SPATIAL ANALYSIS OF RESTORATION POTENTIAL AND POPULATION VIABILITY OF THE WOLF (*Canis lupus*) IN THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO

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EXECUTIVE SUMMARY

Long-term conservation of the gray wolf (*Canis lupus*) in the southwestern U.S. and northern Mexico likely depends on establishment of a metapopulation or several semi-disjunct but viable populations spanning a significant portion of its historic range in this region. We performed a regional-scale population viability analysis for the wolf using a dynamic, individual-based model (PATCH) that links GIS habitat data to estimates of wolf demographic rates in different habitats. The model results help assess threats to wolf population recovery and prioritize areas for reintroduction. We were able to take advantage of several newly-available regional data sets. However, the resolution of the habitat data was still inconsistent between U.S. and Mexico to an extent that significantly limits comparability between Mexican and U.S. reintroduction sites. We evaluated 5 potential or current reintroduction sites in the U.S.: Blue Range (Arizona/New Mexico), Grand Canyon (Arizona), Mogollon Rim (Tonto National Forest, Arizona), San Juans (Colorado), Vermejo/Carson (northern New Mexico), and 4 potential sites in Mexico: the Austin Ranch area (Chihuahua/Sonora near U.S. border), Carmen (northern Coahuila south of Big Bend National Park), northwestern Durango (by Chihuahua border), and the Tutuaca reserve area (westcentral Chihuahua, by Sonora border). The Blue Range site was included to provide comparability with current recovery program results.

The model predicted that vulnerability of wolf populations to landscape change (e.g., development) varied across the region with higher vulnerability within more fragmented habitat in New Mexico than within the larger habitat blocks in Arizona. Most wolves would eventually inhabit general public lands (i.e., U.S. Forest Service non-wilderness lands) in the U.S., and occur on unprotected private lands in Mexico, although core protected areas played a role in lowering the extinction risk of reintroduced populations. The extinction risk of potential

reintroduction sites varied greatly, with the Mogollon Rim site having the highest extinction risk. The Austin Ranch (Chihuahua) and San Juans (Colorado) sites showed some sensitivity to landscape change and moderate extinction risk, which suggests that if either site were selected it might be best to pair it with a second reintroduction site to ensure high overall success. The Blue Range and Grand Canyon sites showed the highest ability to enhance wolf population establishment in the southwestern U.S.. Amongst the Mexican sites, the Durango site has the most productive habitat for wolves, but the Tutuaca and Carmen sites appear to have lower risk from conflict with livestock production. Our results in the U.S. portion of the southwestern Distinct Population Segment (SWDPS) suggest that the best additional candidate reintroduction sites are in the northern portion of the current SWDPS. The U.S./Mexico border country (e.g., the Chiricahua mountains and other parts of the Sky Islands) is likely to serve as sink habitat for wolves, and may thus be a poor choice for a second U.S. reintroduction site. However, the area's key role as the highest potential habitat connecting U.S. and Mexican populations suggests that it be given significant attention in recovery planning, for example as part of an expanded Blue Range Wolf Recovery Area. Although data limitations prevent direct comparison between U.S. and Mexican sites, the level of population linkage predicted between U.S. and Mexican wolf populations in the border region suggests benefits from a binational coordination of recovery strategies.

INTRODUCTION

HISTORY OF WOLF EXTIRPATION AND RECOVERY IN THE SOUTHWEST

The wolf (*Canis lupus*) is a species of conservation concern in the southwestern United States, being listed as endangered under the U.S. Endangered Species Act (Federal Register 68:15804-15882) and also listed as endangered in Mexico (NOM-059-ECOL-94, Diario Official de la Federacion, May 16, 1994). Wolves were extirpated from the southwestern U.S. by the 1940s (Brown 1983). Between 1977 and 1980, under an agreement between the United States and Mexico, trappers captured five Mexican wolves (*Canis lupus baileyi*) in the Mexican states of Durango and Chihuahua. They transported these four males and one pregnant female to the Arizona-Sonora Desert Museum to establish a captive breeding program. Due to the absence of verified sightings or specimens of wild Mexican wolves in recent decades, it is thought that the small population of wolves present in the wild in Mexico in 1980 has been extirpated due to a continuation of the same forces that led to its original endangerment: habitat alteration and conflict with livestock and humans (Brown 1983). In 1979, the U.S. Fish and Wildlife Service formed a Mexican Wolf Recovery Team. That team finalized a binational recovery plan with Mexico in 1982 (U.S. Fish and Wildlife Service 1982). The plan proposes to maintain a captive breeding program and to reestablish a population of at least 100 wolves (U.S. Fish and Wildlife Service 1982). While the plan contains no downlisting or delisting criteria, a new plan will (B. T. Kelly, pers. comm.). Successive recovery program documents reveal an evolution of recovery goals consistent with the maturation of the field of conservation biology and increased awareness of the factors that promote population viability. Goals have progressed from creating a captive and a single small semi-wild population to currently proposed criteria for several interconnected populations or demes (U.S. Fish and Wildlife Service 1995).

Given the probable extirpation of wild Mexican wolves, captive breeding is essential to recovery. By December 2000 the captive breeding program included 205 animals maintained at 31 facilities in the United States and 14 in Mexico (Arizona-Sonora Desert Museum 2001). The American Zoological Association oversees management, guided by a Species Survival Plan (SSP). During the early 1990s, the U.S. Fish and Wildlife Service began developing an EIS for reestablishing a wild population. After considering over 4,000 comments on the draft EIS, Service recommended the reintroduction of Mexican gray wolves to the Blue Range Wolf Recovery Area (BRWRA) (U.S. Fish and Wildlife Service 1996). The U.S. Fish and Wildlife Service signed the Record of Decision in March 1997; an associated final rule later promulgated reintroduction and management specifics (Parsons 1998). The reintroduction plan called for releasing about 15 wolves annually for up to five consecutive years. Aiming to respect the needs and concerns of local citizens , the Service classified these wolves as members of an experimental-nonessential population (Parsons 1998).

The BRWRA encompasses around 18,000 km^2 of the Gila National Forest in New Mexico and the Apache National Forest in Arizona and New Mexico. The final rule (Parsons 1998) authorizes the Service to initially release wolves only in the “primary recovery zone” of the BRWRA, an area that encompasses about 2,664 km^2 of the Apache National Forest. The remainder of the BRWRA comprises the secondary recovery zone, where re-releases of wolves are authorized. Wolves that travel from the primary recovery zone can inhabit the secondary zone. In March 1998, the Service began reintroductions by releasing 11 wolves (Brown and Parsons 2001). From then until March 2001 the Service released another 45 wolves on 61 occasions. The current wild population of ~40 wolves, while representing important progress for southwestern wolf recovery, is small when compared with Yellowstone Park’s population of 119 wolves five years after the start of reintroduction (Smith et al. 2003). The growth of the Mexican wolf population is, however, consistent with the initial growth of the red wolf (*Canis rufus*) population (J. Oakleaf, unpublished data) which was also established via reintroduction of captive-born animals that were initially managed per restrictive regulations (Parker et al. 1986) similar to those currently being applied to the BRWRA project (Parsons 1998) .

Reintroduction of the Mexican wolf in the BRWRA followed decades of successful conservation and restoration work on behalf of the gray wolf in the Great Lake states and the northern Rocky Mountains. By March 2003, the species (including the Mexican wolf) occupied about 5% of its historic range in the conterminous United States and included about 3,500 animals. In response to the improved conservation status for the gray wolf, in April 2003 the U.S. Fish and Wildlife Service published a reclassification rule that removed the species from the federal list of endangered and threatened wildlife (i.e., delisted) in all or parts of 16 southern and eastern states where it historically probably did not occur (U.S. Fish and Wildlife Service 2003a). Elsewhere the reclassification rule divided the lower 48 states into three distinct population segments (DPS) – areas that support wolf populations, are somewhat separated from one another, are significant to the overall conservation of the species, and are considered separately under the ESA.

With the reclassification rule the USFWS retained the experimental-nonessential population areas in the northern Rocky Mountains, but elsewhere downlisted the eastern and western gray wolf DPSs from endangered to threatened and indicated that recovery objectives for both had been met by late winter 1999 and December 2002, respectively (USFWS 2003a). Concomitant with publication of the reclassification rule the USFWS published advanced notices of intent to delist these DPSs (U.S. Fish and Wildlife Service 2003b, 2003c). For the southwestern DPS (SWDPS) (Figure 1), the USFWS retained the experimental-nonessential population area (Parsons 1998) and designated the remainder of the area as endangered since there wolf numbers are low and threats are high. Experimental-nonessential populations are designated by the USFWS per section 10(j) of the ESA to minimize conflicts from endangered species reintroduction projects (Parker and Phillips 1991). The decision to classify the southwestern DPS as endangered indicated a need for comprehensive and science-based recovery planning, including the development of downlisting and delisting criteria (U.S. Fish and Wildlife Service 2003:15811). This process was initiated in October 2003.

Although, as of 2003, wolves have not been released in Mexico, planning is underway to determine suitable habitat and conduct reintroductions there (e.g., Servín et al. 2003, R. Wolf pers. comm.). McBride (1980) noted the landscape characteristics and threats to wolves in their last Mexican refugia in the states of Durango, Chihuahua, and Sonora. Wolves were encountered in the 1970s in the most remote portions of the eastern edge of the Sierra Madre Occidental. In the quarter century since McBride's surveys, there has been an expansion of timber extraction throughout the Sierra Madre Occidental, and expansion of intensive agriculture has occurred in some areas of former wolf habitat on the eastern edge of the range. At the same time, changes in regulations governing land ownership, decline in internal agricultural markets, and expansion of drug cultivation has led to a depopulation of some areas of the Sierra. While this pattern of population migration from interior to urban or coastal areas is also evident on the eastern fringe of the U.S. SWDPS, much of the U.S. SWDPS is experiencing rapid population growth due to an influx of migrants from other regions of the U.S. For example, western Colorado is experiencing among the highest population growth rates in the U.S. (Theobald et al. 1996).

ROLE OF THIS STUDY

Although currently the region's wolf population is limited to reintroduced animals and their progeny in the BRWRA, recovery and long-term conservation of the gray wolf in the southwestern U.S. and Mexico will likely depend on establishment of a metapopulation or several semi-disjunct but viable populations spanning a significant portion of its historic range in the U.S./Mexico transboundary region. To facilitate success recovering the gray wolf to the southwest, we sought to 1) compare the efficacy of alternative conservation management strategies, 2) prioritize areas for reintroduction, and 3) assess threats to population recovery from landscape change and development. To do this, we combined habitat suitability modeling with population viability analysis (PVA) to allow us to assess how subpopulations function within the larger metapopulation (e.g., through dispersal and demographic rescue [Brown and Kodric-Brown 1977]) and evaluate whether an area contains sufficient habitat to ensure population viability. The analysis builds upon previous research concerning carnivore viability in the northern Rocky Mountains and Colorado (Carroll et al. 2001a, 2003a, 2003b, Carroll et al. in press). We modified previous wolf models to incorporate historical data on contrasts in habitat associations and demography between the Mexican wolf and more northerly subspecies (e.g., McBride 1980, Brown 1983). We did not also apply resource selection function (RSF) modeling (Boyce and McDonald 1999) of wolf habitat as we had done in the earlier Colorado study (Carroll et al. 2003a) because data on the distribution of wolves, necessary for building RSF models, was still sparse from the southwestern population. Use of distributional data from the Yellowstone population, while relevant to the Colorado study, would have been less applicable to the semi-arid ecosystems of the southwest.

A comprehensive conservation assessment such as this has not been attempted previously for wolves in the southwest due to challenges associated with 1) gathering consistent habitat data over such a large region spanning two nations, and 2) lack of tools to link population dynamics to mapped habitat data at these scales. To resolve the former problem, we were able to take advantage of several newly-available regional data sets. For example, the availability of new Mexican and U.S. multi-state vegetation coverages was key factor in assessing potential prey productivity in areas lacking detailed surveys of prey abundance (Palacio-Prieto et al. 2000, Vogelmann et al. 2001). To resolve the second problem of linking population performance to habitat, we used the program PATCH (Schumaker 1998), which provides a means of building biologically-realistic regional-scale population models.

METHODS

STUDY AREA

Our study area (Figure 1) within the U.S. consists of the states of Utah, Colorado, Arizona and New Mexico and trans-Pecos Texas. As such it encompasses almost the entire U.S. portion of the Southwestern Distinct Population Segment (SWDPS) (Federal Register 68:15803-15875), as well as adjacent wolf habitat in northern Utah and Colorado. Western Oklahoma and northern Texas, although nominally part of the U.S. SWDPS, were not considered due to their low habitat suitability for wolves and a pattern of land ownership not conducive to large carnivore recovery. The Mexican portion of our study area includes the states of Sonora, Chihuahua, Coahuila, Nuevo Leon, Durango, and Tamaulipas, and portions of Zacatecas and San Luis Potosí (Figure 1). This encompasses the majority of the estimated historic distribution of the Mexican wolf, although a few wolves may have been present further to the south in the Transvolcanic Ranges (Brown 1983, Servín et al. 2003) .

In the mid-1970s the first list of species protected under the Endangered Species Act included the northern Rocky Mountain wolf *C. l. irremotus*) (U.S. Fish and Wildlife Service 1974). In April 1976 the Mexican wolf *C. l. baileyi*) was listed as endangered (Federal Register 41:17736-177740), and in June 1976 *C. l. monstrabilis* was listed as endangered (Federal Register 41:24062-24067). Due to new information about wolf taxonomy and ranges occupied by gray wolf subspecies, in 1978 the U.S. Fish and Wildlife Service reclassified the gray wolf at the species level (i.e., *Canis lupus*) as endangered throughout the contiguous U.S. and Mexico, except for Minnesota where a threatened status was applied (Federal Register 43:9607-9615). In response to an improved status for the gray wolf in the western Great Lakes states and the northern Rocky Mountains, in 2003 the Service finalized another reclassification that created the SWDPS and reaffirmed the U.S. Fish and Wildlife Service's decision to primarily effect wolf recovery at the species level (U.S. Fish and Wildlife Service 1978).

The U.S. Fish and Wildlife Service's decision to focus recovery at the species level is tempered by the agency's long-standing belief that it is important to preserve as much wolf genetic diversity as practicable (Federal Register 43:9607-9615, U.S. Fish and Wildlife Service 2003a:15809-15811). Wolf recovery in the SWDPS thus represents a unique challenge because here there was a historical convergence of five purported subspecies (Hall 1981), suggesting a zone of diverse genetic resources (Garcia-Moreno et al. 1996). The extent of *Canis lupus baileyi's* historic range varied according to author. Hall (1981) described it as including only a small portion of extreme southwestern New Mexico and southeastern Arizona. Bogan and Mehlhop (1980, 1983) recommended that the range be extended to northern Arizona and central New Mexico because their research had indicated that two previously recognized subspecies (i.e., *Canis lupus mogollonensis, Canis lupus monstrabilis*) should be combined with *Canis lupus baileyi*. The U.S. Fish and Wildlife Service adopted their recommendation in the approved Mexican wolf recovery plan, in part because it provided justification for reintroducing wolves in central Arizona and central New Mexico, areas believed to support suitable release habitat (U.S. Fish and Wildlife Service 1982:3); the recovery team felt that such habitat was lacking elsewhere in the southwestern U.S..

Nowak (1995) disagreed with Bogan and Mehlhop (1983) and recommended that the historic range for *baileyi* in the U.S. include only extreme southern Arizona and southern New

Mexico, a position consistent with Hall (1981). Parsons (1996) added knowledge of wolf dispersal patterns to the historic range proposed by Nowak (1995) and concluded that historically Mexican wolves ranged as far north as central New Mexico and east-central Arizona, a position more or less consistent with that posited by Bogan and Mehlhop (1983). The U.S. Fish and Wildlife Service adopted the historic range proposed by Parsons (1996) and included it in the final environmental impact statement for the BRWRA reintroduction project (U.S. Fish and Wildlife Service 1996).

We agree with Parsons (1996) that development of a historic range should include information about a species' dispersal patterns. We note, however, that his use of a 320-km dispersal radius outward from the edge of *baileyi's* historic range [as determined by Nowak (1995)] represents a conservative approach since gray wolves are capable of dispersing 800 km or more (Fritts 1983, Boyd et al. 1995). Had Parsons (1996) utilized a dispersal radius of 640 km, for example, his historic range for *baileyi* would have extended to southern Colorado and southern Utah. Regardless of the dispersal radius chosen, it is certain that gray wolves are capable of traveling great distances. It is equally certain that the boundaries between gray wolf subspecies were wide zones of integradation spanning hundreds of kilometers where genetic mixing occurred.

In the late 1990s, spurred by concern over the lack of recovery habitat for the Mexican wolf from central Arizona and central New Mexico south to Mexico, Phillips began investigating the evolution of thinking about *baileyi's* historic range. In addition to uncovering disagreement amongst researchers who had investigated this topic (see above), he determined that Nowak (1995:384-385) referred to a Mexican wolf specimen collected in 1957 near Concho, Apache County, Arizona, an area about 160 km north of the historic range that Nowak had proposed for *baileyi*. Nowak (1995:385) concluded that such wolves probably regularly dispersed this far north, especially after resident populations had been eliminated by people during the 20th century. He agreed with Phillips who proposed that such wolves had effectively established a contemporary range for the subspecies that should be of paramount importance for recovery planning purposes (R. M. Nowak personal communication). Combining this contemporary range with current knowledge about wolf dispersal tendencies [e.g., a 320-km dispersal radius as proposed by Parsons (1996)] and broad ecological abilities (Mech and Boitani 2003:xv) provides justification for considering areas in the northern half of the SWDPS as reintroduction sites for *Canis lupus baileyi*. Such consideration is consistent with results presented by others researchers (Young and Goldman 1944:471, Bogan and Mehlhop 1983, Wayne and Vila 2003:223, R. K. Wayne personal communication) that support the claim that widespread admixture was a historic characteristic for gray wolf populations.

Despite the information above, by the early 2000s concern existed over the appropriateness of involving *Canis lupus baileyi* in reintroductions in suitable habitat in areas like northern Arizona and northern New Mexico (i.e., that portion of the southwestern U.S. that would become the northern half of the SWDPS), based on the belief that such areas were outside the subspecies' original historic range. In March 2000 Phillips presented information on this matter, with particular reference to the southern Rocky Mountains Ecoregion (i.e., the northeastern portion of what would become the SWDPS), to the IUCN/SSC Wolf Specialist Group which concluded that "The IUCN/SSC Wolf Specialist Group endorses the reintroduction of Mexican wolves (*Canis lupus baileyi*) to the Southern Rocky Mountains ecosystem pending a determination through an Environmental Impact Statement that the areas is suitable for gray wolves and provided that additional scientific review determines that Mexican wolves are the most appropriate source stock...” (IUCN Wolf Specialist Group Resolution – February 23, 2000).

In August 2001 during a Southern Rockies wolf population and habitat viability analysis conducted by the IUCN/SSC Conservation Breeding Specialist Group a team of experts addressed the Wolf Specialist Group’s desire for additional scientific review on the appropriateness of reintroducing Mexican wolves to the southern Rocky Mountains, an ecoregion that extends from northern New Mexico to southern Wyoming. The southern half of the SRM includes the north-eastern quarter of the SWDPS. The experts wrote (Phillips et al. 2001:22): “For several reasons, the Mexican wolf is the most appropriate wolf to use as a reintroduction source to the southern Rocky Mountains. First, the habitats and prey base in the southern Rockies are ecologically similar to both that existing in the northern historic range of the Mexican wolf and the present range of the reintroduced population. Second, the Mexican wolf is the closest geographic source of wolves to the southern portions of the southern Rocky Mountains ecoregion. Third, the Mexican wolf is the most endangered subspecies of gray wolf and would therefore greatly benefit from the additional reintroduction area...... we suggest that the most appropriate initial source of wolves for reintroduction into the southern Rocky Mountains is *C. l. baileyi*. The first priority should be the establishment of this critically endangered subspecies in the southern part of the this ecoregion. The second priority should be the establishment of *C. l. occidentalis* into the more northern part of this region. Eventually a transition of differentiation from *C. l. baileyi* in the south to *C. l. occidentalis* in the north, with a transition zone area in the southern Rocky Mountains would be established. This would serve to provide a genetic gradation similar to that found ancestrally in gray wolves from south to north in this region." Three independent reviewers supported their conclusion (Phillips et al. 2000:97-102).

We are not surprised that the expert opinion reaffirmed the notion that historically extensive admixture characterized gray wolf populations in the southwestern U.S.. On this point, Wayne and Vila (2003:223) concluded that "the division of wolves into discrete subspecies and other genetic units may be somewhat arbitrary and overly typological (conforming to a specific ideal type)". This combined with results from recent genetic investigations that indicate that the Mexican wolf was far more widespread in the U.S. than previously reported (R. K. Wayne personal communication), prompts us to conclude that it is appropriate to reintroduce *Canis lupus baileyi* anywhere in the northern half of the SWDPS where suitable habitat remains..

Consideration of the appropriateness of reintroducing the Mexican wolf in areas like northern Arizona and northern New Mexico has been fueled by concern over the lack of suitable habitat in central Arizona and central New Mexico south to Mexico (U.S. Fish and Wildlife Service 1982:3, U.S. Fish and Wildlife Service 1996:2-2 to 2-5). Nonetheless, it is important to note that evidence indicates that sometimes significant patterns of genetic diversity within wolf populations exist probably due to ecological factors and associated landscape features that operate over relatively small spatial scales (Carmichael et al. 2001, Geffen et al. in press). It is possible that the uniqueness of the Mexican wolf (Wayne and Vila 2003, Nowak 1995) is due largely to the ecological conditions that characterized the subspecies' core historic range in the extreme southwestern U.S. and Mexico. Ecological conditions of importance to the evolution of the gray wolf could have included the presence of relatively small prey [e.g., Coues white-tailed deer (*Odocoileus virginianus couesi*) and collared peccary (*Pecari tajacu*)] that were sparsely distributed because of the aridity of the general region. Early investigators reported that Mexican wolves probably avoided desert scrub and semidesert grasslands which provided little cover, food, or water (Brown 1983). Given that local ecological conditions may have significant affected the evolutionary history of the Mexican wolf, then it is important to consider including habitation of sites like the Sky Islands of southeastern Arizona as an important criterion for recovery of the gray wolf in the southwestern U.S.

Recovering *Canis lupus baileyi* to a significant portion of historic range within the SWDPS would ensure the persistence of a subspecies with unique genetic characteristics (Garcia-Moreno et al. 1996, Hedrick et al. 1997). Effecting wolf recovery to conserve genetic diversity whenever practicable is an appropriate and important objective for the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2003a).

PREVIOUS WOLF HABITAT ANALYSES FOR THE REGION

Several authors have evaluated historical distribution and habitat potential for wolves in the southwestern U.S. and Mexico. Young and Goldman (1944) stated that in 1916-8 the wolf was fairly numerous in Sonora, Chihuahua, and Coahuila. By the time of Leopold (1959), the formerly continuous wolf distribution in northern Mexico had contracted to encompass the Sierra Madre Occidental in Chihuahua, Sonora, and Durango, as well as a disjunct population in western Coahuila (from Sierra del Carmen westward). Leopold (1959) found conflicting reports on the status of the Coahuila population and stated that wolves were likely less abundant there than in the Sierra Madre Occidental.

McBride (1980) surveyed the distribution of the last wild populations of Mexican wolves. He mapped 3 general areas where wolves were recorded as still present in the Sierra Madre Occidental: 1) northern Chihuahua/Sonora border (at least 8 wolves) 2) western Durango (at least 20 wolves in two areas), and 3) a small area in southern Zacatecas (Figure 1). McBride (1980) believed that wolves did not occur in northern and eastern Coahuila despite the existence of what he judged to be excellent wolf habitat there. Brown (1983) summarized historical distribution records for the wolf from McBride (1980) and other sources. His map (Brown 1983: 10) shows most records in the southwestern U.S. as being from the Blue Range and the Animas region of New Mexico.

With the capture of several of the last wild wolves in Mexico and initiation of a U.S. reintroduction program, attention shifted to evaluating the habitat potential of areas in Arizona and New Mexico. Five potential reintroduction areas were identified, with those within each of the two states being evaluated separately. Bednarz (1989) evaluated the suitability of the White Sands Missile Range (WSMR) in central New Mexico. He found the WSMR suitable in terms of habitat security but marginal in habitat productivity (prey abundance). A later assessment concluded that the area could only support 20 to 30 wolves (Green-Hammond 1994). Johnson et al. (1992) evaluated four areas in Arizona: the Blue, Galiuro-Pinaleno, Chiracahua, and Patagonia-Atascosa ranges (Figure 1). Significantly, the New Mexico portion of the current Blue Range Wolf Recovery Area was not considered in either Johnson et al. (1992) or Bednarz (1989). Despite this, the Blue Range was scored by Johnson et al. (1992, see also Groebner et al. 1995) as highest in 7 of 13 habitat factors. The Atascosa/Patagonia ranges were the only one of the remaining three areas to approach the Blue Range in quality (highest in 5 of 13 habitat factors). Parsons (1995) produced a comprehensive reassessment of all 5 of the proposed sites in Arizona and New Mexico. He found that, based on the sum of scores for seven factors affecting wolf habitat suitability (habitat area, ungulate density, water availability, livestock density, human density, road density, and effects on threatened species), WSMR scored highest, followed by the Blue Range, and more distantly, the Atascosa/Patagonia Mountains. The contrast between these results and those of others who strongly discount the potential of the WSMR (e.g., Paquet et al. 2001), is due to the fact that habitat area, for which WSMR scores very low, is only one of seven factors given equal weight in Parsons (1995).

USFWS (1996) evaluated four alternatives for Mexican wolf recovery and chose a preferred alternative involving reintroduction to the Blue Range, with potential use of WSMR as a second reintroduction area if necessary. In the evaluation of Alternative D (No action or natural recolonization), it was estimated that if successful wolf dispersal from Mexico occurred, this might eventually result in 30, 20, and 5 wolves inhabiting southeastern Arizona, southern New Mexico, and Big Bend National Park (Texas), respectively, based on habitat potential there.

However, the document stated "Natural recolonization is considered extremely speculative. Based on historical wolf abundance, recent sighting reports alleged to be wolves, proximity to Mexico, and other factors, the most suitable areas for potential natural recolonization by wild wolves probably would be the mountainous parts of southeastern Arizona and southwestern New Mexico (Fig. 2-5), and Big Bend National Park in southern Texas (Fig. 2-6). This alternative [*Alternative D - Natural Recolonization*] analyzes these three areas. No confirmed sighting reports have come from these areas or from Mexico in recent years. ...evidence from natural gray wolf recolonization along the U.S./Canada border suggests that, even when adequate source populations exist, lone wolves or breeding pairs may repeatedly appear in an area but then die out or be accidentally or illegally killed without establishing a self-sustaining population (USFWS 1993a)." (USFWS 1996: 2-24).

More recent work has evaluated areas within the current U.S. SWDPS but to the north of the more restrictive definitions of the historic range of *Canis lupus baileyi* (see above). Carroll et al. (2003) predicted that northern New Mexico (the Valle Vidal unit of the Carson National Forest and adjacent private lands such as Vermejo Park Ranch) could support a viable wolf population of around 100 animals. Carroll et al. (2003a) further predicted that the entire southern Rocky Mountains ecoregion, encompassing primarily western Colorado and northern New Mexico, could support 1,000 or more wolves.

Sneed (2001) evaluated the Grand Canyon and Mogollon Rim in northern and central Arizona. While this area includes some habitat with relatively low ungulate density due to the arid climate, other portions of the area such as the Kaibab Plateau support ungulate densities comparable to more mesic forest ecosystems of the northern Rockies (> 8 DEPU/km^2 (Sneed 2001)). Sneed (2001) concluded that the North Kaibab and South Colorado Plateau could support between 115 and 187 wolves.

In Mexico, several analyses are in progress or recently completed that evaluate potential habitat. Araiza (2002) evaluated GIS data from Sonora, Chihuahua, and Coahuila and identified a area in the northern Sierra Madre Occidental with relatively high levels of habitat security (low road density and human settlement). However, field measurements of prey abundance indicated deer densities near the lower limit for wolf persistence. This suggested that augmentation of deer herds through revised grazing techniques and reduced hunting might be necessary before the area could support wolves (Araiza 2002). Sanchez (in prep.) examined habitat potential in Coahuila and Nuevo Leon and identified areas in northern Coahuila (Sierra del Carmen) and central Nuevo Leon (Sierra Plegada) as potential wolf habitat.

Servín et al. (2003, see also Servín 1986, 1996) used historic wolf distribution records and regional-scale GIS data on vegetation type, elevation, temperature, and precipitation to define the probable historic distribution of the Mexican wolf. Areas with land use unsuitable for current occupation by wolves (human-altered habitats) were then excluded from the historic distribution to produce an estimate of the area of remaining suitable habitat. A large portion of the Sierra Madre Occidental (90,000 km^2) was predicted to be suitable for wolves under these assumptions, whereas little habitat remained in other areas such as Nuevo Leon and Tamaulipas (Servín et al. 2003).

VARIABLES ASSOCIATED WITH WOLF FECUNDITY

Because compilation of appropriate regional-scale data sets is a significant challenge in this type of study, we summarize the types of data used as model inputs, dividing them into the two categories of those primarily affecting wolf fecundity (vegetation and satellite imagery-derived productivity measures) and those affecting wolf survival (roads, human population, and livestock density).

The biological context of wolf recovery in the southwestern U.S. differs from that of earlier recovery efforts in the northern Rocky Mountains (Brown 1983, Bangs et al. 1998). Because of the semi-arid climate, primary productivity is generally lower in the southwest. In consequence, prey species available to wolves tend to be smaller in size. Their populations also exist at relatively low densities and exhibit patchy distributions. In Mexico, the wolf preyed primarily on Coues deer (*Odocoileus virginianus couesi*), with some use of collared peccaries (*Tayassu tajacu*) (McBride 1980, Brown 1983). In the southwestern U.S. mule deer (*O. hemionus*), and in some areas elk (*Cervus elaphus*) were also available. Pronghorn (*Antilocapra americana*) may also have been preyed upon occasionally. Elk have comprised the bulk of the biomass in the diet of wolves reintroduced to the Blue Range area of Arizona (Paquet et al. 2001).

Ideally our wolf fecundity estimates would be based on prey abundance surveys. However, this data is of variable quality and resolution for the U.S. and essentially unavailable outside of small intensive study areas in Mexico. Although we necessarily depend for our regional habitat evaluation on surrogates for prey productivity, evaluation of prey abundance data for potential reintroduction areas would be a necessary component of subsequent, finer-scale stages of recovery planning (e.g., development of an environmental impact statement). Encouragingly, we have found good concurrence between our surrogate metric and actual prey abundance in earlier studies in Colorado and Utah (Carroll et al. 2003a, Carroll 2003). The source of vegetation data for the United States was the National Land Cover Dataset (NLCD) developed by the Multi-Resolution Land Characterization Consortium of governmental agencies in order to provide a seamless vegetation map spanning the conterminous United States (Vogelmann et al. 1998, Vogelmann et al. 2001). The landcover data were derived from Landsat TM data at a resolution of 30 m. It contains 21 landcover classes and therefore represents a spatially-detailed but thematically coarse data layer when compared with the vegetation maps produced by the Gap Analysis Programs (GAP) of the individual states (Scott et al. 1993). Although we considered using vegetation data derived from a combination of state GAP program maps, this was judged to produce too great a data inconsistency between jurisdictions. We used vegetation data for Mexico from the 2000 National Forest Inventory (Palacio-Prieto et al. 2000). This data mapped land cover across Mexico at a scale of 1:250,000 based on Landsat TM imagery. Land cover was assigned to one of 75 classes, with a minimum mapping unit (MMU) of approximately 1 km^2. Landcover types from both the U.S. and Mexican data sets were ranked as to their value as wolf habitat based on expert opinion and historical records (Tables 4 and 5) (Brown 1983, Carlos Lopez-Gonzalez pers. obs.).

Because ungulate prey density may vary greatly within a particular vegetation type due to variation in primary productivity and other factors, we augmented the vegetation data with satellite imagery-derived metrics that are surrogates for productivity. We derived from MODIS imagery (Wharton and Myers 1999) the tasseled-cap greenness index (Crist and Cicone 1984). The tasseled-cap indices are a standardized means of representing the three principal axes of variation in six spectral bands of the MODIS imagery. “Pseudo-habitat” variables such as greenness that are derived directly from unclassified satellite imagery are correlated to varying degrees with ecological factors such as net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al.1993, White et al. 1997) and have proved useful in modeling wildlife distributions (Mace et al. 1999). Vegetation variables and imagery metrics such as greenness may be expected to be correlated with abundance of prey species through their relationships to primary productivity. In a previous study, we found that summer greenness values were strongly correlated with ungulate density in the northern Rocky Mountains and Pacific Northwest (Carroll et al. 2001b, 2003a). However we would expect the relationship between greenness and prey productivity to be weaker across the much larger and more ecologically varied region addressed in this study. Therefore we combined greenness levels with ranking of vegetation types to produce a composite ranking of prey productivity, which we considered a surrogate for wolf fecundity rate (Figure 2). The fecundity layer also incorporated the negative effect of terrain (slope) on prey availability (Paquet et al. 1996). Because the season of maximum productivity varies across the region, we used the maximum greenness level found in either March or July (2001) MODIS imagery.

VARIABLES ASSOCIATED WITH WOLF SURVIVAL

Similarly to the case with fecundity, our wolf survival estimates in different habitat types would ideally be based directly on modeling of wolf survival data from adjacent recovery areas such as Yellowstone. However, in place of these models, a large body of literature links wolf survival with surrogates for human lethality such as roads and population (reviewed in Fuller et al. 2003). Because much of this data comes from areas without the dispersed public lands grazing patterns found in the western U.S., less is known about the quantitative effects of livestock density, and resulting depredation-related conflicts, on wolf survival. We used “habitat effectiveness”, a composite metric for relative mortality risk to large carnivores based on roads and human population (Merrill et al. 1999) that has proven a robust surrogate for wolf mortality risk in the northern Rocky Mountains (Carroll et al. 2003a, 2003b) (Figure 3). We also explored a more speculative survival index that averaged data on relative levels of cattle density (Figure 4) with the above habitat effectiveness metric. While it is unlikely that the latter index exactly captures the relationship between livestock levels and wolf mortality, it allows us to compare how considering livestock effects would increase or decrease the model’s viability estimates.

Roads data for the U.S. were derived from USGS Digital Line Graphs (DLG) coverage at 1:100,000 scale (USGS, unpublished data). Roads data for Mexico were derived from the Inventario Nacional de Infraestructura para el Transporte (INIT), a national database recently created from state and local level roads data sources at 1:50,000 or coarser scales (Backhoff Pohls et al. 2000). In areas of Mexico that showed human-altered land cover types but no roads (at a resolution of 1 ha), we set minimum road densities of 1.24 km/km^2 for pasture and 2.0 km/km^2 for other human-altered lands, based on an evaluation of road densities in similar land cover types in the U.S.

Population data for the U.S. was derived from 1990 and 2000 censuses (U.S. Census Bureau 2001) at the census block scale. Population data for Mexico was derived from 1990 and 2000 censuses at the locality scale (INEGI 2000). The locality is the finest scale of census data collected in Mexico, and thus corresponds approximately to the census block scale in the United States. However, locality data was available as point locations rather than the polygons used to delineate U.S. census blocks. We predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 2000. Road density was predicted to increase at 1% per year (Theobald et al. 1996). Data on livestock abundance for the U.S. was derived from the 1997 U.S. Census of Agriculture at the county level. These data are therefore at a substantially coarser scale than available human population data. Livestock data for Mexico were derived from the 1991 Census of Agriculture at the municipality level, which is also coarser in scale than are the localities over which human population data were collected.

DATA INCONSISTENCIES BETWEEN THE U.S. AND MEXICO

Although we sought to use the best available data, we inevitably encountered inconsistencies in the resolution and completeness of data between the U.S. and Mexico. This inconsistency was greatest for the roads data, as the mapped roads network in Mexico was quite sparse when compared to the relatively complete mapping of 4WD routes in the U.S.. In contrast, the human population data was relatively consistent in scale between the two countries. Available vegetation data was quite different in scale (at a finer scale in U.S.) and thematic detail (providing more floristic detail in Mexico). However, due to the generalized nature of the rankings of vegetation by wolf habitat value (both due to generalist nature of wolf habitat associations and lack of detailed data on Mexican wolf natural history), and the spatial smoothing inherent in the PATCH model’s evaluation of home range quality, both the thematic and spatial detail of the vegetation data is probably sufficient for the purposes of this study. The availability of the new vegetation data (Palacio-Prieto et al. 2000) for Mexico was also critical to the modeling effort because it is the first detailed national vegetation data set for the area and provided a more accurate record of human impacts (i.e., human-altered landcover types) than did the Mexican roads data.

DETAILS OF MODELING

PATCH is a female-only model designed for studying territorial vertebrates and links the survival and fecundity of individual animals to GIS data on mortality risk and habitat productivity measured at the location of the individual or pack territory (Schumaker 1998). 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. The pixels of the GIS maps are assigned weights based on the relative levels of fecundity and survival rates expected in the various habitat classes. Habitat rankings were calibrated to specific demographic values based on field studies from areas showing similar habitat quality (e.g., road density) to habitat classes in the PATCH input layers (Ballard et al. 1987; Fuller 1989; Hayes and Harestad 2000).

Survival and reproductive rates are then supplied to the model as a population projection matrix (Caswell 2001). The model scales the matrix values based on the mean of the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output. These “expected” demographic rates can then be used to calculate a predicted lambda, or population growth rate, for each territory. However, we based our analysis not on these expected lambda values, but on the lambda values actually observed during the model simulations. Observed lambda values are derived from: 1.0 + (emigration - immigration), with emigration and immigration values for each hexagon expressed as per year per simulation (Schumaker 1998).

The simulations incorporate demographic stochasticity with a random number generator. In the case of survival, a uniform random number between zero and one is selected. An individual dies if this number is less than the sum of the probabilities of making a transition between the current age class and every other class. A random number is also selected to force the number of offspring in a year to take on integer values. Environmental stochasticity is incorporated by drawing each year's base population matrix from a randomized set of matrices whose elements were drawn from a truncated normal distribution. Coefficients of variation were 30% for fecundity, 40% for pup mortality, and 30% for adult mortality for the wolf (Ballard et al. 1987; Fuller 1989). We did not model additional catastrophic mortality events (e.g., disease outbreaks).

Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a site fidelity parameter, but floaters must always search for available breeding sites. We modified PATCH to allow territory holders to be social, with individuals from the same pack able to replace territory holders (alpha females) that die. As pack size increases, members of a pack 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 (tendency to continue in the direction of the last step), and attraction to higher quality habitat (Schumaker 1998). However, there is no knowledge of habitat quality beyond the immediately adjacent territories. Parameters for territory size, dispersal distance, and demographic rates used in PATCH are shown in Table 1.

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. We first used PATCH to assess the overall equilibrium potential of the region to support wolf populations. That is, “current” predictions depict the current “carrying capacity” of an area to support wolf populations over 200 years. This carrying capacity may be greater than current species distribution because a species has not yet been able to disperse to an area. Conversely, it may be less than current species distribution because human-caused habitat change is faster than the rate of response of an affected wolf population. We also modeled specific reintroduction options to assess transient dynamics such as probability of extinction and the probability of an area being colonized by dispersers from a specific reintroduction site. We performed 500 simulations of 200 years each for each equilibrium scenario, and 1000 simulations of 200 years each for each reintroduction scenario.

DESCRIPTIONS OF SCENARIOS

We evaluated four major scenarios of landscape condition using the PATCH model. These landscape scenarios were: (A) current conditions, with wolf mortality risk based on roads and census data, (B) current conditions, with wolf mortality risk based on roads, census, and livestock density data, C) human population as of 2025, with increased road development on private lands only, with wolf mortality risk based on roads and census data, and (D) human population as of 2025, with increased road development on both private and unprotected public lands, with wolf mortality risk based on roads and census data. We did not model future landscape scenarios using the wolf mortality metric that included livestock data because we could make no predictions as to how livestock density would change over time.

After deriving the wolf mortality risk layer, we offset this base mortality risk value to account for differences in human lethality between jurisdictions. For example, in both the United States and Mexico, statutes nominally protects wolves from deliberate killing by humans (Nowak 1978). However, enforcement of these regulations is likely to vary between jurisdictions. In addition, due to contrasts in quality of the roads data between the U.S. and Mexico, it is unlikely that an equivalent level of mapped road density in our data layer corresponds to the same level of wolf mortality risk in both the U.S. and Mexico. To explore sensitivity of model results to these inconsistencies between the two nations, we offset wolf mortality risk values using the formula $y = 1 - ((1 - H) * z)$, where H is habitat effectiveness, the surrogate of wolf survival, and z is the offset factor.

An offset of 0.50 was used in strictly-protected areas (subsequently termed “parks” here) in both countries where no hunting or trapping of wolves or other game animals is permitted. That is, in these areas an additional increment of human impacts (e.g., a road density level of 2 km/km^2 rather than 1 km/km^2) had an effect in decreasing wolf survival that is 50% of that in other areas. These areas form 6.8% of the U.S. SWDPS and 0.2% of the Mexican SWDPS (Gap Analysis Program unpublished data, INEGI unpublished data). U. S. Department of Defense (DOD) lands, which usually have restricted access and no livestock, were treated as “parks” in the analysis. High levels of hunting activity for other species may cause enough incidental mortality of carnivores to cause protected areas where hunting is allowed to function as population sinks (Mace and Waller 1998), although this risk may differ between wolves and other large carnivores such as grizzly bears. For comparison, the larger class of “protected lands”

(GAP categories 1 and 2) form 10.8% of the U.S. SWDPS and 3.2% of the Mexican SWDPS ((Gap Analysis Program unpublished data, INEGI unpublished data). We treated both parks and protected lands differently from unprotected habitat (GAP categories 3 and 4) in the landscape change analysis in that we assumed no increase in road density over time in any of the landscape scenarios.

Offsets of either 0.75, 1.00 (no offset), or 1.25 were used in non-“park”areas within the United States. The offset factor on non-park lands in Mexico was varied between 1.00 (no offset), 1.25, 1.50, and 1.75 to assess the effect of different assumptions concerning the effect of contrasts in wolf management policies between the two nations. The base scenarios used an offset of 1.00 on non-park lands in the U.S., and 1.75 on non-park lands in Mexico. The high offset used in Mexico was a result of initial sensitivity analyses that revealed the sparseness of the available data on mapped human impacts (roads and altered habitat types) in that country.

DESCRIPTION OF CANDIDATE RESTORATION ZONES

GIS data used as model inputs are informative in themselves as to the patterns of factors promoting or limiting wolf recovery in the region. The vegetation types historically occupied by Mexican wolves (Brown 1983) are currently scattered in island-like patches across the SWDPS, with the largest patches located from the Blue Range northward along the Mogollon Rim, in southern Colorado/northern New Mexico, and in the central Sierra Madre Occidental (Figure 2). Human settlements and roads are at low levels in many portions of the region, primarily the more arid areas of the Colorado Plateau and northern interior Mexico, but also including mountainous areas with vegetation types more suitable for wolf habitat (Figure 3). Livestock density is lowest in arid areas as expected, but the Mogollon Rim/Kaibab Plateau and portions of northern New Mexico also show low livestock numbers (Figure 4).

POTENTIAL RESTORATION ZONES

Based on the results of initial equilibrium PATCH simulations, we identified eight potential reintroduction sites in the U.S., four in the U.S. and four in Mexico: Grand Canyon (Arizona), Mogollon Rim (Tonto National Forest (NF), Arizona), San Juans (Colorado), Vermejo/Carson (New Mexico), the Austin Ranch area (Chihuahua/Sonora near U.S. border), Carmen (northern Coahuila south of Big Bend National Park), northwestern Durango (by Chihuahua border), and the Tutuaca reserve area (westcentral Chihuahua, by Sonora border) (Figure 1). A ninth site in the Blue Range (Arizona/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 5 adjacent potential wolf territories, totaling 2500 km^2 in size. PATCH only models the females in a population to reduce computational time. The assumption that males are not a limiting factor at the relevant scales of the model is common in spatially explicit models like PATCH (Dunning et al. 1995), and is probably accurate except for the smallest populations. This feature of PATCH makes it necessary to translate the standard reintroduction protocol in terms of females only. In the PATCH model, individuals are added as breeding females at the start of a simulation. Therefore 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 five years at close to 100% under the assumption that new animals would be released to replace mortality among the initial releases. In an actual reintroduction project these five females would be released with five adult males and about five other animals of differing ages and sex resulting in the reintroduction of about 15 wolves per year. Additionally, following standard protocol up to 15 such wolves would be released every year for five consecutive years resulting in the involvement of more than five adult females over the course of the reintroduction effort. Consequently, our model probably underestimates the catalyzing effect of the standard reintroduction protocol on population establishment.

We also evaluated the broader habitat context of each reintroduction site by summarizing results for a larger 10,000 km^2 reintroduction zone centered on each 2,500 km^2 site. In addition, we compiled summary statistics based on equilibrium simulations, but did not perform individual reintroduction scenarios, for 4 additional sites that have been previously evaluated as potential wolf habitat: the Galiuro/Pinaleno, Chiricahua, and Atascosa/Patagonia Mountains in Arizona, and White Sands Missile Range and National Monument (WSMR) in New Mexico. We did not simulate reintroduction at these latter 4 sites because none showed sufficient potential as source habitat in the initial PATCH simulations.

While we describe the potential reintroduction sites briefly here, a more detailed evaluation of local land ownership, land use, and prey abundance patterns would be a necessary subsequent stage of recovery planning (e.g., development of an environmental impact statement). The 2,500 km^2 Blue Range reintroduction site lies within the larger Blue Range Recovery Area located on the Apache and Gila National Forests (NFs) along the Arizona/New Mexico border. The Grand Canyon site lies within the Grand Canyon Ecoregion which extends from southernmost Utah through northern Arizona, and is centered on the 4900 km^2 Grand Canyon National Park and adjacent 13,300 km^2 of Kaibab and Coconino NF lands. The Mogollon Rim site lies on the Tonto NF at the center of the block of forested public lands stretching between the Blue Range and Grand Canyon sites. The San Juans (Colorado) site lies within the greater San Juan Mountains region which extends across portions of the San Juan National Forest (8,345 km^2), Rio Grande National Forests (7,440 km^2), and Grand Mesa, Uncompahgre, and Gunnison National Forests (12,600 km^2), which include 4,000 km^2 of formally protected Wilderness Areas. The Vermejo/Carson site lies in northern New Mexico within the Valle Vidal unit of the Carson NF and adjacent private lands of Vermejo Park Ranch. The Carson National Forest and adjacent Santa Fe National Forest total 12,400 km^2 of public land, augmented by several large tracts of private land under conservation management.

The Austin Ranch site lies in the Sierra San Luis and adjacent ranges along the Chihuahua/Sonora/New Mexico border. Large private holdings in this area are under conservation management and have been submitted for designation as Mexican Natural Protected Areas. The Carmen site, located in northern Coahuila, includes the Maderas del Carmen protected area and areas to its east in the Sierras del Carmen and El Burro range. This area is the site of current private lands conservation initiatives (e.g., by the CEMEX corporation). However, questions remain whether the area held *C. l. baileyi* historically, and why wolves were apparently eradicated there long before their extirpation from the Sierra Madre Occidental (McBride 1980). The Durango site, in northwestern Durango along the Chihuahua border, was a historical refuge for wolves (McBride 1980) and was among the last areas in Sierra Madre Occidental to be invaded by roads and intensive logging. The Tutuaca site, centered on the "Area de Proteccion de Flora y Fauna Tutuaca" in Chihuahua on the Sonoran border, lies in an area of small-scale logging and grazing. However, areas on the eastern edge of the Sierras in this region are largely accessible by vehicle and were historically characterized by high levels of wolf persecution due to livestock depredation (McBride 1980). An additional area of potential habitat which we did not evaluate in detail but where McBride (1980) reported wolves, is the Copper Canyon area of southwestern Chihuahua. Although this area has few roads and towns, it may have relatively low prey density due to high hunting pressure by the indigenous Tarahumara population.

RESULTS

EQUILIBRIUM PREDICTIONS

CARRYING CAPACITY UNDER DIFFERENT SCENARIOS

Under current landscape conditions (Scenario A), the U.S. portion of the SWDPS is predicted to potentially support 3,166 wolves, while the Mexican portion would support 2,600 wolves. Under Scenario B (current conditions with wolf survival a function of both levels of human presence and livestock density), 4,570 wolves could potentially occur in the U.S. SWDPS and 1,746 in Mexico. Under scenario C (future landscape conditions, development on private lands but no additional development on public lands), 2,306 wolves could potentially occur in the U.S. SWDPS and 2,264 in Mexico. Under Scenario D (future landscape conditions, development on private and public lands), 1,894 wolves could potentially occur in the U.S. SWDPS and 2,288 in Mexico. Under current conditions, 12.7, 50.5, and 36.8% of the U.S. SWDPS wolf population might inhabit protected, general public (GAP category 3), and private lands respectively. The importance of private lands as habitat would decrease over time (to 30.9% after 25 years) as they became more developed. In Mexico, less than 5% of the wolf population might inhabit protected areas.

Due to the uncertainties inherent in complex models such as spatially-explicit population models (SEPM), the above population estimates are best used to judge the relative rather absolute size of wolf populations under differing assumptions about landscape conditions. It can be seen that approximately two-thirds of the decline in wolf carrying capacity in the U.S. SWDPS is due to the effects of development on private lands. If no additional development occurred on public lands, decline over 25 years would be 27.2% rather than 40.2%. Wolf populations in New Mexico and Colorado are most vulnerable to landscape change because habitat in those states is relatively more fragmented than in Arizona and areas of wolf habitat in those states are experiencing more rapid development (Table 2). Outside of those two states, the U.S. SWDPS shows vulnerability levels similar to those in the U.S. Northern Rockies - about a 25% decline in wolf carrying capacity over 25 years (Carroll et al. 2003b). Adding data on livestock density into the evaluation of wolf survival greatly reduces carrying capacity in Mexico, for without the livestock data, the sparse data on human settlement patterns and roads present an artificially optimistic assessment of wolf survival there. Similar to the U.S. situation, peripheral populations in Nuevo Leon and Tamaulipas are most at risk from landscape change (Table 2).

The general pattern of wolf distribution within the U.S. SWDPS under Scenario A (Figure 5) shows a broad arc of potential wolf habitat stretching northwestward from the Blue Range to the Grand Canyon and northward through Utah's mountain ranges. Utah habitat is more tenuously connected to a large block of habitat in western Colorado, and sink habitat in southeastern Arizona connects the Blue Range with habitat in northern Mexico. Scenario B, which adds information on livestock density (Figure 6), results in similar patterns in most of the U.S. SWDPS, with the exception of New Mexico where substantially more habitat is predicted in a north-south axis through the center of the state from the Carson NF south to WSMR. (Use of the livestock data could increase estimates of wolf survival in areas with few livestock because the influence of livestock on wolf mortality was not purely additive to the influence of roads and population). Scenarios C and D, which assess the effects of development trends (Figures 7-8), show wolf distribution contracting to be primarily confined to the major blocks of source habitat in the Blue Range, Grand Canyon, and smaller areas in southern Utah, Colorado's San Juans, and the Vermejo/Carson area. Much of southeastern Arizona is no longer occupied in these scenarios, and connectivity between the Blue Range and Mexico is only tenuously maintained by means of a corridor of occupied habitat along the Arizona/New Mexico border.

EVALUATION OF ALTERNATE REINTRODUCTION SITES

EXTINCTION PROBABILITY

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 to near 10% for the Mogollon Rim and San Juans (Table 3). Under scenario B, Mogollon and Austin Ranch have higher extinction probabilities (9.3 and 19.9%) while San Juans and other sites are near zero (i.e., 100% success). Under scenario D, Mogollon and San Juans increase in extinction probability to 16-20%. Other sites increase slightly but remain low (< 3%). With the exception of the 3 sites mentioned above, the low extinction probabilities shown by southwestern sites are more similar to those shown by Yellowstone National Park than by sites in western Colorado evaluated in a previous study (Carroll et al. 2003a). Two sites, San Juans and Vermejo/Carson, are common to both Carroll et al. (2003a) and this study. In Carroll et al. (2003), both sites showed slightly higher extinction probabilities for scenarios A and D (13.3 and 31.6% vs. 10.5 and 19.6% for the San Juans, and 6.7 and 14.5% vs. 0.8 and 2.7% for Vermejo/Carson). Results in this study are influenced by the expansion of the study area boundary southwards from that analyzed in Carroll et al. (2003a) (adding new habitat that may reduce extinction risk), and the use of a modified fecundity model. However, we judge the agreement between the two studies to be good, in that the qualitative conclusions and ranking of these two sites did not change between studies.

Occupancy of the larger 10,000 km^2 reintroduction zone surrounding each 2,500 km^2 reintroduction site gives a sense of the extent of suitable habitat within the immediate area of reintroduction that might be important in the early stages of recovery. The Blue Range zone has the highest occupancy at 72.5% followed closely by the Vermejo/Carson and Grand Canyon zones. The lower occupancy zones, San Juans and Mogollon, are still higher than the Chiricahua Mountains, and especially the Galiuro/Pinaleno and Atascosa/Patagonia Mountains in Arizona (Johnson et al. 1992). However, these Sky Islands sites are predicted as potentially occupied by wolves, and hence play an important role in maintaining connectivity between U.S. and Mexican populations. In contrast, White Sands (WSMR and WSNM) is essentially non-habitat with very low probability of occupancy by wolves (Table 3). Among the Mexican sites, Durango shows highest occupancy followed by Tutuaca, Austin and Carmen. Population density estimates support the same ranking of sites as shown by occupancy. Grand Canyon is more resilient to landscape change than the Blue Range or Vermejo/Carson, so it shows the highest wolf density amongst U.S. sites under scenario D.

Because candidate reintroduction sites were selected based on preliminary results from the PATCH model, it is not surprising that all of them were found to be source habitat in the subsequent simulations. Grand Canyon shows the highest lambda (population growth rate) of U.S. sites, while Carmen and Durango show the highest lambda among the Mexican sites (Table 3). The Galiuro/Pinaleno, Chiricahua Mountains, and Atascosa/Patagonia Mountains in Arizona are sink habitat, while the WSMR, due to its low occupancy, shows a lambda close to 1 (neither source or sink).

The regional population size achieved at the end of the PATCH reintroduction simulations (year 200) gives an indication of the ability of a particular reintroduction site to enhance the broader regional population, due to factors such as ease of dispersal to other suitable habitat. The Grand Canyon site achieves the highest regional population within the U.S. SWDPS. There is little difference among the Mexican sites unless livestock data enters into mortality risk estimates, in which case Tutuaca and Carmen appear superior. Whereas Mexican reintroductions achieve populations nearly as large (99%) as the maximum carrying capacity predicted in the equilibrium simulations, the largest U.S. population (1896) from a single reintroduction is only about 60% of maximum carrying capacity. This is due to the more realistic mapping of mortality risk in the U.S., which more accurately represents sink habitat and other barriers to population spread.

We conclude from the extinction analysis and other metrics that all candidate sites besides Mogollon have low enough extinction risk that they can be included for further consideration. The Austin Ranch and San Juans sites show sensitivity to landscape change and/or moderate extinction risk, suggesting caution in their use as a single site for reintroduction, and if used, pairing with a second site. The three previously proposed Arizona sites (Galiuro/Pinaleno, Chiricahua Mountains, and Atascosa/Patagonia Mountains [Johnson et al. 1992]) appear to be poorer choices for a role as an initial reintroduction site due to being sink habitat and to their proximity to an existing strong source (the Blue Range), which increases their likelihood of being recolonized by natural dispersal. However, they do play a key role in connecting U.S. and Mexican wolf populations, and might thus be appropriate areas to receive animals relocated from the Blue Range. In contrast, based on our results, the WSMR is unsuitable for further consideration as an element in recovery strategy.

SENSITIVITY ANALYSIS

Several aspects of the sensitivity analysis have been summarized previously in the results. Sensitivity of results to assumptions regarding development (road construction) on public lands is summarized in comparisons of scenarios C and D. Sensitivity to assumptions as to whether wolf mortality risk is primarily correlated with human presence or also independently with livestock density is summarized in comparisons of scenarios A and B.

Because of the larger uncertainty in mapped estimates of wolf mortality risk in Mexico, we evaluated the sensitivity of results to Mexican mortality risk parameterization, that is, the level of offset used in creating the mortality risk layer. We found that decreasing this offset from 1.75 to 1.25 caused predicted Mexican population size to increase by 59%,. However peripheral populations in Nuevo Leon and Tamaulipas were more sensitive, increasing by 78%. In the core of potential wolf habitat in the Sierra Madre Occidental, there was little change in the distribution of potential habitat with different mortality offsets, despite the increase in wolf population size. This implies that the lack of detailed data on human impacts in remote areas of the Sierra Madre Occidental cannot be remedied by proportionately increasing the mortality offset level. Without any change in U.S. mortality risk, U.S. population predictions still increased in response to lower mortality in Mexico, by 52%. This suggests either that border subpopulations would form a demographically interlinked metapopulation, or more pessimistically, that uncertainty regrading mortality risk in Mexico propagates a strong element of uncertainty into U.S. population estimates.

To further assess the effects of uncertainty about habitat in Mexico on U.S. predictions, we performed simulations with a reflecting barrier to dispersal at the U.S. border to simulate a situation where Mexico was neither a source nor a sink to U.S. dispersers. As expected, Utah and Colorado population estimates were insensitive to the absence of interaction with Mexico, Arizona and New Mexico were moderately sensitive, and Texas's small population was very sensitive. Percentage reduction under Scenario A was 1.4, 0.7, 9.4, 14.0, and 58.5% for Utah, Colorado, Arizona, New Mexico, and Texas, respectively. Percentage change under Scenario D was 1.2, 8.7, 15.5, 19.0, and 98.6%, respectively. Results of these simulations differ from those that include Mexico in that most of southeastern Arizona and trans-Pecos Texas are unoccupied by wolves without dispersal from Mexico. Population size estimates for the BRWRA, WSMR, and Galiuro/Pinaleno Mountains were insensitive to loss of Mexican populations, the Chiricahua Mountains were sensitive (reduction of 33% (Scenario A) to 72% (Scenario D)), and the Atascosa/Patagonia Mountains became nearly unoccupied.

A sensitivity analysis of model results to estimates of wolf mortality risk in the U.S. indicated similar patterns as had the contrast between scenarios A and D. A change in the offset used for habitat effectiveness within the U.S. from 0.75 (25% below the base parameter offset) to 1.25 (25% above the base parameter offset) resulted in an overall decline of 71.3% in predicted U.S. population size (Figure 10). Mexican population size was little effected, decreasing by only 1.6%. Population estimates for Colorado and New Mexico were most sensitive to this parameter, declining by 89.9 and 83.5%, respectively. Declines for Arizona, Utah, and Texas were 60.2, 49.0, and 21.7%, respectively.

We assessed whether a mortality risk index based only on human population (without roads data) would give a more consistent assessment of comparative mortality risk between the U.S. and Mexico, given that census data was relatively similar between the two countries. Although there was little effect on distribution estimates in Mexico, areas in the U.S. with low human population but many roads, such as ranching areas in eastern New Mexico and eastern

Texas, were predicted to be sources using this parameterization. We therefore judged this to be an unrealistic model scenario.

We also compared predictions using the fecundity metric based on both vegetation type and greenness with one based exclusively on greenness as had been used in an earlier study (Carroll et al. 2003a). We found that a greenness-based metric performed poorly as an estimator of fecundity in a large study region spanning both arid grassland and mesic forest ecosystems. Greenness-based scenarios added suitable habitat in semi-arid grasslands and desert areas of northwestern Sonora and the Chihuahua/Coahuila border characterized by seasonally ephemeral plant production.

Sensitivity to dispersal parameterization is often identified as a key weakness of SEPMs (Kareiva et al. 1996). We found that population predictions were most sensitive to dispersal in peripheral areas with fragmented habitat; New Mexico (13% relative change) in the U.S., and Nuevo Leon and Tamaulipas (17-20% relative change) in Mexico, with most other areas showing < 5% relative change. Encouragingly, 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 > 0.5% (absolute %), with a maximum of 1.6% change.

We varied wolf territory size in the model by changes in the parameter for maximum territory size. This parameter does not actually change the size of the hexagon used by PATCH. Instead it changes the ability of marginal quality territories to become suitable for breeding by "borrowing" habitat from adjacent hexagons. We found that a shift of maximum territory size from 600 to 650 km^2 greatly increased the extent of predicted wolf distribution in arid portions of northern Mexico (eastern Chihuahua, western Coahuila, and northern Sonora). In semi-arid habitat where low prey density often limits wolf distribution, PATCH estimates of population size will have higher uncertainty due to sensitivity to this parameter.

DISCUSSION

Complex spatially-explicit population models (SEPMs) such as PATCH (Schumaker 1998) may be more biologically realistic than simpler tools, but this may come at the expense of increased sensitivity of the results to lack of detailed demographic, habitat, and movement data (Kareiva et al. 1996). Therefore, it is important to assess which conservation questions can be answered with relative confidence despite model uncertainty. For example, we can place more confidence in the relative rankings of management options than in exact population numbers, and more confidence in the predicted carrying capacity or equilibrium distribution than in the predicted probability of rare events such as recolonization (Carroll et al. 2003a, b). (Carroll et al. (2003a) predicted a low probability of establishment of a Colorado population by natural dispersal from Yellowstone. As of 2004, a wolf or wolves have dispersed this distance, but have not established territories.)

Although results from SEPMs may be sensitive to variation in poorly known parameters such as dispersal distance (Ruckelshaus et al. 1997), this may be most evident in simplified SEPMs that lack a demographic context (South 1999), use a dispersal function that is not sensitive to landscape quality, and vary dispersal mortality across a wider range than is usually plausible for a particular species (Mooij and DeAngelis 1999). Real landscapes often contain a few large patches with very low extinction probability. The resultant mainland-island dynamics tend to stabilize metapopulations and reduce sensitivity to dispersal success (South 1999). As evident in other realistic SEPMs (Pulliam et al. 1992; South 1999), our results were more sensitive to the demographic parameters used and how they were assigned to habitat classes than to variation in dispersal distance. However, the complex long-distance dispersal behavior of wolves, which results in a “long-tailed” distribution with a small fraction of dispersers traveling up to 800 km (Fritts 1983), is not realistically modeled by PATCH or most other dispersal models (Shigesada and Kawasaki 2002). Therefore, SEPMs may be useful for evaluating regional population dynamics but not for judging probabilities of inter-regional colonization events. Unlike in a previous study that considered the chance of long-distance dispersal from Yellowstone to Colorado (Carroll et al. 2003a), the current study is not primarily concerned with long-distance natural recolonization events.

SEPM predictions for wolves have been found to be strongly correlated with the species’ distributions in the northern Rockies (GYE: D. Smith, unpublished data), in contrast with the poorer performance of distribution models for mesocarnivores (Carroll et al. 2002). This is 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). The use of roads and human population (Merrill et al 1999) as a surrogate for mortality risk is likely to be relatively robust in southwestern landscapes, as we can expect most wolf mortality, as in the northern Rockies, to be associated with access to an area by humans (Ream et al. 1998). The influence of variation in livestock abundance and associated depredation on overall wolf survival rates is poorly known and thus treated in the sensitivity analyses. The effect of contrasts in enforcement of protective regulations between the U.S. and Mexico is also uncertain, and thus treated in the sensitivity analysis. No effective solution was found for the lack of detailed human impacts (roads) data for Mexico. Alternatives such as basing the habitat effectiveness metric only on population, or offsetting habitat effectiveness values, added little detail in the remote areas of the Sierra Madre Occidental that appeared to be the best candidates for wolf reintroduction sites. Inflated estimates of wolf survival rate in Mexico may make predictions of dispersal flow from Mexico overly optimistic. This would result in areas in the U.S. adjacent to the Mexican border showing artificially high occupancy estimates. Areas shown as occupied sink habitat in southernmost Arizona and trans-Pecos Texas might actually be unoccupied, but this effect diminishes rapidly as one moved northward.

The relationship of wolf fecundity to prey availability is relatively robust across different ecosystems (Fuller 1989). Semi-arid ecosystems show a strong gradient in vegetation type and primary productivity that is more easily mapped from remote sensing data than are more subtle gradients in mesic regions (Carroll in review). However, although prey species in the U.S. are often managed near carrying capacity, in Mexico they may be locally depleted by heavy hunting pressure, lowering the match between vegetation productivity and wolf habitat. Although we used the best available regional-scale data in our study, data resolution was still inconsistent between U.S. and Mexico. However, our results for the Sierra Madre Occidental agree qualitatively with the location of the last relict wild Mexican wolf populations (Figure 1, McBride 1980). They should thus be of use as an initial screening of possible reintroduction sites, which can then be followed by local surveys of land use and prey abundance.

More generally, we should be aware of the uncertainty in the relative strength of the two factors, fecundity rate variation and survival rate variation, in determining persistence. For example, we can contrast model predictions for western Colorado (which has both high prey abundance and higher human impacts) with those for the Grand Canyon (which has lower prey abundance and lower human impacts). This uncertainty is compounded in the latter area by the assumptions we made concerning the effects of parks with no firearms or livestock in increasing wolf survival. Because previous reintroductions were to sites in the GYE and central Idaho which have both high prey abundance and low human impacts, they provide little guidance as to whether model results accurately capture the relative strength of these two factors. This uncertainty is accentuated in arid ecosystems, which often have low human impact, but also show prey abundance near the lower threshold for wolf persistence. Because of our poor knowledge of thresholds to wolf occupancy in low-productivity arid ecosystems, our model results are sensitive, for example, to the parameterization of territory size.

Despite the uncertainty inherent in complex models, our results suggest that spatial PVAs can be useful for organizing knowledge about recovery options and ranking their likelihood of success. Decision making under uncertainty is often necessary for species at risk, and spatial models should be used as one source of information in a multi-faceted decision-support process (Breitenmoser et al. 2001).

APPROPRIATE CONTEXT FOR USE OF MODEL RESULTS

We received valuable comments from several reviewers that made it evident that we should further clarify the context in which model results should be used. We group these into the three themes of 1) appropriate scale for interpreting results, 2) scenarios versus predictions, and 3) uncertainties in parameterization of fecundity (prey productivity).

APPROPRIATE SCALE FOR INTERPRETING RESULTS

It was noted that our results do not provide insights for managers seeking, for example, to decide whether the Grand Canyon’s South or North Rim would be most appropriate for a reintroduction. In fact, our Grand Canyon “reintroduction site” overlaps both the North and South Rims, which would likely be logistically unfeasible for an actual reintroduction strategy. Our results from the Grand Canyon, and from other modeled reintroduction sites, are an attempt to provide a general evaluation of the suitability of the surrounding area (e.g., the Grand Canyon reintroduction zone) as a whole. For each reintroduction zone, we chose the contiguous block of 2500 km^2 of highest quality source habitat for our reintroduction site in order to give the best chance of reintroduction success in the model. Identification of specific release sites should occur during subsequent feasibility analysis that would make use of detailed data (e.g., on landuse conflicts, prey density) that was not available for the entire study area.

SCENARIOS VERSUS PREDICTIONS

Although we use the term prediction (e.g., “predicted source habitat”) in reporting our results, these results should be seen as arising from scenarios rather than predictions. A scenario is an attempt to say, not that this WILL occur, but IF this occurs, what will the consequences be? The aphorism “all models are wrong, some models are useful” helps illustrate this point. For example, although we examine the results of current human population growth on wolf habitat by extending trends from census data for 25 years into the future, it is certain that unforeseen socioeconomic trends will result in actual human population distribution in 2025 differing from our scenario. However, we believe that this model scenario is useful and informative because strong elements of current population trends will still be evident. While our human population parameters are based on local (block-level) census trends, our road density parameters simply incorporate a 1% per year increase (proportional to the current road density at the 1 km^2 scale) across the study area. Because available regional-scale roads data is of varying dates, it is not possible given the resources of the current study, to, as one reviewer suggested, assemble a regional chronosequence of road distribution and determine e.g., county by county rates of increase in roads. We chose to use a rate (1%/year) that is half of that seen in the most rapidly growing portions of our study region (western Colorado). Despite these limitations, we believe that, because road construction is an important force fragmenting wildlife habitat in the region, it is instructive to examine a scenario which involves increase in this factor.

UNCERTAINTIES IN PARAMETERIZATION OF FECUNDITY (PREY PRODUCTIVITY)

Several reviewers questioned the assumptions we made concerning the relative prey productivity and resultant wolf fecundity to be expected in different vegetation types of the region. However, comments were divided between those who felt we had overrated the more xeric habitats typical of the southwest, and those who felt we had given them insufficient value. The former view resulted in a concern that the Colorado site (San Juans) was likely of higher potential than shown in our results. The latter view resulted in a concern that our results underestimated the potential of the Sky Islands region of southeastern Arizona and southeastern New Mexico. Because we chose an intermediate view, areas such as the Blue Range and Grand Canyon that show elements of Madrean vegetation but not extreme aridity were rated as among the most productive habitat. This agrees with previous assumptions as to Mexican wolf habitat (e.g., the 1982 recovery plan states a goal to reintroduce wolves to habitat above 1200 m (4,000 feet) elevation [USFWS 1982]). To make our assumptions more transparent, we have included the rankings in Tables 4 and 5. Uncertainty surrounding the relative habitat value of southwestern vegetation types for wolves is due to the spotty historical record, and lack of extant wolf populations in similar habitats, with the exception of the relatively recently established Blue Range population. Historical records of occurrence of wolves in an area may not indicate that the area was a population source, but rather dispersal or sink habitat. It is also important to consider habitat associations across the historic range of e.g., *C. l. baileyi*, rather than primarily focusing on the more accessible data from the U.S. portion of the subspecific range. We sought to balance historical records of wolf occurrence from the southwestern U.S. and northern Mexico (e.g., that wolves used xeric habitats but prey and wolves were more abundant in the Madrean oak woodlands and pine forests [Brown 1983]) with more extensive knowledge of relationships between wolf viability and prey density from across North America (e.g., Fuller 1989). In the end, however, the level of uncertainty means that other assumptions could be defended and would result in somewhat differing results. However, once these initial assumptions are made (e.g., as to the relative value of xeric versus higher elevation forested habitat), the PATCH results can illustrate their implications (e.g., whether an area with fragmented habitat patches can sustain a viable population).

LESSONS FOR RECOVERY PLANNING

Reestablishment of wolf populations via reintroduction of naive, captive-born animals is problematic because such animals often have poor survival rates after reintroduction (Griffith at al. 1989, Beck et al. 1994, Wilson and Stanley-Price 1994, Phillips et al. 2003). Mindful of this trend, Phillips (2000) proposed to develop a management facility in northern New Mexico that would promote recovery of the Mexican wolf by providing captive-born adults with opportunities to enhance survival behaviors; allowing some adults to produce wild-born pups for reintroduction; and designed to evolve into an official reintroduction project once the need to provide experienced wolves to another reintroduction effort had been satisfied. Lack of an extant wild population also contributes to a scarcity of data on field ecology and historic distribution which could inform recovery efforts. Wolf restoration to fragmented landscapes such as the southwest that lack areas of secure habitat as large as Yellowstone and central Idaho requires a greater focus on regional-scale planning across many jurisdictions. The binational distribution of *C. l. baileyi* potentially further complicates planning due to a contrast in available data on habitat suitability as well as contrasting socioeconomic and regulatory contexts. These factors combine with the patchy prey distribution and lower prey density in semi-arid landscapes to make wolf recovery in the SWDPS a significant challenge.

The key to successful wolf recovery in the southwest's fragmented landscapes is to establish strong well-distributed source populations and then allow natural dispersal to reestablish peripheral populations. The reintroduction sites we evaluated with PATCH are all predicted source habitat, as that was a criteria for their initial selection. Therefore, to rank them for recovery planning we must look at their relative vulnerability and ability to facilitate regional population growth. Our results suggest that, next to the current reintroduction site in the Blue Range, the Grand Canyon area may be the reintroduction site with the highest probability of success and greatest effect on enhancing regional wolf populations through dispersal. This is due to both a large area of park and other public lands with low mortality risk for wolves, and the connectivity from that habitat southward through the Mogollon Rim towards the Blue Range and northward to the public lands of the mountains of central Utah. Similarly to the Grand Canyon, the Vermejo/Carson (northern New Mexico) and San Juans (southern Colorado) would also aid the reestablishment of well-distributed wolf populations northward to the public lands in western Colorado. However, these sites appear to have somewhat higher vulnerability to habitat reduction (San Juans) or isolation (Vermejo/Carson) by landscape change. All of these sites in the northern SWDPS could contribute significantly to restoration of rangewide connectivity from Canada to Mexico. Similarly, the Sky Islands of the U.S./Mexico border country, although generally not high quality source habitat, could, if occupied, play a key role in restoring connectivity between U.S. and Mexican wolf populations. Conversely, an area such as the White Sands Missile Range (WSMR), even in the doubtful event that it could support a viable population, would make little contribution to regional recovery goals due to its isolation and small size. In support of the experience to date in the southwest, and in contrast with wolf recovery in the northern Rockies, our results suggest that more than one reintroduction project will be necessary for recovering the gray wolf to a significant portion of its historic range within the SWDPS, and that a longer-term initial reintroduction effort should be anticipated.

Restoration of a extirpated species such as the wolf that has high area requirements for viable populations (Woodroffe and Ginsberg 1998) and yet whose protection potentially conflicts with other land uses inevitably causes contentious debate over what level of recovery is necessary or desirable. The Endangered Species Act (ESA) and conservation science arguably suggest that our goal should be recovery over a significant portion of the historic range. Our results can help inform this debate by providing an estimate of the distribution of suitable habitat and what habitat trends may compromise future wolf persistence. Knowing the distribution of suitable habitat allows us to more rigorously define what constitutes a significant portion of range. This combined with knowledge of potential future threats should inform the development of recovery criteria for the SWDPS.

Basing recovery on large-scale patterns of habitat suitability and connectivity contrasts with the current policy of wolf management in the Blue Range Wolf Recovery Area (BRWRA), which requires that some wide-ranging wolves be captured and returned to select tracts of public land, even in the absence of an identifiable problem (U.S. Fish and Wildlife Service 1996). Although it makes sense that federal lands should play the major role in species recovery where possible, it is important to consider the entire regional landscape rather than minimal core recovery areas, and assess the role of all land categories, including private lands, in promoting or endangering wolf persistence. Our results suggest that general public (e.g., non-wilderness) lands will play an important role in wolf recovery in the SWDPS. Identifying key habitats on general public lands and coordinating their management as buffer and connective habitat to adjacent protected lands will greatly enhance the resiliency of the initial core populations. This, of course, is contingent on revising the current Blue Range policy to allow dispersal of non-problem animals, as is consistent with wolf recovery policy in other areas (Paquet et al. 2001). Thus our prediction as to the source value of the BRWRA under a policy of natural dispersal is not inconsistent with Paquet et al. (2001)'s more pessimistic assessment of the status of the BRWRA population under current policy. Our results may also allow us to anticipate conflict zones that may become occupied by wolves but are predicted to remain sink habitat due to high wolf mortality and low productivity. For example, previously-evaluated areas in southeastern Arizona (Johnson et al. 1992) are lower in carrying capacity and potential occupancy than other potential reintroduction sites (except for the Mogollon site). They are only predicted to be occupied due to their proximity to Mexico and the Blue Range area and are at risk of extirpation due to landscape change. However, because of their key role as connective habitat, our results suggests the importance of planning to mitigate existing threats and negative landscape trends to insure maintenance of connectivity. This could occur through establishment of occupancy of the Galiuro/Pinaleno and/or Chiricahua Mountains as a recovery goal, and through expansion of the Blue Range Wolf Recovery Area to allow natural dispersal and relocation of wolves from the Blue Range to the Sky Islands.

Our results strongly establish the importance of habitat in the northern portion of the SWDPS. Recovering the Mexican wolf to a significant portion of the historic range within the SWDPS would ensure the persistence of a subspecies with unique genetic characteristics (Garcia-Moreno et al. 1996, Hedrick et al. 1997, Wayne and Vila 2003). Moreover, by also involving northern wolves (e.g., *Canis lupus occidentalis* or *Canis lupus nubilus*) (Nowak 1995) in recovery actions in the SWDPS it would be possible to restore historic patterns of gene flow (Phillips et al. 2000:22). Effecting wolf recovery to maximize genetic diversity whenever practicable is an appropriate and important objective for the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2003a). The challenge before the current recovery team is to devise a strategy that both recognizes the unique genetic heritage of *Canis lupus baileyi* (Wayne and Vilà 2003) and fully exploits the abundance of habitat in the northern portion of the SWDPS to reestablish a robust southwestern wolf population linked to other regional populations along a natural gradient of genetic diversity.

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Table 1. Base parameters used in the PATCH model of wolf population dynamics in the SWDPS. Fecundity is given as number of female offspring per adult female or pack.

PARAMETER	
Territory size (km^2)	504
Maximum dispersal distance (km)	750-1500
Survival rates (maximum)	
young, year 0	0.46
subadult - year 1	0.86
adult - > 2 years	0.96
at senescence (at year 8)	0.69
Fecundity rates (maximum/mean)	
subadult Year 1	0
adult Year 2	2.29
adult > 3 years	3.21

Table 2. Landscape change vulnerability by state, expressed as percentage change in population from scenario A to scenario D. Only those portions of Utah, Colorado, and Texas within the SWDPS are considered.

Utah	23.3
Colorado	58.3
Arizona	33.4
New Mexico	53.9
Texas	15.9
Sonora	5.6
Chihuahua	11.1
Coahuila	4.1
Nuevo Leon	38.1
Tamaulipas	44.4
Sinaloa	5.9
Durango	16.0

Table 3. Comparative summary of results for potential wolf reintroduction areas in terms of model predictions.

Scenario	Area (km^2)	Population A/B/D	Occupancy A	Lambda A	Extinction risk (%) A/B/D	Vulnerability (A - D)/A
SITES EVALUATED WITH DETAILED REINTRODUCTION SCENARIOS						
B - Blue Range	10000	92/122/67	72.5	1.04	0/0.2/1.4	27.2
G - Grand Canyon	10000	91/109/79	68.5	1.06	0/0.1/0.4	13.2
M - Mogollon Rim	10000	71/96/45	60.3	1.00	8.6/9.3/15.8	36.6
S - San Juans	10000	79/99/51	63.6	1.04	10.5/1.0/19.6	35.4
V - Vermejo/Carson	10000	84/111/66	68.2	1.04	0.8/0/2.7	21.4
A - Austin Ranch	10000	72/57/69	55.9	1.05	1.5/19.9/1.8	4.2
C - Carmen	10000	67/56/66	46.8	1.08	0.1/0.3/0.2	1.5
D - Durango	10000	128/108/116	96.8	1.07	0.2/0.3/0	9.4
T - Tutuaca	10000	88/97/77	72.8	1.01	0.5/0/1.2	12.5
OTHER SITES						
Entire Blue Range WRA	18617	185/224/143	77.3	1.05	N/A	22.7
1 - Galiano/Pinaleno Mountains	8950	50/68/27	51.4	0.98		46.0
2 - Chiricahua Mountains	6836	42/45/32	57.3	0.97		23.8
3 - Atascosa/Patagonia Mountains	6066	30/36/19	50.4	0.93		36.7
4 - White Sands Missile Range	10102	5/8/3	4.4	1.00		40.0

Table 4. Relative ranks and resulting habitat value (scaled 0 to 1) assigned Mexican vegetation types in the creation of the wolf fecundity layer.

VEGETATION	RANK	VALUE
AGRICULTURA DE HUMEDAD	26	0.0
AGRICULTURA DE RIEGO (INCLUYE RIEGO EVENTUAL)	26	0.0
AGRICULTURA DE TEMPORAL CON CULTIVOS ANUALES	26	0.0
AGRICULTURA DE TEMPORAL CON CULTIVOS PERMANENTES Y SEMIPERMANENTES	26	0.0
AREA SIN VEGETACION APARENTE	27	0.0
ASENTAMIENTO HUMANO	29	0.0
BOSQUE BAJO-ABIERTO	6	0.55
BOSQUE BAJO-ABIERTO CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	6	0.55
BOSQUE DE ENCINO	7	0.5
BOSQUE DE ENCINO CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	7	0.5
BOSQUE DE OYAMEL (INCLUYE AYARIN Y CEDRO)	3	0.8
BOSQUE DE OYAMEL (INCLUYE AYARIN Y CEDRO) CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	3	0.8
BOSQUE DE PINO	1	1.0
BOSQUE DE PINO CON VEGETACION PRIMARIA Y SECUNDARIA ARBOREA	1	1.0
BOSQUE DE PINO CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	1	1.0
BOSQUE DE PINO-ENCINO (INCLUYE ENCINO-PINO)	5	0.6

VEGETATION	RANK	VALUE
BOSQUE DE PINO-ENCINO (INCLUYE ENCINO-PINO) CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	5	0.6
BOSQUE DE TASCATE	4	0.7
BOSQUE DE TASCATE CON VEGETACION PRIMARIA Y SECUNDARIA ARBOREA	4	0.7
BOSQUE DE TASCATE CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	4	0.7
BOSQUE MESOFILO DE MONTANA	8	0.45
BOSQUE MESOFILO DE MONTANA CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	8	0.45
CHAPARRAL	9	0.4
CHAPARRAL CON VEGETACION SECUNDARIA	9	0.4
CUERPO DE AGUA	28	0.0
MANGLAR	24	0.0
MATORRAL CRASICAULE	10	0.35
MATORRAL CRASICAULE CON VEGETACION SECUNDARIA	10	0.35
MATORRAL DE CONIFERAS	2	0.85
MATORRAL DE CONIFERAS CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	2	0.85
MATORRAL DESERTICO MICROFILO	10	0.35
MATORRAL DESERTICO MICROFILO CON VEGETACION SECUNDARIA	11	0.3
MATORRAL DESERTICO ROSETOFILO	11	0.3
MATORRAL DESERTICO ROSETOFILO CON VEGETACION SECUNDARIA	11	0.3
MATORRAL ESPINOSO TAMAULIPECO	11	0.3

VEGETATION	RANK	VALUE
MATORRAL ESPINOSO TAMAULIPECO CON VEGETACION SECUNDARIA	11	0.3
MATORRAL ROSETOFILO COSTERO	12	0.25
MATORRAL ROSETOFILO COSTERO CON VEGETACION SECUNDARIA	12	0.25
MATORRAL SARCOCAULE	10	0.35
MATORRAL SARCOCAULE CON VEGETACION SECUNDARIA	11	0.3
MATORRAL SARCOCRASICAULE	10	0.35
MATORRAL SARCOCRASICAULE CON VEGETACION SECUNDARIA	10	0.35
MATORRAL SARCOCRASICAULE DE NEBLINA	10	0.35
MATORRAL SARCOCRASICAULE DE NEBLINA CON VEGETACION SECUNDARIA	11	0.3
MATORRAL SUBMONTANO	10	0.35
MATORRAL SUBMONTANO CON VEGETACION SECUNDARIA	10	0.35
MATORRAL SUBTROPICAL	13	0.2
MATORRAL SUBTROPICAL CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	13	0.2
MEZQUITAL (INCLUYE HUIZACHAL)	9	0.4
MEZQUITAL (INCLUYE HUIZACHAL) CON VEGETACION SECUNDARIA	9	0.4
PALMAR	25	0.0
PASTIZAL CULTIVADO	26	0.0
PASTIZAL INDUCIDO	22	0.1
PASTIZAL NATURAL (INCLUYE PASTIZAL-HUIZACHAL)	9	0.4
PLANTACION FORESTAL	21	0.1

VEGETATION	RANK	VALUE
POPAL-TULAR	25	0.0
PRADERA DE ALTA MONTANA	9	0.4
RIEGO SUSPENDIDO	26	0.0
SABANA	9	0.4
SELVA ALTA Y MEDIANA PERENNIFOLIA	20	0.1
SELVA ALTA Y MEDIANA PERENNIFOLIA CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	20	0.1
SELVA ALTA Y MEDIANA SUBPERENNIFOLIA	18	0.1
SELVA ALTA Y MEDIANA SUBPERENNIFOLIA CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	18	0.1
SELVA BAJA CADUCIFOLIA Y SUBCADUCIFOLIA	15	0.1
SELVA BAJA CADUCIFOLIA Y SUBCADUCIFOLIA CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	15	0.1
SELVA BAJA ESPINOSA	14	0.1
SELVA BAJA ESPINOSA CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	14	0.1
SELVA MEDIANA CADUCIFOLIA Y SUBCADUCIFOLIA	16	0.1
SELVA MEDIANA CADUCIFOLIA Y SUBCADUCIFOLIA CON VEGETACION SECUNDARIA ARBUSTIVA Y HERBACEA	16	0.1
VEGETACION DE DESIERTOS ARENOSOS	13	0.2
VEGETACION DE DUNAS COSTERAS	25	0.0
VEGETACION DE GALERIA (INCLUYE BOSQUE, SELVA Y VEGETACION DE GALERIA)	23	0.1
VEGETACION HALOFILA Y GIPSOFILA	25	0.0

Table 5. Relative ranks and resulting habitat value (scaled 0 to 1) assigned U.S. vegetation types in the creation of the wolf fecundity layer.

VEGETATION	RANK	MULTIPLIER
Bare Rock/Sand/Clay	27	0.0
Commercial/Industrial/Transportation	29	0.0
Deciduous Forest	7	0.5
Emergent Herbaceous Wetlands	24	0.0
Evergreen Forest	1	1.0
Fallow	26	0.0
Grasslands/Herbaceous	9	0.4
High Intensity Residential	29	0.0
Low Intensity Residential	29	0.0
Mixed Forest	5	0.6
Open Water	28	0.0
Orchards/Vineyards/Other	26	0.0
Pasture/Hay	26	0.0
Perennial Ice/Snow	27	0.0
Quarries/Strip Mines/Gravel Pits	28	0.0
Row Crops	26	0.0
Shrubland	10	0.35
Small Grains	26	0.0
Transitional	26	0.0
Urban/Recreational Grasses	29	0.0
Woody Wetlands	23	0.1

FIGURES (see file carrolletal_figures.pdf)

Figure 1. Map of the study area considered in the habitat and viability modeling for southwestern wolves.

Figure 2. Ranking of habitat in terms of wolf fecundity rate as used in viability modeling for southwestern wolves. Fecundity rate was modeled as a function of vegetation type, greenness (a satellite-imagery derived metric associated with plant productivity), and slope.

Figure 3. Ranking of habitat in terms of wolf survival rate as used in viability modeling for southwestern wolves. Survival rate was modeled as an inverse function of human population and roads.

Figure 4. Cattle density in the southwestern U.S. and northern Mexico.

Figure 5. Potential distribution and demography of wolves as predicted by the PATCH model in the southwestern U.S. and northern Mexico under landscape scenario A - current conditions, with wolf mortality risk based on roads and census data. Only those areas with a predicted probability of occupancy of greater than 50% are shown.

Figure 6. Potential distribution and demography of wolves as predicted by the PATCH model in the southwestern U.S. and northern Mexico under landscape scenario B - current conditions, with wolf mortality risk based on roads, census, and livestock density data. Only those areas with a predicted probability of occupancy of greater than 50% are shown.

Figure 7. Potential distribution and demography of wolves as predicted by the PATCH model in the southwestern U.S. and northern Mexico under landscape scenario C - human population as of 2025, with increased road development on private lands only, with wolf mortality risk based on roads and census data. Only those areas with a predicted probability of occupancy of greater than 50% are shown.

Figure 8. Potential distribution and demography of wolves as predicted by the PATCH model in the southwestern U.S. and northern Mexico under landscape scenario D - human population as of 2025, with increased road development on both private and unprotected public lands, with wolf mortality risk based on roads and census data. Only those areas with a predicted probability of occupancy of greater than 50% are shown.

Figure 9. Composite of figures 5-8 shown for comparison of 4 scenarios of potential distribution and demography of wolves as predicted by the PATCH model in the southwestern U.S. and northern Mexico. Scenarios are as labeled A through D.

Figure 10. Results of sensitivity analysis for U.S. wolf mortality risk parameters. Potential distribution and demography of wolves is shown as predicted by the PATCH model in the southwestern U.S. and northern Mexico under landscape scenario A, but with mortality risk reduced proportionately by 25% in the U.S. (A), or increased proportionately by 25% in the U.S..

Figure 11. Results of sensitivity analysis for the influence of Mexican populations on U.S. population estimates. Potential distribution and demography of wolves is shown as predicted by the PATCH model in the southwestern U.S. under (A) landscape scenario A, and (B) landscape scenario D, but with a reflecting barrier to dispersal at the U.S./Mexico border and no wolves in Mexico.