated at <1 for the natural recolonization option, 10.7 for option 2, 20.5 for option 3, and 29.4 for option 4 (Fig. 4).

When the separate reintroduction areas are consid-

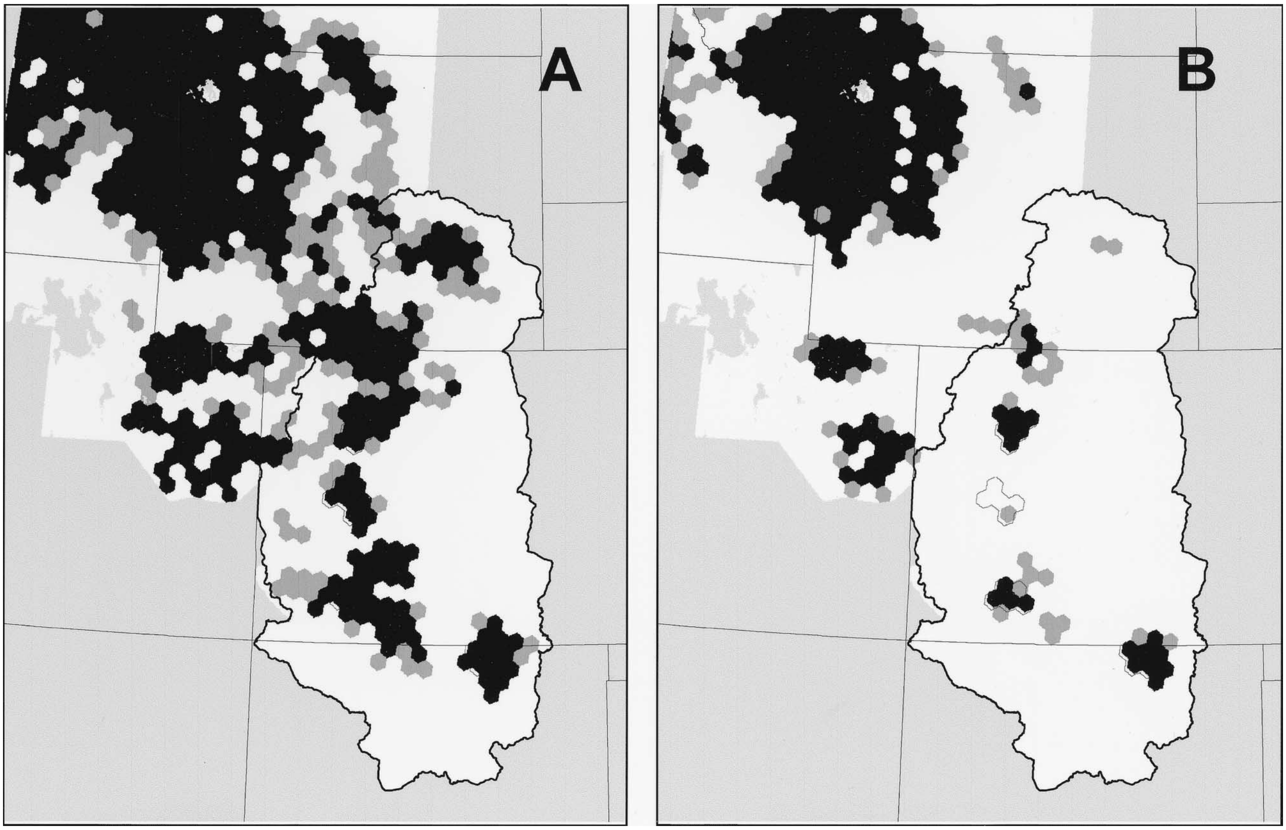


Figure 3. Contrasts between predicted wolf distribution in simulations with and without environmental stochasticity under (a) current conditions (scenario A) and (b) future conditions (scenario C, development on both public and private lands through 2025). Areas in black are occupied in simulations with environmental stochasticity, whereas areas in gray are occupied only in the absence of environmental stochasticity.

Table 2. Relative ranking of potential wolf reintroduction areas in terms of model predictions, with Yellowstone National Park added for comparison.

Area	*mean RSF*[a] *value*	*occupancy probability*[b] *(PATCH), 2000*	*occupancy probability, 2025 (scenario B)*	*occupancy probability, 2025 (scenario C)*	*extinction probability (PATCH), 2000*	*extinction probability, 2025 (scenario C)*
Northern New Mexico	15.7	80.0	67.6	67.1	6.7	14.5
Southwest Colorado	12.0	75.9	68.4	53.1	13.3	31.6
West-central Colorado	17.3	64.4	37.3	23.8	26.7	58.8
Northwestern Colorado	21.9	78.7	58.1	54.8	11.4	31.6
Yellowstone National Park	221.6	99.1	98.7	98.6	<1	<1

[a] *Resource selection function.*
[b] *Occupancy probability is given as averaged over all pack territories in an area.*

ered alone (Fig. 5), rather than as part of the multisite options, extinction probability is 26.7% for a reintroduction to only west-central Colorado, 13.3% for southwestern Colorado, 11.4% for northwestern Colorado, and 6.7% for northern New Mexico (Table 2).

Under future landscape scenario B, extinction probability is 26.3% for a reintroduction to only west-central Colorado, 12.5% for southwestern Colorado, 11.8% for northwestern Colorado, and 16.6% for northern New Mexico. Under future landscape scenario C, extinction probability increases, reaching 58.8% for a reintroduction to only west-central Colorado, 31.6% for southwestern Colorado, 31.6% for northwestern Colorado, and 14.5% for northern New Mexico (Table 2).

Discussion

Spatial models such as ours contribute a new perspective to population viability analysis and endangered species recovery planning. The resource-selection-function (RSF) model extracts new information from the successful reintroduction of wolves into a neighboring region, revealing regionally specific habitat associations not evident in more-general models or those adapted from the central United States (e.g., Mladenoff et al.1995). The RSF model may be too specific, however, because wolves in the GYE, which were reintroduced in 1995, have not yet dispersed to inhabit a full range of potential habitats, and some characteristics of currently occupied habitat (e.g., association with boreal forest types) may be coincidental rather than actual limiting factors. The probability of such extrapolation error grows as distance increases from the source of the wolf-distribution data, the GYE.

The spatially explicit population model (SEPM) allows a greater level of biological realism because it integrates data on demography and habitat and can explore the response of wolf populations to new habitat scenarios and examine long-term viability requirements, which may differ from short-term requirements for occupation of habitat. How-

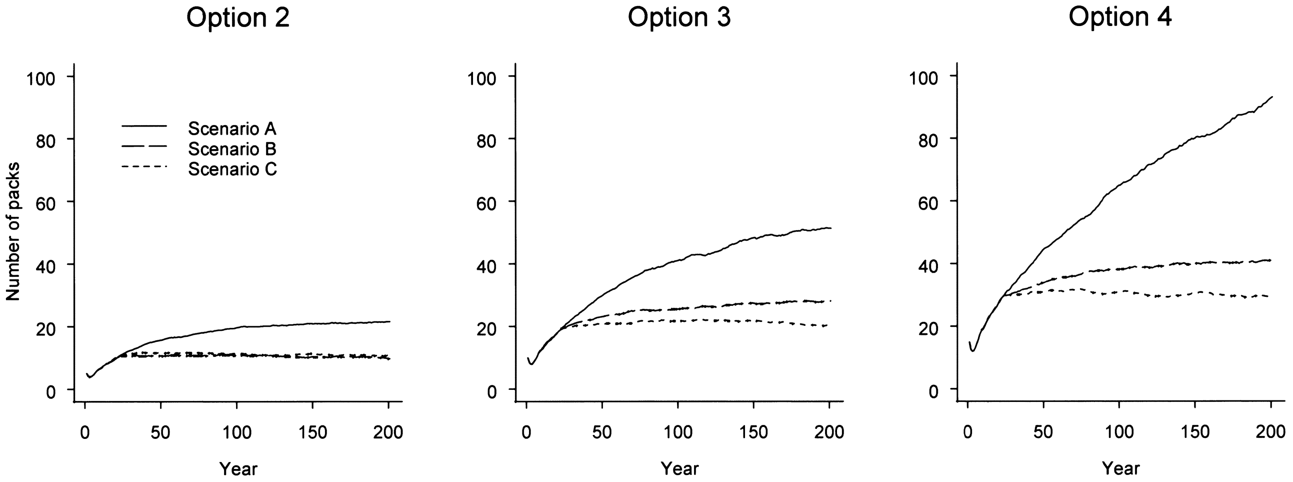


Figure 4. Mean wolf population trajectory as predicted by the PATCH model for three reintroduction options under current and future conditions. Option 2 would involve reintroduction of wolves to northern New Mexico, option 3 would add a second reintroduction site in southwestern Colorado, and option 4 would add a third reintroduction site in northwestern Colorado.

ever, this model's added complexity may make its results more sensitive to variation in poorly known parameters such as dispersal behavior (Karieva et al. 1996). This increased variability makes SEPMs more appropriate for ranking management options than predicting actual population levels. Both the static and dynamic models provide a structure for considering restoration potential and making qualitative comparisons between regions. Both approaches are also useful for generating testable hypotheses that can be refined in an adaptive management context based on new field research, improved modeling techniques, and data from successful and unsuccessful restoration efforts and natural recolonization events (Murphy & Noon 1992).

Contrasts between the static and dynamic model predictions derive in part from how they quantify human impacts. The static model includes management status as a surrogate for human impacts, rather than the road or human population variables used as input to the PATCH model. Road density is one of the most significant univariate predictors of wolf distribution in the north-central United States (Mladenoff et al. 1995). Low road density, along with public land ownership, forested land cover, and high elk density are also significantly correlated with the locations of wolf-pack territories in the U.S. northern Rockies (Houts 2000). The absence of road density from the multivariate RSF model we developed is the result of collinearity between habitat variables, specifically the negative correlation between road density and other significant variables such as snowfall and slope. Candidate multivariate models that included road density along with the latter variables often resulted in positive coefficients for road density, which would have caused poor model generality when extrapolated to areas of high road density outside the GYE.

The remaining variables included in the static model were consistent with field knowledge of wolf habitat associations and with previous static carnivore habitat models (Carroll et al. 2001*a*). Because wolves are coursing predators, they generally avoid areas with steep slopes where prey vulnerability is low (Paquet et al. 1996). Areas of high snowfall also limit winter movement because of the wolf's high foot loading compared with snow-adapted predators such as the lynx (Paquet et al. 1996). Fall wetness is correlated with early snow cover, accounting for its negative coefficient here. Both elk winter range and summer greenness are indicators of prey productivity (Carroll et al. 2001*a*).

The static and dynamic models give similar estimates of the potential size of the wolf population in the SRM region, but the spatial distribution of predicted wolf abundance differs between the models. The static model predicts that a larger proportion of the region's wolves occurs within parks and wilderness areas than does the PATCH model. Because it ignores the influence of social structure (e.g., interpack aggression) on limiting wolf density, the static model likely overpredicts density in highly suitable areas.

The results of the PATCH model emphasize the importance of mortality risk in limiting wolf distribution. Although wolves may be more demographically resilient than some large carnivores (Weaver et al. 1996), adult survival is still of overriding importance. Contrasts between the predictions of the static and dynamic models derive primarily from area effects and the effects of landscape change. Small, isolated areas of predicted habitat in the static model are rarely occupied in the dynamic model. In contrast, predicted occupancy in areas adjacent to other populations is higher in the PATCH model than in the static model because wolves there benefit from a demographic rescue effect (Brown & Kodric-Brown 1977). For example, the re-introduction area in northwestern Colorado benefits from its location within a larger constellation of habitat patches. Incorporating landscape change into the dynamic model caused areas such as southwestern Colorado, with relatively low human population growth and a high proportion of protected areas, to increase their ranking under future conditions as other more threatened areas become degraded (Table 2). The reintroduction location in northern New Mexico is unique in that it is a highly protected core area that has little risk of future degradation but is surrounded by a relatively unprotected and at-risk regional landscape. Although the core protected area there is larger than areas that support isolated wolf populations, its regional value for wolf conservation may be affected by loss of connectivity.

Model predictions may be inaccurate if extensive land uses, such as public-lands grazing, are more important than intensive land uses, such as development trends, in limiting wolf restoration. Most mortalities in the early stages of restoration of wolves to the GYE have been associated with control of livestock depredation (Bangs et al. 1998). Our model effectively assumes that the risk of encounters between wolves and livestock is correlated with other human-impact factors such as roads, or that intensive human impacts form more-important long-term limiting factors. It can be argued that it is relatively easy to reduce public-lands grazing through changes in management policy but more difficult to reverse development once it occurs. Wolves in the north-central United States, which are in a later stage of range expansion, are more limited by intensive than extensive land use (Mladenoff et al. 1995). However, patterns of low-density public-lands grazing in the western United States may create greater potential for livestock depredation there. Livestock grazing on U.S. Forest Service lands increases from south to north in the SRM region (Bennett 1994). This may place wolves in northwestern Colorado at greater short-term risk than shown in our model and hinder dispersal between the GYE and Colorado.

Turning from the individual sites to the composite reintroduction options, our results suggest that adding a second release site results in a large reduction in extinction probability. Of the options we considered, option 3 of reintroduction to two sites in northern New Mexico and

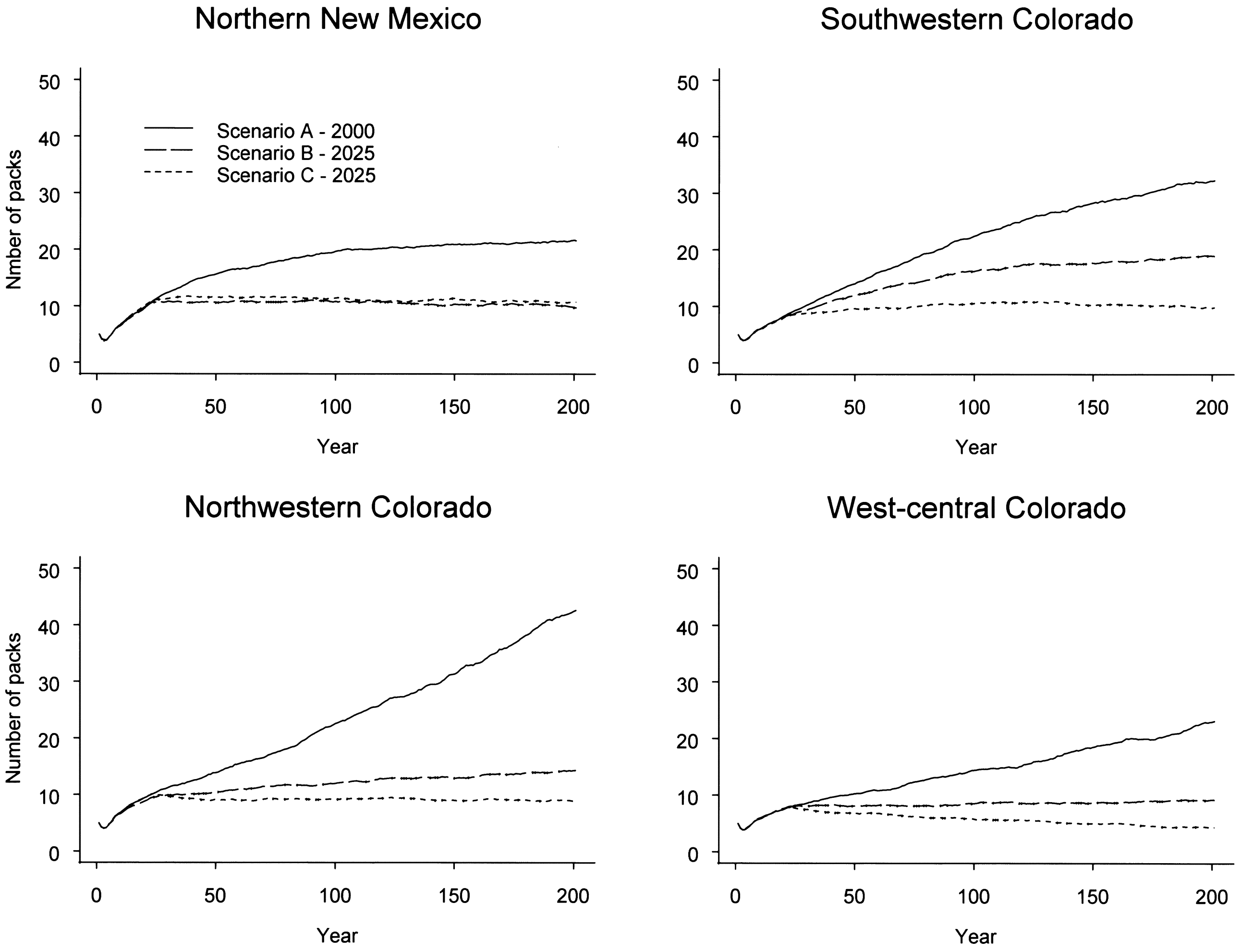


Figure 5. Mean wolf population trajectory as predicted by the PATCH model for the individual candidate reintroduction areas under current and future conditions.

southwestern Colorado may best balance the goals of maximizing the probability of success and minimizing the cost of restoration. The prospects for long-term viability with this option under future scenario C (94.7%) compare favorably with those for wolves in the GYE (>99%). Therefore, despite the effects of landscape change, our results suggest a high potential for successful wolf restoration to the SRM region.

Lessons for Reintroduction Planning

Overall, a consistent message emerges from our two models regarding what portions of the SRM have the highest potential to support wolves and how that potential compares with previous reintroduction areas. Comparison of the RSF and PATCH results from Colorado with those from the GYE and Idaho suggest that the latter two areas are unique in the western United States in the size of their core areas. Resource-selection-function values for the GYE are an order of magnitude greater than those for the Colorado reintroduction sites (Table 2). Although wolves often occur outside core protected areas, they may depend on them for long-term population persistence (Fritts & Carbyn 1995; Haight et al. 1998). Semi-developed, mixed-ownership landscapes such as those found in western Colorado may both support high prey densities and create a high risk of human-caused wolf mortality (Mladenoff et al. 1997). More effort and time may be necessary for wolves in Colorado to reach the population levels seen in the GYE and Idaho after relatively short reintroduction efforts. However, wolf-recovery efforts in the north-central United States suggest that, given favorable human attitudes, wolves can coexist with development at surprisingly high levels. In Wisconsin, wolves currently inhabit more area than was predicted in empirical habitat models based on road density (Mladenoff et al. 1999). Both the RSF and PATCH results suggest that a large proportion of the packs of the SRM region will be found on general public lands rather than in parks or wilderness, but the PATCH results suggest that core refugia remain the key to whether a particular reintroduction area can maintain wolves under future conditions.

The smaller size and greater isolation of core refugia in Colorado compared with those of the GYE and Idaho will likely make maintenance of connectivity between subpopulations of greater importance (Haight et al. 1998). The reduction in carrying capacity caused by landscape change in the SRM is two and four times that seen in the GYE and southern Canadian Rockies, respectively (C.C., unpublished), pointing to the higher pace of development in the SRM, its isolation from more northerly populations, and its current status closer to the threshold for large-carnivore persistence.

Because wolf dispersal behavior is too complex to model realistically, we must consider the variation in results due to dispersal behavior when evaluating model output. Wolves may exhibit a pattern of dispersal termed "stratified diffusion," a mixture of short-distance dispersal that expands existing colonies and long-distance dispersal that creates new colonies (Shigesada & Kawasaki 1997). Although the PATCH model cannot currently predict this type of mixed-dispersal dynamics, it may be instructive regarding the influence of short-distance dispersal on source-sink dynamics within a region. For example, the contrasts in predicted population trajectories between the subregions (Fig. 5) relate to the dispersion of core habitat and the level of connectivity in each area. Occasional long-distance dispersal events may cause the long-term distribution predicted in the PATCH reintroduction options to be achieved more rapidly. The relative levels of connectivity shown by the different scenarios are significant, however, in that they show that even if dispersers from the GYE may potentially colonize Colorado over the long term, the level of connectivity between the GYE and Colorado is low enough that a separate Colorado reintroduction would significantly hasten establishment of that population. This may be important given the pace of landscape change in the region. Our results suggest that although their sensitivity to dispersal parameters make spatially explicit population models unsuitable for some aspects of reintroduction planning, they nevertheless can provide other insights not available from less complex models.

Comparison of the model results also suggests more-general guidelines for large-carnivore conservation. Lambda values observed in the dynamic model were lower than expected from the model input. These more pessimistic predictions are the result of area and connectivity factors that reduce the potential of small and isolated habitat patches to support species with large area requirements. A comparison of the spatial distribution of expected (Fig. 2a) and observed (Fig. 2c) sources and sinks suggests that weak source habitat isolated from strong sources has a low probability of occupancy. The key territories occupying strong source habitat tend to consist of large packs in our model. As the size and demographic value of these packs is reduced with future landscape change, they are less able to support peripheral packs. The high lambda of the largest packs is the inverse of what might be predicted by a density-dependent PVA model, but it is consistent with patterns observed in the GYE population.

An additional reduction in potential occurs when environmental stochasticity is incorporated in the model because territories located in the periphery are most affected by stochastic factors (Fig. 3). This "extinction vortex" (Gilpin & Soulé 1986) is an example of the novel results provided by combining spatial and demographic data. As predicted (Woodroffe & Ginsberg 1998), this effect is more noticeable in the wolf than in solitary large carnivores such as the grizzly bear (C.C., unpublished data) and may be generally relevant to other threatened social carnivores such as the African wild dog (*Lycaon pictus*) (Creel & Creel 1998). This reduction in the viability of peripheral populations may partially negate the added resilience (sensu Weaver et al. 1996) conferred by the wolf's high fecundity and vagility. Our results suggest that dynamic models and less complex models such as resource-selection functions can be complementary tools for the design of reintroduction strategies for carnivores and other area-sensitive species in increasingly human-dominated landscapes.

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