The following packet contains:

- Draft Biological Report for the Mexican Wolf, June 22, 2017 version
- Population Viability Analysis for the Mexican Wolf, June 13, 2017 version
- Mexican Wolf Habitat Suitability Analysis in Historical Range in Southwestern US and Mexico, April 2017 version

The U.S. Fish and Wildlife Service is providing the above versions of the Draft Biological Report and two supporting analyses, “Population Viability Analysis for the Mexican Wolf” and “Mexican Wolf Habitat Suitability Analysis in Historical Range in Southwestern US and Mexico,” to the public as supplemental background information during the public comment period on the Draft Mexican Wolf Recovery Plan, First Revision. We submitted previous versions of these documents for peer review from May 2 to June 2, 2017 and received responses from 5 peer reviewers. This version of the Draft Biological Report (June 22, 2017) and population viability analysis (June 13, 2017) include some revisions that are responsive to those reviews, but additional revisions will continue to be made until the document and its appendices are finalized. We will finalize the Biological Report concurrent with the 2017 Mexican Wolf Recovery Plan, First Revision, and will update the Biological Report as needed in the future to maintain a compendium of the best available scientific information upon which to base our recovery efforts for the Mexican wolf.

DRAFT
BIOLOGICAL REPORT
for the
Mexican wolf
(*Canis lupus baileyi*)

(June 22, 2017)

U.S. Fish and Wildlife Service
Southwest Region (Region 2)
Albuquerque, New Mexico

2017

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We gratefully acknowledge the continuing engagement of our current and former interagency partners in the reintroduction and recovery effort, including Arizona Game and Fish Department, U.S. Forest Service, White Mountain Apache Tribe, U.S. Department of Agriculture-Wildlife Services, New Mexico Department of Game and Fish, as well as the counties of Gila, Graham, Greenlee, Navajo, and the Eastern Arizona Counties Organization in Arizona and New Mexico. We are grateful for the continuing collaboration with the Comisión Nacional de Áreas Naturales Protegidas (CONANP) and the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) in Mexico, and recognize the contributions of these agencies’ staff and leaders to the Mexican wolf recovery effort.

We owe perhaps our biggest thank you to the binational Mexican Wolf Species Survival Plan breeding facilities of the Association of Zoos and Aquariums, without whom the reintroduction of the Mexican wolf would not be possible. We are grateful for the member institutions and their many staff who maintain these facilities, conduct research and annual reproductive planning, educate the public, and facilitate the transport of captive wolves between facilities and to the wild as needed.

An enourmous thank you is owed to the Interagency Field Team for their tireless effort throughout the years to establish and maintain Mexican wolves on a working landscape. Reintroductions require an extensive group of dedicated personnel to collect data and accomplish the goal of establishing a population. Data for this project has been collected by personnel from the Arizona Game and Fish Department, the New Mexico Department of Game and Fish, the U.S. Fish and Wildlife Service, U.S. Department of Agriculture – Wildlife Services, and the White Mountain Apache Tribe. There are too many employees to list from 1998 – 2016, but we appreciate your efforts and dedication. In particular, Colby Gardner (U.S. Fish and Wildlife Service) assisted with the databases that were required to initially populate the population viability model. A group of dedicated pilots with the Arizona Game and Fish Department have kept many employees safe during flights to collect data. We also appreciate the continued partnership of the U.S. Forest Service in recovery of the Mexican wolf.

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LITERATURE CITATION AND AVAILABILITY

Literature citation should read as follows:
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Copies are available on-line at:
http://www.fws.gov/southwest/es/mexicanwolf

Copies of the document can also be requested from:

U.S. Fish and Wildlife Service
Mexican Wolf Recovery Program
New Mexico Ecological Services Field Office
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INTRODUCTION TO THE BIOLOGICAL REPORT

This biological report informs the U.S. Fish and Wildlife Service's (Service, we) revision of the 1982 Mexican Wolf Recovery Plan.

We are revising the recovery plan to provide an updated strategy to guide Mexican wolf (*Canis lupus baileyi*) conservation efforts. As a supplement to the recovery plan, the biological report enables us to streamline the recovery plan to focus on the statutorily required elements of the Endangered Species Act (Act, or ESA):

- A description of site-specific management actions that may be necessary to achieve the plan's goal for the conservation and survival of the Mexican wolf;
- Objective, measurable criteria which, when met, would result in a determination that the Mexican wolf may be removed from the List of Threatened and Endangered Wildlife and Plants;
- Estimates of the time required and the cost to carry out those measures needed to achieve the plan's goal and to achieve intermediate steps toward that goal.

In this biological report, we briefly describe the biology and ecology of the Mexican wolf, its abundance, distribution and population trends, and stressors to recovery. We then consider the concepts of resiliency, redundancy, and representation as they apply to the recovery of the Mexican wolf. The biological report draws on the substantial amount of information available from the course of our reintroduction effort and in the scientific literature. We cite our existing regulations, annual reports, and related documents when possible rather than providing an exhaustive recounting of all available information.

The biological report is accompanied by two technical analyses: "Population Viability Analysis for the Mexican Wolf (*Canis lupus baileyi*): Integrating Wild and Captive Populations in a Metapopulation Risk Assessment Model for Recovery Planning" (Miller 2017), and "Mexican Wolf Habitat Suitability Analysis in Historical Range in the Southwestern U.S. and Mexico" (Martínez-Meyer et al. 2017). The population viability analysis assesses the conditions needed for Mexican wolf populations to maintain long-term viability. The habitat suitability report assesses the current condition of the landscape in portions of Arizona, New Mexico, and Mexico based on habitat features required to sustain Mexican wolf populations. Together, the biological report and two accompanying technical analyses provide a succinct accounting of the best available science to inform our understanding of the current and future viability of the Mexican wolf, and therefore serve as a foundation for our strategy to recover the Mexican wolf.

Our development of a biological report is an interim approach as we transition to using a species status assessment as the standard format to analyze species and make decisions under the Act. We intend for species biological reports to support all functions of the Endangered Species Program from Candidate Assessment to Listing to Consultations to Recovery and Delisting. For the Mexican wolf, which is already listed, we have developed a biological report as part of the ongoing recovery process.

The biological report, the revised recovery plan, and a separate detailed implementation strategy provide a three-part operational vision for Mexican wolf recovery. The biological report and implementation strategy will be updated as new information is gained or annual implementation progress informs adaptation of our management actions over time. The recovery plan is broader in its scope, providing an overarching strategy, objective and measurable criteria, and actions that we intend will remain valid, potentially for the entire course of the recovery process. In addition, tribes and pueblos in the Southwest have developed a white paper to describe the ecological, cultural, and logistical aspects of Mexican wolf recovery to their communities, "Tribal Perspectives on Mexican Wolf Recovery." This report is available on our website, at: https://www.fws.gov/southwest/es/mexicanwolf/MWRP.cfm.

BRIEF DESCRIPTION OF MEXICAN WOLVES IN CAPTIVITY AND THE WILD

Recovery efforts for the Mexican wolf have been underway in the United States and Mexico since the late 1970s. Both countries are working to reestablish Mexican wolves in the wild and are involved in maintaining a binational captive population of Mexican wolves.

In the United States, a single population of at least 113 Mexican wolves inhabits portions of Arizona and New Mexico in an area designated as the Mexican Wolf Experimental Population Area (MWEPA) (U.S. Fish and Wildlife Service [USFWS] 2017a) (Figure 1). Mexican wolves are not present in the wild in the United States outside of the MWEPA. The Service and its partners began releasing Mexican wolves from captivity into the MWEPA in 1998, marking the first reintroduction of the Mexican wolf since their extirpation in the late 1970s. The Service is now focused on inserting gene diversity from the captive population into the growing wild population. Additional detailed history of the reintroduction of Mexican wolves in the MWEPA is available in our "Final Environment Impact Statement for the Proposed Revision to the Regulations for the Nonessential Experimental Population of the Mexican Wolf" (USFWS 2014) and in annual progress reports. (These documents are available online at: https://www.fws.gov/southwest/es/mexicanwolf/).

Mexican Wolf Experimental Population Area

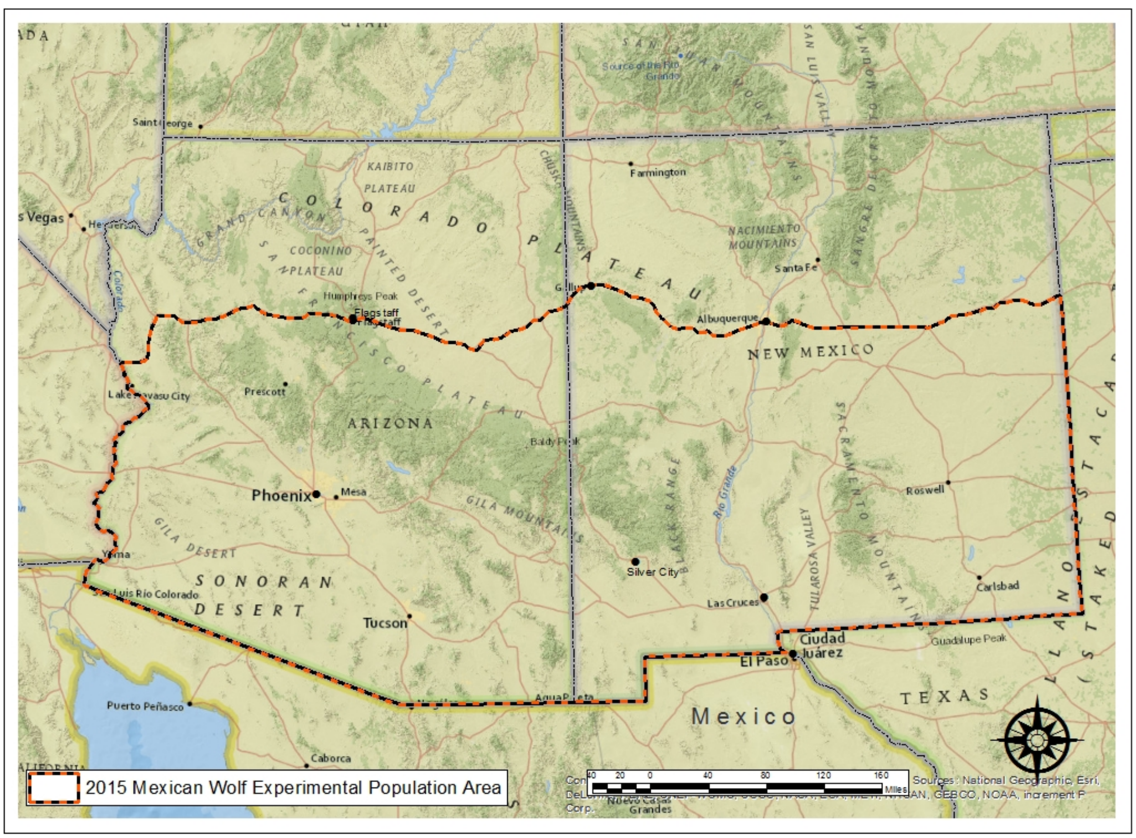

Figure 1. Mexican Wolf Experimental Population Area in the Arizona and New Mexico, United States (U.S. Fish and Wildlife Service files).

Mexico began reestablishing a population of Mexican wolves in the Sierra Madre Occidental in 2011 (Siminski and Spevak 2016). As of April 2017, approximately 28 wolves inhabit the northern portion of these mountains in the state of Chihuahua (Garcia Chavez et al. 2017) (Figure 2). Natural reproduction was documented in 2014, 2015, and 2016 (personal communication with Dr. López-González, Universidad Autónoma de Querétaro, March 13, 2017). Additional detailed information about the status of Mexican wolves in Mexico is available in updates from the Comisión Nacional de Áreas Naturales Protegidas (available online at http://procer.conanp.gob.mx/noticias.html).

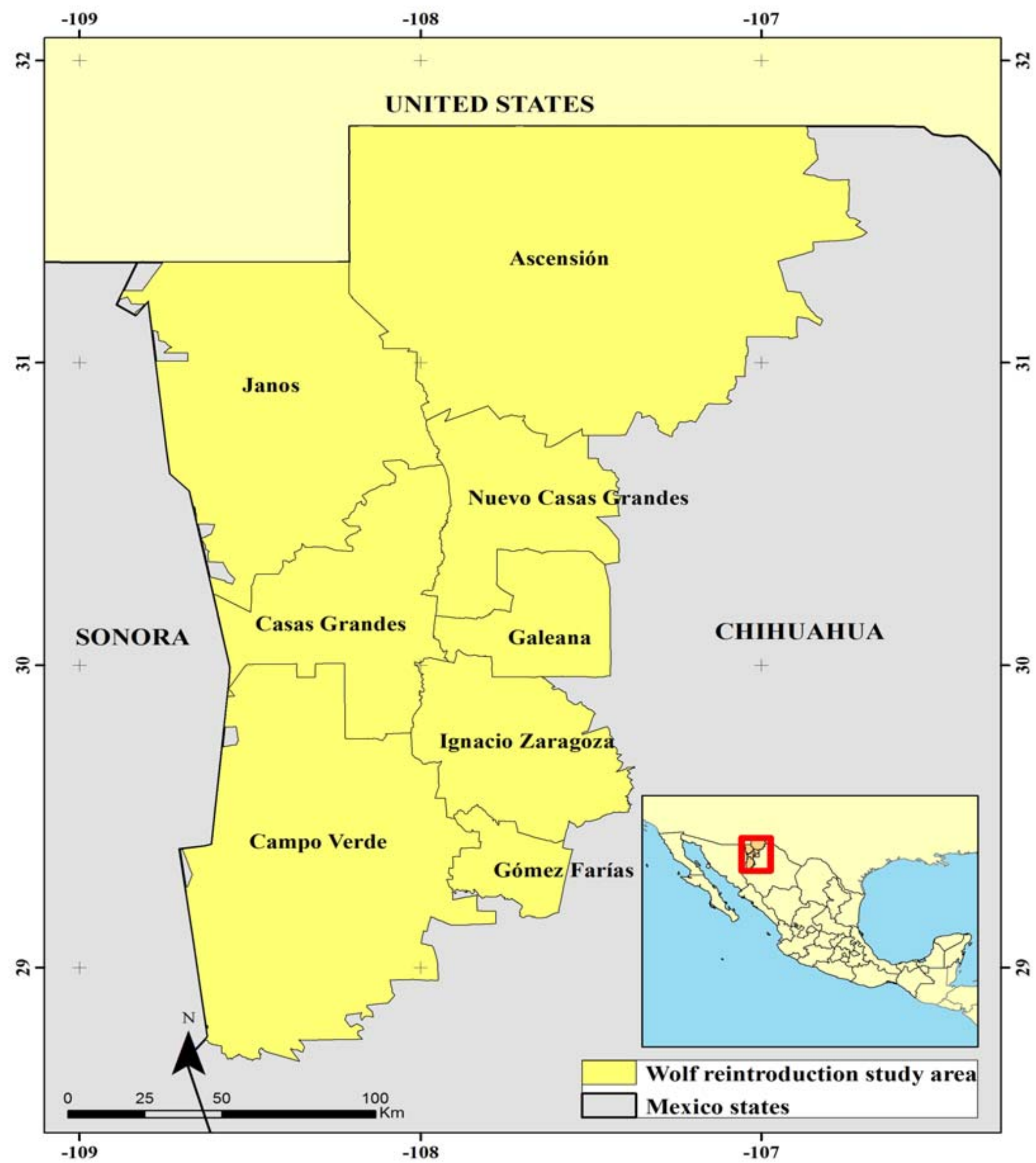

Figure 2. Approximate range of Mexican wolves in Mexico as of March 2017 (map provided by Dr. López-González, Universidad Autónoma de Querétaro, March 13, 2017). The names on the map within the yellow polygon represent municipalities within the state of Chihuahua.

The Mexican wolf captive population is managed under the Mexican Wolf Species Survival Plan (SSP), administered by the Association of Zoos and Aquariums. The Mexican wolf SSP is a binational program whose primary purpose is to produce Mexican wolves for reintroduction in the United States and Mexico, and to conduct public education and research. The captive population is the sole source of Mexican wolves available to reestablish the subspecies in the wild and is therefore an essential component of the Mexican wolf recovery effort. The Mexican wolf captive breeding program was initiated in 1977 to 1980 with the capture of the last remaining Mexican wolves in the wild in Mexico and the subsequent addition of several wolves already in captivity, for a total of seven unrelated “founders.” This is a small number of founders compared with many species recovery efforts and presents challenges to the recovery of the Mexican wolf. The founding wolves represented three family groups referred to as the McBride (originally referred to as Certified), Aragon, and Ghost Ranch lineages (Siminski and Spevak 2016). Each of the animals from these lineages has been confirmed to be pure Mexican wolves (García-Moreno et al. 1996). All Mexican wolves alive today in captivity or the wild are descendants of the seven founders.

The SSP strives to maintain at least 240 Mexican wolves in captivity. As of October 21, 2016, the binational captive program houses 251 wolves in 51 institutions (Siminski and Spevak 2016) (Figure 3). Although the captive population is spread over many institutions in two countries, annual reproductive planning and transportation of wolves between facilities to facilitate breeding results in management of the animals as a single population. Wolves that are genetically well-represented in the captive populations can be selected for release to the wild (Siminski and Spevak 2016). The SSP maintains a pedigree of Mexican wolves in captivity and in the wild, although maintaining the wild pedigree will become more challenging over time as the populations in the United States and Mexico grow and it becomes more difficult to track the parentage of each individual wolf.

Mexican Wolf SSP Facilities - 2016

Figure 3. General locations of Mexican wolf captive breeding facilities in the U.S. and Mexico (U.S. Fish and Wildlife Service files).

LEGAL AND HISTORICAL CONTEXT

Legal Status of the Species

The Mexican wolf, *C. l. baileyi*, is listed as an endangered subspecies under the Act. The Service originally listed the Mexican wolf as an endangered subspecies in 1976, but subsequently subsumed it into a rangewide listing for the gray wolf species (41 FR 17736 April 28, 1976; 43 FR 9607, March 9, 1978). In 2015 we finalized a rule to separate the Mexican wolf subspecies from the gray wolf listing, retaining the Mexican wolf's status as endangered (80 FR 2488, January 16, 2015). Critical habitat has not been designated for the Mexican wolf.

The Service designated a Mexican wolf nonessential experimental population under section 10(j) of the Act in 1998, which was revised in 2015 (80 FR 2512, January 16, 2015). Mexican wolves' status in the southwestern United States is dependent on their location: Mexican wolves within the MWEPA boundaries are considered part of the nonessential experimental population; Mexican wolves outside of the MWEPA boundary are considered endangered. There are currently no known Mexican wolves outside of the MWEPA boundaries in the United States. The protections and prohibitions for the nonessential experimental population of Mexican wolves are provided in our rule, "Revisions to the Regulations for the Nonessential Experimental Population of Mexican wolves" (80 FR 2512, January 16, 2015; available on our website at https://www.fws.gov/southwest/es/mexicanwolf).

The Mexican wolf is protected under State wildlife statutes as the gray wolf, and by federal regulation as a subspecies in Mexico. In Arizona, the gray wolf is identified as a Species of Greatest Conservation Need (Arizona Game and Fish Department 2012). The gray wolf is listed as endangered in New Mexico (Wildlife Conservation Act, 17-2-37 through 17-2-46 NMSA 1978; List of Threatened and Endangered Species, 19.33.6 NMAC 1978) and Texas (Texas Statute 31 T.A.P). In Mexico, the Mexican wolf is assigned a status of "probably extinct in the wild" under Mexican law (Norma Oficial Mexicana NOM-059-SEMARNAT-2010) (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT; Federal Ministry of the Environment and Natural Resources] 2010). The Norma Oficial Mexicana NOM-059-SEMARNAT-2010 provides the regulatory framework for assessing and categorizing extinction risk levels, although the Mexican wolf has not been assessed because prior to the initiation of the reintroduction effort in 2011, the existence of live individuals in the wild had not been affirmed.

Historical Causes of Decline

When the Mexican wolf was listed as endangered under the Act in 1976, no wild populations were known to remain in the United States, and only small pockets of wolves persisted in Mexico, resulting in a complete contraction of the historical range of the Mexican wolf (Brown 1988, and see USFWS 2010). Reintroduction efforts in the United States and Mexico have begun to restore the Mexican wolf to portions of its former range in Arizona, New Mexico, and Mexico.

The near extinction of the Mexican wolf was the result of government and private campaigns to reduce predator populations during the late 1800s- to mid- 1900s due in part to conflict with the expanding ranching industry (Brown 1988). While we know that efforts to eradicate Mexican wolves were effective, we do not know how many wolves were on the landscape preceding their rapid decline. Some trapping records, anecdotal evidence, and rough population estimates are available from the early 1900s, but they do not provide a rigorous estimate of population size of Mexican wolves in the United States or Mexico. In New Mexico, a statewide carrying capacity (potential habitat) of about 1,500 gray wolves was hypothesized by Bednarz (1988), with an estimate of 480 to 1,030 wolves present in 1915. We hypothesize, based on this information, that across the southwestern United States and Mexico Mexican wolves numbered in the thousands in multiple populations.

SPECIES DESCRIPTION AND NEEDS

Taxonomy and Description

The Mexican wolf, *C. l. baileyi*, is a subspecies of gray wolf (Nelson and Goldman 1929) and member of the dog family *(Canidae: Order Carnivora).* The genus *Canis* also includes the red wolf (*C. rufus*), Eastern wolf (*C. lycaon*), dog (*C. familiaris*), coyote (*C. latrans*), several species of jackal (*C. aureus*, *C. mesomelas*, *C. adustus*) and the dingo (*C. dingo*) (Mech 1970). The type locality of *C. l. baileyi* is Colonia Garcia, Chihuahua, Mexico based on a gray wolf killed during a biological investigation in the mountains of Chihuahua, Mexico in 1899. Thirty years later this animal was combined with additional specimens to define the Mexican wolf (Nelson and Goldman 1929).

Goldman (1944) provided the first comprehensive treatment of North American wolves. Since that time, gray wolf taxonomy has undergone substantial revision related to the grouping of subspecies. Most notably, Nowak (1995) condensed 24 previously recognized North American gray wolf subspecies into five subspecies, including *C. l. baileyi* as one of the remaining five. Gray wolf taxonomy continues to be an unsettled area of scientific inquiry for gray wolves in some parts of North America (e.g., Chambers et al. 2012, vonHoldt et al. 2011). However, the distinctiveness of *C. l. baileyi* and its recognition as a subspecies is resolved and is not at the center of these ongoing discussions.

The uniqueness of the Mexican wolf continues to be supported by both morphometric (Bogan and Mehlhop 1983, Hoffmeister 1986, Nowak 2003) and genetic (Chambers et al. 2012, Garcia-Moreno et al. 1996, Hedrick et al. 1997, Leonard et al. 2005, vonHoldt et al. 2011) evidence. Most recently, Cronin et al. (2014) challenged the subspecies concept for North American wolves, including the Mexican wolf, based on their interpretation of other authors' work (most notably Leonard et al. 2005 relative to mtDNA monophyly); however there is broad concurrence in the scientific literature that the Mexican wolf is differentiated from other gray wolves by multiple morphological and genetic markers (and see Fredrickson et al. 2015). Further, Leonard et al. (2005) found that haplotypes associated with the Mexican wolf are related to other haplotypes that have a southerly distribution they identified as a southern clade. A clade is a taxonomic group that includes all individuals that are related and sometimes assumed to have descended from a common ancestor. The Service continues to recognize the Mexican wolf as a subspecies of gray wolf (80 FR 2488-2567, January 16, 2015). Limited discussion of the historical range of the Mexican wolf is ongoing in the scientific literature (see below).

The Mexican wolf is the smallest extant gray wolf in North America; adults weigh 23-41 kilogram (kg) (50-90 pounds (lbs)) with a length of 1.5-1.8 meters (m) (5-6 feet (ft)) and height at shoulder of 63-81 centimeters (cm) (25-32 inches (in)) (Young and Goldman 1944, Brown 1988). Females are typically smaller than males in weight and length. Mexican wolves are typically a patchy black, brown to cinnamon, and cream color, with primarily light underparts (Brown 1988); solid black or white Mexican wolves have never been documented as seen in other North American gray wolves (Figure 4).

Figure 4. Mexican wolf (credit: U.S. Fish and Wildlife Service).

Distribution

As explained by Heffelfinger et al. (2017), when the Mexican wolf was more common on the landscape and originally described in the literature, its range was defined as southern Arizona, southwestern New Mexico, and the Sierra Madre of Mexico south at least to southern Durango (Nelson and Goldman 1929). In the following decades, observers working in this region reaffirmed this geographic range based on body size and skull morphology through first-hand observation and examination of Mexican wolves and specimens (Bailey 1931; Young and Goldman 1944; Hoffmeister 1986; Nowak 1995, 2003, as cited by Heffelfinger et al. 2017). (See above discussion of Taxonomy and our discussion of historical range in our final listing rule "Endangered Status for the Mexican Wolf" (80 FR 2488-2567, January 16, 2015)). The taxonomic issues surrounding the validity of the Mexican wolf subspecies are largely resolved, but there remain some differing opinions in the literature of what areas should be considered for recovery.

Bogan and Mehlhop (1983) analyzed measurements from 253 adult wolf skulls from throughout the Southwest and reported that wolves from northern New Mexico and southern Colorado were distinct from Mexican wolves in southeastern Arizona, southern New Mexico, and Mexico.

Specimens from the Mogollon Rim in central Arizona were intermediate between those two forms, with females showing affinity to the larger northern group and males being more similar to Mexican wolves in the south. They recognized the Mogollon Rim as a wide zone of intergradation, but suggested including wolves from this area (*C. l. mogollonensis*) and Texas (*C. l. monstrabilis*) with Mexican wolves. In the 1982 Mexican Wolf Recovery Plan, the Service cited Bogan and Mehlhop (1983) as support for reintroducing wolves into the areas previously considered the historical ranges of *C. l. mogollonensis* and *C. l. monstrabilis*. Subsequently, the Service adopted the expanded historical range for *C.l. baileyi* proposed by Parsons (1996), with a 200-mile northward extension of the historical range of *C. l. baileyi* into central New Mexico and east-central Arizona, based on potential dispersal patterns (USFWS 1996; 63 FR 1752; January 12, 1998) (Figure 5). The Service's adoption of Parsons' (1996) historical range was used to support reintroduction of the Mexican wolf north of *C. l. baileyi*'s range as originally described in early accounts (e.g., Nelson and Goldman 1929; Young and Goldman 1944; Hall and Kelson 1959, Nowak 1995, 2003, Chambers et al. 2012).

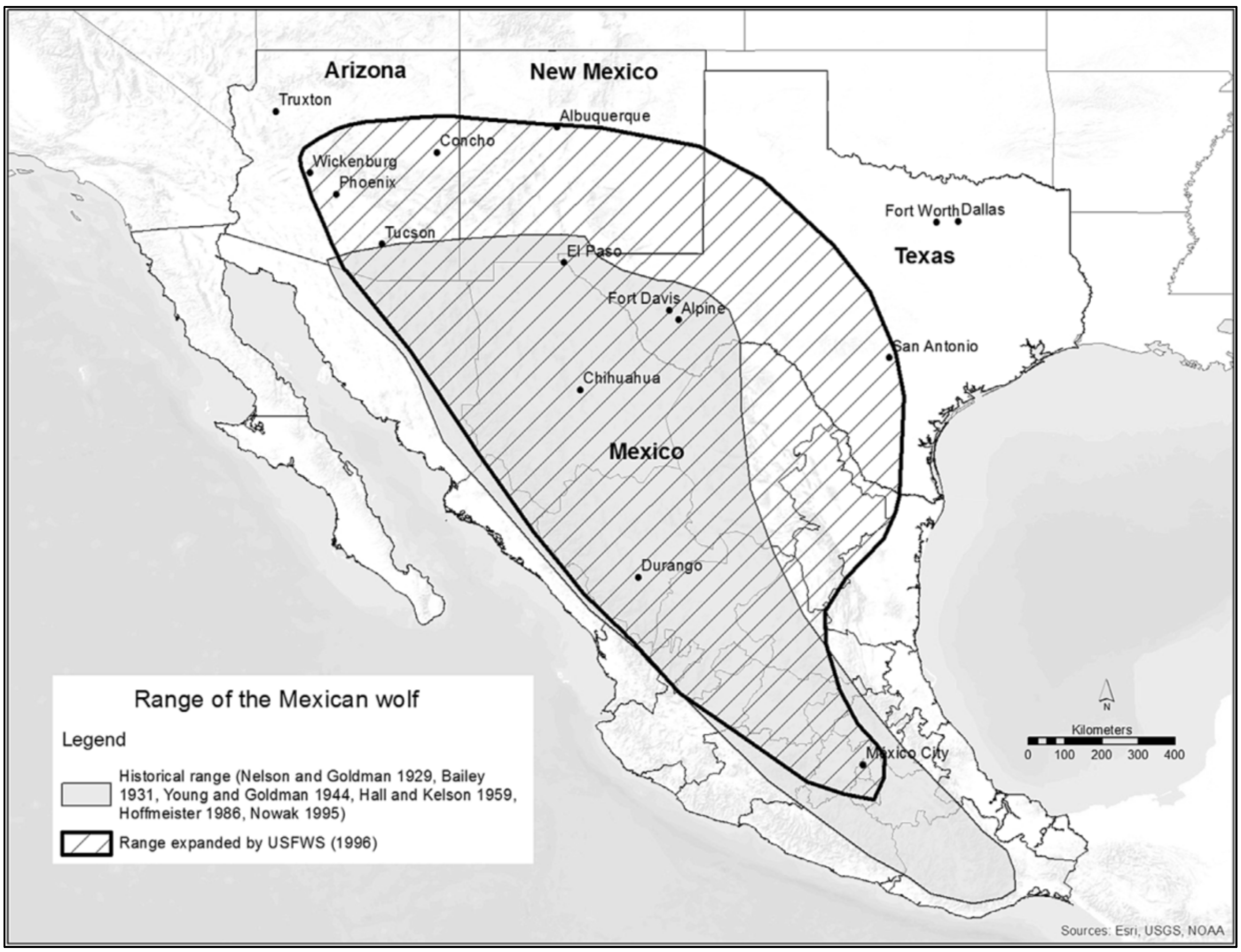

Figure 5. Generalized historical range of the Mexican wolf defined by most authorities compared with the range expanded by Parsons (1996) and adopted by the United States Fish and Wildlife Service (USFWS 1996:1–4) as "probable historic range" (map and title from Heffelfinger et al. 2017).

In recent years, the analysis of molecular markers has led some to suggest the historical range of the Mexican wolf may have extended as far north as Nebraska and northern Utah (Leonard et al. 2005), and as far west as southern California (Hendricks et al. 2015, 2016). Distribution of those molecular markers has led those researchers and others to suggest a larger geographic area could be used for recovery of the Mexican wolf. Heffelfinger et al. (2017) counter that these interpretations and recommendations overstep the power of the studies' limited data sets, inappropriately discount historical accounts of distribution, and conflict with the phylogeographic concordance Mexican wolves share with other southwestern species and subspecies associated with the Madrean Pine-Oak woodland.

The Service acknowledges that intergradation zones between Mexican wolves and other gray wolf populations likely occurred in central Arizona and New Mexico (Bogan and Mehlhop 1983, Heffelfinger et al. 2017) as incorporated into the historical range expanded by Parsons (1996). The Service continues to recognize the concordance in the scientific literature depicting the Sierra Madre of Mexico and southern Arizona and New Mexico as Mexican wolf core historical range and will continue to recognize the expanded range as per Parsons (1996) that extends into central New Mexico and Arizona (USFWS 1996). We note that although Heffelfinger 2017 depicts Mexican wolf historical range with definitive lines (Figure 5), "fuzzy", or broader lines would likely better delineate the historical distribution of Mexican wolves. The Service will continue to monitor the scientific literature for exploration of this topic.

<u>Life History</u>

Gray wolves have a relatively simple life history that is well documented in the scientific literature and generally familiar to the public. Published studies specific to the Mexican wolf subspecies are less readily available, but can be inferred from gray wolf information, given the similarity in life history. Our monitoring data from the MWEPA is useful in pointing out Mexican wolf characteristics or needs that may differ from the gray wolf. Although Mexico has not gathered extensive data due to the short timeframe of their reintroduction, we use available information to the extent possible. Because we previously summarized life history information for the gray wolf/Mexican wolf in our Mexican Wolf Conservation Assessment (USFWS 2010), only a brief summary is provided here to highlight the essential needs of the Mexican wolf at the level of the individual animal and the population as they relate to conditions for viability.

Mexican wolves are social animals born into a family unit referred to as a pack. A wolf pack is typically some variation of a mated (or breeding) pair and their offspring, sometimes of varying ages (Mech and Boitani 2003). Pack size in the MWEPA between 1998 and 2016 has ranged from 2 to 12 (mean = 4.1) wolves (U.S. Fish and Wildlife Service files), consistent with historical pack size estimates (Bednarz 1988 (two to eight wolves); Brown 1988 (fewer than six wolves). Pack size in Mexico between 2011 and 2017 has ranged from 2 to 14 Mexican wolves (personal communication Dr. López-González, Universidad Autónoma de Querétaro, April 10, 2017).

Gray wolves reach sexual maturity just before two years of age and have one reproductive cycle per year. Females are capable of producing a litter of pups, usually four to six, each year (Mech 1970). In the wild, Mexican wolf pups are generally born between early April and early May (Adaptive Management and Oversight Committee and Interagency Field Team [AMOC and IFT]

2005) and remain inside the den for three to four weeks. Some pup mortality is expected prior to den emergence. Our data suggest that on average 4.65 pups are born while 3.25 are counted post den emergence (U.S. Fish and Wildlife Service files). Mexican wolves typically live for four to five years in the wild, although we have documented wolves living to 13 years (U.S. Fish and Wildlife Service files); this is consistent with average gray wolf life expectancy documented in other populations (Mech 1988). Annual survival rate of yearling and adult gray wolves is estimated at 0.55 to 0.86 (Fuller et al. 2003: table 6.6). In the MWEPA, survival rate of pups, yearlings, and adults is estimated at 0.50 (inclusive of den bound mortality), 0.67, and 0.81, respectively between 2009 and 2014 (U.S. Fish and Wildlife Service files).

A wolf pack establishes and defends an area, or territory, within which pack members hunt and find shelter (Mech and Boitani 2003). Daily and seasonal movements of individual wolves and the pack vary in response to the distribution, abundance, and availability of prey, and care of young. Wolf pack territories vary in size depending on prey density or biomass and pack size; minimum territory size is the area in which sufficient prey exist to support the pack (Fuller et al. 2003). Bednarz (1988) predicted that reintroduced Mexican wolves would likely occupy territories ranging from approximately 78 to 158 square miles (mi^2) (200-400 square kilometers (km^2), and hypothesized that Mexican wolf territories were historically comparable in size to those of small packs of northern gray wolves, but possibly larger, due to habitat patchiness (mountainous terrain that included areas of unsuitable lowland habitat) and lower prey densities associated with the arid environment. Between 1998 and 2015, home range size of 138 denning packs in the MWEPA population averaged 197 mi^2 +/- 125mi^2 (SD) (510 km^2 +/- 324 km^2 (Mexican Wolf Annual Reports 1998-2002 & 2004-2015). The average home range size for 30 non-denning packs during the same time period was 343 mi^2 +/- 313 mi^2 (SD) (888km^2 +/- 811 km^2). Average pack home range size for denning packs has remained fairly consistent during the last 10 years. In Mexico, no estimates of denning versus non-denning pack home ranges have been made. However, López González et al. (2017) estimated the area of activity of 20 Mexico wolf individuals, belonging to three packs, from July to December 2016 ranged from: 1) 23.73 to 34.94 km^2 in Pies ligeros pack; 2) 137.5 to 200.9 km^2 for the Mesa de lobos pack; and 3) 4.26 to 837.9 km^2 for the La Escalera pack.

An individual wolf, or rarely a group, will disperse from its natal pack in search of vacant habitat or a mate, typically between nine to 36 months of age. These dispersals may be short trips to a neighboring territory, or a long distance journey of hundreds of miles (Packard 2003). Wolves that disperse and locate a mate and an unoccupied patch of suitable habitat usually establish a territory (Rothman and Mech 1979, Fritts and Mech 1981). Dispersing wolves tend to have a high risk of mortality (Fuller et al. 2003). In the MWEPA population, some dispersal events events ended in mortality (16.5 %). In addition, dispersal was hindered by a rule from 1998 through 2014 that prohibited Mexican wolf occupancy outside the boundaries of the Gila and Apache National Forests (63 FR 1752; January 12, 1998; and see “Abundance, Trend, and Distribution of Mexican Wolves in the United States”). Therefore, a proportion of dispersal events ended with the removal or translocation of the wolf due to the boundary rule (12%). However, 55% of dispersal events documented between 1998-2015 ended with the wolf successfully locating a mate (U.S. Fish and Wildlife Service files). In Mexico, mortality associated with dispersal has not yet been analyzed (personal communication, Dr. López-González, Universidad Autónoma de Querétaro, April 10, 2017).

Ecology and Habitat Characteristics

Historically, Mexican wolves were associated with montane woodlands characterized by sparsely to densely-forested mountainous terrain and adjacent grasslands in habitats found at elevations of 1,219-1,524 m (4,500-5,000 ft) (Brown 1988). Wolves were known to occupy habitats ranging from foothills characterized by evergreen oaks (*Quercus* spp.) or pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.) to higher elevation pine (*Pinus* spp.) and mixed conifer forests. Factors making these habitats attractive to Mexican wolves likely included an abundance of prey, availability of water, and the presence of hiding cover and suitable den sites. Early investigators reported that Mexican wolves probably avoided desert scrub and semidesert grasslands that provided little cover, food, or water (Brown 1988). Wolves traveled between suitable habitats using riparian corridors, and later, roads or trails (Brown 1988).

We recognize that the suitability of an area to sustain wolves is influenced by both biophysical (vegetation cover, water availability and prey abundance) and socioeconomic (human population density, road density, and land status) factors (Sneed 2001). Today, we generally consider the most important habitat attributes needed for wolves to persist and succeed in pack formation to be forest cover, high native ungulate density, and low livestock density, while unsuitable habitat is characterized by low forest cover, and high human density and use (74 FR 15123, pp. 15157-15159, Oakleaf et al. 2006; see the Service's 2009 Northern Rocky Mountains distinct populations segment delisting rule for more information on wolf habitat models (74 FR 15123, pp. 15157-15159). Suitable wolf habitat has minimal roads and human development, as human access to areas inhabited by wolves can result in increased wolf mortality (e.g., due to illegal killing, vehicular mortality, or other causes). Public lands such as national forests are considered to have more appropriate conditions for wolf reintroduction and recovery efforts in the United States than other land ownership types because they typically have minimal human development and habitat degradation (Fritts and Carbyn 1995). Recovery of Mexican wolves in the MWEPA relies on the occupancy of national forests (USFWS 2014). The reestablishment effort in Mexico is also located in an area of low human density and roads, although not on federal lands. Land tenureship in Mexico differs in that the federal government does not hold large tracts of land; rather, private lands and communal landholdings, such as ejidos, comprise the largest forms of land tenure in Mexico (Valdez et al. 2006) (see Species' Current Conditions).

Description of the MWEPA in the United States

As described by Wahlberg et al. 2016, the MWEPA varies considerably in elevation and topography, ranging from 3,048 m (10,000 ft) in the mountains to below 305 m (1,000 ft) in southwestern Arizona. The dominant physical feature is in the southern-most portion of the Colorado Plateau, known as the Mogollon Rim, which extends from central Arizona to west-central New Mexico. The Mogollon Rim forms the source of the Gila-Salt-Verde River system, which combine in Arizona and flow westward into the Colorado River. The eastern portion of the Mogollon Rim forms the western boundary of the Rio Grande River valley in New Mexico, which has its origin in Colorado, north of the MWEPA, and flows north to south. East of the Rio Grande Valley, mountains also separate the Rio Grande from the Pecos River, which flows south to join the Rio Grande in Texas. In southeastern Arizona/southwestern New Mexico, the isolated mountain ranges separating these river systems are referred to as the "Sky Islands" of the Southwest.

The drainages associated with these river systems contain riparian vegetation dependent on the water table and stream flows, with elevation and disturbance patterns influencing the specific type of vegetation. The amount of riparian vegetation (Table 1), though less than 1% of the total MWEPA, is very important to wolves since it provides water, and in many cases cover, and often serves as a means of easy movement in areas with rapid changes in elevation (Wahlberg et al. 2016).

The elevation variations found within the MWEPA result in considerable variation in vegetation communities. The low elevation areas of southern Arizona and southern New Mexico are desert communities dominated by creosote bush (*Larrea tridentata*) and succulent species (e.g., *Agave* spp., *Opuntia* spp.), intergrading to semi-desert grasslands and shrublands at higher elevation. Much of the area in southeastern New Mexico is part of the southwestern Great Plains. Together, the desert communities and grasslands make up more than 70% of the area of the MWEPA (Table 1) (Wahlberg et al. 2016).

Between 900-1200 m (approximately 3,000 to 4,000 ft in elevation, transition to woodlands begins. Most woodlands in the MWEPA are dominated by junipers (*Juniperus* spp.), with pinyon (*Pinus* spp.) and oaks (*Quercus* spp.) also present. Woodlands make up more than 16% of the MWEPA (Table 1), and are typically found just below the high-elevation forest communities. These higher elevation forest communities (beginning at approximately 1500 m (approximately 5,000 ft), are characterized by Ponderosa pine (*Pinus ponderosa*) at the lower elevations, with increasing occurrence of Douglas fir (*Pseudotsuga menziesii*), true firs (*Abies* spp.) and spruce (*Picea* spp.) higher in elevation. While only about 7% of the total area of the MWEPA (Table 1) is composed of these vegetation types, forested communities dominate most of the Mogollon Rim and at higher elevations of the Sky Islands in southeastern Arizona, and southwestern and southeastern New Mexico (Wahlberg et al. 2016).

More than 40% of the MWEPA is administered by Federal agencies, with the Bureau of Land Management and Forest Service administering the most land. The BLM lands are predominately desert and grassland communities (approximately 89% of BLM lands, 17% of the MWEPA), while the Forest Service lands are predominately woodland and forest (approximately 72% of national forests, 11% of the MWEPA). Approximately 31% of the MWEPA is privately owned; about 19% of these privately owned lands are grasslands, and about 10% are either desert or woodlands. Very little forest land is in private ownership, compared with a substantial amount of riparian areas that are in private ownership (Table 1) (Wahlberg et al. 2016).

State and Tribal lands comprise approximately 25% of the MWEPA. As with private lands, much of these lands are deserts, grasslands, and woodlands, though forests constitute a higher percentage on tribal lands than either state or private lands (Table 1) (Wahlberg et al. 2016).

Table 1. Land ownership and vegetation types (acreage and percentage) within the Mexican Wolf Experimental Population Area (or MWEPA), United States (derived from Wahlberg et al. 2016).[1]

Vegetation	BLM	Forest Service	Other Federal	State	Tribal	Private	Total
Developed/ Non-vegetated	251,100 (0.30%)	122,100 (01.10%)	214,500 (0.20%)	138,800 (0.10%)	54,500 (0.10%)	311,800 (0.30%)	**1,092,900 (0.10%)**
Riparian	59,500 (0.10%)	226,100 (0.20%)	118,600 (0.10%)	59,700 (0.10%)	52,300 (0.00%)	236,700 (0.20%)	**752,900 (0.70%)**
Desert	9,024,400 (9.20%)	855,200 (0.90%)	6,290,000 (6.40%)	4,303,400 (4.50%)	3,386,400 (3.50%)	5,278,500 (5.60%)	**29,137,900 (30.20%)**
Grassland	7,866,100 (8.10%)	2,042,000 (2.10%)	1,369,200 (1.40%)	8,073,900 (8.50%)	2,222,200 (2.30%)	18,326,000 (19.30%)	**39,899,400 (41.70%)**
Shrubland	530,500 (0.40%)	1,101,700 (1.10%)	108,700 (0.10%)	803,100 (0.40%)	484,900 (0.40%)	1,415,700 (0.50%)	**4,444,700 (3.00%)**
Woodland	1,266,400 (1.30%)	6,196,900 (6.30%)	286,800 (0.30%)	1,574,000 (1.60%)	2,158,000 (2.20%)	4,664,700 (4.70%)	**16,146,700 (16.40%)**
Forest	87,000 (0.10%)	4,720,800 (4.80%)	42,900 (0.00%)	98,700 (0.10%)	1,322,000 (1.30%)	493,800 (0.50%)	**6,765,100 (6.90%)**
Total MWEPA Acres	**19,085,000 (19.40%)**	**15,264,900 (15.50%)**	**8,430,700 (8.60%)**	**15,051,600 (15.30%)**	**9,680,300 (9.90%)**	**30,727,300 (31.30%)**	**98,239,800 (100.00%)**

Due to the variety of terrain, vegetation, and human land use within the MWEPA, a mixture of suitable and unsuitable habitat for Mexican wolves exists. We previously estimated that approximately 68,938 km^2 (26,617 mi^2) of suitable habitat exists in the MWEPA (of 397,027 km^2 (153,293 mi^2) including Zone 3 of the MWEPA; not including tribal lands) (USFWS 2014). More recently, Martínez-Meyer et al. (2017) estimate 33,674 km^2 (13,001 mi^2) of high quality habitat exists in the MWEPA.

Description of the Sierra Madre Occidental in Mexico

The Sierra Madre Occidental is the longest mountain range in Mexico, extending from near the U.S.-Mexico border to northern Jalisco (González-Elizondo et al. 2013). It has a rugged physiography of highland plateaus and deeply cut canyons, with elevations ranging from 300 to 3,340 m (984 to 10,958 ft) (González-Elizondo et al. 2013). Three primary ecoregions occur in the Sierra Madre Occidental, the Madrean, Madrean Xerophylous and Tropical regions (González-Elizondo et al. 2013). Five major vegetation associations occur within the Madrean region, including pine forests, mixed conifer forests, pine-oak forests, oak forests, and temperate mesophytic forests (González-Elizondo et al. 2013). Two major vegetation types occur within the Madrean Xerophylous region, including oak or pine-oak woodland and evergreen juniper scrub (González-Elizondo et al. 2013).

[1] Totals may not add up due to rounding acres to the nearest 100.

In Mexico, López González et al. (2017) found that Mexican wolves use pine oak forest and pine forest according to availability, but avoid other types of vegetation, thus indicating a preference for pine oak and pine forests (Figure 6). According to González-Elizondo et al. (2013) pine-oak forests cover about 30% of the Sierra Madre Occidental from 1,250 to 3,200 m (4,101 to 10,498 ft), while pine forests cover 12% of the Sierra Madre Occidental and occur between 1,600 and 3,320 m (5,249 to 10,892 ft). Other major vegetation types in the Sierra Madre Oriental include oak forests which cover almost 14% and occur from 340 to 2,900 m (1,115 to 9,514 ft), and oak or pine-oak woodlands which cover more than 13% and occur from 1,450 to 2,500 m (4,757 to 8,202 ft) (González-Elizondo et al. 2013).

Martínez-Meyer et al. (2017, Table 10) estimate there are two large patches of high quality habitat of 25,311 km^2 (9,773 mi^2) and 39,610 km^2 (15,293 mi^2) in the Sierra Madre Occidental that are connected by areas of lower quality habitat and small interstitial patches of high quality habitat. Three Áreas Naturales Protegidas (or Natural Protected Areas) in Chihuahua (Tutuaca-Papigochi, Campo Verde, and Janos), one in Sonora (Ajos-Bavispe) and one in Durango (La Michilía, as well as the proposed protected area Sierra Tarahumara) partially overlap with the largest high-quality Mexican wolf habitat patches in the Sierra Madre Occidental. Between 2011 and 2017, wolves have occasionally been documented in these natural protected areas; use of these areas may increase as the wolf population expands (personal communication, Dr. López-González, Universidad Autónoma de Querétaro, April 10, 2017).

Figure 6. Mexican wolf habitat in Chihuahua, Mexico (credit: Laura Saldivar, Universidad Autónoma de Querétaro/CONANP).

Mexican Wolves and Prey

Wolves are highly-adaptable prey generalists that can efficiently capture a range of ungulate prey species of widely varying size. Studies of gray wolf hunting behavior indicate that wolf hunting strategy is plastic and capable of adjusting for variously sized prey (MacNulty 2007, Smith et al. 2004) by varying the age, size (males vs. females), behavior, and hunting group size within one pack depending on the situation and species of prey (MacNulty et al. 2009, 2012). Wolf density is positively correlated to the amount of ungulate biomass available and the vulnerability of ungulates to predation (Fuller et al. 2003).

Wolves play a variable and complex role in ungulate population dynamics depending on predator and prey densities, prey productivity, vulnerability factors, weather, alternative prey availability, and habitat quality (Boutin 1992, Gasaway et al. 1992, Messier 1994, Ballard et al. 2001). Ungulates employ a variety of defenses against predation (e.g., aggression, altered habitat use, behavioral, flight, gregariousness, migration) (MacNulty et al. 2007, Creel et al. 2008, Liley and Creel 2008), and wolves are frequently unsuccessful in their attempts to capture prey (Mech and Peterson 2003, Smith et al. 2004). Generally, wolves tend to kill young, old, or injured prey that may be predisposed to predation (Mech and Peterson 2003, Eberhardt et al. 2007, Smith and Bangs 2009). Wolves have been found to regulate prey populations at lower densities, but only in extreme circumstances have they been documented exterminating a prey population, and then only in a relatively small area (Dekker et al. 1995, Mech and Peterson 2003, White and Garrott 2005, Becker et al. 2009, Hamlin and Cunningham 2009).

Elk (*Cervus elaphus*), which are common in portions of the MWEPA (USFWS 2014), comprise the bulk of the biomass in the diet of wolves in the MWEPA (Paquet et al. 2001, Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009). Although white-tailed deer (*Odocoileus virginianus*) and mule deer are present, Mexican wolves' preference for elk may be related to the gregariousness, higher relative abundance, and consistent habitat use by elk. There is also a possibility that the methodologies of diet studies may be biasing data analysis because only large scats were collected and analyzed to minimize the probability of including coyote scat (Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009). This may have excluded some adult and all juvenile Mexican wolves from the analyses. However, investigations of ungulate kill sites using locations from GPS-collared wolves support the scat analysis showing most ungulates killed are elk (Arizona Game and Fish Department files). Mexican wolves in the MWEPA have also been found to feed on adult and fawn deer, cattle, small mammals, and occasionally birds (Reed et al. 2006, Merkle et al. 2009).

In Mexico, Salvídar Burrola (2015) detected the presence of 16 distinct prey species in the scat of reintroduced Mexican wolves. White-tailed deer was the most important prey both in terms of frequency of occurrence (37.6) and percentage biomass consumed (30.65). Other prey items included cattle (*Bos taurus*), Eastern cottontail (*Sylvilagus floridanus*), yellow-nosed cotton rat (*Sigmodon ochrognathus*), woodrats (*Neotoma*), skunks (*Mephitis* and *Spilogale*), as well as other rodents and birds. Domestic pigs (*Sus scrofa*), which were provided as supplemental food for wolves, were also an important food item (Salvídar Burrola 2015). Hidalgo-Mihart et al. (2001) found that coyotes in southern latitudes had a greater dietary diversity and consumed smaller prey items than northern latitudes. The small endangered red wolf also has a diet that includes more small items than does the diet of larger northern wolves (Phillips et al. 2003, Dellinger et al. 2011).

Mexican wolves will also prey on livestock in the MWEPA and Sierra Madre Occidental in Mexico. In the MWEPA, between 1998 and 2015, 288 confirmed cattle depredations were documented with an average depredation rate of 27 cattle per 100 wolves per year. This depredation rate may represent an underestimate due to incomplete detection of wolf-killed cattle (Oakleaf et al. 2003, Breck et al. 2011). In Mexico, from 2013 to 2017, 16 confirmed cattle depredations were documented in Chihuahua from Mexican wolves (Garcia Chavez et al. 2017). In both the MWEPA and Mexico, Mexican wolves receive supplemental/diversionary feeding of ungulate carcasses or carnivore logs (ground horse meat and meat byproduct) for various management reasons, such as to allow a pair or pack to adapt to the wild after release (supplementary) or to reduce the likelihood of cattle depredation (diversionary).

Historically, Mexican wolves were believed to have preyed upon white-tailed deer, mule deer (*Odocoileus hemionus*), elk, collared peccaries (javelina) (*Pecari tajacu*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), jackrabbits (*Lepus spp*.), cottontails (*Sylvilagus spp.*), wild turkeys (*Meleagris gallopavo*), and small rodents (Parsons and Nicholopoulos 1995). White-tailed deer and mule deer were believed to be the primary sources of prey (Brown 1988, Bednarz 1988, Bailey 1931, Leopold 1959), but Mexican wolves may have consumed more vegetative material and smaller animals than gray wolves in other areas (Brown 1988) as do coyotes in southern latitudes (Hidalgo-Mihart et al. 2001). The difference between historical versus current prey preference in the United States is likely due to the lack of elk in large portions of historical Mexican wolf range.

Ungulate population dynamics in the Southwest differ from that of the same species in other ecoregions due to the lower overall primary productivity of the habitat (Short 1979). Although vegetation and climate vary across the range of the Mexican wolf, the region as a whole is generally more arid than other regions of North America with recovered gray wolf populations such as the Northern Rocky Mountains and Western Great Lakes, resulting in lower primary productivity in the range of the Mexican wolf than in these areas (Carroll et al. 2006). The lower productivity of the vegetative community influences productivity through several trophic levels resulting in lower inherent herbivore resiliency in the Southwest than their northern counterparts (Heffelfinger 2006). Deer species available to Mexican wolves may be smaller in size, have lower population growth rates, exist at lower densities, and exhibit patchy distributions. However, lack of widespread winterkill of ungulates means that lower recruitment is able to sustain a stable population compared to northern ungulate populations. Southwestern deer herds (mule deer and white-tailed deer) require 35-50 fawns per 100 does to remain stable (Heffelfinger 2006), while those in the northern Rocky Mountains require 66 fawns per 100 does for population maintenance (Unsworth et al. 1999).

Predator-prey dynamics may differ in the Southwest compared to other systems as well. Predator populations are sustained more by the productivity of prey populations than by the standing biomass at one point in time (Seip 1995, National Research Council 1997, Carbone and Gittleman 2002). In southwestern deer populations, a compensatory response in deer survival or recruitment would not be expected because deer density is usually kept below the fluctuating carrying capacity through chronically low recruitment (Deyoung et al. 2009, Bowyer et al. 2014). Computer population simulations of Arizona and New Mexico deer herds showed that an increase in adult doe mortality by only 5-10% was enough to cause population declines because of low and erratic recruitment and no compensatory response (Short 1979). When excluding human harvest, adult female elk survival has been found to be relatively high (Ballard et al. 2000). As such, additional adult mortality sources of adult female elk would tend to be more additive and may contribute to population declines.

Kill rates of individual gray wolves vary significantly, from 0.5 to 24.8 kg/wolf/day (1 to 50 lbs/wolf/day), based on a variety of factors such as prey selection, availability and vulnerability of prey, and the effects of season or weather on hunting success (Mech and Peterson 2003, see Table 5.5). Minimum daily food requirements of a wild, adult gray wolf have been estimated at 1.4 kg/wolf (3 lbs/wolf) to 3.25 kg/wolf (7 lbs/wolf), or about 13 to 30 adult-sized deer per wolf per year, with the highest kill rate of deer reported as 6.8 kg/wolf/day (15 lbs/wolf/day) (Mech and Peterson 2003, Peterson and Ciucci 2003).

The Mexican Wolf Interagency Field Team used clusters of wolf GPS locations to estimate kill rates (prey killed/wolf/day) (or kg/wolf/day). The results indicated that during 2015 and 2016 a single Mexican wolf would kill on average the equivalent of 16.5 cow elk, scavenge 1.2 cow elk, and kill 3.9 mule deer does and 0.5 white-tailed deer annually, which equates to 7.19 kg/wolf/day. However, the Interagency Field Team notes that: "The average standardized impacts of Mexican wolves on prey we calculated are likely overestimated because of the four months of hunting season outside of the winter and summer study periods when scavenging likely makes up a significant portion of the diet of Mexican wolves. This estimate is slightly higher than the average, but within the range observed in similar studies conducted on northern gray wolves."

Wolves may also affect ecosystem diversity beyond that of their immediate prey source in areas where their abundance affects the distribution and abundance of other species (sometimes referred to as "ecologically effective densities") (Soule et al. 2003, 2005). For example, in a major review of large carnivore impacts on ecosystems, Estes et al. 2011 concluded that structure and function as well as biodiversity is dissimilar between systems with and without carnivores. Wolves could affect biodiversity and ecosystem processes through two mechanisms: a behaviorally mediated or numeric response on prey – or both (Terborgh et al. 1999). Such trophic cascade effects have been attributed to gray wolf reintroduction in Yellowstone National Park and elsewhere (e.g., Ripple and Beschta 2003, Wilmers et al. 2003, Ripple and Beschta 2004, Hebblewhite et al. 2005, Hebblewhite and Smith 2010, Ripple and Beschta 2011, Baril et al. 2011).

Kauffman et al. (2010) used a more rigorous experimental design than previous studies and found no widespread general reduction in browsing on aspen, nor an increase in plant height that would be evidence of a behaviorally mediated trophic cascade. They noted that plant height and browsing are both strongly influenced by many environmental forces unrelated to wolves (Kauffman et al. 2013). Middleton et al. (2013) found no relationship between the risk of an elk being preyed upon by wolves and elk body fat and pregnancy. These finding also failed to support the existence of behaviorally mediated trophic cascades operating in Yellowstone

National Park. The dramatic numerical reduction in elk abundance in Yellowstone National Park has relaxed browsing pressure on some plants and resulted in a spatially inconsistent recovery of riparian vegetation, but not to the extent reported widely in the popular media.

Numerous studies conducted in the Northern Range of Yellowstone National Park demonstrate that fire and hydrologic changes strongly influence willow growth and recruitment (Johnston et al. 2007, Bilyeu et al. 2008, Tercek et al. 2010), snow strongly influences elk habitat selection (Mao et al. 2005), use of aspen sites (Brodie et al. 2012), and intensity of browsing versus grazing (Creel and Christianson 2009). Studies in Yellowstone National Park also cast doubt on the cascading effects of wolf recovery on willows (Bilyeu et al. 2008; Johnston et al. 2007, 2011; Wolf et al. 2007; Creel and Christianson 2009; Tercek et al. 2010). In addition, other ecological changes that can impact vegetation recovery have occurred in Yellowstone National Park concurrent with wolf recovery. Moose abundance has declined markedly following the extensive fires in 1988 (Tyers 2006), grizzly bear abundance has increased dramatically (Schwartz et al. 2006) with a threefold increase in elk calf predation rates (Barber-Meyer et al. 2008), a drought in the mid- to late-1990s, human antlerless elk harvest, and heavy winter snows have impacted elk population abundance (Creel and Christianson 2009). It is now widely understood that assuming the presence of wolves is responsible for all variance in plant growth or recovery in Yellowstone National Park (Beschta and Ripple 2013) is an oversimplification of a complex system.

Wolves and Non-prey

Wolves also interact with non-prey species. Although these interactions are generally not well documented, competition and coexistence may occur between wolves and other large, medium, or small carnivores (Ballard et al. 2003). In the Southwest, Mexican wolves may interact with coyotes, mountain lions (*Puma concolor*), and black bears (*Ursus americanus*) (AMOC and IFT 2005; USFWS 2010). We do not have data suggesting competition with non-prey species is impacting population dynamics for Mexican wolves in the MWEPA or Mexico under current population levels for these predators: however, predator population changes could result in differing impacts to Mexican wolves.

Wolf – Human Interactions

Wolves' reactions to humans include a range of non-aggressive to aggressive behaviors, and may depend on their prior experience with people. For example, wolves that have been fed by humans, reared in captivity with frequent human contact or otherwise habituated to humans may be more apt to show greater fearless or aggressive behavior towards humans than wild wolves; diseased wolves may also demonstrate fearless behavior (McNay 2002, Fritts et al. 2003). In North America, wolf-human interactions have increased in the last three decades, likely due to increasing wolf populations and increasing visitor use of parks and other remote areas (Fritts et al. 2003). Generally, wild wolves are not considered a threat to human safety (McNay 2002). In 2014, we summarized wolf-human interactions in the MWEPA in our EIS, "Final Environment Impact Statement for the Proposed Revision to the Regulations for the Nonessential Experimental Population of the Mexican Wolf" (USFWS 2014). In short, prior to the extirpation of Mexican wolves in Arizona and New Mexico in the 1970s, there are no confirmed or reliable reports of Mexican wolf attacks that occurred on humans, or wolf-caused human fatalities. Subsequent to the 1998 initiation of the reintroduction of Mexican wolves, wolf-human interactions have occurred but there have been no attacks on humans (USFWS 2014). In Mexico, since the reintroduction in 2011, no attacks or aggression toward humans by wolves have been documented (personal communication Dr. López-González, Universidad Autónoma de Querétaro, April 10, 2017).

Humans can be a significant source of mortality for wolves. Human-caused mortality is a function of human densities in and near occupied wolf habitat and human attitudes toward wolves (Kellert 1985, Fritts and Carbyn 1995, Mladenoff et al. 1995). Sources of mortality may include accidental incidents such as vehicle collision, or intentional incidents such as shooting (including legal shooting to protect livestock, pets, or rarely for human safety). In areas where humans are tolerant to the presence of wolves, wolves demonstrate an ability to persist in the presence of a wide range of human activities (e.g., near cities and congested areas) (Fritts et al. 2003). In the most recent analysis of habitat suitability, Martínez-Meyer et al. (2017) used 1.52 humans/km^2 as a threshold of Mexican wolf habitat suitability based on Mlandenoff (1995). In the MWEPA, gunshot related mortality is the biggest mortality source for Mexican wolves (USFWS 2017b; 80 FR 2488, January 16, 2015).

SPECIES' CURRENT CONDITION

Abundance, Trend, and Distribution of Mexican Wolves in the United States

The MWEPA population can be characterized as a relatively small but growing population. After exhibiting moderate growth in the initial years of the reintroduction (1998-2003), followed by a period of relative stagnation from 2003-2009, the MWEPA has exhibited sustained population growth for the last seven years (with the exception of 2014-2015) with relatively high adult survival. The 2016 annual minimum population estimate for the MWEPA was 113 wolves, the largest population size reached by the MWEPA population in its 19 years (U.S. Fish and Wildlife Service files) (Figure 7).

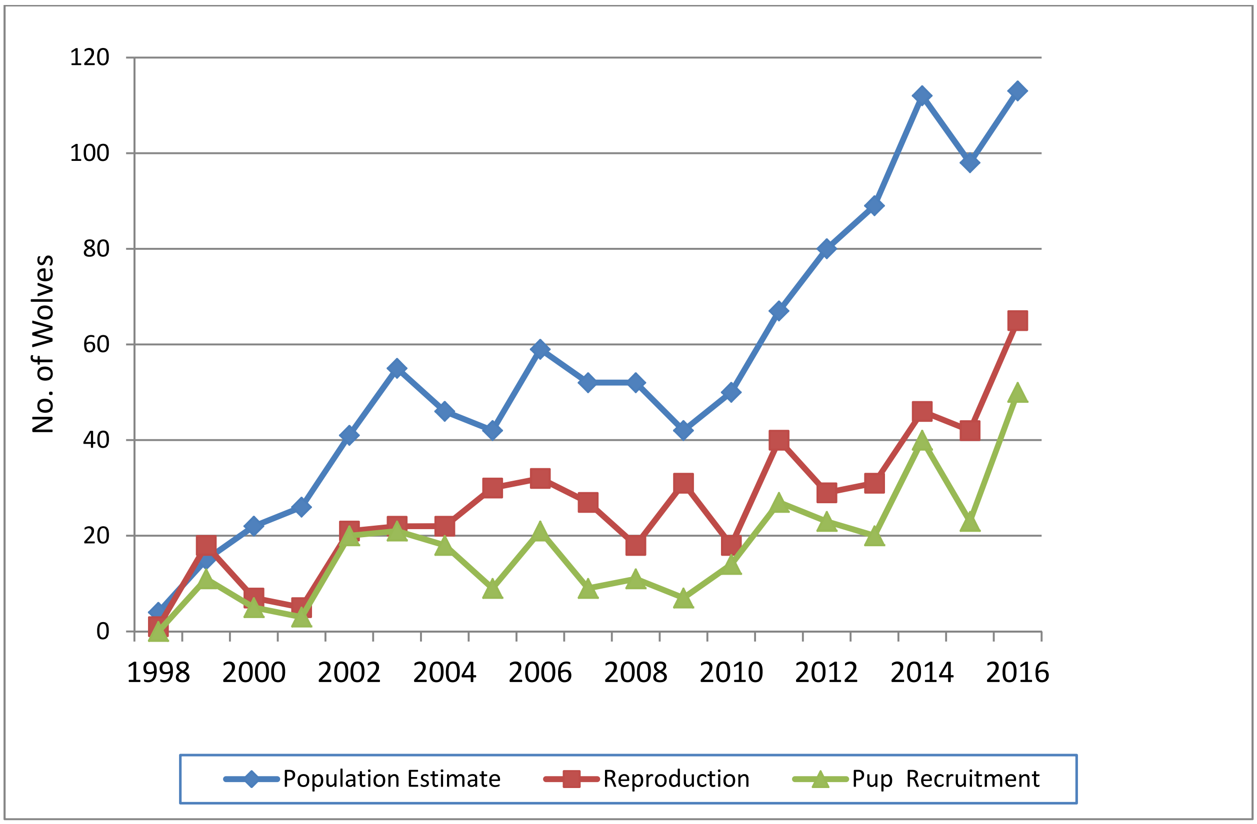

Figure 7. Annual Minimum Population Estimate of Mexican Wolves in the MWEPA, 1998-2016 (U.S. Fish and Wildlife Service files).

The demographic performance of the MWEPA population is influenced by both natural and anthropogenic forces, which is not surprising given the intensity of management of wild wolves. In 2016, all of the wolves in the MWEPA were wild-born, with the exception of surviving cross-fostered pups from captivity (a minimum of one), demonstrating that population growth is driven by natural reproduction rather than the release of wolves from captivity; only 10 initial releases, including 6 cross-fostered pups from captivity, were conducted between 2009-2016. 2016 marked the 15th consecutive year in which wild born wolves bred and raised pups in the wild. Our data suggest that probability of an adult pair producing pups in the wild is a function of age of the dam and relationship of the paired female to her mate (i.e., the predicted inbreeding coefficient of the pups). Average litter size in the MWEPA has been estimated at 4-5 pups between 1998-2016 (U.S. Fish and Wildlife Service files). However, our monitoring data suggest that the maximum number of pups in the summer is affected by feeding efforts. Packs that have received diversionary feed (road-killed native prey carcasses or carnivore logs) are larger than those that have not, likely due to improved summer survival of pups due to reduced pup mortality (See Miller 2017, “Calculation of litter size”).

Survival, or conversely mortality, of Mexican wolves in the MWEPA is substantially affected by anthropogenic forces. The average Mexican wolf in the MWEPA is 3.37 years old and has been monitored for 2 years at the time of its mortality or removal from the wild, with estimated survival rates of 0.5 for pups (0-1 year old, inclusive of estimated mortality from time of birth to one year based on observational (4.652 pups born versus 2.699 pups observed prior to September 30) and radio collar information after September 30), 0.67 for subadults (1-2 years old), and 0.81 for adults (greater than 2 years old) from 2009 to 2014 (See Appendix D in Miller 2017 for more information). Causes of Mexican wolf mortality in the MWEPA have been largely human-related, including vehicle collision and gunshot and trapping related incidents. Natural causes such as dehydration, disease, intraspecific and interspecific attack account for less than 17% of documented mortality, and unknown causes have been documented to account for 11% of known mortality. The combination of human caused mortality from shooting and trapping incidents (77 of 133 documented mortalities [only four of these were trapping incidents], or 58% of total documented mortalities) and human caused mortality from vehicular collision (16 of 133 documented mortalities, or 12% of total mortalities) accounts for 70% of documented wolf mortalities from 1998 to 2016 (USFWS 2017b).

Our removal of Mexican wolves from the MWEPA for management reasons is also functionally the same as mortality to the wild population. The majority of wolf removals are the result of conflicts or interactions with humans, including removals associated with livestock. Wolf removals were conducted in response to livestock depredation (76, including 13 lethal removals), boundary violations (49; conducted under the previous 1998 10(j) rule), nuisance behavior (24), and other reasons (28) (USFWS 2017b). In some years, wolf mortality in addition to removals and missing wolves has resulted in decreasing or stagnant population trends, such as the period from 2004-2009 (AGFD 2007; USFWS 2004, 2005, 2006, 2008, 2009).

Over the course of the reintroduction, our management of the MWEPA population has impacted its performance. We consider the MWEPA population to have gone through three stages of management: the period from 1998 through 2003, which was characterized by a high number of initial releases and translocations and a moderate number of removals; the period from 2004 through 2009, during which we conducted a moderate number of initial releases and translocations and a high number of removals; and the period from 2010 through 2016, which was characterized by a low number of releases and translocations but also a low number of removals (Miller 2017:figure 1).

Our shift in management response to depredating wolves was the driving factor behind the transition from the second to the third management stage. For several years (in particular 2005-2007) we conducted a high number of depredation-related removals to address social and economic concerns from local ranching communities. After observation of the negative impact the high number of removals was having on population performance, we lessened our removal rate by focusing on working with landowners and permittees to implement proactive management techniques such as range riders, fladry, and non-lethal ammunitions to minimize the likelihood of depredations. One of our proactive techniques is diversionary feeding. Diversionary food caches are road-killed native prey carcasses or carnivore logs provided to denning wolves to reduce potential conflicts with livestock in the area. Diversionary food caches have been used on increasing proportions of the population since 2009, providing about 10 pounds of meat per wolf every two to three days sometimes for several months when the likelihood of depredations are high (e.g., during denning season). In 2016, we provided diversionary feeding for approximately 70% of the breeding pairs during denning season (U.S. Fish and Wildlife Service files). This management change away from wolf removal and toward proactive management, coupled with a shift toward mostly wild-born wolves was accompanied by a lower mortality rate in the population.

The wolf distribution in the MWEPA is also influenced by both natural and anthropogenic forces, primarily habitat availability and quality, and management of dispersing wolves. Mexican wolves occupied 13,329 mi^2 (34,522 km^2) of the MWEPA during 2015 (USFWS 2015). We expect that over the next few years the distribution of the population will continue to expand naturally within the MWEPA as the size of the population increases. As previously described, Mexican wolves are capable of dispersing long distances. Our management regime curtailed the natural movement patterns of Mexican wolves in the MWEPA due to the geographic regulatory restrictions from 1998 to 2014 requiring capture of wolves that dispersed outside of the Gila and Apache National Forests (63 FR 1752; January 12, 1998) and Fort Apache Indian Reservation: 12% of dispersal events resulted in mortality due to the boundary rule (U.S. Fish and Wildlife Service files). Similarly, wolves are now not allowed to disperse beyond the revised MWEPA boundaries established in 2015 (80 FR 2512-2567, January 16, 2015). The revised boundaries, although considerably more expansive than the boundaries originally established in 1998, may still limit some dispersal movements. (The revised regulations expand the total area Mexican wolves can occupy from 7,212 mi^2 -- the size of the Gila and Apache National Forests in the 1998 regulations -- to 153,293 mi^2 -- Zones 1, 2, and 3 in the new regulations). Our dispersal data for the MWEPA is, and may continue to be, limited in its ability to inform our complete understanding of the frequency, duration, or distance of longer dispersal events that would typically occur and related changes in distribution.

<u>Abundance, Trend, and Distribution of Mexican Wolves in Mexico</u>

The Mexican wolves that occupy northern Sierra Madre Occidental can be characterized as an extremely small, establishing population. In October 2011, Mexico initiated the establishment of a wild Mexican wolf population in the Sierra San Luis Complex of northern Sonora and Chihuahua, Mexico, with the release of five captive-bred Mexican wolves into the San Luis Mountains in Sonora just south of the US-Mexico border (SEMARNAT e-press release, 2011). Since that time, from 2012 to 2016, 41 Mexican wolves have been released into the state of Chihuahua, 18 of which died within a year after release (Garcia Chavez et al. 2017). Out of 14 adults released from 2011 to 2014, 11 died or were believed dead, and 1 was removed for veterinary care. Of these 11 Mexican wolves that died or were believed dead, 6 were due to illegal killings (4 from poisoning and 2 were shot), 1 wolf was presumably killed by a mountain lion, 3 causes of mortality are unknown (presumed illegal killings because collars were found, but not the carcasses), and 1 disappeared (neither collar nor carcass has been found) (80 FR 2491, January 16, 2015). One pair released in 2013 in Chihuahua has produced three litters (Garcia Chavez et al. 2017). This pair first reproduced in 2014, with 5 pups documented, marking the first successful reproductive event in Mexico since reintroductions were initiated in 2011 (80 FR 2491, January 16, 2015). As of April 2017, approximately 28 wolves inhabit the northern portion of the Sierra Madre Occidental in the state of Chihuahua (Garcia Chavez et al. 2017).

<u>Genetic Status of the Mexican Wolf</u>

In Captivity

The Mexican wolf captive population is an intensively managed but genetically depauperate population. The small number of founders of the captive population and the resultant low gene diversity available with which to build a captive population have been a concern since the beginning of the project (Hedrick et al. 1997) and remain a concern today (Siminski and Spevak 2016).

As of 2016, the captive population has retained approximately 83% of the gene diversity of the founders, which is lower than the recommended retention of 90% for most captive breeding programs (Siminski and Spevak 2016). In its current condition, the population would be expected to retain 75% gene diversity over 60 years and only 70.22% in 100 years. Long-term viability or adaptive potential depends on genetic variability. It is desirable to retain as much genetic variability as possible, but it is uncertain when loss of variability could have negative impacts on individuals or populations (Soulé et al 1986). Loss of variability might manifest in compromised reproductive function or physical and physiological abnormality. Reducing the rate of loss could be achieved by increasing the annual population growth rate, increasing the representation of under-represented founders, and by using the genome bank (Siminski and Spevak 2016).

The SSP actively supports both the MWEPA and northern Sierra Madre Occidental reintroductions. Today, relatively few initial releases are conducted into the MWEPA compared with the early years of the program (i.e., 74 captive wolves released in the first five years) because the population is established and population growth occurs via natural reproduction rather than augmentation through releases from captivity (USFWS 2017b). Initial releases are conducted into the MWEPA mostly for genetic management or other specific management purposes, and we expect this pattern to continue. Mexico, currently in the early phase of reintroduction, will likely continue to release a higher number of captive wolves to grow its population for the next few years (i.e., 41 wolves released in the first five years, including both initial releases and translocated wolves from the MWEPA). Releases in Mexico can simultaneously achieve demographic and genetic management objectives. For both wild populations, it is desirable to establish adequate gene diversity while the population is small, and then allow the population to grow.

The major challenges facing the SSP include: the limited number of founders; insufficient captive space; and the current demographic instability of the population. The number and relationship of animals founding the SSP population limit the amount of genetic diversity available to the SSP program. As a result, the SSP manages breeding to minimize the rate of loss of the genetic diversity over generations. This includes planned annual pairings with priority to those wolves with the least genetic representation in the population. It also means slowing the rate of loss over time by cryopreserving sperm and eggs beyond the natural life of the individual wolf for use in artificial pairings in the future. The development and application of assisted reproductive technologies like artificial insemination and *in vitro* fertilization are a priority for the SSP. The SSP established the genome bank in 1990 by collecting and preserving eggs and sperm from Mexican wolves. Males are selected for collection based on their representation in the gamete bank; as of 2016, material from 155 males has been cryopreserved. The collection process for females involves removing the ovaries resulting in permanent sterilization. Therefore, females are selected for collection opportunistically (prior to scheduled euthanasia, for example) or as individuals reach reproductive senecense. As of 2016, material from 51 females has been cryopreserved. Techniques to use the material in the gamete bank such as artificial insemination are still under development but have been used successfully in a limited number of instances (Siminski and Spevak 2016). For example, in 2017 the SSP documented successful production of a healthy Mexican wolf pup produced through artificial insemination using frozen semen (U.S Fish and Wildlife Service, our files).

The SSP seeks to increase the number of holding facilities in recognition that a larger population will retain genetic diversity longer than a small population. In order to promote demographic stability, the SSP needs to breed a greater proportion of its population each year. This requires increased space and greater efficiency in managing the SSP population. Improvements in SSP wolf husbandry through regular revisions of its husbandry manual are another priority for the SSP.

The captive population is currently demographically unstable because the age pyramid of the population is top heavy with older animals (that is, the population consists of many more older animals than young). The SSP population grew slowly from its founding in the late 1970s through the 80s, and then grew exponentially through the 90s hitting a peak population in 2008 of 335 wolves. In response to the reduction in releases to the wild and having reached maximum capacity in about 47 holding facilities, the SSP deliberately reduced its reproduction to stabilize the SSP population below 300 wolves within a stable age pyramid in the mid-2000s. Maintaining a stable age pyramid between 280 and 300 has proven difficult however, and the SSP estimates it may take another five years to achieve a stable age pyramid at a population size below 300.

In the Wild

The genetic status of Mexican wolves in the wild is as much or more of a concern as that of the captive population, namely due to high mean kinship (or, relatedness of individuals to one another) in the MWEPA, as well as ongoing loss of gene diversity and concerns over the potential for inbreeding depression to have negative demographic impacts on either the MWEPA or Mexico populations in the future. Unlike the captive breeding program, where specific wolves can be paired to maximize the retention of gene diversity, we cannot control which wolves breed in the wild. Due to this, and because introductions of wolves from the captive population is limited to those wolves that are over-represented in captivity, we expect gene diversity in the wild to be lower than in the captive population. As of 2016, the MWEPA population has a retained gene diversity of 75.91% of the founding population, while the wolves in Mexico have a retained gene diversity of 66.26%. In the early phase of the MWEPA reintroduction, we intended to mirror the SSP's original goal for lineage representation: 80% McBride, 10% Aragon, and 10% Ghost Ranch. This SSP goal has since been modified to slowly increase the lineage representation for Ghost Ranch and Aragon (Siminski and Spevak 2016). The representation of the three lineages in the MWEPA are 76.97% McBride, 7.21% Aragon, and 15.83% Ghost Ranch, and 60.94% McBride, 19.79% Aragon and 19.27% Ghost Ranch in Mexico. While lineage representation is still monitored and reported, current evaluation to select release candidates, for example, focuses more directly on under- representation which inherently serves to improve founder, or lineage, representation (i.e., a wolf that is considered under-represented in the wild is likely to contribute positively to lineage representation).

As of 2016, Mexican wolves in the MWEPA population were on average as related to one another as siblings. This "relatedness," as measured through population mean kinship, in the MWEPA was 0.2409, and in Mexico was 0.3374 (Siminski and Spevak 2016). High relatedness is concerning because of the risk of inbreeding depression (the reduction in fitness associated with inbreeding). Inbreeding depression may affect traits that reduce population viability, such as reproduction (Fredrickson et al. 2007), survival (Allendorf and Ryman 2002), or disease resistance (Hedrick et al. 2003) (and see USFWS 2010 and 80 FR 2504-2506). Improving gene diversity and reducing population mean kinship of both wild populations can be achieved by the introduction of under-represented wolves from the captive population.

Recent exploration of inbreeding depression has been conducted in the captive and MWEPA populations. Fredrickson et al. (2007) analyzed 39 litters (1998-2006) from the MWEPA and reported a negative association between pup inbreeding coefficient (*f*) and "litter size" (maximum number of pups counted during the summer). However, a more recent analysis of 89 wild litters from 1998 to 2014 found no significant relationship using all available data (Clement and Cline 2016 in Miller 2017, Appendix C). Clement and Cline (ibid) found estimated effect of inbreeding differed during different time periods. The effect of pup *f* on maximum pup count was negative in the early period (1998-2006), not significant for the entire time period (1998-2014), and positive but not significant for the late time period (2009-2014). They went on to state, "Given the lack of experimental control, it is difficult to understand the cause of the changing relationship through time. However, it could be due to a shift in the population from captive-born animals to wild-born animals, changes in population density, changes in the survey protocol for wild animals, or some unmeasured individual effect"(see Miller 2017, Appendix B for detailed description of methodology changes through time).

We are able to positively influence the genetic condition of the MWEPA and northern Sierra Madre Occidental population through the release of genetically advantageous Mexican wolves to the wild from captivity, cross-fostering genetically-valuable pups, translocating wolves between wild populations, or potentially by removing Mexican wolves whose genes are over-represented. Management recommendations suggest that the Aragon and Ghost Ranch lineages should be increased to as much as 25% each in the MWEPA (Hedrick et al. 1997) because wolves from these lineages are currently under-represented (Siminski and Spevak 2016).

We have been striving to decrease mean kinship and increase the retention of gene diversity in the MWEPA through the release of wolves from the captive breeding program. In 2014, the

Service and our interagency partners began utilizing a technique referred to as cross-fostering. Instead of releasing adult wolves from captivity into the wild, which have a lower survival rate than wild born wolves and a higher incidence of nuisance behavior (AMOC and IFT 2005), we have placed genetically advantageous pups from captive litters into wild dens to be raised with the wild litter. In our first cross-fostering event in 2014, we placed two pups from one wild litter into another wild litter. In 2016, we placed six pups from captivity into three wild litters (two pups into each litter). The success of cross-fostering efforts is measured by pups surviving and breeding, such that their genetic material is integrated into the wild population. To date, we are aware of one instance in which a cross-fostered pup has survived and bred, but a second was paired with a mate at the end of 2016 (U.S. Fish and Wildlife Service files). We will continue to monitor the success of cross-fostering efforts.

Several other genetic issues, including hybridization (between Mexican wolves and dogs or coyotes) and introgression of gray wolves with Mexican wolves are of potential concern to our management of wild Mexican wolves. In the MWEPA population, three hybridization events between Mexican wolves and dogs have been documented since wolves were first reintroduced in 1998. In each case, hybrid litters were humanely euthanized with the exception of one pup of unknown status (80 FR 2504, January 15, 2016). No hybridization events between Mexican wolves and coyotes have been documented. No hybridization events with coyotes or dogs have been documented in Mexico (personal communication Dr. López-González, Universidad Autónoma de Querétaro, April 10, 2017). We recognize that hybridization events could occur and therefore have management protocols in place to respond swiftly if hybridization is detected; however, hybridization is not a significant genetic or management concern to Mexican wolves at the level at which it has occurred to date.

We recognize the potential for introgression of gray wolves into Mexican wolf range. Several long-distance dispersal events from other gray wolf populations in recent years suggest that gray wolves could disperse into the MWEPA, where they could breed with Mexican wolves. While the introduction of gray wolf genes into the MWEPA population could result in genetic rescue of the population (Hedrick and Fredrickson 2010, Whiteley et al. 2015), multiple introgression events could quickly swamp the Mexican wolf genome by introducing alleles that might change the natural history or behavior of the population (e.g., Fitzpatrick et al. 2010). Careful evaluation of the potential effects of introgression of gray wolves is needed to determine whether allowing gray wolves to breed with Mexican wolves could be appropriate during a later stage of recovery or after recovery (Hedrick and Fredrickson 2010). Until such evaluation occurs and pending its results, we would manage against such breeding events occurring in the MWEPA.

<u>Stressors</u>

The most important biological stressors, or conditions, that may influence the current and ongoing recovery potential of the Mexican wolf include: 1) adequate habitat availability and suitability; 2) excessive human-caused mortality; 3) demographic stochasticity associated with small population size; and 4) continuing or accelerated loss of genetic diversity in the captive or wild populations. In addition to their individual impacts, these stressors can have synergistic effects. For example, high mortality rates may result in declining populations that become less demographically stable and lose gene diversity more rapidly than a more stable, growing population.

Habitat availability/suitability

Wolf reintroduction and recovery efforts require large areas. As previously discussed, suitable habitat for the Mexican wolf is forested, montane terrain containing adequate biomass of wild prey (elk, white-tailed deer, mule deer, and other smaller prey) to support a wolf population. Suitable habitat has minimal roads and human development, as human access to areas inhabited by wolves can result in wolf mortality by facilitating illegal killing. A recent habitat assessment conducted by Martínez-Meyer et al. (2017) assessed information on abiotic climatic variables, land cover and vegetation types, ungulate biomass, human population density, and road density to determine the extent of suitable habitat in the southwestern United States and Mexico. Their study identifies the MWEPA and two areas in the Sierra Madre Occidental of Mexico as the most suitable areas within historical range (per Parsons 1996) to establish Mexican wolf populations to contribute to recovery. These areas have been identified in previous habitat assessments (summarized in USFWS 2010) and two of the three areas (the MWEPA and the northern Sierra Madre Occidental site in Mexico) are the current locations of Mexican wolf reintroductions.

As Martínez-Meyer et al. (2017) recognize, ground-truthing is needed to verify the results of their niche modeling exercise to ensure the areas identified as suitable habitat adequately contain the biological characteristics necessary to support Mexican wolves. Specifically, verifying the availability of ungulate biomass in Mexico is of particular importance, as wolf density is positively correlated to the amount of ungulate biomass available and the vulnerability of ungulates to predation (Fuller et al. 2003). Adequate ungulate monitoring data are available for the MWEPA to inform our understanding of the size of Mexican wolf populations that could be supported. We previously estimated that a population of 300-325 Mexican wolves could be supported in the MWEPA without unacceptable impacts to ungulates (USFWS 2014). However, in Mexico ungulate monitoring methodologies are more variable and data are not readily available in the area of interest, making predictions about ungulate biomass as a characteristic of habitat suitability less certain (Martínez-Meyer et al. 2017). We recognize that ungulate availability is lower in the Sierra Madre Occidental sites compared with the MWEPA, in large part due to the absence of elk in Mexico, as well as lower deer densities (Martínez-Meyer et al. 2017). Lower density of ungulates in Mexico would suggest that wolves in Mexico will likely have smaller pack sizes and larger home ranges relative to wolves in the MWEPA (Fuller et al. 2003). Historically Mexican wolves subsisted in this area, likely with a larger proportion of small mammals in their diet compared to wolves in other areas (Brown 1988). As Mexico continues efforts to establish a population of Mexican wolves in the Sierra Madre Occidental, information about ungulate (or other prey) abundance and density will be informative to more fully understand the area's ability to support wolves.

In addition to ecological differences between the United States and Mexico reintroduction sites, we also recognize that land tenure in areas of suitable habitat in each country is significantly different. Land tenure differences may result in different opportunities and challenges in each country to establish and maintain Mexican wolf populations. In the United States, we consider federal land to be an important characteristic of the quality of the reintroduction area. Federal lands such as National Forests are considered to have the most appropriate conditions for Mexican wolf reintroduction and recovery efforts because they typically have significantly less human development and habitat degradation than other land-ownership types (Fritts and Carbyn 1995). The majority of suitable habitat for Mexican wolves in the MWEPA occurs on the Apache, Sitgreaves, Coconino and portions of the Tonto, Prescott, and Coronado National Forests in Arizona, as well as on the Fort Apache Indian Reservation and San Carlos Apache tribal lands. In New Mexico, the Gila and portions of the Cibola and Lincoln National Forests are important large blocks of public land (USFWS 2014).

In Mexico, there are three primary types of land: federal, private, and communal (Valdez et al. 2006). Large tracts of federally owned lands managed solely for conservation do not exist in Mexico. Ejidos are a type of communal property distributed among individuals but owned by the community that may have conservation objectives but are typically managed for multiple uses including extraction of natural resources such as timber or mining (Valdez et al. 2006). Natural Protected Areas are managed by the federal government in Mexico for the protection, restoration, and sustainable use of the natural resources, but many have native or rural communities living within their boundaries, and are a mix of private, federal, and communal land. Most Natural Protected Areas do not have comprehensive management plans, and extractive uses are allowed (Valdez et al. 2006). Because the Mexican landscape is dominated by privately and communally owned lands, landowner approval is necessary before Mexican wolves can be released onto private land. As in the United States, landowner support for the reintroduction of Mexican wolves ranges from supportive to antagonistic (López González and Lara Díaz 2016). Federal agencies in Mexico continue to work with landowners to seek support for the reintroduction of Mexican wolves and have obtained signed agreements from several cooperative landowners who have allowed for the reintroductions to date.

Successful Mexican wolf recovery will require that Mexican wolf populations occupy large areas of ecologically suitable habitat. Prey availability will need to be adequate to support populations, and land tenure and management, although potentially different between the two countries, will need to support the occupancy and management of Mexican wolves across the landscape.

Human-Caused Mortality

Results from research on gray wolves (Fuller et al. 2003, Carroll et al. 2006), our monitoring data, and the Vortex population modeling analysis (Miller 2017) suggest that Mexican wolf populations are highly sensitive to adult mortality. For populations to grow or maintain themselves at demographic recovery targets, mortality rates will need to stay below threshold levels (Miller 2017).

As previously described, human-caused mortality is the most significant source of documented mortality in the MWEPA (USFWS 2017b; 80 FR 2488, January 16, 2015), and therefore the most important single source of mortality to address during the recovery process. The impact of human-caused mortality has varied from a small impact in a given year to reducing the population by about 20% (U.S. Fish and Wildlife Service files). Human-caused mortality may occur at levels significant enough to cause a population decline, or at lower levels may hinder how quickly the population grows (that is, the population is still able to grow, but at a slower rate than it otherwise would). Ongoing and increased law enforcement presence and education to reduce misinformation will continue to be necessary in the MWEPA for the full extent of the recovery effort.

We have also observed that wolves experience a greatly increased likelihood of mortality in their first year after initial release or translocation. Survival of released or translocated wolves is markedly lower than average survival rates for wild wolves (See Miller 2017, Table 3). Functionally this means that a greater number of wolves need to be released to the wild than the number expected to survive and contribute to the population (e.g., we release 10 wolves in order to get 2 wolves that survive as potentially reproductive members of the population).

As we have observed in the MWEPA, the combination of mortality and management removals (which serve as mortality to a population) can have a significant impact on population performance. While some level of removal is a useful management tool to address conflicts with livestock or humans, excessive removals can be counterproductive to population performance, particularly during years when the population is experiencing higher mortality rates or slower growth. Livestock depredations and conflicts with humans are the major causes of management removals that are likely to continue in the future, and therefore the most important source of removal to consider as it relates to the recovery of the Mexican wolf. Many considerations are taken into account when determining whether to remove wolves, including the status of the population and the genetics of individual wolves. During years in which a population exhibits robust growth (low mortality rates), higher levels of removal could occur without hindering the population (Miller 2017). During years with higher mortality rates, removal rates would need to be lessened or eliminated to support population stability. Maintaining and expanding the use of proactive techniques to deter depredation events will continue to be necessary throughout the recovery effort, and possibly indefinitely.

In summary, populations that contribute to recovery will need to experience levels of human-caused mortality that do not hinder population growth. Furthermore, while we recognize that management removals will remain a useful management tool during the recovery process, we envision that the populations that contribute to recovery will be managed with a suite of tools to reduce conflicts, of which removal will be only one. To track the impact of mortality and removals, ongoing monitoring and data collection will need to continue in both the MWEPA and Mexico, with frequent adjustments in management to respond to the status and performance of populations. Improving the survival of released and translocated wolves could greatly improve our progress toward demographic or genetic recovery goals.

Demographic stochasticity

As explained in the final listing rule for the Mexican wolf, Mexican wolves in the wild have a high demographic risk of extinction due to small population size. Scientific theory and practice generally agree that a subspecies represented by a small population faces a higher risk of extinction than one that is widely and abundantly distributed (Goodman 1987, Pimm et al. 1988).

One of the primary causes of this susceptibility to extinction is the sensitivity of small populations to random demographic events (Shaffer 1987, Caughley 1994). In small populations, even those that are growing, random changes in average birth or survival rates could cause a population decline that would result in extinction. This phenomenon is referred to as demographic stochasticity. As a population grows larger and individual events tend to average out, the population becomes less susceptible to extinction from demographic stochasticity and is more likely to persist.

At their current sizes, both the MWEPA and northern Sierra Madre Occidental populations have a high risk of extinction that must be ameliorated during the recovery process. Miller 2017, suggests that if both populations were maintained at or near their current population size for 100 years, the MWEPA would have approximately a 45% risk of extinction, and then northern Sierra Madre Occidental wolves would have a 99% risk of extinction (see Conclusions and Discussion: Analysis of the Status Quo).

We envision populations that contribute to recovery to exhibit moderately low levels of demographic stochasticity, meaning that they demonstrate population dynamics (as growing or stable populations) that suggest they are unlikely to go extinct now or in the foreseeable future (50-100 year time horizon). Neither the ESA nor the Service equate a specific extinction risk with the definitions of "endangered" or "threatened", but rather the Service recognizes this is a species specific determination that should be explored during the development of conservation measures and recovery plans for listed species. Therefore, population growth will be necessary for both populations to reduce the risk of stochastic population fluctuations that could threaten their ability to persist over time (see additional discussion in subsection "Resiliency").

Loss of genetic diversity

As described above, both the captive and wild Mexican wolf populations lose gene diversity every year as animals die or reach reproductive senescence. Because there are no new founders to bring new genes to the population, we focus our efforts on slowing the rate of loss of diversity. This is more easily accomplished in captivity than the wild due to our ability to manage pairings.

Inbreeding depression is not currently operating at a level that is suppressing demographic performance in the MWEPA (in fact, the population has exhibited robust growth in recent years), yet we remain aware that the population has high levels of mean kinship and does not likely contain an adequate amount of the gene diversity available to it from the captive population. Currently, our data analysis suggests that inbreeding depression is impacting the probability of producing a litter, but is not significantly influencing litter size as previously thought (see discussion of genetic threats under Factor D at 80 FR 2488, January 16, 2015). However, we also recognize that the high level of supplemental feeding may be clouding our ability to detect inbreeding impacts on litter size (see Miller 2017, "Calculation of litter size"). The recent growth of the MWEPA in its current genetic condition compounds our concern, because it becomes harder to improve gene diversity as the population grows larger. In other words, releasing more Mexican wolves would be necessary to shift the genetic composition of the population than at a smaller population size. Miller 2017 demonstrates that without active genetic management in the form of releases and translocations (including cross-fostering) in either reintroduction area, genetic drift leads to reduced genetic variability over time (see

Scenario Set 1). When active genetic management is conducted, populations in the Vortex model are able to maintain a more robust genetic condition that minimizes the likelihood of genetic issues and may provide for longer term adaptive potential (Miller 2017, Scenario Set 2).

We are unable to make statements about the degree to which genetic issues may be influencing the demographic performance of the northern Sierra Madre Occidental wolves due to the short time frame of the reintroduction effort and specifically a lack of data on reproduction.

We envision populations that contribute to recovery will be sufficiently genetically robust as to not demonstrate demographic-level impacts from inbreeding depression or other observable, detrimental impacts. We expect that active genetic management will be necessary during the recovery process through a combination of initial releases, translocations, cross-fostering events, and removals, as a precautionary measure to avoid the negative impacts that may occur at higher levels of inbreeding depression, such as reduced likelihood of litter production or other reproductive effects.

RESILIENCY, REDUNDANCY, AND REPRESENTATION

The Service has recently begun using the concepts of resiliency, redundancy, and representation to identify the conditions needed for species recovery. We previously assessed the resiliency, redundancy, and representation of Mexican wolves in the MWEPA in our 2010 Conservation Assessment (USFWS 2010). Since that time, the MWEPA population has grown in abundance and distribution, and Mexico has initiated the establishment of a population in Mexico. We incorporate this new information in our updated discussion of the "3 R's". In combination with our identification of stressors, assessing the resiliency, redundancy, and representation of the MWEPA and northern Sierra Madre Occidental populations will guide development of an effective recovery strategy in our revised recovery plan for the Mexican wolf that will result in recovered populations across its range.

The Service describes resiliency, redundancy, and representation as follows (USFWS 2016):

Resiliency describes the ability of the populations to withstand stochastic events. Measured by the size and growth rate of each population, resiliency gauges the probability that the populations comprising a species are able to withstand or bounce back from environmental or demographic stochastic events.

Redundancy describes the ability of a species to withstand catastrophic events. Measured by the number of populations, their resiliency, and their distribution (and connectivity), redundancy gauges the probability that the species has a margin of safety to withstand or can bounce back from catastrophic events.

Representation describes the ability of a species to adapt to changing environmental conditions. Measured by the breadth of genetic or environmental diversity within and among populations, representation gauges the probability that a species is capable of adapting to environmental changes.

Lengthier descriptions of these concepts and their applicability to Mexican wolf conservation and recovery are provided in the 2010 Conservation Assessment (USFWS 2010).

<u>Resiliency</u>

We used population viability analysis to explore the conditions for viability, or resiliency, of wild Mexican wolf populations in the United States and Mexico (Miller 2017). We consider a resilient population to be one that is able to maintain approximately a 90% or greater likelihood of persistence over a 100 year period. Given that the Service does not equate specific levels of viability with endangered or threatened status, we use 90% persistence as a general guideline indicating that populations are highly demographically stable, rather than as an absolute threshold. This benchmark is well supported by the community of practice in recovery planning (Doak et al. 2015) and is appropriate because we have a high degree of certainty of the status of populations based on monthly and annual monitoring, we recognize that wolf populations are able to grow and rebound from population fluctuations rapidly (Fuller et al. 2003), and we want to strike a balance between achieving a reasonable level of viability while also considering the needs of local communities and the economic impact of wolves on some local businesses. In addition to the natural variability in demographic rates used as input for the analysis, an element of extreme stochasticity was incorporated in the model in all scenarios to ensure populations are able to withstand single year reductions in population growth or reproductive rate (See "Catastrophic Event") as may occur during disease events or other unexpected "catastrophes."

Miller's (2017; Scenario Set 1) results suggest that resiliency (~90% persistence over 100 years) of wild Mexican wolf populations can be achieved by various combinations of population size and mortality rate, with larger population sizes needed to accommodate higher mortality rates. The MWEPA population is able to achieve the 90% guideline when managed for a long term abundance of around 300 wolves when adult mortality is below 25%. Given predicted annual variation in abundance, managing for a population of around 300 wolves means that in some years the population will grow larger than 300. At higher mortality rates, larger population sizes are needed to achieve and maintain resiliency. In the northern Sierra Madre Occidental, a population of less than 200 wolves is unable to reach the 90% benchmark except at the lowest tested mortality rate (approximately 19%), which is well below the population's current average adult mortality rate and expected to be unlikely to be achieved during the early years of the reintroduction. Larger population sizes at or above 200-250 are needed for persistence of this population at a mortality rate of approximately 25%, while populations of 200-250 are not able to achieve persistence at mortality rates of 28% and 31%.

<u>Redundancy</u>

The scientific literature does not recommend a specific number or range of populations appropriate for conservation efforts, although rule of thumb guidelines for the reintroduction of a species from captivity recommends that at least two populations be established that are demographically and environmentally independent (Allendorf and Luikart 2007). Recent habitat analysis (Martínez-Meyer et al. 2017) supports previous findings (see USFWS 2010) that there are limited areas within the core historical range of the Mexican wolf with the ecological conditions and size necessary to support Mexican wolf populations: the MWEPA in the United States, and two locations in the Sierra Madre Occidental of Mexico. Previous studies (Carroll et al. 2004; Carroll et al. 2006) identified potential areas north of the MWPEA with suitable habitat for Mexican wolf reintroduction.

The Mexican wolf is currently distributed in the MWEPA and northern Sierra Madre Occidental in different phases of establishment, as discussed in Current Conditions. The initiation of the reintroduction effort in northern Mexico demonstrates progress in establishing *redundancy* since the 2010 Conservation Assessment (USFWS 2010), but it does not yet fully satisfy this objective. To achieve *redundancy*, populations in these two geographic areas, at minimum, will need to demonstrate sufficient *resiliency* (as described above) such that they provide a true measure of security against extinction for one another. If the southern Sierra Madre Occidental area were used as a reintroduction site and managed to establish *resiliency* and *representation* (see below), this area could provide an additional level of *redundancy*. Therefore, at minimum we expect *redundancy* can be satisfied by the maintenance of two *resilient*, *representative* populations in the MWEPA and northern Sierra Madre Occidental, with the southern Sierra Madre Occidental potentially providing support to the northern Sierra Madre Occidental site or independently functioning as another opportunity for *redundancy*. The relationship between redundant populations (whether they are connected by natural or assisted migration) is described below in Representation.

Representation

We consider *representation* to have both genetic and ecological aspects that are important to recovery of the Mexican wolf. The population viability analysis of Miller (2017) enabled us to quantify and predict the maintenance of gene diversity in wild and captive populations over time, while the habitat assessment conducted by Martínez-Meyer et al. 2017 enabled our understanding of the ecological conditions across the range of the Mexican wolf, together providing a detailed assessment of *representation*.

We consider the degree to which wild populations contain the gene diversity available from the captive population to be an important indication of genetic *representation* for recovery. As Miller (2017:17) states, “As the SSP population represents the origin of all wolves following the taxon’s extirpation to the wild, it is the source of all genetic variation that can be transferred to wild populations.” Additionally, translocation of wolves between wild populations may also be a method for transferring gene diversity between wild populations. Ensuring wild populations represent approximately 90% of the gene diversity retained by the captive population provides a guideline for *representation* based on community of practice in the management of captive populations (Siminski and Spevak 2016). We consider approximately 90% to be a reasonable bar for recovery because it ensures wild populations contain a high degree of the genetic diversity available, while recognizing that we cannot control breeding events in the wild and need flexibility in our management of wolves (e.g., removals may impact the gene diversity the population).

Using the pedigree maintained by the SSP for the captive and wild populations, Miller tracked gene diversity (expected levels of heterozygosity) of Mexican wolf populations across several scenario sets of initial release and translocation combinations that could be conducted to improve the genetic condition of wild populations (Miller 2017, table 2). Miller’s results suggest that the number of initial releases from the SSP to the MWEPA that we recommended in our 2014 EIS to improve the genetic condition of the MWEPA (USFWS 2014) would be insufficient for attaining the approximately 90% guideline we consider for recovery. We note that these results were predicted based on assumed survival of only 0.284 of adult wolves their first year of release from captivity (Miller 2017, table 3). Model results suggest that this guideline could be reached by increasing the number of releases, increasing survival of released animals, or a combination. We recognize there may be additional release and translocation combinations (including cross-fostering and selective removals) beyond those explored by Miller (2017) by which MWEPA or Sierra Madre Occidental populations could reach the genetic diversity guideline.

Ecological *representation* is addressed by the distribution of Mexican wolves across large portions of their range in the United States and Mexico. Habitat conditions vary between the MWEPA and Sierra Madre Occidental sites in both terrain and vegetation, as well as the abundance and distribution of prey. As previously discussed, historically Mexican wolves likely preyed upon a larger proportion of smaller prey in Mexico than the United States. Our data from the MWEPA and northern Sierra Madre Occidental currently show that Mexican wolves are likely to reestablish this pattern, given the lack of elk in Mexico and lower deer densities in portions of the Sierra Madre Occidental compared to the MWEPA. We anticipate that genetically diverse wild populations in both reintroduction areas will be better able to respond to not the current range of habitat conditions, but also future changing conditions such as shifts in prey availability, drought, or other environmental fluctuations.

Martinez-Meyer et al.'s (2017) habitat model shows that large patches of high quality habitat in the MWEPA and Sierra Madre Occidental are connected by large patches of low quality habitat in the U.S.-Mexico border region (see Martinez-Meyer et al. 2017, figure 19) . These results and monitoring data from the MWEPA and northern Sierra Madre Occidental were used to inform Miller's (2017) exploration of whether natural connectivity via dispersing wolves is likely to occur between reintroduction sites and whether connectivity between these *redundant* populations is necessary for recovery of the Mexican wolf. We recognize benefits and drawbacks to either connected or isolated populations, as described in our 2010 Conservation Assessment. Miller (2017) assumed a low level of dispersal between the MWEPA and northern Sierra Madre Occidental population, and a slightly higher level of dispersal between the northern and southern Sierra Madre Occidental populations (see "Metapopulation Dynamics"). Modeling results predict that assumed levels of natural dispersal would not be sufficient to maintain the desired genetic *representation* for the Mexican wolf (Miller 2017, Scenario Set 1). Therefore, genetic management such as releases, translocations, and cross-fostering of pups is a necessary tool to achieve appropriate *representation* (Miller 2017, Scenario Set 2). This management is a form of artificial, or assisted, connectivity that will be necessary for at least portions of the recovery process.

Conclusion

The recovery of the Mexican wolf is well underway, with reintroduction occurring in the MWEPA in the United States and the northern Sierra Madre Occidental in Mexico. The MWEPA population, which has shown a positive growth trend in recent years, needs to continue to increase in size. Meanwhile, the release of wolves from captivity (including cross-fostered pups) into the MWEPA needs to continue in order to improve the genetic condition of the population. In Mexico, the establishing population will be strengthened by continued releases from captivity (or translocations) to both assist in population growth as well as improving the gene diversity of that population. The MWEPA and northern Sierra Madre Occidental sites, potentially supported by wolves in the southern Sierra Madre Occidental in the future, have the potential to provide *representation*, *resiliency*, and *redundancy* for the recovery of the Mexican wolf.

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APPENDIX A. Population Viability Analysis for the Mexican Wolf (*Canis lupus baileyi*): Integrating Wild and Captive Populations in a Metapopulation Risk Assessment Model for Recovery Planning (Miller 2017).

APPENDIX B. Mexican Wolf Habitat Suitability Analysis in Historical Range in the Southwestern US and Mexico (Martínez-Meyer et al. 2017).

Population Viability Analysis for the Mexican Wolf (*Canis lupus baileyi*)

Integrating Wild and Captive Populations in a Metapopulation Risk Assessment Model for Recovery Planning

Report prepared by

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Introduction

This document describes the demographic and genetic simulation model developed for population viability analysis (PVA) of the Mexican wolf (*Canis lupus baileyi*) to assist in the recovery planning effort for the species in the United States and Mexico. The modeling tool used in this analysis is the stochastic individual-based software *Vortex* (Lacy and Pollak 2017). This most current PVA project, initiated in December 2015, builds upon previous work led by Rich Fredrickson and Carlos Carroll in 2013-2015 (itself based on the published analysis of Carroll et al. (2014)). The previous analysis relied on demographic information from other wolf populations, most notably the Greater Yellowstone Ecosystem, while this analysis uses a majority of data collected through direct observation of Mexican wolves in the wild. In addition, the earlier effort used an older version of the *Vortex* software platform; an important new feature of this latest effort is the explicit addition of a captive population component to the metapopulation model. This new capability now allows us to incorporate the pedigree of all existing wild and captive wolves, thereby establishing an accurate portrayal of the genetic relationships among all living wolves. Using this expanded capability, we can explore specific scenarios of wolf release from the captive population (based on specific genetic criteria) to existing populations in the U.S. or Mexico, or to currently unoccupied habitat patches in Mexico as defined by the ongoing habitat suitability analysis (Martinez-Mayer et al. 2017) conducted as part of the larger recovery planning process. In addition, we can more accurately track the changes in gene diversity (expected heterozygosity) over time across all wild and captive populations – thereby providing more useful guidance in deriving both demographic and genetic population recovery criteria.

Presentation of the extensive model input datasets is organized by population. Specification of wild population input data focuses strongly on the Mexican Wolf Experimental Population Area (MWEPA) which has been the subject of targeted research and monitoring since 1998 by biologists from the U. S. Fish and Wildlife Service and cooperating state wildlife agencies. The separate population currently inhabiting northern portions of Mexico's Sierra Madre Occidental, hereafter referred to as Sierra Madre Occidental – North or simply SMOCC-N, was established much more recently; consequently, we have comparatively little detailed knowledge of its demographic dynamics. A second habitat patch in the southern Sierra Madre Occidental, hereafter referred to as SMOCC-S, is currently unoccupied. Any model of wolf population dynamics in this area must assume demographic rates based on those that define both MWEPA and SMOCC-N populations. Input data for the captive population, hereafter referred to as the SSP (Species Survival Plan) population, are derived from analysis of the Mexican Wolf International Studbook (as of 31 December 2015) compiled annually by P. Siminski. Where appropriate, captive population input data have been checked with the recently completed demographic analysis of this population (Mechak et al. 2016) through the assistance of Kathy Traylor-Holzer (CBSG).

Population viability analysis (PVA) can be an extremely useful tool for investigating current and future demographic dynamics of Mexican wolf populations in the northern portion of the species' range. The need for and consequences of alternative management strategies can be modeled to suggest which practices may be the most effective in managing Mexican wolf populations. *Vortex*, a simulation software package written for PVA, was used here as a vehicle to study the interaction of a number of Mexican wolf life history and population parameters, and to test the effects of selected management scenarios.

The *Vortex* package is a simulation of the effects of a number of different natural and human-mediated forces – some, by definition, acting unpredictably from year to year – on the health and integrity of wildlife populations. *Vortex* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or random variables that follow specified distributions. The package simulates a population by recreating the essential series of events that describe the typical life cycles of sexually reproducing organisms.

PVA methodologies such as the *Vortex* system are not intended to give absolute and accurate "answers" for what the future will bring for a given wildlife species or population. This limitation arises simply from two fundamental facts about the natural world: it is inherently unpredictable in its detailed behavior; and we will never fully understand its precise mechanics. Consequently, many researchers have cautioned against the exclusive use of absolute results from a PVA in order to promote specific management actions for threatened populations (e.g., Ludwig 1999; Beissinger and McCullough 2002; Reed et al. 2002; Ellner et al. 2002; Lotts et al. 2004). Instead, the true value of an analysis of this type lies in the assembly and critical analysis of the available information on the species and its ecology, and in the ability to compare the quantitative metrics of population performance that emerge from a suite of simulations, with each simulation representing a specific scenario and its inherent assumptions about the available data and a proposed method of population and/or landscape management. Interpretation of this type of output depends strongly upon our knowledge of Mexican wolf biology, the environmental conditions affecting the species, and possible future changes in these conditions. Under thoughtful and appropriate interpretation, results from PVA efforts can be an invaluable aid when deriving meaningful and justifiable endangered species recovery criteria (Doak et al. 2015).

Guidance for PVA Model Development

An important set of information that can be used to guide the development of a proper PVA model input dataset is the recent trend in Mexican wolf population abundance in the MWEPA – the largest, oldest, and most well-studied wild population of Mexican wolves currently in existence. The abundance trend for this population is shown in Figure 1 from its initiation in 1998 to 2016. These data can shed light on population growth rates across different phases of population management following the initial releases, and can also be used to propose mechanistic hypotheses to explain differences in population growth across these different phases of the release program. Such an analysis is critical for retrospectively analyzing our model to determine overall realism and reliability when forecasting future abundance trends under alternative management scenarios.

While recognizing the value of this retrospective analysis of historic demographic data as a means of assessing PVA model realism, it is important to recognize that our projections of future Mexican wolf abundance and genetic structure encompass a broad range of potential demographic states that may or may not be diagnostic of existing wild wolf populations. These exploratory analyses are designed to identify demographic conditions that are likely to lead to long-term wild population recovery, i.e., will result in an acceptably low risk of a population's decline to extinction or an acceptably small extent of loss of population genetic viability (gene diversity).

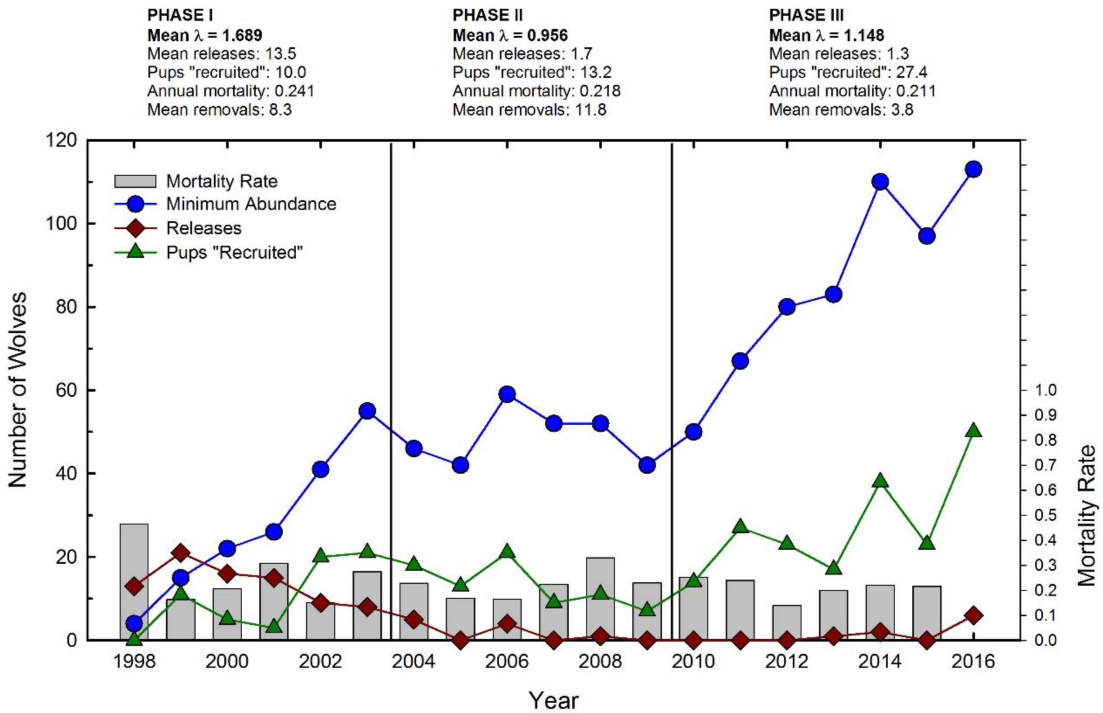

Figure 1. Population statistics for the MWEPA Mexican wolf population, 1998-2016. Data include minimum abundance, annual adult mortality rate, number of animals released from the SSP ex situ population, and the number of pups "recruited" (defined here as surviving to 31 December of their year of birth). Primary data sources: Annual USFWS Population Reports.

Input Data for PVA Simulations: Wild Populations

Initial Population Specification

All models for this analysis are based on the status of the wild and captive populations as of 31 December, 2015. This specification allows us to construct a full pedigree of all populations up to the date we choose to begin the population projection. This pedigree, uploaded to the software as a simple text file, includes the age and gender of all animals produced since the initiation of the captive management program between 1961 and 1980 (Hedrick et al. 1997). Additionally, the pedigree flags those adults that are paired at the time of initiation of the simulation, thereby providing a starting point for the population breeding structure. Based on information collated by the US Fish and Wildlife Service and Mexico's Protected Areas Commission (CONANP), we set the population abundance for MWEPA at 97 individuals and for SMOCC-N at 17 individuals.

Reproductive Parameters

Breeding system: Wolves display a long-term monogamous breeding system. In the context of *Vortex* model development, adult breeding pairs are assumed to remain intact until either individual in the pair dies.

Age of first reproduction: We assume that both females and males are capable of producing pups when they are two years of age.

Maximum breeding age / longevity: In our demographic specification of wolf breeding biology, wolves remain capable of producing pups throughout their adult lifespan, i.e., reproductive senescence is not a feature of our models. We assume that wild Mexican wolves will not live beyond eleven years of age, based in part on the very low frequency of observing a wolf of this age or greater in the MWEPA. Also note that the approximate generation length for Mexican wolves is four years; therefore, a 100-year projection constitutes approximately 25 generations.

Litters per year: Wolves will produce one litter of pups per year.

Maximum number of pups per litter: For our modeling purposes, we are defining pup production at the mean time of first observation at or near the den. We recognize, therefore, that this does not account for *in utero* mortality or the unobserved death of pups before they are first seen after emergence from the den. With this as our definition, the largest litter documented from the MWEPA population is 7 pups. We will use this as our maximum litter size, recognizing that it is a rare occurrence. Note that the specification of litter size for each successfully breeding female in a given year is determined by a complex function involving a number of independent variables (see "Distribution of litters per year" below).

Sex ratio of observed pups: This ratio will be set at 50:50 for wild populations, with the understanding that the actual ratio within any one litter may deviate from this expected value through random variability.

Percentage of adult females "breeding" in a given year: For our specific Mexican wolf model, this input parameter is more accurately defined as the percentage of adult females that pair up with an adult male in a given year. This parameter is calculated through the complex function FPOOL derived by R. Fredrickson in the earlier 2013 PVA modeling effort. FPOOL determines which adult females pair within any one year, as a function of whether they were paired last year, the availability of breeding-age males in the population, and adult female age. We have retained this function for our current model.
The long-term annual mean expected proportion of paired adult females was set at 0.78. In other words, we expect approximately 78% of the wild adult females in a given year to be paired with an adult male. This value was informed by two sets of data analyzed by J. Oakleaf and M. Dwire, USFWS: (1) direct observations of collared animals age 2+ that were seen to be paired, and (2) estimates of the number of females (1+ years old) in the entire population at time t-1 compared to the number of observed pairs at time t. Each of these two methods have inherent biases that serve to either underestimate or overestimate this parameter; consequently, the group decided to use the mean parameter value obtained by these two methods as model input. See Appendix A for more information on the process used to derive this parameter value.

Male mate availability is controlled by another related parameter, MPOOL, also derived by R. Fredrickson as part of the previous PVA modeling effort. This function identifies male mates on the basis of their current paired status and adult male age. We also assume that wolves will avoid pairing with their siblings or their parents in an attempt to avoid excessive levels of inbreeding. This assumption is based on limited observation of successful reproduction (one pack) through the 2016 breeding season, although a full-sib mating observed in 2017 has produced a litter whose fate is currently unknown.

Probability of litter production among paired females: Once the identification of pairs is complete using FPOOL and MPOOL above, we must specify the proportion of those paired adult females that fail to produce pups. Detailed analysis by J. Oakleaf and M. Dwire (USFWS) of the probability of live birth among wild adult females, using data on both denning behavior and litter production, indicates that probability of litter production is a function of both the age of the dam and the kinship (KIN) of that female with her mate (equal to the inbreeding coefficient of the resulting litter). The functional relationship was obtained through logistic regression; therefore, the direct expression for probability of litter production takes the form

Pr(pair produces a litter) = $\frac{1}{(1+e^{-x})}$, with

x = 1.266+1.819-(8.255**KIN*) for females age 2-3;
x = 1.266+2.2645-(8.255**KIN*) for females age 4 – 8; and
x = 1.266-(8.255**KIN*) for females age 9+.

See Appendix B for more information on the derivation of this function. Among prime-aged breeding females age 4-8, the above functions predicts that approximately 95% of paired females are expected to produce a litter with a kinship coefficient with her mate of 0.1. This probability drops to approximately 80% when the kinship coefficient of the pair increases to 0.3. The reduction in probability of litter production among paired females is greater among younger (age 2-3) and older (age 8+) paired females.

Calculation of litter size: Once the litters have been assigned to each successful adult female breeder, the size of each litter for each breeding female must be determined. Extensive analysis of the available breeding data appears to indicate only a very weak relationship between litter size and inbreeding coefficient of either the dam or the pups. This differs from the conclusion previously reported by Fredrickson et al. (2007), suggesting that the larger dataset now available no longer demonstrates the deleterious impacts of inbreeding affecting litter size. [Note that some inbreeding depression is now captured in the calculation of litter production as described above.] It is recognized that some unknown magnitude of inbreeding depression for various aspects of fitness may currently be masked by confounding factors such as the presence of diversionary feeding. Furthermore, issues around small available sample sizes and associated detection difficulties make the specification of inbreeding depression effects in wild wolf populations difficult at best. In light of this, our detailed analyses of the best available data indicate a relatively modest inbreeding impact across the demographic components that were studied. In contrast, the presence of supplemental (diversionary) feeding, which started in earnest in 2009 in response to significant rates of wolf removal following an increase in cattle depredation rates, does appear to influence litter size. Detailed statistical analysis of the available data by M. Clement (AZ Game and Fish Dept.) and M. Cline (NM Dept. of Game and Fish), ultimately led to the group to conclude that the presence of diversionary feeding was a causal factor influencing mean litter size, along with the age of the dam producing the litter.

The Poisson regression yields a result that is transformed through exponentiation to generate the final form of the functional relationship:

Litter size = e^x, with

$x = 1.0937+(0.49408*Fed)+(0.09685*((FAge-5.292)/2.217))+(-0.12114*((FAge-5.292)/2.217)^2)$

where

FAge = female age;
Fed = categorical variable describing if a female is fed (1 if fed, 0 if not fed).

Note that *FAge* is *z*-transformed to accommodate the structure of the Poisson regression. Among 6-year-old adult females, the analysis shows that reproducing dams receiving diversionary feeding produced litters of 5 pups on average, while those that were not fed produced litters of 3 pups on average. Each female that is determined to produce a litter in a given year is evaluated as to whether or not she receives diversionary feeding, according to a random number draw against a specified probability (see “Dynamic Diversionary Feeding” below for more information on this parameter). The size of her litter is then determined based on her age and the presence of feeding. See Appendix C for more information on the derivation of this function.

Annual environmental variability in reproduction: Expected mean reproductive rates will vary from year to year in response to variability in external environmental fluctuations. This process is simulated by specifying a standard deviation around the mean rate. The mean and variance for parameters defining reproductive success follow binomial distributions. We set the environmental variation (standard deviation) for the probability of pairing at 0.105 based on the extent of observed annual variation in pairing rates. Additionally, the standard deviation for mean litter size was set at 1.8 in accordance with the dispersion of data on litter size observed among wild reproducing females. Explicit estimation of natural variability in reproductive success from MWEPA data is tenuous at best, given the ongoing intensive management of this population since its inception.

Density-dependent reproduction: Wolves are likely to exhibit lower rates of pup production as population density increases towards the habitat's ecological carrying capacity. However, because of the mechanics of wolf management expected to take place on the landscape (see below), it is considered highly unlikely to see wolf densities approach a level where this effect would be observed. Consequently, we have not implemented a density-dependent mechanism for reproduction in our model.

<u>Mortality Parameters</u>

Data were used from the most recent phase of Mexican wolf population management in MWEPA (2009 – 2015) to develop baseline age-specific mortality estimates. This time period is characterized by a management strategy generating relatively robust population growth due to high pup survival rates and few individual removals after conflict with local human populations. Furthermore, it is likely that this strategy will continue into the future, making it an appropriate context for establishing baseline conditions. These baseline estimates were used as a guide to inform model scenarios exploring threshold mortality rates consistent with wolf population recovery. We assume no difference in mortality between males and females, in accord with available data and with other studies of wolf population demographics (e.g., Fuller et al. 2003, Adams et al. 2008, Smith et al. 2010). For more information on data collection related to age-specific wolf mortality in MWEPA, and the analytical methods used to estimate these mortalities, refer to Appendix D.

Pup (0-1) mortality: 28.2 ± 10%. The mortality estimate consists of two phases: an early phase from first observation of pups after emergence from the den (before 30 June) to the time of collaring (approx. mid-September), and a second phase from time of collaring to the next breeding season. The survival rates for these two phases are estimated as 0.83 and 0.865, respectively. Therefore, the total pup mortality rate from first observation to the next breeding cycle is 1 – [(0.83)*(0.865)] = 0.282.

<u>*Subadult (1-2) mortality*:</u> 32.7 ± 6.5%.

<u>*Adult (2+) mortality*</u>: 18.9 ± 6%. The recent period of population growth is at least in part characterized by a strong rate of adult survival. Specifically, radio-collar data indicates a mean annual adult mortality rate of 18.9%. This rate is likely to be on the low end of rates observed in other wolf populations exhibiting positive growth, such as the Greater Yellowstone Area population described by Smith et al. (2010) with an average adult rate of 22.9%. Therefore, for the purposes of using the PVA tool to explore demographic conditions that can lead to population recovery, we developed a set of scenarios featuring alternative estimates of mean annual adult mortality rates in addition to the aforementioned baseline value: 21.9%, 24.9%, 27.9%, and 30.9%. We focus on adult mortality and its impact on population performance because this parameter is a major factor driving population dynamics in wolves and other species with a similar life history (e.g., Carroll et al. 2014).

We have retained the density-dependent function for adult mortality that was included in the most recent PVA modeling effort (Carroll et al. 2014). This functional relationship is loosely based on observations of wolf dynamics in the Greater Yellowstone Area (Smith et al. 2010), although these same authors note the difficulty in detecting and interpreting this mode of density dependence across different wolf populations. We also must recognize that Mexican wolves in both the MWEPA and the Sierra Madre Occidental will likely persist at relatively low population densities, and therefore may not be significantly influenced by density-dependent processes.

“Catastrophic” Event

The most recent PVA effort (Carroll et al. 2014) identified an “episodic threat” to wolf populations in the form of a disease outbreak, with the primary impact targeting pup survival. They used data on canine distemper outbreaks in the Greater Yellowstone wolf population (Almberg et al. 2010) to specify the characteristics of this event. Participants in the current PVA effort broadened this definition of catastrophe to include any kind of event that would lead to major pup loss, with some associated increased mortality among adults.

The Yellowstone data suggest that three such outbreaks occurred there over a 20-year period, yielding an annual probability of occurrence of approximately 0.15. In the absence of data specific to Mexican wolves, we assumed the same frequency for a similar type of event occurring in the future in either the MWEPA or SMOCC populations. If such an event were to occur, the Yellowstone wolf population data cited above were used to estimate the impact to survival of both pups and adults in the year of the event. We assume that pup survival is reduced by 65% during the event, while adult mortality is reduced by 5%. As the primary impact of the simulated event is targeting pup survival, we do not incorporate an additional impact in the form of reduced reproductive output of adults.

Carrying Capacity

Estimates of the ecological carrying capacity (*K*) for all habitat areas to be considered in the recovery planning process are specified in the model. In the typical *Vortex* modeling framework, a population is allowed to increase in abundance under favorable demographic conditions until *K* is reached, after which time individuals are randomly removed from the population to bring the population back down to the value of *K*, thereby simulating a ceiling-type density dependence. Estimates of *K* for each population in this analysis are based on the habitat suitability analysis of Martínez-Meyer et al. (2017). Based on this analysis, we estimate *K* for the MWEPA, SMOCC-N and SMOCC-S populations to be 1000, 300, and 350 individuals, respectively. Note that this parameter is different from the management target parameter used to manage wolf populations at a specified abundance (see below). Because the population-specific management targets described below are less than the estimates for carrying capacity, the simulated populations will not increase in abundance beyond the targets and approach *K*. Nevertheless, the carrying capacity is specified for purposes of model completeness.

Management Target

In contrast to the ecological carrying capacity parameter described above, a critical feature of the current demographic model is the specification of a management target abundance. This target is defined as the wolf population abundance that is both biologically viable (according to identified recovery criteria) as well as socially acceptable in light of the expected ongoing issues around livestock depredation and other forms of wolf-human conflict.

Within the mechanics of the PVA model, the management target works much like the ecological carrying capacity parameter, except that population regulation in response to the management target is implemented through a type of “harvest” within the *Vortex* model framework. If a given population exceeds its management target abundance in a given year, both adults and pups are "harvested" from the population in equal numbers until the target abundance is reached. For example, if the population abundance at the beginning of the removal step is 320 and the management target is 300, *Vortex* would be expected to remove, on average, ten adults and ten pups at random from the population, with some variability around that mean resulting from random sampling of individuals for removal. This "harvest" occurs only if the population abundance exceeds the specified management target after the year's cycles of pup production and age-specific mortality have occurred.

An important goal of this PVA was to identify those population-specific management targets that would generate long-term population dynamics that are consistent with recovery. Therefore, we explored a range of reasonable management targets for analysis: 300, 340, and 379 for MWEPA; and 150, 200, and 250 for both SMOCC-N and SMOCC-S. The largest management target explored for MWEPA is based on previous analyses within the scope of this project, and is partly informed by existing management regulations for the Mexican wolf population in the United States. Under the elk abundance estimate utilized in the EIS for the MWEPA (80,811 elk: USFWS 2014), the wolf:elk ratio for the management targets of 300, 340 and 379 are estimated to be 3.7, 4.2, and 4.7 wolves per 1000 elk, respectively. These ratios are near the level (4-6 wolves per 1000 elk) where impacts have been proposed to begin occurring in the Northern Rockies (Hamlin et al. 2009). However, there is considerable uncertainty related to wolf:elk ratios and the climatic, hunting and prey refugia characteristics in the Southwest that would trigger the onset of these impacts (Hamlin et al. 2009; Vucetich et al. 2011; Hebblewhite 2013).

Dynamic Diversionary Feeding

As described earlier in the explanation of litter size calculations for wild adult females, the presence of diversionary feeding influences the size of that female's litter. Management authorities in the United States and Mexico estimate that about 70% of pairs are currently receiving diversionary feeding in each country. As the populations grow, the extent of feeding will decline due to logistical complexities and other sociological factors. The rate at which feeding declines will be a function of the rate of population growth to the management target; populations that are growing at a faster rate will experience a more rapid decline in the rate at which they are fed.

This dynamic diversionary feeding process was incorporated into all our population simulations. We assumed that feeding will begin to decline five years into the simulation, with the subsequent rate of decline from 70% feeding determined by the extent of growth toward that population's management target. Authorities assume that the long-term feeding rate will not drop to zero but will likely be maintained at approximately 15% to allow for management of occasional livestock depredations.

Metapopulation Dynamics

Our PVA model features a metapopulation structure in which wolves may naturally disperse from one population to another according to defined probabilities. We assume that only younger (1 to 4 years old), unpaired individuals are capable of dispersal, with males and females displaying equal tendencies to disperse. Furthermore, we assume a form of "stepping stone" model, where both the northernmost MWEPA population and the southernmost SMOCC-S populations are linked by dispersal to the central SMOCC-N population. In this linear spatial configuration, we assume that there is no functional connectivity between MWEPA and SMOCC-S (See Martínez-Meyer 2017 for more information on the geography of these populations).

Rates of dispersal among candidate individuals are based loosely on wolf behavioral dynamics, the distances between populations and the nature of the intervening terrain. We assume that the distance from MWEPA to SMOCC-N, along with the presence of an international border subject to intense scrutiny, will severely limit the extent of demographic connectivity. In contrast, while the intervening terrain between the two Sierra Madre Occidental populations is more rugged than that across the international border, the closer proximity between these two Mexico habitat units likely increases the probability of successful dispersal among them. Therefore, in the absence of specific dispersal data for Mexican wolves across this recovery landscape, we set the individual dispersal probability between MWEPA and SMOCC-N at 0.175% and between Mexican SMOCC populations 0.875%. These rates are symmetric between pairs of populations and are within the range of plausible values suggested by wolf population biologists participating in the current PVA effort. In addition, we assume that wolves pay a high cost to attempt cross-country dispersal. We use the estimate of 37.5% dispersal survival from the most recent PVA effort based on the published analysis of Carroll et al. (2014). In terms of absolute numbers and with a candidate population of 100 unpaired wolves age 1-4, the MWEPA – SMOCC-N rate corresponds to approximately one wolf dispersing to the recipient population every sixteen years. Note that the dispersal survival estimate does not include the probability of successful reproduction among dispersing animals.

Input Data for PVA Simulations: SSP Population

Initial Population Specification

All models for this analysis are based on the status of the wild and captive populations as of 31 December, 2015. This specification allows us to construct a full pedigree of all populations up to the date we choose to begin the population projection. This pedigree, uploaded to the software as a simple text file, includes the age and gender of all animals produced since the initiation of the captive management program between 1961 and 1980 (Hedrick et al. 1997). Additionally, the pedigree file includes the following information: age, sex, ID of the parents, reproductive status (number of offspring previously produced), ID of the current mate (if paired), and the SSP status (in the managed population or a non-breeder that is excluded from the genetic analysis). Based on information collated by the Mexican wolf SSP, we set the initial abundance for the captive population at 214 individuals, with the appropriate age-sex structure.

Reproductive Parameters

Breeding system: Wolves display a long-term monogamous breeding system. In the context of *Vortex* model development, adult breeding pairs are assumed to remain intact until either individual in the pair dies.

Age of first reproduction: We assume that both females and males are capable of producing pups when they are two years of age.

Maximum breeding age / longevity: Studbook data indicate that captive female wolves can reproduce through 12 years of age (14 for males), and can live in a post-reproductive state until about 17 years of age.

Litters per year: Wolves will produce one litter of pups per year.

Maximum number of pups per litter: Pup production in captivity is defined slightly differently from that in the wild, as litters are often observed at an earlier age in an intensively managed setting. Studbook analysis reveals a maximum litter size of 10-11 pups in rare occurrences. Note that the specification of litter size for each successfully breeding female in a given year is determined by a complex function involving a number of independent variables (see “Distribution of litters per year” below).

Sex ratio of observed pups: This ratio will be set at 50:50 for captive-born litters, with the understanding that the actual ratio within any one litter may deviate from this expected value through random variability.

Percentage of adult females "breeding" in a given year: As in the specification of this parameter for wild populations, we define this parameter as the proportion of adult females that are paired across years. Initial pairs for the onset of the simulation are specified in the studbook file, and all adults of suitable breeding age are considered a part of the "managed SSP population" and therefore capable of producing a litter in a given year.

Probability of litter production among paired females: The probability of a paired female successfully producing a litter is a complex function of a number of variables: dam age, sire age, age difference between dam and sire, and the past reproductive success of each adult (a categorical variable set to 1 if the individual has produced pups in the past and set to 0 otherwise). Data from the studbook are analyzed using logistic regression (J. Sahrmann, St. Louis Zoo, unpubl.); therefore, the functional form of the relationship is the inverse logit of the regression results:

Pr(pair produces a litter) = $\frac{1}{(1+e^{-x})}$, with

x = -1.489+(0.479**MAge*)-(0.048**MAge*^{2})+(0.415**MPar*)-(0.062**FAge*)+(1.092**FPar*)+(0.11803**dAge*)

where

MAge = male age;
FAge = female age;
MPar = male parity (reproductive success);
FPar = female parity (reproductive success); and
dAge = absolute value of difference in male and female age.

This gives a different probability of success for each pair. For example, a pair of 5-year-old proven breeders has a 71% chance of producing a litter, while a pair of 11-year-old wolves, neither of which have previously bred, has a 6% chance of success.

Calculation of litter size: Analysis of the studbook reveals that the size of a given litter among captive Mexican wolves is best predicted by a functional expression that includes the inbreeding coefficient of the dam, her age, and her past reproductive success (parity) as before. The Poisson regression yields a result that is transformed through exponentiation to generate the final form of the functional relationship:

Litter size = e^x, with

x = 1.64-(2.70**FDam*)-(0.274**FPar*)+(0.0823**FAge*)-(0.0000866*(*FAge*^{4})

where

FDam = inbreeding coefficient of the dam;
FPar = female parity (reproductive success); and
FAge = female age.

Using the above expression, we estimate that a middle-aged adult female with an inbreeding coefficient of 0.13 (mean *F* in the captive population as of 31 December 2015) would be expected to produce a litter of 4 – 5 pups, depending on whether or not she had produced a litter in the past. This is consistent with the mean litter size of just over 4 pups estimated from studbook analysis (Mechak et al. 2016). Variability in litter size (standard deviation around the mean) as analyzed from the studbook was 2.5 pups.

Mortality Parameters

Based on studbook data, we were able to generate the following age-specific mortality schedule (Table 1) that closely resembles that of Mechak et al. (2016):

Table 1. Age/sex-specific annual mortality rates for the Mexican wolf SSP population.

	Rate $q(x)$	
Age	Male	Female
0 – 1	39.0	36.0
1 - 2	2.0	2.0
2 - 5	2.0	2.0
6 - 9	6.0	6.0
10 – 12	15	10.0
13	25	15
14	36	35
15	42	40
16	71	67

There is little to environmental stochasticity in the relatively highly controlled captive environment; therefore, we do not specify a standard deviation for these mean mortality rates and allow variability across years to result purely from demographic stochasticity.

Carrying Capacity

The concept of carrying capacity for a captive population is different than that for a wild population. In the captive setting, *K* is functionally defined by the number of spaces (enclosures) available across all the zoological institutions currently holding the species of interest. Additionally, the institutions may choose to manage the breeding among adult pairs so as to maintain the population at a level slightly below the space allotment, thereby minimizing the risk of producing more animals than the available space can support. In our models, we define *K* for the SSP at 255 individuals, representing an abundance slightly below the maximum number of spaces to allow for some flexibility in long-term population management. If the population increases above *K* in a given year, *Vortex* will apply a small additional mortality risk to each wolf to try to bring the population back to 255 animals. Reproduction will also be slowed to allow just enough breeding to keep the population around *K* and not produce excess pups (see below). This is all simulated stochastically, so the population will show small fluctuations around *K*.

Simulating the SSP Masterplanning Process

Each year *Vortex* calculates the number of litters that are required to maintain the population at or near the maximum abundance (K), based on available space and the current population abundance and age structure (to estimate the expected number of deaths). The model algorithm then uses the demographic input data for the captive population, couple with an average breeding success rate of 42% (based on studbook analysis) to determine the number of breeding recommendations to create in that year. *Vortex* will initiate the pairing process at the top of the list of genetically important animals (ranked by the metric mean kinship, MK) and will assign a breeding recommendation to those high-priority females needed to produce the desired number of litters, taking into account the probability of breeding success (e.g., assuming a 25% success rate, a target of three 3 litters means the identification of sufficient breeding recommendations given to the top-ranked females to result in 12 pairings). The further the population is below available capacity, the more recommendations that would be made. If a recommended female does not have a mate, she is paired with the next highest ranked available male. As in the wild population component of the model, *Vortex* will not put together full siblings or parent-offspring pairs for mating.

Breeding pairs are split up, with the animals available to receive a new mate, under the following conditions:

- One of the wolves dies or becomes post-reproductive (i.e., turns 13 years old if a female, 15 years old if a male)
- One of the wolves has a mean kinship value that has dropped below the average MK value for the entire population.
- The pair has been together for two years but has not produced any offspring.

Input Data for PVA Simulations: Transfer (Release and Translocation) Dynamics

In order to enhance the viability of wild Mexican wolf populations, management authorities in the United States and Mexico want to use the PVA modeling effort to evaluate the potential benefits of (1) continued releases of wolves from the SSP to the existing MWEPA and SMOCC-N populations; (2) starting releases of wolves from the SSP to a new SMOCC-S population; and (3) proposed translocations of wolves from the larger MWEPA population to one or both SMOCC populations. These management alternatives can be simulated using the "Harvest" and "Supplement" modules of *Vortex*. Specifically, we can instruct the software to conduct an explicit transfer of individual wolves from one population to another, thereby retaining their individual demographic and genetic identities for the potential benefit of the recipient (and sometimes source) population.

A consistent feature of both releases and translocations is the transfer of an adult pair and their associated offspring (assuming that pair produced offspring in the year of their transfer). Unfortunately, while the software is sufficiently flexible to incorporate this mechanic, the current Mexican wolf model structure does not allow us to precisely identify a mated pair, along with the exact offspring they produced in that year, for transfer. Instead, we more simply choose an adult female and adult male, and three Age-0 individuals, to be designated for transfer. This simplification to our model mechanics will likely overestimate the genetic impact of a given release, since a set of two adults and three pups selected for release will not represent a true family unit but will be made up of animals that are likely to be unrelated (given the stochastic nature of animal selection in the model algorithm). The magnitude of this overestimate is unknown at present but could be the subject of more detailed future study. On the other hand, this overestimate will be diminished by the rather low survival rate of released and translocated animals (see Table 3 below). The transfer of one pair with pups therefore constitutes the removal of a total of five animals from the source population, while transferring two or four pairs means the removal of 10 or 20 animals, respectively. Our choice of the number of pups to be transferred is based on the assumption of some level of pup mortality between birth and the time of release. Where appropriate, the gender of the pups is assigned randomly by *Vortex* through probabilistic rounding.

Releases from the SSP: The choice of specific animals to release from the SSP is to a large degree informed by genetic criteria. Specifically, animals are chosen for release whose individual mean kinship (MK) is greater than the average MK of the full captive population. With this criterion in place, we are choosing individuals for release into the wild that are genetically over-represented in captivity. The strategy is meant to preserve the genetic integrity of the captive population, while also not compromising the genetic status of the wild population. Moreover, we are choosing younger adults, less than five years old, for release in order to increase their reproductive value to the wild population.

First, we included the actual release of wolves from the SSP to SMOCC-N that took place in 2016. Given that our simulations were initialized as of 1 January 2016, we wanted to include these releases to Mexico in order to more accurately portray the early dynamics of this population following the substantial demographic and genetic augmentation received from the SSP. While a total of 18 wolves were released

in two separate events during the second half of the year, it is estimated that only 12 of those animals survived to the next breeding season: nine pups (seven females, two males) and three subadults (all male). This release takes place in all simulations in model year 1 (calendar year 2016).
Second, the current Mexican Wolf EIS states that releases from the SSP to MWEPA will be conducted according to the following generic schedule:

- Release of two pairs with pups in model years 2 and 6;
- Release of one pair with pups in model years 10, 14 and 18.

This strategy, referred to hereafter as the "EIS" strategy, was included in all of the release scenarios discussed below. The interval between releases was to roughly correspond to the duration of one average wolf generation.

Third, in addition to the EIS releases into MWEPA, we evaluated releases from the SSP into the SMOCC-N and SMOCC-S populations. Either two or four pairs with pups were released every year into the Mexico populations over a total period of five years. Releases into SMOCC-N would begin in simulation year 2 (corresponding to calendar year 2017, given the initiation of our models on 1 January 2016), while releases into SMOCC-S would not begin until simulation year 7 (calendar year 2022).

Translocations from MWEPA: In addition to the releases of captive-bred wolves, we evaluated the utility of translocating wild-born wolves from MWEPA to either or both of the SMOCC populations. Either two or four pairs with pups were harvested from MWEPA and delivered to the SMOCC-N and SMOCC-S populations, with translocation events into each recipient population occurring every other year. A total of five events were scheduled for each population. We assumed that translocations into SMOCC-N would begin early in the simulation (model year 2), while translocations into SMOCC-S would require more time for organization and local approval, thereby beginning in model year 7.

Taken together, our analyses focused on four alternative wolf transfer strategies (Table 2):

- "000_00": No releases or translocations taking place throughout the duration of the simulation, thereby evaluating the potential to generate at least two viable wild Mexican wolf populations in the absence of additional transfer events beyond calendar year 2016.
- "EIS20_20": EIS releases into MWEPA; releases of two pairs with pups into SMOCC-N every year for five years (in addition to 2016 releases); no releases into SMOCC-S; translocations from MWEPA to SMOCC-N of two pairs with pups every other year in model years 2-10; no translocations from MWEPA to SMOCC-S.
- "EIS40_40": EIS releases into MWEPA; releases of four pairs with pups into SMOCC-N every year for five years (in addition to 2016 releases); no releases into SMOCC-S; translocations from MWEPA to SMOCC-N of four pairs with pups every other year in model years 2-10; no translocations from MWEPA to SMOCC-S.
- "EIS22_22": EIS releases into MWEPA; releases of two pairs with pups into SMOCC-N every year for five years (in addition to 2016 releases); releases of two pairs with pups into SMOCC-S every year for five years; translocations from MWEPA to SMOCC-N (two pairs with pups every other year in model years 2-10); translocations from MWEPA to SMOCC-S (two pairs with pups every other year in model years 7-15).

In addition to this base set of transfer schemes, a second set of strategies was developed to address specific issues that emerged from analysis of the original strategy set. This second set is composed of the following three strategies:

- "[EISx2]20_20": Based closely on the standard "EIS20_20" scheme, but now featuring a doubling of the extent of initial releases from the SSP to MWEPA. This means that four pairs with pups are transferred from the SSP to MWEPA in model years 2 and 6, and two pairs with pups are transferred in years 10, 14 and 18.
- "[EISx2]30_10": Doubled releases from SSP to MWEPA; releases of three pairs with pups from SSP to SMOCC-N every year for five years (in addition to 2016 releases); no releases into SMOCC-S; translocations from MWEPA to SMOCC-N of one pair with pups every other year in model years 2-10; no translocations from MWEPA to SMOCC-S.
- "[EISx2]40_00": Doubled releases from SSP to MWEPA; releases of four pairs with pups from SSP to SMOCC-N every year for five years (in addition to 2016 releases); no releases into SMOCC-S; no translocations from MWEPA to SMOCC-N or SMOCC-S.

All scenarios using these additional strategies feature a mean annual adult mortality rate of 24.9%, and the population management targets for the MWEPA and Sierra Madre Occidental populations were set at 379 and 200, respectively.

Note that, in practice, a translocation event could involve a wild-born wolf being brought into captivity for some length of time and then being returned to the wild in another location. The *Vortex* model used for this PVA does not keep track of the long-term location history of individuals to this level of detail; consequently, we simulate translocations only as direct wild-wild transfers.

The numbers in Table 2 actually refer to the number of wolves that are removed from the source population (either SSP or MWEPA) – not the final number of animals that survive after release. Detailed analysis of release data from MWEPA by J. Oakleaf indicate that a substantial fraction of those wolves released from the SSP die within the first year following release from captivity or after translocation from another wild population. The results of this analysis are presented in Table 3. Translocation data include those events that involve an intermediate stop in a captive facility as described in the previous paragraph. These survival rates (mean only) were incorporated directly into the *Vortex* supplementation module, thereby specifying an "effective" number of released or translocated individuals that are assumed to survive to the next breeding season. For example, if we were to release two pairs with pups from the SSP to MWEPA, we would harvest four adults from the SSP but would only successfully release [4*0.284] = 1.136 adults into the MWEPA population. Those individuals that do not "survive" (are not selected for release) would be permanently removed from the simulation. In using this mechanic, we assume that all mortality takes place relatively quickly after the transfer event – thereby preventing those animals from reproducing before they die. This is consistent with recent observations of wolf transfers into and among wild populations. For more information on how these post-transfer mortalities were derived, refer to Appendix D.

Table 2. Release / translocation schedules for three of the four alternative transfer strategies included in the Mexican wolf PVA. The "EIS" label refers to the proposed schedule of wolf releases from the SSP to MWEPA currently described in the Mexican Wolf EIS. The first pair of two numbers after the "EIS" label refers to the scheduled number of adult pairs to be released from the SSP to the SMOCC-N and/or SMOCC-S population, respectively. The second pair of numbers refers to the scheduled number of adult pairs to be translocated from the MWEPA population to the SMOCC-N and/or SMOCC-S population, respectively. The information presented within each table cell describing a scheduled transfer is of the format [#pairs x (#adults,#pups)]. See accompanying text for more information on the strategies and their simulation in the PVA model.

		EIS20_20					**EIS40_40**					**EIS22_22**				
Model Year	Calendar Year	SSP – MWEPA	SSP – SMOCC-N	SSP – SMOCC-S	MWEPA – SMOCC-N	MWEPA – SMOCC-S	SSP – MWEPA	SSP – SMOCC-N	SSP – SMOCC-S	MWEPA – SMOCC-N	MWEPA – SMOCC-S	SSP – MWEPA	SSP – SMOCC-N	SSP – SMOCC-S	MWEPA – SMOCC-N	MWEPA – SMOCC-S
1	2016															
2	2017	**2 x (2,3)**	**2 x (2,3)**		**2 x (2,3)**		**2 x (2,3)**	**4 x (2,3)**		**4 x (2,3)**		**2 x (2,3)**	**2 x (2,3)**		**2 x (2,3)**	
3	2018		**2 x (2,3)**					**4 x (2,3)**					**2 x (2,3)**			
4	2019		**2 x (2,3)**		**2 x (2,3)**			**4 x (2,3)**		**4 x (2,3)**			**2 x (2,3)**		**2 x (2,3)**	
5	2020		**2 x (2,3)**					**4 x (2,3)**					**2 x (2,3)**			
6	2021	**2 x (2,3)**	**2 x (2,3)**		**2 x (2,3)**		**2 x (2,3)**	**4 x (2,3)**		**4 x (2,3)**		**2 x (2,3)**	**2 x (2,3)**		**2 x (2,3)**	
7	2022													**2 x (2,3)**		**2 x (2,3)**
8	2023				**2 x (2,3)**					**4 x (2,3)**				**2 x (2,3)**	**2 x (2,3)**	
9	2024													**2 x (2,3)**		**2 x (2,3)**
10	2025	**1 x (2,3)**			**2 x (2,3)**		**1 x (2,3)**			**4 x (2,3)**		**1 x (2,3)**		**2 x (2,3)**	**2 x (2,3)**	
11	2026													**2 x (2,3)**		**2 x (2,3)**
12	2027															
13	2028															**2 x (2,3)**
14	2029	**1 x (2,3)**					**1 x (2,3)**					**1 x (2,3)**				
15	2030															**2 x (2,3)**
16	2031															
17	2032															
18	2033	**1 x (2,3)**					**1 x (2,3)**					**1 x (2,3)**				
19	2034															
20	2035															

Table 3. Estimated survival rates (mean ± 95% CI) of pups and adults within one year of their transfer to another population as simulated in the Mexican wolf PVA. A release involves the transfer of captive individuals in the SSP population to the wild, while a translocation involves the transfer of wolves in the MWEPA population to one or both of the proposed habitat areas in Mexico's Sierra Madre Occidental. Refer to Tables D-5 and D-7 (Appendix D) for sample sizes (radio days) used to derive these estimates.

Age Class	Release	Translocation
Pup	0.496 (0.268, 0.917)	0.555 (0.246, 1.000)
Adult	0.284 (0.173, 0.465)	0.527 (0.406, 0.685)

PVA Simulation Structure

As described in the previous section, a select set of simulation input parameters – wild population management target, annual adult mortality rate, and transfer (release / translocation) schedule – span a range of alternative values for the purposes of evaluating the required conditions for wild population viability. Our simulations must therefore test multiple combinations of those parameter values to identify the parameter space that predicts the demographic and genetic conditions that meet the appropriate recovery criteria. In the context of our PVA modeling effort, this means that we construct an array of model scenarios that are defined by combinations of those parameter values.

Figure 2 maps out the scenario structure for this analysis. Each set of population management targets is tested against each combination of annual adult mortality rate and transfer schedule, yielding 100 separate scenarios for analysis ((5 management targets) x (5 mortality rates) x (4 transfer schedules)). A smaller set of additional scenarios were constructed to address more detailed questions that will be discussed in the Results section.

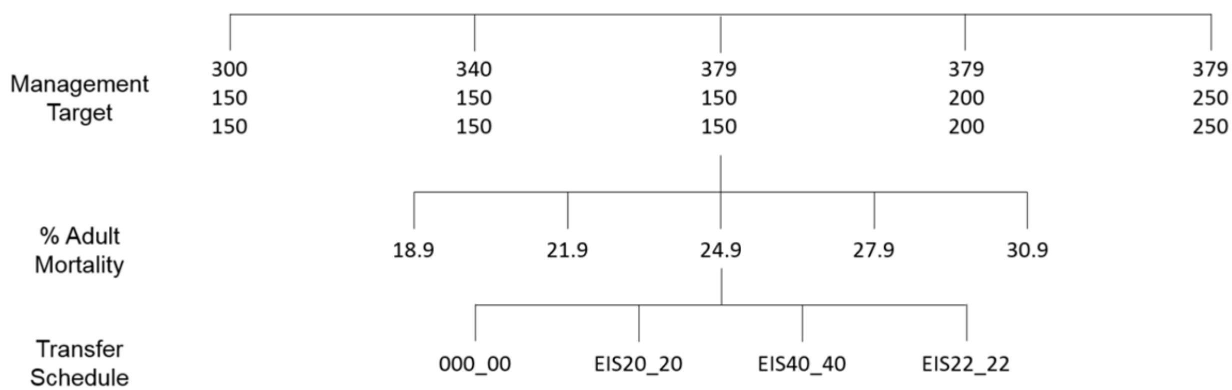

Figure 2. Diagrammatic sketch of Mexican wolf PVA scenario structure. The three values for population management target are listed as MWEPA (top), SMOCC-N (middle) and SMOCC-S (bottom). Adult mortality rates are listed as annual mean rates, and the transfer schedule nomenclature is defined in Table 2.

All scenarios projected wild and captive wolf population dynamics over a period of 100 years, starting approximately from the initiation of the first breeding cycle in the spring of 2016. Each scenario was repeated 1,000 times in order to assess the impact of stochastic variation in demographic and genetic processes as described in the previous section. Scenario output was reported in a manner intended to best inform the derivation of demographic and genetic recovery criteria. Specifically, the following output metrics are reported for each wild population in each scenario:

- Probability of population extinction within the 100-year timeframe of the simulation;
- Mean long-term population abundance (where appropriate);
- Mean final gene diversity (expected heterozygosity) at the end of the 100-year simulation;
- Proportional retention of final gene diversity relative to the starting value for that population; and
- Proportional retention of final gene diversity relative to the final value for the SSP population.

This final output metric is intended to assess the genetic integrity of the wild populations relative to the source of animals used to initiate those populations: the SSP population maintained among numerous zoological institutions across North America. As the SSP population represents the origin of all wolves following the taxon’s extirpation in the wild, it is the source of all genetic variation that can be transferred to wild populations. Stated another way, it is reasonable to assume that, at least in the broad statistical sense, the amount of gene diversity in any one wild population is itself a proportion of the gene diversity currently retained in the SSP. Consequently, it may be instructive for the purposes of recovery planning to consider the proportion of that genetic variation remaining in the source population that is present in each of the wild populations.

Results of Simulation Modeling

Confirmation of Selected Model Performance Elements

Before discussing the detailed results of specific scenarios, it is instructive to briefly review the broad demographic performance of simulated Mexican wolf populations in a representative scenario. In particular, it is important to confirm the reproductive performance of the simulated populations, as this is the most complex component of the model. A summary of the relevant demographic parameters is presented below for a typical MWEPA wolf population.

- Mean annual proportion of adult females paired: 0.77. This is consistent with expectations defined through the specification of the FPOOL pairing function. This value is also in accord with field observations of the number of packs observed in the MWEPA population.
- Mean annual proportion of paired females producing a litter: 0.72 (maximum) to 0.64 (end). These values are consistent with the values predicted from the relationship discussed in Appendix B (Figure B-1) across all adult ages and as inbreeding levels increase broadly from about 0.2 at the beginning of any given scenario to about 0.3 in the absence of significant genetic input from the SSP population.
- Mean litter size across reproducing females: 3.5 (early) to 2.95 (late). This is consistent with expectations defined through the specification of mean litter size in Appendix C (Figure C-1). Given that mean litter size among middle-aged females is predicted to be approximately five pups and the extent of diversionary feeding present at the start of the simulations is 0.7, we would expect approximately 3.5 pups per litter in the early years. Similarly, in the later stages of the simulation when the extent of diversionary feeding declines to about 0.15, a mean litter size of approximately three pups fits with the litter size predicted in the absence of diversionary feeding.

The simulated populations in Mexico demonstrate this same degree of consistency in population demographic performance. Therefore, we believe our prospective models can be viewed as internally consistent and generating demographic dynamics that agree with baseline expectations of Mexican wolf reproductive characteristics.

Analysis of the Status Quo

Before evaluating the full set of prospective analyses making up this PVA, a preliminary scenario was designed where the population-specific management targets for MWEPA and SMOCC-N were set to a small increase above the 31 December 2015 abundances. This is meant to explore the viability of these two populations at approximately their current abundance. The management target for MWEPA was set at 135 wolves, while that for SMOCC-N was set at 40 wolves. Neither population receives releases or translocations beyond the 2016 release to SMOCC-N from the SSP.

Under these conditions, the MWEPA population has a probability of persisting for the next 100 years of 0.539, while the probability for SMOCC-N is just 0.001. Even if the MWEPA population persists for this period of time, the mean expected population size is likely to decline to less than 50 animals after an initial increase to about 120 wolves over 10-20 years. Gene diversity for the MWEPA population declines to 0.541, significantly below its original value and far below the final value for the SSP. The accumulation of inbreeding and a reduction in the extent of diversionary feeding, with the resultant decrease in pup production, is the likely cause of this steady decline that begins about 20 years into the simulation.

Demographic Sensitivity Analysis

This PVA effort does not include the presentation of a formal sensitivity analysis of demographic parameters. The sensitivity analysis conducted by Carroll et al. (2014) provides much of the relevant information in this regard, where adult mortality rate, female breeding rate, population abundance threshold and strength of inbreeding depression were identified as the primary factors influencing population extinction risk. Additional sensitivity analyses (not reported here) were conducted in the early phases of the current modeling effort, largely as a method for prioritizing efforts to generate more accurate estimates of parameter values identified as sensitive.

Scenario Set 1: No Additional Transfers to and among Wild Populations

The first set of scenarios explores the capacity for each of the three population units to achieve viability on their own, with no further introgression of wolves from SSP releases or from wild-wild translocations. Under these conditions, the SMOCC-N population may receive individuals through occasional dispersal from MWEPA, while the SMOCC-S unit – which starts the simulation with no wolves – can only receive wolves through occasional dispersal from SMOCC-N.

MWEPA population: Under the condition of no additional transfers, extinction risks for the simulated MWEPA populations remain below 10% as long as the mean adult mortality rate is below 24.9% (Figure 3). Above this rate, extinction probabilities increase more rapidly to nearly 0.7 when the management target is 300 wolves. At the lower mortality rates (< 25%), extinction risk is negligible and there is very little influence of management target on the extinction risk. While the risk of extinction is low at intermediate mortality rates, the long-term abundance typically reaches a maximum of 80 to 90% of the management target approximately 40 years into the simulation and then begins to decline thereafter. The decline is likely due to a combination of higher adult mortality in the face of reduced litter production as inbreeding increases and reduced litter size as the extent of diversionary feeding drops from 70% of reproducing females to 15% over the first 15 – 25 years of the simulation.

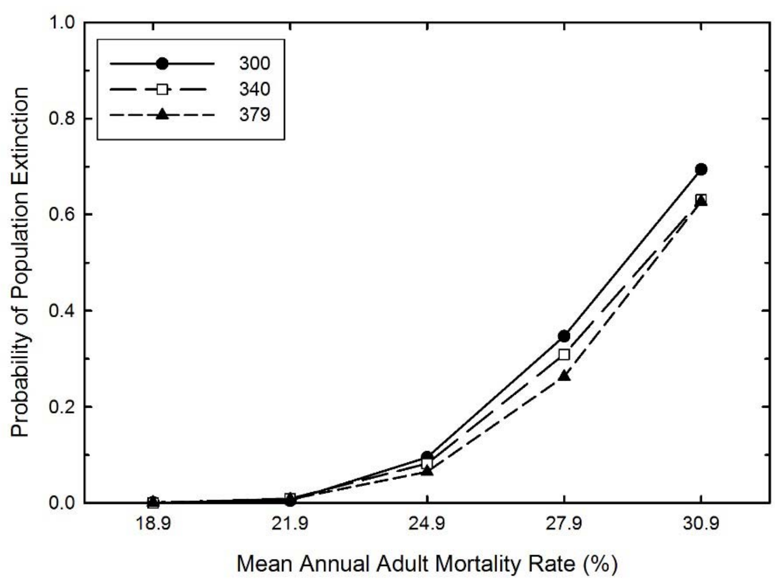

Figure 3. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "000_00".

At low to intermediate adult mortality rates, simulated MWEPA populations retain approximately 88% to 91% of the initial gene diversity present in that population at the beginning of the simulation (Table 4). As expected, larger management targets result in larger GD retention, although the gains are modest. Despite reasonable GD retention relative to the initial starting conditions, the final GD value for MWEPA is just 83% to 86% that of the SSP population at the end of the simulation. This reduced relative retention reflects the greater capacity for genetic diversity maintenance in the SSP through more intensive breeding management, as well as the improved genetic starting conditions for the SSP relative to MWEPA.

Table 4. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the MWEPA population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets and with the "000_00" wolf transfer scheme. The first value in each cell gives the final gene diversity value for that simulation at year 100. The first value in parentheses gives the proportional GD retention at year 100 relative to the starting value for MWEPA for all simulations (GD = 0.741), while the second value in parentheses gives the proportional GD retention at year 100 relative to the ending value for the SSP population (GD = 0.785). The last row of the table gives the GD and extent of retention for the SSP population as a reference.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.677 (0.913; 0.862)	0.668 (0.902; 0.852)	0.651 (0.878; 0.829)	0.624 (0.842; 0.795)	0.595 (0.803; 0.758)
340	0.682 (0.920; 0.869)	0.675 (0.910; 0.860)	0.659 (0.889; 0.840)	0.633 (0.854; 0.807)	0.604 (0.815; 0.770)
379	0.687 (0.927; 0.875)	0.679 (0.916; 0.865)	0.665 (0.897; 0.847)	0.644 (0.869; 0.821)	0.615 (0.830; 0.784)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

SMOCC-N population: The SMOCC-N population demonstrates a low risk of extinction at the lowest adult mortality rate, but the risk begins to increase at higher mortality rates (Figure 4). The rate of increase in extinction probability is greater when the management target is set to its lowest level (150 wolves), rising to greater than 0.3 at the intermediate mortality rate of 24.9%. This is a result of the higher rates of inbreeding and associated genetic impacts acting on this smaller population, as well as the negative impacts of occasional stochastic events reducing survival and/or reproduction from one year to the next. Note that the extinction probability is not markedly impacted by the size of the MWEPA management target. This is because the level of demographic connectivity between these two populations is very small, meaning that the SMOCC-N population is effectively isolated under the conditions described in this set of scenarios. Separate analysis of PVA model output not reported in detail here indicates that the level of dispersal featured in the model results in an annual rate of immigration from MWEPA into SMOCC-N of just 0.05 – 0.1 wolves.

Gene diversity retention rates for the SMOCC-N population, relative to the value at the start of the simulation, are actually higher than that for the MWEPA population at lower adult mortality rates (Table 5). This is due to the 2016 SSP releases into SMOCC-N which result in a significant infusion of genes from the SSP into the wild. However, the smaller size of this population means that it will lose gene diversity more rapidly over time so that the final GD relative to the final value for the SSP is lower for SMOCC-N than for MWEPA. Again, the effective isolation of these populations means that both demographic and particularly genetic stability may be compromised over the longer-term as stochastic events reduce demographic rates and inbreeding genetic drift lead to reduced genetic variability in these smaller populations.

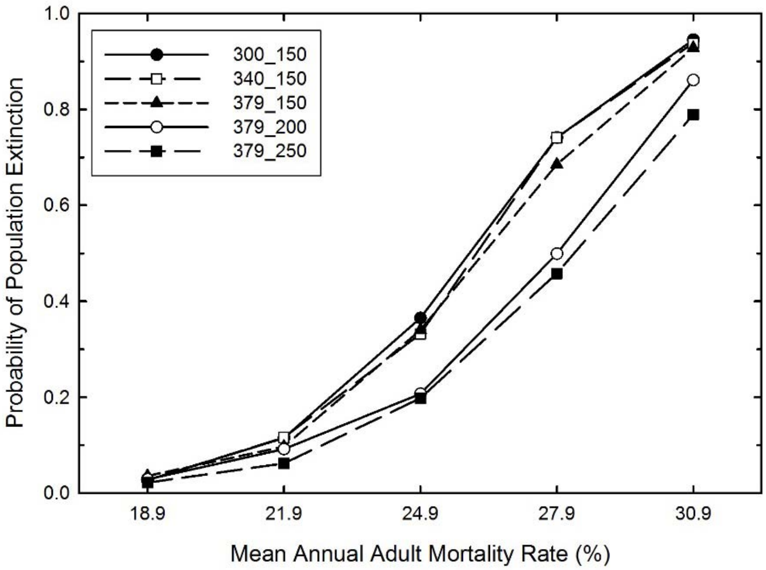

Figure 4. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “000_00”. The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-N target.

Table 5. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-N population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets, and with the “000_00” wolf transfer scheme. The first value in each cell gives the final gene diversity value for that simulation at year 100. The first value in parentheses gives the proportional GD retention at year 100 relative to the starting value for SMOCC-N for all simulations (GD = 0.691), while the second value in parentheses gives the proportional GD retention at year 100 relative to the ending value for the SSP population (GD = 0.785). The last row of the table gives the GD and extent of retention for the SSP population as a reference.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.649 (0.939; 0.827)	0.630 (0.912; 0.803)	0.598 (0.865; 0.762)	0.571 (0.826; 0.728)	0.540 (0.781; 0.688)
340_150	0.651 (0.942; 0.830)	0.635 (0.919; 0.809)	0.607 (0.878; 0.773)	0.561 (0.812; 0.715)	0.526 (0.761; 0.670)
379_150	0.652 (0.944; 0.831)	0.636 (0.920; 0.811)	0.609 (0.881; 0.776)	0.577 (0.835; 0.735)	0.528 (0.764; 0.673)
379_200	0.672 (0.973; 0.856)	0.660 (0.955; 0.841)	0.637 (0.922; 0.812)	0.602 (0.871; 0.767)	0.563 (0.815; 0.717)
379_250	0.684 (0.990; 0.871)	0.672 (0.973; 0.856)	0.650 (0.941; 0.828)	0.625 (0.904; 0.796)	0.584 (0.845; 0.744)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

SMOCC-S population: The initially vacant SMOCC-S population unit can potentially be colonized with wolves under the conditions explored in this set of scenarios, via occasional successful dispersal of wolves from the SMOCC-N population to the north. When the management target is just 150 wolves for both Sierra Madre populations, the probability of failing to establish a population in SMOCC-S is significant at all mean adult mortality rates, and regardless of the MWEPA management target (Figure 5). This is expected since the MWEPA population is again effectively isolated from its counterparts in Mexico, so establishing a population in SMOCC-S is solely dependent on successful dispersal from SMOCC-N followed by successful reproduction once they have arrived. Interestingly, the probability of failing to establish a SMOCC-S population drops to just 0.143 when the SMOCC management targets are each expanded to 250 wolves and under the most optimistic adult mortality rate. Under the intermediate mortality rate, that probability of failure increases to 0.53. If a population were to become established there under conditions of intermediate adult mortality, the mean expected wolf abundance estimate from the model is 64, 106 or 163 wolves for management targets of 150, 200 or 250, respectively.

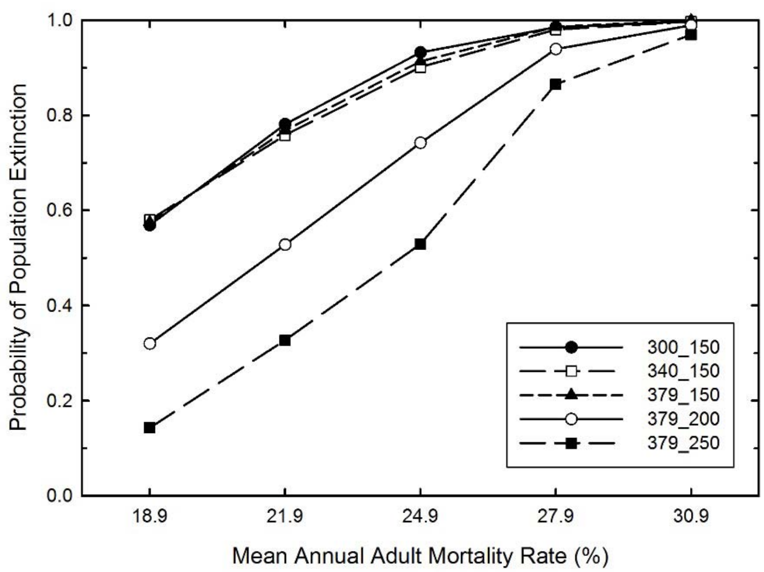

Figure 5. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “000_00”. The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-S target.

The extent of gene diversity retained in the SMOCC-S population, as a proportion of that which is present in the SSP population, ranges from approximately 64% to 76% depending on the size of the SMOCC-S management target and the underlying mean adult mortality rate (Table 6). Actual GD values among extant populations are quite low, on the order of just 0.46 to 0.59. This is due to the small size of any wolf population that may persist in the SMOCC-S population unit for any extended period of time, with the resulting rapid loss of genetic variants through random genetic drift and inbreeding.

Table 6. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-S population of Mexican wolves, under the range of tested annual adult mortality rates and with the “000_00” wolf transfer scheme. The first value in each cell gives the final gene diversity value for that simulation at year 100. The value in parentheses gives the proportional GD retention in SMOCC-S at year 100 relative to the ending value for the SSP population (GD = 0.785). The last row of the table gives the GD and extent of retention for the SSP population as a reference.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.542 (0.691)	0.526 (0.670)	0.513 (0.654)	0.484 (0.617)	0.462 (0.587)
340_150	0.538 (0.686)	0.519 (0.661)	0.501 (0.638)	0.499 (0.636)	0.449 (0.572)
379_150	0.540 (0.688)	0.530 (0.675)	0.504 (0.642)	0.514 (0.655)	0.457 (0.582)
379_200	0.567 (0.722)	0.558 (0.711)	0.534 (0.680)	0.514 (0.655)	0.496 (0.632)
379_250	0.594 (0.757)	0.575 (0.733)	0.557 (0.710)	0.531 (0.677)	0.492 (0.627)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

The trajectories of average gene diversity through time among populations from a representative scenario in the “000_00” transfer scheme are shown in Figure 6. Note the attenuated rate of loss in gene diversity in the SSP population, especially in the first 10 years of the simulation as genetically over-represented wolves are selected for the 2016 release to the SMOCC-N population. Of particular interest is the significant gain in gene diversity in the SMOCC-N population after the 2016 release from the SSP, where GD increases from its initial value of 0.691 to 0.781 – a 13% proportional increase immediately after the release. At the same time, also note the more rapid rate of GD loss in this population as its smaller size leads to more rapid accumulation of inbreeding and greater rates of random genetic drift in the absence of significant dispersal of wolves from MWEPA. The erratic nature of the trajectory for the SMOCC-S population reflects the smaller number of extant populations used to estimate the average gene diversity value at each timestep, as well as the very small population abundances after wolves disperse there from the neighboring SMOCC-N population

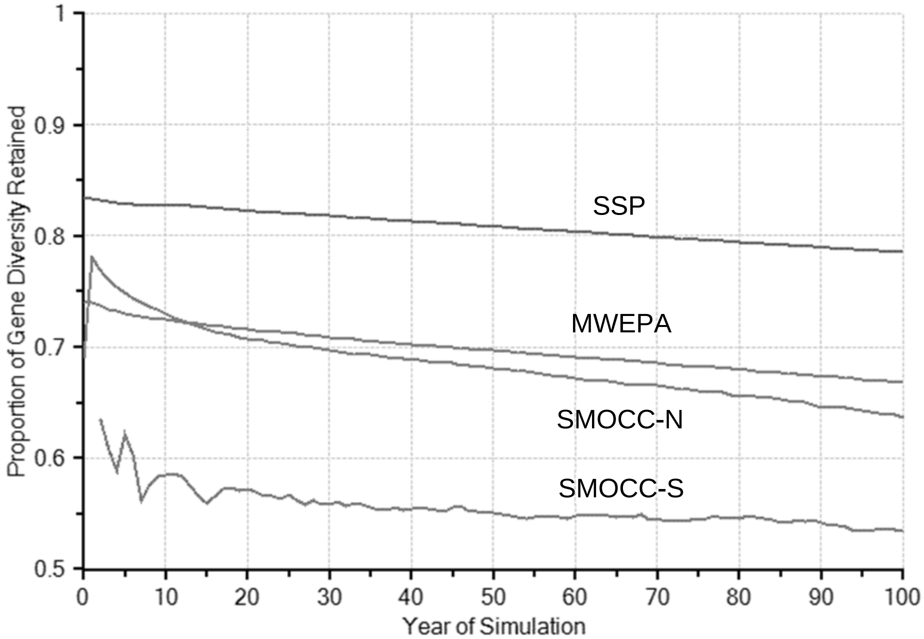

Figure 6. Average gene diversity over time for Mexican wolf populations subject to 24.9% mean annual adult mortality and under the "000_00" transfer scheme. Management targets are set at 379 for MWEPA and 200 for SMOCC-N and SMOCC-S.

Scenario Set 2: Releases to MWEPA; Releases and Translocations to SMOCC-N

We will now explore scenarios that feature releases to the MWEPA and SMOCC-N populations from the SSP as well as translocations from the MWEPA population to the SMOCC-N population. The goal with these scenarios is to determine if the proposed release strategies assist in generating a viable population of wolves in the northern Sierra Madre, with perhaps the associated creation of a linked population of wolves to the south. Related to this is the question of the degree to which removing pairs from MWEPA for translocation may negatively impact its long-term demographic and/or genetic stability.

MWEPA receives wolves according to the release strategy outlined in the Mexican wolf EIS across all scenarios in this scenario set. In addition, the first set of scenarios (the "EIS20_20" strategy) features the release of two pairs of wolves with pups to SMOCC-N at each of five release events, as well as the translocation of two pairs with pups from MWEPA to SMOCC-N at each of five translocation events. No wolves are explicitly transferred to the SMOCC-S population unit. See Table 2 for more information on the nature of these transfer strategies.

EIS20_20 – MWEPA population: Under the EIS_20_20 strategy, the extinction risk for MWEPA remains low over the low and intermediate adult mortality rates, and again increases rapidly at higher mortality rates (Figure 7). Comparison with the "000_00" strategy featuring no releases or translocation reveals that the risk of extinction in MWEPA increases slightly with the inclusion of translocations out of MWEPA to SMOCC-N. For example, at the intermediate mortality rate of 24.9%, the risk of extinction increases from 0.095 to 0.114. This is indeed a rather minor increase, but it highlights the additional demographic burden that a source population may incur when animals are moved out for translocation. It is important to recognize that the input of wolves to MWEPA through the release strategy does not balance the removal of wolves for translocation to SMOCC-N. The “EIS20_20” means that ten pairs with pups will be removed from MWEPA over five years, and is slated to receive seven pairs with pups from the SSP over about 16 years. However, the high rate of post-release mortality included in the models means that just less than two pairs (7*0.284) are expected to survive to the next breeding cycle. This rather large net loss of wolves over the early years of the simulation is likely the cause of any increased extinction risk. In particular iterations, stochastic processes in early years may lead to significant reductions in MWEPA population size that are exacerbated by removals for translocation. This could begin a cycle of continued demographic and genetic instability that, infrequently, could lead to the extinction of that population.

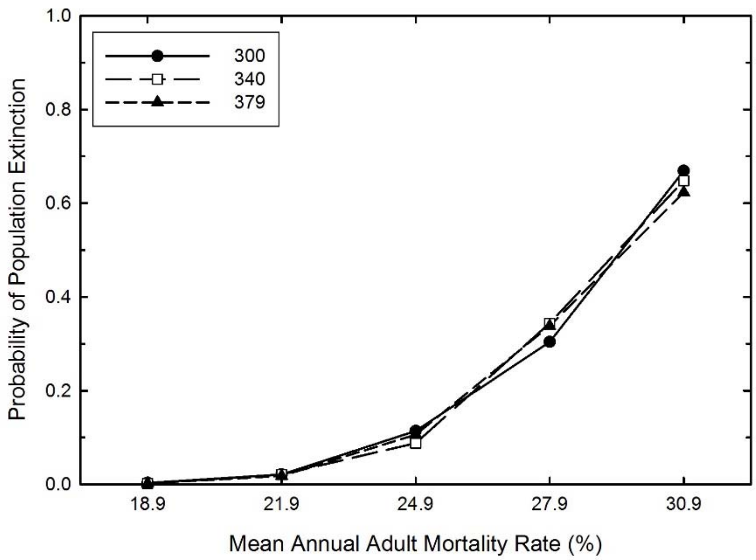

Figure 7. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS20_20”.

Among extant populations, the mean population abundance reaches a maximum at approximately 80% of the management target (240 to 300 at management targets of 300 to 379) at the intermediate adult mortality rate (24.9%), but then begins to decline slowly at the smallest management target as pup production declines, likely due to inbreeding and reduced diversionary feeding. Lower mortality rates lead to more stable populations at 85% to 95% of the management target.

Gene diversity in the MWEPA population increases slightly in this set of scenarios compared to the “000_00” transfer strategy as some new genetic variation is added through the EIS releases strategy. Retention of GD in MWEPA is 90% to 94% of the initial value for that population over the low to intermediate mortality rates tested, and across the three proposed management targets (Table 7). However, the population retains only about 85% to 89% of the gene diversity present in the SSP. Higher mortality rates result in only 84% to 90% retention relative to MWEPA original values, and 79% to 85% GD retention relative to the SSP.

Table 7. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the MWEPA population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets and with the “EIS20_20” wolf transfer scheme. See legend for Table 4 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.690 (0.931; 0.879)	0.683 (0.921; 0.870)	0.670 (0.904; 0.853)	0.650 (0.877; 0.828)	0.619 (0.835; 0.788)
340	0.696 (0.939; 0.886)	0.691 (0.932; 0.880)	0.678 (0.914; 0.864)	0.660 (0.890; 0.841)	0.633 (0.854; 0.806)
379	0.700 (0.944; 0.892)	0.694 (0.936; 0.884)	0.683 (0.921; 0.870)	0.664 (0.896; 0.846)	0.647 (0.873; 0.824)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS20_20 – SMOCC-N population: The addition of wolves to the SMOCC-N population through both releases from the SSP and translocations from MWEPA lead to low extinction probabilities at low and intermediate adult mortality rates (Figure 8). In fact, the risk drops below 0.10 at larger management targets when the annual adult mortality rate increases to 27.9%. Note that at the highest mortality rate, the SMOCC-N extinction risk at the largest management targets is less than that for the largest MWEPA target (Figure 7). This likely results from relatively high removal rates from MWEPA depressing population abundance in the early years, and from a lower level of gene diversity in MWEPA despite its larger abundance. At the same time, SMOCC-N is receiving wolves from both the SSP and from MWEPA in those same early years, helping to reduce risk when the population is at its smallest abundance. Even with the high post-transfer mortality rates included in the model, the transfer of an initial total of 20 pairs with pups over the first ten years of the simulation acts to significantly increase population demographic stability. The value of the MWEPA management target has little impact on SMOCC-N demographic performance.

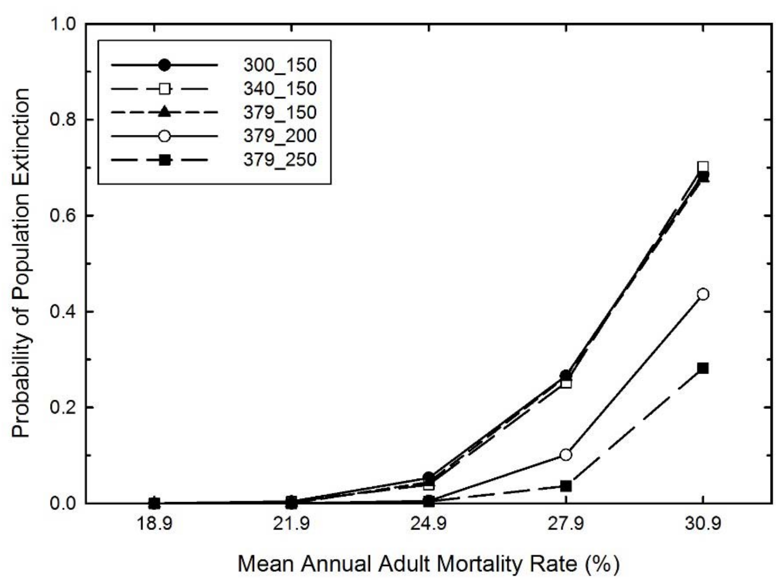

Figure 8. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS20_20”. The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-

Among extant populations, the long-term population abundance reaches a maximum around year 40 at approximately 80% to 90% of the management target at low to intermediate adult mortality rates, but begins to decline after that, with more rapid declines to about 60% of the management target at the intermediate mortality rate.

The "EIS20_20" transfer schedule also leads to significant increases in gene diversity in the SMOCC-N population (Table 8). Once again, the impact of the 2016 releases to SMOCC-N is dramatic; the final GD value is 96% to 106% relative to the initial value before the releases at low to intermediate mortality rates. The retention relative to the SSP under these same mortality rates is 84% to 94%. When the SMOCC-N management target increases to 200-250, GD retention approaches and exceeds 90% relative to the SSP.

Table 8. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-N population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets, and with the "EIS20_20" wolf transfer scheme. See legend for Table 5 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.691 (1.000; 0.880)	0.681 (0.986; 0.868)	0.660 (0.955; 0.841)	0.622 (0.900; 0.792)	0.583 (0.844; 0.743)
340_150	0.692 (1.001; 0.882)	0.682 (0.987; 0.869)	0.660 (0.955; 0.841)	0.625 (0.904; 0.796)	0.584 (0.845; 0.744)
379_150	0.693 (1.003; 0.883)	0.683 (0.988; 0.870)	0.664 (0.961; 0.846)	0.624 (0.903; 0.795)	0.585 (0.847; 0.745)
379_200	0.718 (1.040; 0.915)	0.711 (1.029; 0.906)	0.699 (1.012; 0.890)	0.668 (0.967; 0.876)	0.624 (0.903; 0.795)
379_250	0.734 (1.062; 0.935)	0.728 (1.054; 0.927)	0.718 (1.039; 0.915)	0.696 (1.007; 0.887)	0.659 (0.954; 0.839)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS20_20 – SMOCC-S population: The increased demographic stability of the SMOCC-N population under the "EIS20_20" release strategy leads to an increased opportunity for population establishment in SMOCC-S, even when transfers are not explicitly included in Mexican wolf management as simulated in this set of scenarios. When the management target is 200 or 250, the probability of failing to establish a population in SMOCC-S drop to 5% to 40% at low to intermediate adult mortality rates (Figure 9). The probability of establishing a population remains low at a management target of 150. If a population were to become established in SMOCC-S, the abundance at year 100 would range from about 60 to 90 wolves at intermediate mortality rates and at a management target of 200 or 250.

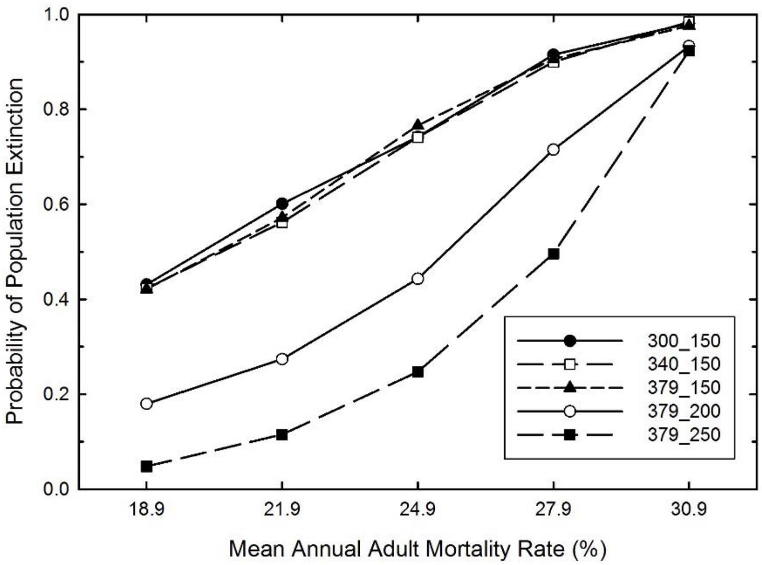

Figure 9. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS20_20”. The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-

Despite some level of demographic stability that may be observed in an established SMOCC-S population under the conditions or our simulations, the extent of gene diversity retention in the population remains low (Table 9). Under the smallest management target of 150 wolves and at low to intermediate adult mortality rates, the extent of GD retained relative to the final value for the SSP ranges from 70% to 74%. Increasing the management target to 200 or 250 increases final GD retention in SMOCC-S to 75% to 82% of the final SSP value.

Table 9. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-S population of Mexican wolves, under the range of tested annual adult mortality rates and with the “EIS20_20” wolf transfer scheme. See legend for Table 6 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.582 (0.741)	0.564 (0.718)	0.550 (0.701)	0.531 (0.676)	0.498 (0.634)
340_150	0.583 (0.743)	0.566 (0.721)	0.556 (0.708)	0.520 (0.662)	0.523 (0.666)
379_150	0.580 (0.739)	0.570 (0.726)	0.557 (0.710)	0.520 (0.662)	0.518 (0.660)
379_200	0.619 (0.789)	0.603 (0.768)	0.588 (0.749)	0.562 (0.716)	0.539 (0.687)
379_250	0.643 (0.819)	0.632 (0.805)	0.617 (0.786)	0.597 (0.761)	0.582 (0.741)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

The trajectories of average gene diversity through time among populations from a representative scenario in the "EIS20_20" transfer scheme are shown in Figure 10. The general nature of the trajectories is similar to that shown in Figure 6 for the "000_00" transfer scheme, with the notable exception of the SMOCC-N trajectory. When SMOCC-N receives releases from the SSP and translocations from MWEPA, the initial jump in GD following the 2016 releases is now sustained to a much greater degree compared to the scenario featuring only the 2016 releases (Figure 6). In fact, the final gene diversity value for SMOCC-N is higher than that for the MWEPA population. Notice the small gains in gene diversity in the MWEPA population in the first 20 years of the simulation, resulting from the EIS release schedule. However, the smaller size of those releases, particularly in light of the larger recipient population, yields relatively little gain to MWEPA.

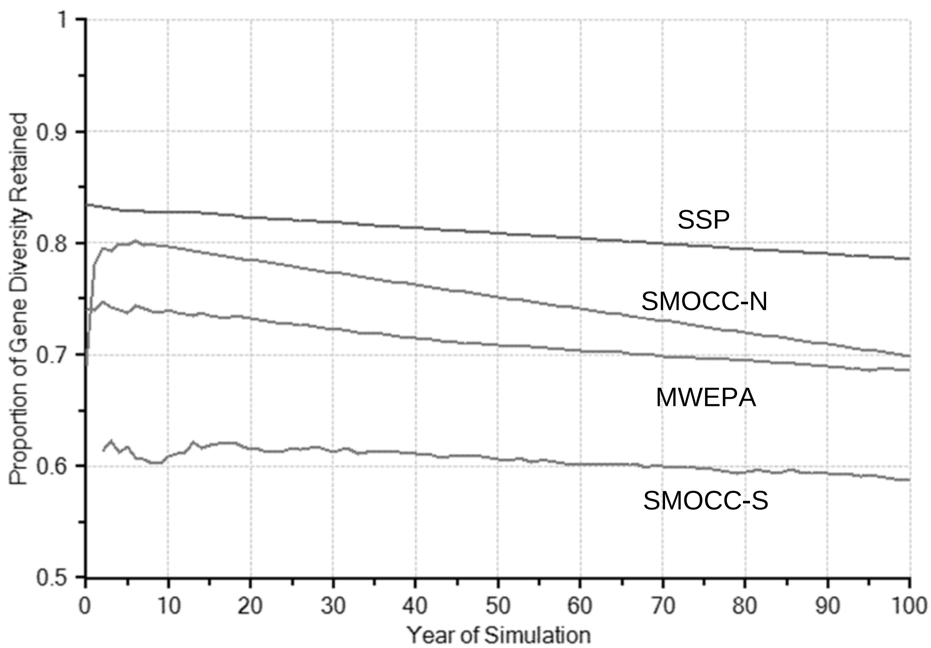

Figure 10. Average gene diversity over time for Mexican wolf populations subject to 24.9% mean annual adult mortality and under the "EIS20_20" transfer scheme. Management targets are set at 379 for MWEPA and 200 for SMOCC-N and SMOCC-S.

The second group of scenarios in the set feature the "EIS40_40" strategy. Once again, MWEPA receives wolves according to the release strategy outlined in the Mexican wolf EIS across all scenarios in this group. In addition, the extent of releases and translocations to SMOCC-N is now doubled so that four pairs of wolves with pups are now released to SMOCC-N from the SSP at each release event, and four pairs with pups are now translocated from MWEPA to SMOCC-N at each translocation event. No wolves are explicitly transferred to the SMOCC-S population unit. See Table 2 for more information on the nature of these transfer strategies.

EIS40_40 – MWEPA population: Despite the infusion of SSP wolves into the population through the EIS release strategy, the removal of 20 pairs of wolves with pups in the first ten years of the simulation leads to a further reduction in viability of the MWEPA population (Figure 11). Extinction risk is low (<0.10) only at the lowest adult mortality level (18.9%) and increases to 0.36 at the intermediate mortality rate of 24.9%. As before, the risk of MWEPA population extinction is not impacted by the size of the management target, suggesting that the removals for translocation in the early years of the simulation can set in motion a process of demographic and genetic destabilization that leads to ultimate extinction.

Extant populations reach a long-term population abundance of about 220 to 280 wolves when the management target is set to 300 to 379, respectively. The approach to this long-term abundance is slower as the larger set of removals limits growth; the abundance levels reported above are not attained until about 60 – 70 years into the simulation.

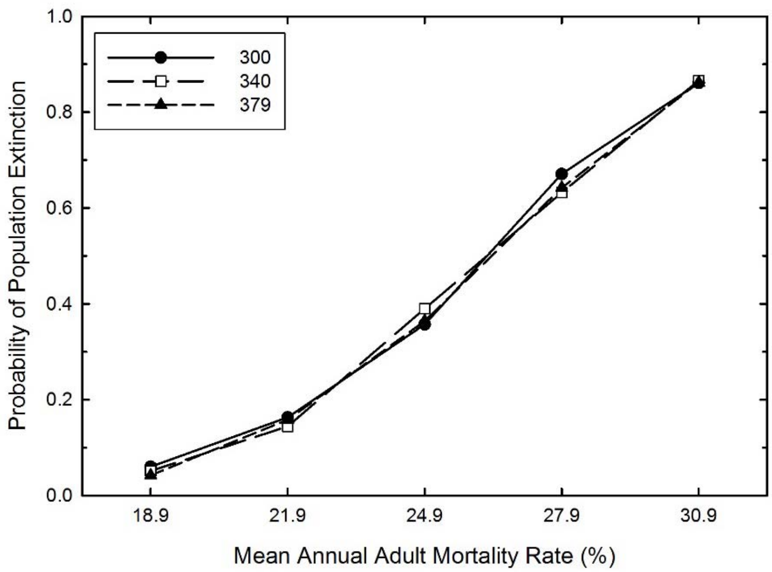

Figure 11. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS40_40”.

Gene diversity in the MWEPA population does not improve relative to the less intense release strategy previously described. Retention of GD in MWEPA is 90% to 94% of the initial value for that population over the low to intermediate mortality rates tested, and across the three proposed management targets (Table 10). However, the population retains only about 85% to 88% of the gene diversity present in the SSP. Higher mortality rates result in only 85% to 88% retention relative to MWEPA original values, and 80% to 84% GD retention relative to the SSP.

Table 10. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the MWEPA population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets and with the "EIS40_40" wolf transfer scheme. See legend for Table 4 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.686 (0.926; 0.874)	0.677 (0.914; 0.862)	0.665 (0.897; 0.847)	0.642 (0.866; 0.818)	0.628 (0.848; 0.800)
340	0.692 (0.934; 0.882)	0.682 (0.920; 0.869)	0.669 (0.903; 0.852)	0.654 (0.883; 0.833)	0.637 (0.860; 0.811)
379	0.694 (0.937; 0.884)	0.685 (0.924; 0.873)	0.673 (0.908; 0.857)	0.658 (0.888; 0.838)	0.639 (0.862; 0.814)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS40_40 – SMOCC-N population: Viability in the SMOCC-N population continues to improve relative to the "EIS_20_20" strategy as more wolves are transferred into the population, although the gains are relatively slight given the appreciable post-transfer mortality included in the models. Once again, extinction risk drops below 0.10 at larger management targets when the annual adult mortality rate increases to 27.9% (Figure 12). As before, the value of the MWEPA management target has little impact on SMOCC-N demographic performance. The population increases rapidly to a maximum mean abundance of about 180 wolves at a management target of 200 and at intermediate adult mortality levels (24.9%, but this growth is followed by the now-familiar decline over time to about 160 wolves at the end of the simulation.

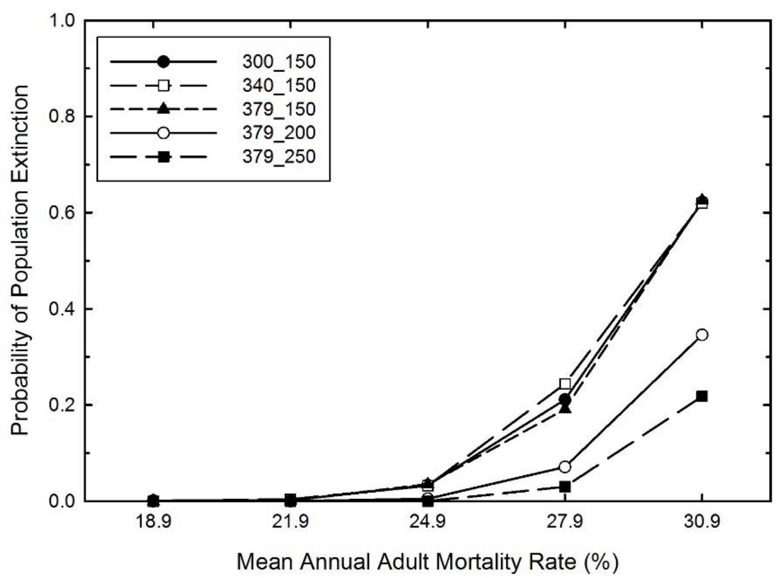

Figure 12. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS40_40". The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-

At low to intermediate adult mortality rates, final gene diversity retention ranges from 97% to 107% relative to the initial value for SMOCC-N, and from 85% to 95% relative to the final SSP value (Table 11). When the management target is at least 200 wolves, final GD relative to the final SSP value is at or above 90% for all low and intermediate adult mortality levels. The maximum GD retention relative to the final SSP value that is observed under the smallest SMOCC-N management target (150) is 89%, at the lowest adult mortality rate tested (18.9%).

Table 11. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-N population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets, and with the “EIS40_40” wolf transfer scheme. See legend for Table 5 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.697 (1.009; 0.888)	0.687 (0.994; 0.875)	0.669 (0.968; 0.852)	0.627 (0.907; 0.799)	0.591 (0.855; 0.753)
340_150	0.698 (1.010; 0.882)	0.688 (0.996; 0.876)	0.667 (0.965; 0.850)	0.630 (0.911; 0.803)	0.585 (0.847; 0.745)
379_150	0.699 (1.011; 0.890)	0.688 (0.996; 0.876)	0.666 (0.964; 0.848)	0.634 (0.918; 0.808)	0.588 (0.851; 0.749)
379_200	0.726 (1.051; 0.925)	0.719 (1.041; 0.906)	0.706 (1.022; 0.899)	0.681 (0.986; 0.868)	0.641 (0.928; 0.817)
379_250	0.742 (1.074; 0.945)	0.737 (1.067; 0.939)	0.729 (1.055; 0.929)	0.708 (1.025; 0.902)	0.667 (0.965; 0.850)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS40_40 – SMOCC-S population: The extinction/establishment dynamics for the SMOCC-S population are for the most part unchanged from the results of the “EIS20_20” models, with the exception of slightly reduced extinction risks at the larger population management targets of 200 and 250 (Figure 13). With a population management target of 250, low adult mortality rates (18.9% - 21.9%) result in extinction risk (failure to establish a population) of 0.041 to 0.113. At the intermediate adult mortality rate of 24.9%, this risk increases to 0.193 – 0.443 at a management target of 250 to 200, respectively. If a population becomes established here, the population abundance at the end of the simulation ranges from 65 wolves at a management target of 150 to 160 wolves at a management target of 250.

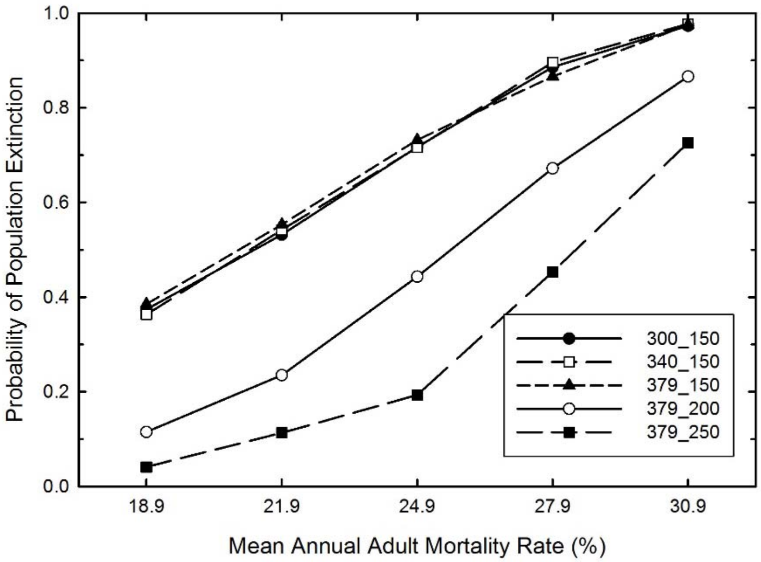

Figure 13. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS40_40”. The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-

Increasing the extent of transfers to the SMOCC-N population in the “EIS40_40” strategy brings only modest improvements to gene diversity retention in the SMOCC-S population (Table 12). Under the smallest management target of 150 wolves and at low to intermediate adult mortality rates, the extent of GD retained relative to the final value for the SSP ranges from 71% to 75%. Increasing the management target to 200 or 250 increases final GD retention in SMOCC-S to 76% to 83% of the final SSP value.

Table 12. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-S population of Mexican wolves, under the range of tested annual adult mortality rates and with the “EIS40_40” wolf transfer scheme. See legend for Table 6 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.585 (0.745)	0.574 (0.731)	0.560 (0.713)	0.549 (0.699)	0.541 (0.689)
340_150	0.584 (0.744)	0.577 (0.735)	0.559 (0.712)	0.545 (0.694)	0.530 (0.675)
379_150	0.590 (0.752)	0.576 (0.738)	0.558 (0.711)	0.545 (0.694)	0.522 (0.665)
379_200	0.623 (0.794)	0.617 (0.786)	0.598 (0.762)	0.579 (0.738)	0.554 (0.706)
379_250	0.651 (0.829)	0.641 (0.817)	0.625 (0.796)	0.609 (0.776)	0.588 (0.749)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

Scenario Set 3: Releases to MWEPA; Releases and Translocations to SMOCC-N and SMOCC-S

The final set of models evaluated in this report feature an “EIS22_22” transfer strategy. This strategy is built upon the “EIS20_20” strategy, but with the important inclusion of the release of two additional pairs with pups from the SSP and the translocation of two additional pairs with pups from MWEPA to the SMOCC-S population unit. These models are designed to explore the ability of direct transfers to the SMOCC-S unit to augment natural dispersal from SMOCC-N in order to generate a demographically and genetically viable wolf population in that habitat.

EIS22_22 – MWEPA population: As with the “EIS40_40” transfer strategy, the relatively high rate of wolf off-take for translocations to the Sierra Madre populations results in an increased risk of extinction in the MWEPA population, compared to models where such off-take is absent (Figure 14). The seemingly counter-intuitive result of higher risk of the largest management target at the lowest mortality rate occurs simply because of stochastic variation around low-probability events. At intermediate adult mortality rates (24.9%), the risk exceeds 0.2 for all population management targets and increases substantially under higher mortality rates. Following the pattern discussed earlier, the risk of MWEPA population extinction is not impacted by the size of the management target, suggesting that removals in the early years of the simulation are an important factor influencing later extinction risk. Long-term abundance among extant populations ranges from approximately 230 wolves under a management target of 300 to approximately 300 wolves under a management target of 379.

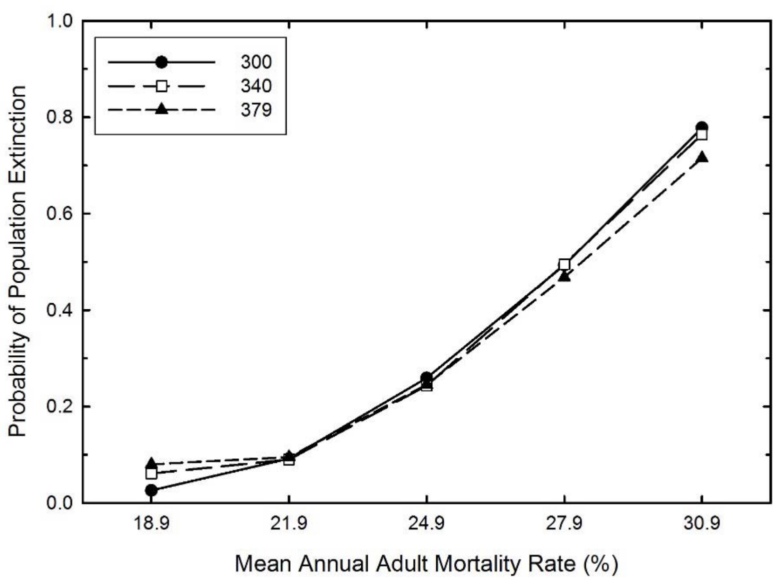

Figure 14. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS22_22”.

Gene diversity retention in the MWEPA population closely follows that for the “EIS40_40” transfer strategy. Retention of GD in MWEPA is 90% to 94% of the initial value for that population over the low to intermediate mortality rates tested, and across the three proposed management targets (Table 13). However, the population retains only about 85% to 89% of the gene diversity present in the SSP. Higher mortality rates result in only 85% to 89% retention relative to MWEPA original values, and 80% to 85% GD retention relative to the SSP.

Table 13. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the MWEPA population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets and with the “EIS22_22” wolf transfer scheme. See legend for Table 4 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.688 (0.928; 0.876)	0.682 (0.920; 0.869)	0.669 (0.903; 0.852)	0.646 (0.872; 0.823)	0.630 (0.850; 0.803)
340	0.695 (0.938; 0.885)	0.686 (0.926; 0.874)	0.677 (0.914; 0.862)	0.660 (0.891; 0.841)	0.637 (0.860; 0.811)
379	0.696 (0.939; 0.887)	0.691 (0.933; 0.880)	0.682 (0.920; 0.869)	0.668 (0.901; 0.851)	0.652 (0.880; 0.831)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS22_22 – SMOCC-N population: When the SMOCC-S population is targeted for releases and translocations, the SMOCC-N population appears to show a slightly lower risk of population extinction compared to the “EIS40_40” strategy described earlier (Figure 15). For example, with a SMOCC-N management target of 200 and with the largest MWEPA management target of 379, the risk of extinction to the SMOCC-N population under the “EIS22_22” population declines to 0.016 compared to 0.035 in the “EIS40_40” strategy. While this specific difference may result from stochastic variation across the set of iterations that make us this analysis, this qualitative difference is consistent across the majority of scenarios that were tested across these two transfer strategies. The slight improvement in demographic stability of the SMOCC-N population may result from occasional dispersal events of wolves from SMOCC-S into SMOCC-N throughout the duration of the simulation, acting to bolster SMOCC-N populations through time. Extant populations reach a long-term abundance of approximately 140 to 220 wolves with a population management target of 150 to 250, respectively. Under the 250 management target, the populations is able to maintain at that level but smaller management targets tend to lead to slow rates of decline in abundance to 160 or 100 wolves for management targets of 200 and 150, respectively. As discussed previously, factors playing a role in reducing reproductive output in these populations over time can lead to gradual erosion of demographic and genetic viability.

Retention of gene diversity in the SMOCC-N population under the “EIS22_22” transfer strategy follows the results of the “EIS40_40” analyses, with perhaps a slightly higher level of GD retention in these scenarios in the presence of occasional connectivity with SMOCC-S as it becomes established. At low to intermediate adult mortality rates, final gene diversity retention ranges from 99% to 107% relative to the initial value for SMOCC-N, and from 87% to 95% relative to the final SSP value (Table 14). When the management target is at least 200 wolves, final GD relative to the final SSP value is at or above 90% for all low and intermediate adult mortality levels. The maximum GD retention relative to the final SSP value that is observed under the smallest SMOCC-N management target (150) is 90%, at the lowest adult mortality rate tested (18.9%).

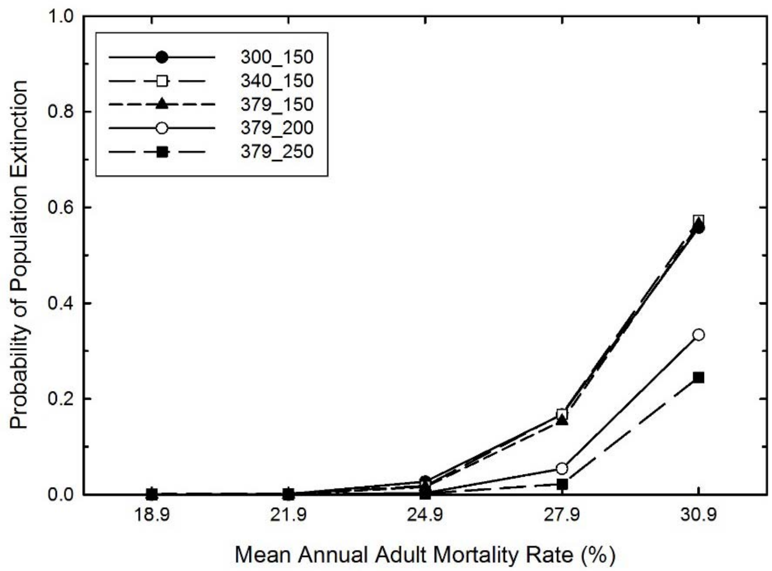

Figure 15. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS22_22". The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-

Table 14. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-N population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets, and with the "EIS22_22" wolf transfer scheme. See legend for Table 5 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.706 (1.022; 0.899)	0.699 (1.012; 0.890)	0.682 (0.987; 0.869)	0.649 (0.939; 0.827)	0.606 (0.877; 0.772)
340_150	0.707 (1.023; 0.901)	0.698 (1.010; 0.889)	0.683 (0.988; 0.870)	0.646 (0.935; 0.823)	0.598 (0.865; 0.762)
379_150	0.707 (1.023; 0.901)	0.700 (1.013; 0.892)	0.684 (0.990; 0.871)	0.651 (0.942; 0.829)	0.603 (0.873; 0.768)
379_200	0.729 (1.055; 0.929)	0.725 (1.049; 0.924)	0.715 (1.035; 0.911)	0.690 (0.999; 0.879)	0.648 (0.938; 0.825)
379_250	0.743 (1.075; 0.946)	0.739 (1.069; 0.941)	0.731 (1.058; 0.931)	0.712 (1.030; 0.907)	0.678 (0.981; 0.864)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS22_22 – SMOCC-S population: When releases and translocations are implemented in the SMOCC-S population unit, the dynamics of this southernmost unit of the Mexican wolf metapopulation model begin to mirror those of the SMOCC-N population. The risks of population extinction (in the case of SMOC-S, the risk of establishment failure) for the two populations is nearly identical for the low and intermediate adult mortality rates tested here (Figure 16). At an adult mortality rate of 24.9%, SMOCC-S extinction risk is no more than 0.04 across the range of population management targets explored in this analysis. Perhaps more importantly, if the SMOCC-S population becomes established, the long-term abundance trajectories are very similar to those of the SMOCC-N population. Although the population growth rate may be slightly lower, leading to a longer time period required to reach the maximum long-term population abundance, the mean abundance for SMOCC-S is essentially identical to that for SMOCC-N.

Extending transfers to the SMOCC-S population in the "EIS22_22" strategy brings significant improvements to gene diversity retention (Table 15). While the extent of GD retained relative to the final value for the SSP ranged from 71% to 83% across the three population management targets under conditions of low to intermediate adult mortality rates in the absence of direct releases and translocations (Table 12), GD retention under the "EIS22_22" strategy in the SMOCC-S population increases across that same set of scenarios to a range of 85% to 93% (Table 15). Even under the highest rates of annual adult mortality tested here, GD retention relative to the final SSP value remained above 85% when the population management target was set at 250.

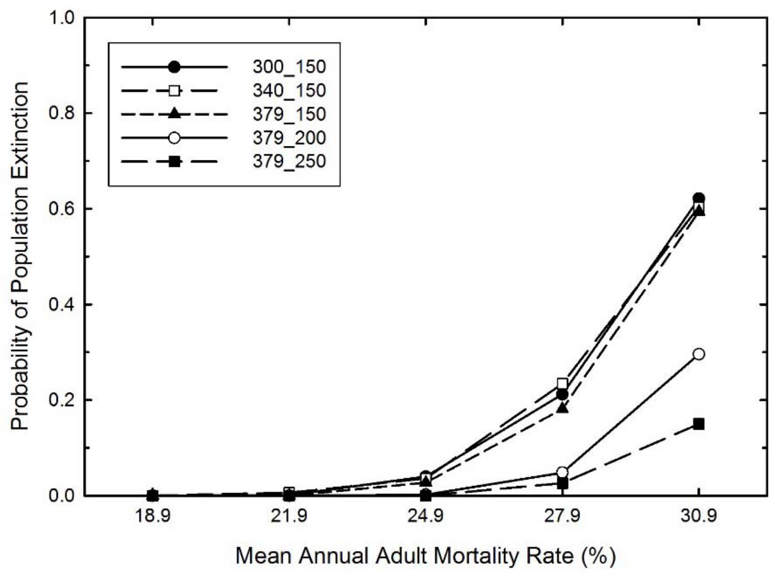

Figure 16. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS22_22". The first value in the plot legend gives the management target for the MWEPA population, while the second value is that for the SMOCC-

Table 15. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-S population of Mexican wolves, under the range of tested annual adult mortality rates and with the "EIS22_22" wolf transfer scheme. See legend for Table 6 for additional information on the meaning of the listed values.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.692 (0.882)	0.684 (0.871)	0.668 (0.851)	0.633 (0.806)	0.589 (0.750)
340_150	0.693 (0.883)	0.685 (0.873)	0.666 (0.848)	0.635 (0.809)	0.580 (0.739)
379_150	0.693 (0.883)	0.685 (0.873)	0.667 (0.850)	0.630 (0.803)	0.587 (0.748)
379_200	0.715 (0.911)	0.710 (0.904)	0.700 (0.892)	0.675 (0.860)	0.632 (0.805)
379_250	0.728 (0.927)	0.725 (0.924)	0.717 (0.913)	0.702 (0.894)	0.668 (0.851)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

The trajectories of average gene diversity through time among populations from a representative scenario in the "EIS22_22" transfer scheme are shown in Figure 17. As in Figure 10 under the "EIS20_20" transfer scheme, the increased gene diversity in SMOCC-N is plainly evident under the "EIS22_22" transfer scheme. In addition, the dramatic gain in gene diversity in the SMOCC-S population is plainly evident. This transfer scheme feature direct releases and translocations to both Sierra Madre Occidental populations, thereby providing significant boosts to local gene diversity. The MWEPA population, receiving only the EIS-scheduled releases, does not see a similar genetic benefit; in fact, the sustained off-take of wolves from this population leads to a slightly lower level of final gene diversity compared to the "EIS20_20" transfer scheme, and results in the lowest level of gene diversity among the three wild wolf populations.

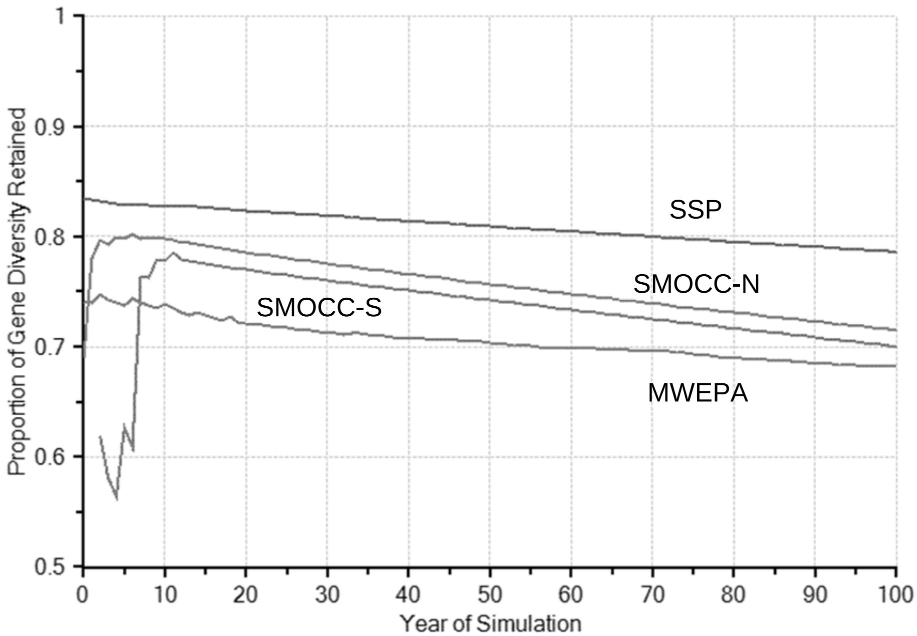

Figure 17. Average gene diversity over time for Mexican wolf populations subject to 24.9% mean annual adult mortality and under the "EIS22_22" transfer scheme. Management targets are set at 379 for MWEPA and 200 for SMOCC-N and SMOCC-S.

Scenario Set 4: Additional Transfer Strategy Scenarios

Based on the models discussed above, the MWEPA population was shown to experience a relatively low (0.11) risk of extinction over the 100-year simulation timeframe, and to retain a reasonable level (0.870) of gene diversity relative to the intensively managed SSP population in captivity, under an intermediate level of mean annual adult mortality (24.9%), with the "EIS20_20" wolf transfer management scheme, and with a long-term population management target of 379 wolves Under alternative transfer schemes that placed a higher demographic burden on the MWEPA population in the form of additional removals of wolves for translocation to Mexico, model results indicated that extinction risks would increase and gene diversity retention would decline. The mean MWEPA population trajectory under the "EIS20_20" transfer scheme and a population management target of 379 wolves revealed that the mean long-term abundance would stabilize at approximately 300 wolves, but it would require about 50 years to reach this abundance. These results stimulated further interest in identifying the management conditions – defined in terms of transfers of wolves among populations – that would lead to more robust levels of viability in the

MWEPA population and a more rapid approach to the long-term population abundance consistent with population recovery.

In light of the above discussion, this additional scenario set is designed to explore two issues of relevance to the derivation of robust recovery criteria:

1. The impact on demographic and genetic viability of the MWEPA through the implementation of a more aggressive initial release strategy from the SSP population; and
2. The consequences for time to MWEPA population recovery of modifications to the proposed transfer schedules.

The "[EISx2]20_20" scheme with its enhanced release strategy from SSP to MWEPA is designed to address issue #1 above. Similarly, the "[EISx2]30_10" and "[EISx2]40_00" schemes are designed to address issue #2 above through a reduced reliance on MWEPA as a source of individuals for translocation to Mexico, instead relying on the more demographically robust SSP population for a larger number of wolves targeted for initial release into the Northern Sierra Madre Occidental population area.

MWEPA Outcomes (Table16, Figure 18): In the original "EIS20_20" transfer scheme as described in Miller (2017), and with a mean annual adult mortality rate of 24.9%, the risk of the MWEPA population declining to extinction within the 100-year simulation timeframe was 0.11 and the extent of gene diversity retention in that population relative to that retained in the SSP was 0.872. If the population were to remain extant, it would increase in abundance at an average rate of approximately 5% per year for the first 20 years of the simulation and would ultimately equilibrate at a mean abundance of 300 wolves after 50 years.

When the EIS release schedule from the SSP to the MWEPA population is doubled (transfer scheme "[EISx2]20_20"), the risk of extinction declines to 0.032 and the length of time required to reach a population abundance of 300 wolves (chosen here arbitrarily for comparative purposes) is reduced in half to just 25 years. The mean population abundance stabilizes at 320 wolves, and the extent of gene diversity retained relative to that in the SSP also increases to just under 90%. When the number of wolves pulled from MWEPA for translocation to SMOCC-N is reduced and replaced by a larger number of wolves pulled from the SSP for initial releases to Mexico (transfer schemes "[EISx2]30_10" and "[EISx2]40_00"), the MWEPA population grows at a more rapid rate, achieves a larger long-term equilibrium abundance, and retains a larger proportion of gene diversity relative to that retained in the SSP.

SMOCC-N Outcomes (Table 16, Figure 19): The output metrics for SMOCC-N across these new transfer scheme scenarios show very little deviation from the "EIS20_20" scenario used here for reference. The population demonstrates less than a 1% chance of extinction through the 100-year simulation, grows to its maximum abundance of about 175 wolves in 15 to 18 years, and retains approximately 89% to 90% of gene diversity relative to the SSP population at the end of the simulation. The SMOCC-N population displays a tendency to decline from the maximum abundance of 175 at year 15 to approximately 155 – 160 wolves by the end of the simulation, as a result of reduced litter production through slow accumulation of inbreeding depression and reduced incidence of diversionary feeding.

Table 16. Output metrics for the MWEPA and SMOCC-N populations from the PVA scenarios featuring alternative transfer schemes. See accompanying text for transfer scheme definitions. Prob(Ext), probability of population extinction over 100 years; N, extant population abundance; $GD(SSP)_{100}$, proportion of population gene diversity retained in the wild populations after 100 years relative to the proportion retained within the captive SSP population.

	Transfer Scheme			
	EIS20_20	[EISx2]20_20	[EISx2]30_10	[EISx2]40_00
MWEPA				
Prob(Ext)	0.110	0.032	0.018	0.008
Years to N=300	50	25	18	15
N_{Eq}	300	320	330	335
$GD(SSP)_{100}$	0.872	0.897	0.900	0.900
SMOCC-N				
Prob(Ext)	0.005	0.006	0.009	0.012
Years to N=175	15	15	15	18
N_{100}	156	154	159	156
$GD(SSP)_{100}$	0.890	0.893	0.896	0.891

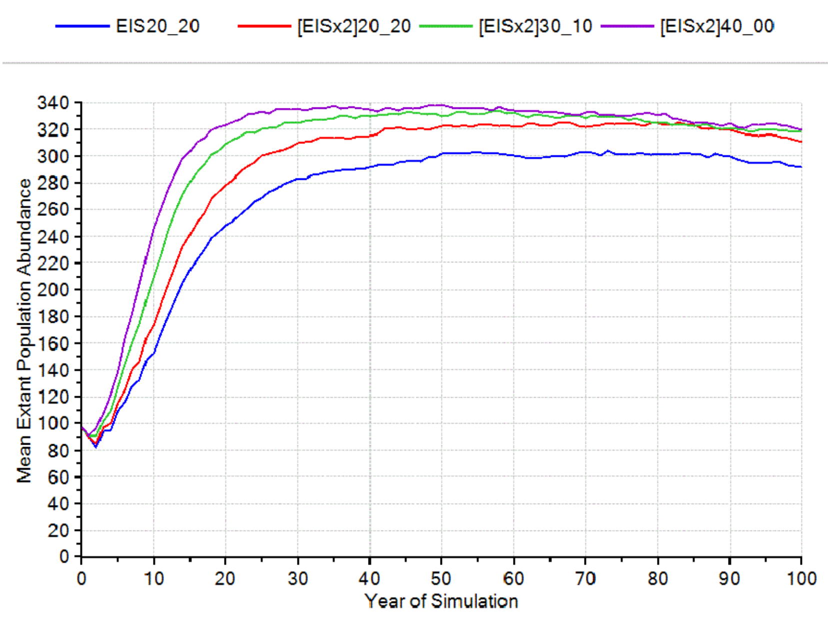

Figure 18. Mean MWEPA population abundance among extant iterations across alternative transfer scheme scenarios. See accompanying text for transfer scheme definitions and underlying scenario characteristics.

The consistency of results for the SMOCC-N population across these scenarios is not surprising, as the total number of pairs transferred into the population (four) remains the same. The difference across the scenarios lies in the source of these individuals: the "20_20" scenarios have two pairs each from release and translocation, while the "30_10" scenario has three released pairs and one translocated pair and the "40_00" scenario features all initial releases and no translocations. The total number of effective transfers into the SMOCC-N population is lowest for the "40_00" scenario since all individuals are transferred through initial releases with the associated low post-release survival rates presented in Table 3.

Across all new transfer schemes tested here, the SSP population remains demographically and genetically robust – even under the highest demand for wolves defined by the "[EISx2]40_00" scenario in which 34 pairs with pups are removed from the SSP over a period of 17 years (model years 2 – 18). Under this scenario, the captive population does not increase appreciably for the first 5-6 years above its initial abundance of 214 wolves, but soon thereafter – once the primary demand for wolves to be released is relaxed – the population is able to rapidly grow to near its long-term carrying capacity of about 250 animals. Additionally, the proportion of gene diversity retained in the SSP population after 100 years remains nearly constant across the scenarios at 0.785, or approximately 94% of the diversity present in that population at the beginning of the simulation.

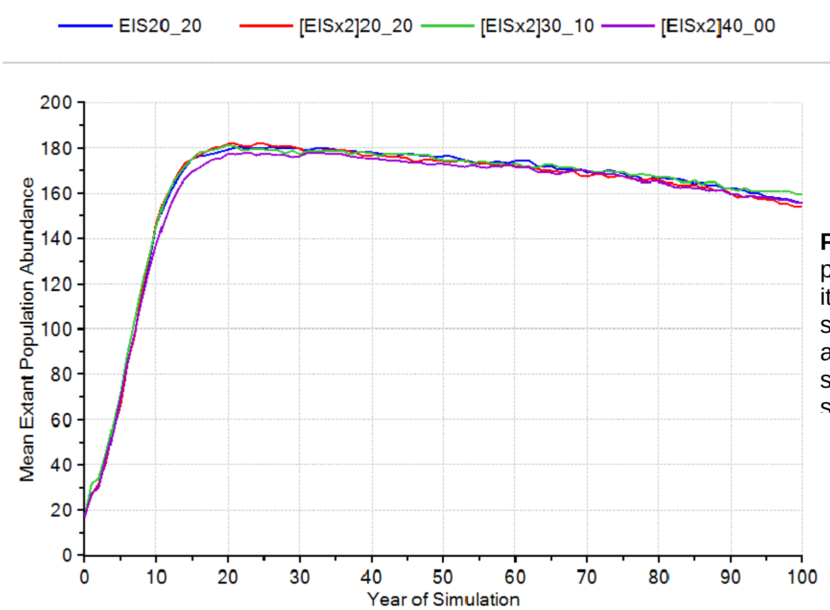

Figure 19. Mean SMOCC-N population abundance among extant iterations across alternative transfer scheme scenarios. See accompanying text for transfer scheme definitions and underlying scenario characteristics

Conclusions and Discussion

The population simulation model described in detail in this report, constructed using the *Vortex* modeling software framework, provides a flexible platform to explore the demographic and genetic conditions – abundance, adult mortality, population genetic structure – that could result in a viable metapopulation of Mexican wolves in the southwestern United States and northern Mexico. This model explicitly includes the captive wolf population and its full pedigree, thereby allowing us to evaluate a suite of metapopulation management alternatives featuring explicit linkage across captive and wild populations. This exploration of captive population dynamics is made possible by recent improvements to the *Vortex* software that were not available at the time of the most recent published PVA effort for Mexican wolves (Carroll et al. 2014).

Figure 20 presents a summary of extinction risk for each of the three wild wolf populations and across the full set of simulated transfer schemes, assuming for the purposes of clarity an intermediate mean annual adult mortality rate of 24.9%. Under the conditions simulation in this analysis, the increased risk to the MWEPA population as a consequence of transferring animals to Mexico is evident. The risk is greatest under the "EIS40_40" transfer scheme, as a relatively large number of wolves – 20 pairs with pups – are removed from the population over a period of only five years. Note that while the "EIS22_22" scheme results in the same total number of wolves being removed from MWEPA, the number of pairs removed in any one year is smaller and the total removal schedule is spread out over a longer period of time, thereby putting less demographic stress on the source population.

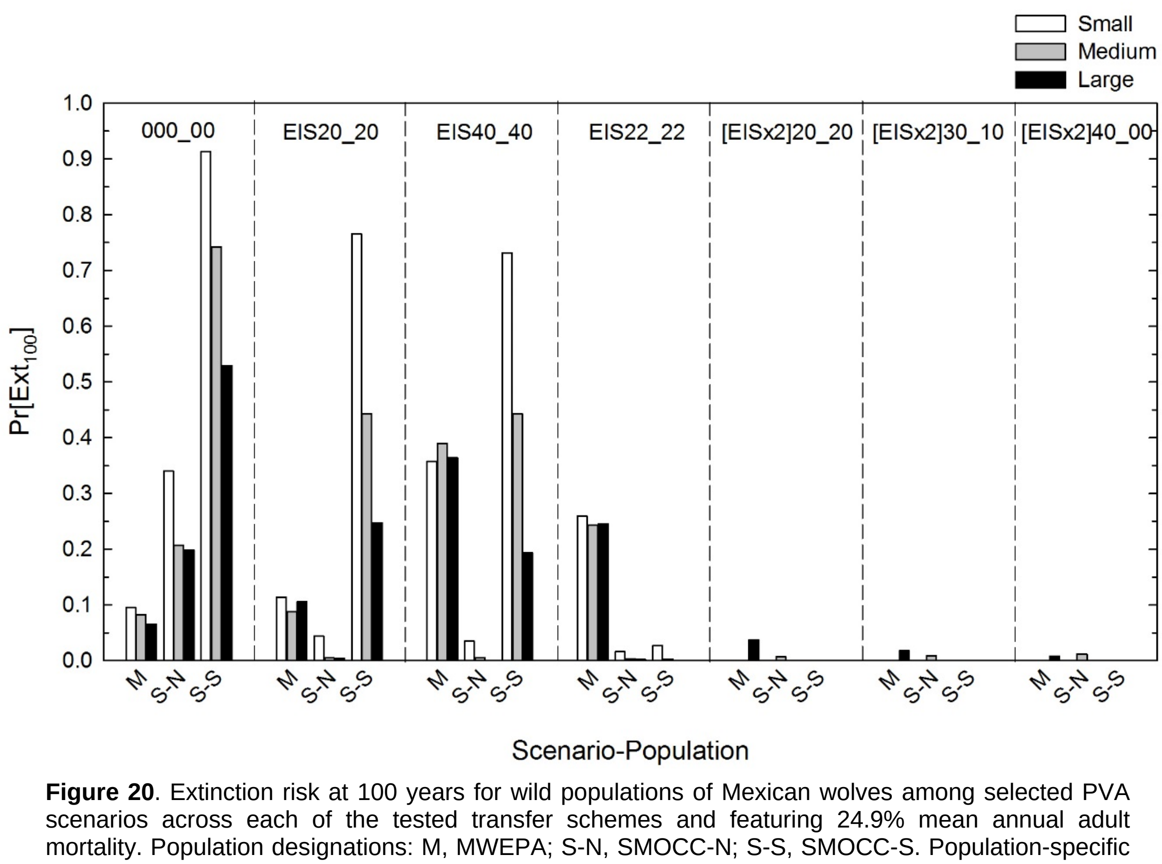

Figure 20. Extinction risk at 100 years for wild populations of Mexican wolves among selected PVA scenarios across each of the tested transfer schemes and featuring 24.9% mean annual adult mortality. Population designations: M, MWEPA; S-N, SMOCC-N; S-S, SMOCC-S. Population-specific management targets are designated Small (MWEPA, 300; SMOCC-N/SMOCC-S, 150), Medium (MWEPA, 340; SMOCC-N/SMOCC-S, 200), or Large (MWEPA, 379; SMOCC-N/SMOCC-S, 250). Smaller set of [EISx2] scenarios restricted to the Large and Medium management target for MWEPA and SMOCC-N, respectively.

Also clearly evident from examination of Figure 20 is the reduced extinction risk in the Sierra Madre Occidental populations in those scenarios featuring explicit transfer to those populations. The risk virtually disappears for the SMOCC-N population under all simulated transfer schemes, although population stability is more difficult to achieve in the presence of smaller management targets. Similarly, the direct addition of wolves to SMOCC-S through releases and translocations results in a dramatic reduction in risk to that population. As with its northern Mexico counterpart, long-term demographic stability in the SMOCC-S population would likely require larger population management targets, i.e., on the order of at least 200 wolves. It is also evident that the Mexico populations contribute little to the demographic or genetic viability of the MWEPA population – a consequence of the very low levels of natural connectivity between these populations across the international border. Nevertheless, the existence of the population(s) in Mexico contributes significantly to overall viability of Mexican wolves in the event of local decline or extirpation of the United States population. While specific estimates of overall metapopulation extinction risk are not reported here, it is reasonable to conclude that this risk will not be greater than the largest extinction probability reported for any of the component populations.

The summary observations for genetic diversity retention are much the same as those for demographic stability (Figure 21). More intensive transfer schemes such as the "EIS40_40" strategy put increased genetic strain on the source MWEPA population, without providing significant added genetic benefit to the recipient SMOCC-N population. In contrast, the "EIS22_22" scheme reduces the burden on MWEPA and leads to marked benefits to the Sierra Madre Occidental populations – particular SMOCC-S. Overall, the extent of proportional gene diversity retention for a given population is greater when comparing the population's final value to the initial value for that same population, compared to comparisons with the final value for the intensively-managed SSP population. Although these higher retention values relative to a population's initial GD value may seem appealing, the low absolute values for this metric across all wild populations do not generate the same appeal. Retaining a larger proportion of a small amount of starting material does not necessarily indicate a large measure of success. This is why it may be more appropriate to consider the retention of GD relative to that value present in the captive population, which is the source of all genetic variants among wild Mexican wolves and currently shows the highest expected gene diversity values across all populations.

The information summarized in Figures 20 and 21 comes from model scenarios that feature the best estimates for the full range of demographic parameters discussed in the Input Data sections. There is, however, uncertainty in these parameter values through inaccurate measurement, small sample sizes used to make the measurements, etc. This parametric uncertainty leads to a similar uncertainty in the prediction of demographic and genetic estimates of population viability. The PVA presented in this report does not include a full analysis of the impact of parametric uncertainty on population viability estimates. Consequently, the risk estimates reported here are likely underestimates of the true risk, although the magnitude of this effect is unknown (Bakker et al. 2009). While this issue of risk underestimation is recognized here, it is unlikely that it will significantly impact the practical application of the analyses as they are presented here.

The demographic and genetic characteristics of the MWEPA population of Mexican wolves can be improved through a more intensive effort focusing on initial releases of wolves from the SSP population, and simultaneously through a reduced reliance on using MWEPA wolves for translocations to Mexico (Scenario set 4). Extinction risk can be reduced, retention of gene diversity can be enhanced, and the time required for the population to increase to its long-term average abundance can be reduced through this intensive management option. The SMOCC-N population remains capable of growing to its specific management-mediated abundance in a manner very similar to that discussed in detail in the original PVA report.

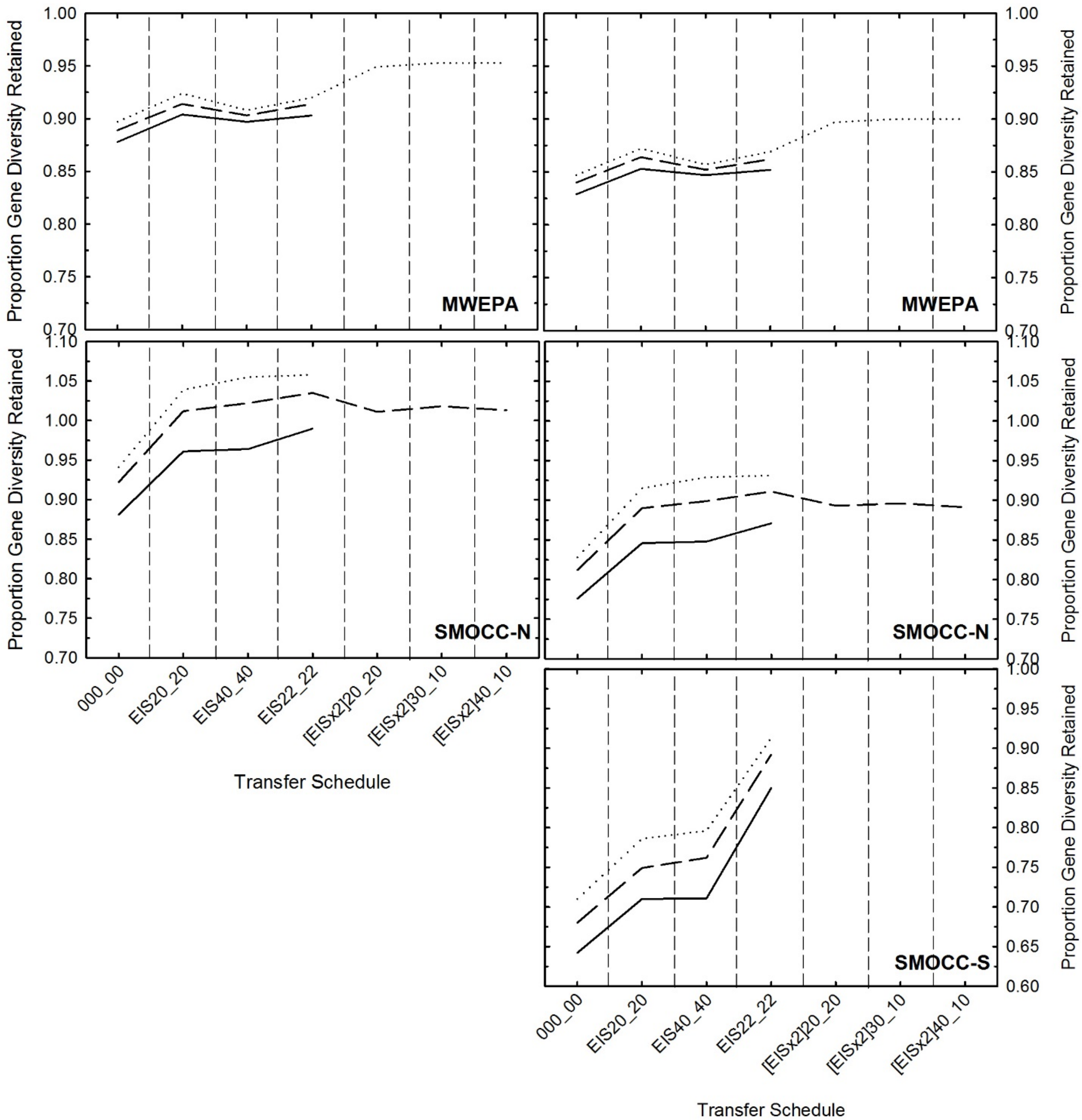

Figure 21. Proportional gene diversity (GD) retention for wild populations of Mexican wolves among selected PVA scenarios across each of the transfer schemes addressed in this analysis, and featuring 24.9% mean annual adult mortality. Lines within each plot refer to alternative population management targets: Small (solid line), Medium (dashed line) or Large (dotted line) (See Figure 20 legend for management target definitions). Panels on the left show final (year 100) gene diversity retention proportional to the starting value for that population at year 1, while panels on the right show final retention relative to the final GD value for the SSP. Smaller set of [EISx2] scenarios restricted to the Large and Medium management target for MWEPA and SMOCC-N, respectively.

Across all simulations presented here, the SSP population can be easily maintained at the specified "carrying capacity" of about 255 wolves, defined in the context of captive population management by the number of available spaces across zoological institutions housing Mexican wolves. Although the demographic stability of the captive population is not in question on the basis of this analysis, the genetic viability of that population could perhaps be improved by either improving reproductive success among selected breeding pairs or by increasing the number of available spaces for more adult pairs. This general management recommendation is also discussed in more detail by Mechak et al. (2016).

Under the complex set of conditions portrayed in this modeling effort, the MWEPA wolf population in the United States can grow in abundance to designated management target levels as long as annual adult mortality rates are below 25%. If further wolf releases from the SSP are discontinued, resulting in effective isolation of this population into the future, demographic and genetic processes can work together to destabilize the population and inhibit its continued growth. This destabilizing force can also be strengthened if wolves are removed from MWEPA in the near future – before the population is able to grow to some designated management target – and translocated to the existing SMOCC-N population or the new SMOCC-S population unit. Of course, the value of using these wolves to augment existing populations or help to create new populations cannot be argued. However, the intensity and (perhaps more importantly) the timing of these removals from MWEPA for translocation need to be considered so that the viability of this valuable source population is retained.

Both demographic and genetic viability of the MWEPA population is improved through releases of wolves into this population from the SSP. The results of the PVA reported here indicate that it is difficult to retain relatively high levels (e.g., at least 90%) of population-level gene diversity in MWEPA relative to the SSP, even if the risk of the MWEPA population declining to extinction is very low. This suggests that the current release schedule laid out in the Mexican Wolf EIS may be insufficient to adequately bolster the genetic integrity of the MWEPA. Under the conditions simulated in this analysis, the transfer schedule laid out in the EIS specifies a total of seven pairs and associated pups. Our modeling effort therefore removed 14 adults and 21 pups from the SSP population. However, because of the documented levels of post-release mortality discussed in this report (see Table 3 page 16), only four adults and 10.4 pups survive after release to the next breeding cycle. The pups will have another round of mortality before they are recruited into the adult stage; hence, a total of seven pups survive after release to adulthood, meaning that a grand total of eleven adults are added to the MWEPA population from 35 wolves released from the SSP. If this effective number of adults added to MWEPA through releases were, for example, doubled to 22 wolves, the genetic benefit may be substantial. Preliminary analysis of this scenario (not reported in detail here) suggests just such an outcome. Interpretation of these types of results is critically dependent on the threshold by which genetic integrity will be judged, but the general concept remains highly relevant. An alternative to increasing the number of wolves released from the SSP is to increase the survival of the same number of animals immediately following release, so that a specified target of effective releases can be achieved. Careful consideration must be given to the relative costs and benefits of each alternative before changes to management activities are recommended.

Long-term management of the MWEPA population involves removing wolves from the landscape when the population is at or near the designed management target. Simulation of this management activity in the current PVA may not be as flexible or as nuanced as what may be undertaken in reality, as decisions may be made in the presence of a broader range of information than what is being considered here. Nevertheless, it may be instructive to briefly explore the extent of removals required to maintain a population at a designated management target. Assuming a mean annual adult mortality rate of 24.9% in MWEPA, and under the "EIS20_20" transfer scheme, our model suggests that an average of no more than approximately 24 to 36 wolves would need to be removed in a given year to keep the wolf population at the management target of 379 to 300, respectively. The larger number of wolves removed at the smaller management target is a by-product of that population reaching that target earlier in the 100-year projection (on the order of 20 years) compared to those simulations with a larger management target (approximately 40 years). As time progresses through the simulation and longer-term population growth rates are expected to decline through processes discussed earlier, the rate of removal declines.

The wolf population currently occupying the northern portions of the Sierra Madre Occidental is likely to benefit significantly from the recent 2016 releases of wolves from the SSP. The extent of genetic variation now in this population is predicted to be higher than that currently within the MWEPA population; however, that diversity is likely to erode more quickly as inbreeding and genetic drift act to eliminate genetic variation in the smaller SMOCC-N population. Given our depiction of metapopulation connectivity, the northern Sierra Madre wolf population receives individuals only very occasionally from MWEPA – almost certainly less frequently than the desired rate of at least 1-2 effective (breeding) migrants per generation discussed by Carroll et al. (2014) that would ameliorate many genetic problems associated with small populations. Therefore, it is likely that the SMOCC-N population's future viability will depend at least in the near term on continued releases from the SSP and, if considered appropriate, on translocations from MWEPA. Once the SMOCC-N population begins to grow to a more stable abundance, it can serve as a more reliable source of dispersers to the SMOCC-S population unit. The actual capacity for wolves to successfully disperse southward is still up for debate, but members of the PVA Development Team with expertise in this area are confident that the probability of successful dispersal between the two Sierra Madre Occidental population units is markedly greater than that across the US – Mexico border.

In the absence of explicit releases from the SSP or translocations from MWEPA, the SMOCC-S population unit has a very low probability of supporting a wolf population at reasonable levels of adult mortality. Even if wolves colonize the area in our simulations, the number of individuals is not consistent with typically acceptable levels of demographic or genetic viability. This is true even when the SMOCC-N population is augmented through releases and translocations, although the prospects for population establishment begin to increase as a larger northern Sierra Madre Occidental population produces more dispersing individuals through time. On the other hand, the prospects for population establishment increase greatly when releases and translocations become an active component of management for this southern population. Under more favorable conditions – a larger management target and reasonable levels of adult mortality – the SMOCC-S population can demonstrate similar growth dynamics to its northern Mexico counterpart. Wolf abundance can approach the designated management target, and retention of gene diversity (measured as a proportion of that measured in the SSP) is at a level comparable to that expected for the SMOCC-N population. This outcome can have major implications for the long-term conservation and recovery of Mexican wolves in the wild. To reiterate, however, it is important to consider the full suite of costs and benefits to one or more complementary components of the Mexican wolf wild and captive metapopulation before implementing transfers to both wolf populations in Mexico.

Acknowledgements

Many thanks to the Mexican Wolf PVA Development Team and many other professionals who participated in this latest modeling effort, dating back to December 2015. Extra thanks go to Rich Fredrickson for his special level of dedication to this project and for his support in resurrecting the original *Vortex*-based simulation model, which forms the foundation of this current effort.

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Appendix A.

Estimation of the Mean Pairing Rate among Wild Mexican Wolves[1]

Prepared By: John Oakleaf, U.S. Fish and Wildlife Service.

Date: 19 October, 2016 and 25 January, 2017

Methods

Method 1: Direct observation

Direct observations of paired status were made on radio-collared females only, which likely biases the data towards a higher proportion of females reproducing because the Interagency field Team tries to capture and maintain collars on breeding adults but not necessarily on one- or two-year-old animals with a pack. Data from 1998 – 2000 were censored due to sample size constraints. Only animals that made it to two years of age in a given year were considered. This may also result in an upward bias because those 1.5-year-old individuals that could pair up in the winter but died prior to reaching 1 April in a given year. Finally, all wolves that were released during the previous four months before observation were not included in the analysis. The data considered for analysis are summarized in Table A-1.

Table A-1. Paired status of adult (age-2+) female Mexican wolves in the MWEPA population, 2001 – 2015.

Year	Adult Females	Number Paired	Proportion Paired
2001	8	5	0.63
2002	9	6	0.67
2003	9	9	1.00
2004	10	8	0.80
2005	9	7	0.78
2006	9	8	0.89
2007	8	8	1.00
2008	8	6	0.75
2009	13	10	0.77
2010	10	10	1.00
2011	11	9	0.82
2012	10	10	1.00
2013	7	7	1.00
2014	5	5	1.00
2015	5	5	1.00
Total	131	113	0.863

The mean proportion of adult females Mexican wolves in a paired status over the period of observation was estimated across the total dataset to be 0.863. This estimate may be biased high because of the following issues:

[1] Sections of the larger report relevant to model input reproduced here for clarity.

1. Collared animals only were utilized, which should bias the data towards higher proportion of females reproducing because the Interagency Field Team attempted to capture and maintain collars on breeding adults but not necessarily one or two year old animals with a pack.
2. Only females that made it to 2 years old in a given year were utilized, which may bias the data slightly higher because we are not considering all of the short two year old's (1.5 year old) that could pair up in the winter but died prior to reaching 4/1 of a given year.
3. Animals were censured that were released during the previous four months to remove potential bias associated with released animals and adaptation to the wild.

Method 2: Indirect estimation

As an alternative approach to using only radio-collared females and whether individuals female where paired at the start of breeding season (recognized as biased high), we attempted to estimate the number of females (1+ years old) in the entire population at time *t* compared to the number of pairs at time *t*+1 over the period 2007 – 2016. We accomplished this by:

(1) Using the number of animals in collared packs that were not pups (1+ years old) at the time of the end of year count (Nov-Jan) and applying a 50:50 (m:f) sex ratio to estimate the number of females available to breed in the population at time t-1.
(2) Dividing the number of pairs present at the start of time t plus any pairs that formed prior to breading season by the estimated number of adult females from 1 above (Table 2).

The data obtained through this method are summarized in Table A-2.

Table A-2. Paired status of adult (age-2+) female Mexican wolves in the MWEPA population, 2007 – 2016.

Year	Adult Females	Number Paired	Proportion Paired
2007	13.5	10	0.741
2008	15.5	12	0.774
2009	16	9	0.563
2010	12	10	0.833
2011	12	8	0.667
2012	16	13	0.813
2013	19.5	14	0.718
2014	25.5	16	0.628
2015	27.5	18	0.655
2016	31.5	20	0.635
Total	189	130	0.688

These data yield a 10-year average pairing rate of 0.688.

Similar to the radio collar data, these data come with potential biases:

1. Uncollared packs that were documented in the count data were excluded from both the number of pairs and the number of females because an appropriate breakdown of the number of animals 1+ year old was not available. This should not have a net impact, or at the most a negligible downward bias of pairing rates.
2. Single uncollared animals were included as >1 both on and off Reservations for 2016 and 2015 where data was available. The number of single uncollared animals on the reservations for other years was pooled with uncollared groups on the reservations and thus all single

uncollared animals on the reservation were excluded for 2014 to 2007. Slight upward bias of pairing rates.

3. The assumption is that females and males are produced and survive at the same rate. This is the same assumption by *Vortex*. However, it appears that there is an overabundance of males and fewer females in the Mexican wolf population based on dispersal and pairing patterns of collared animals (females generally disperse shorter distances and for shorter time periods in dispersal status). This would result in a downward bias of pairing rates, but depending on *Vortex* assumptions this could be consistent with the model parameterization.

As a way to utilize both of these datasets, the decision was made by the Mexican Wolf PVA Development Team to use the average result from the two methods discussed above. This yields a mean pairing rate of 0.78.

Appendix B.

Analysis of Independent Variables Impacts on the Probability of Live Birth and Detection in Wild Mexican Wolves in Arizona and New Mexico[2]

Prepared By: John Oakleaf and Maggie Dwire, U.S. Fish and Wildlife Service.

Date: 16 September, 2016

Methods

Population Monitoring and Pup Counts

The Mexican Wolf Interagency Field Team (IFT) implemented varied methods of population monitoring and pup counts during the duration of our study. Initially (1998-2004), the IFT determined population estimates and pup counts using non-invasive methods such as howling surveys, tracks and scats, and visual observations during aerial (fixed wing) and ground radiotelemetry. Visual observations were collected opportunistically through the least intrusive methods possible and we avoided any disturbance of den areas. Pups were born from early April to late May and were counted post-emergence from the den (> 6 weeks of age) whenever opportunity allowed. During the initial time period, the Mexican wolf population was generally below 50 animals and consistent field efforts allowed for pack composition to be monitored.

In more recent years (2005-2014), the IFT incorporated helicopter counts in January or early February to verify and collect additional population information. In addition, the IFT implemented more aggressive methods to document reproduction earlier in the year due to concerns about reproduction and recruitment. Ultimately, the IFT incorporated the increased use of remote cameras, earlier observations in and at den sites, and trapping for younger pups (2009-2014). Because of the variability in methods used from 1998-2014, we incorporated a structural dummy variable for early (1998-2004), middle (2005- 2008), and late (2009-2014) count methodology to evaluate and control for these evolving methodologies, if necessary. Regardless of the count methodologies, each year the IFT conducted a year-end population survey which resulted in a minimum population count for that year. The minimum population count incorporated the total number of collared wolves, uncollared wolves, and pups, documented as close to December 31 of the given year as possible.

We assessed if a pair of wolves that were together during the breeding season produced detectable pups (probability of detection of live pups). We assessed this based on whether pups were ever documented during the year. Although some pairs may have produced pups that died prior to detection, the IFT was successful in documenting pups in the majority of pairs that had the potential to produce pups (78%, n = 104 out of 134 pairs). Thus, documenting pups was utilized as a dependent variable in an analysis (probability of detecting live pups). This analysis was necessary because Appendix C excludes packs where pups were not documented. Thus, Appendix C was utilized to describe the number of pups that would be detected, while this analysis was utilized to describe whether packs had detectable litters or not.

Statistical Methodology

[2] Sections of the larger report relevant to model input reproduced here for clarity.

We used general linear mixed models with a binomial distribution for the dependent variables of probability of live birth and probability of detecting live pups. The random effect was individual female producing litters. We developed a complete set of candidate models from the independent variables (Table B-1). Thus, the number of models was equivalent (balanced) between independent variables, with the exception of models that were removed from consideration because of uninformative variables (Arnold 2010). We did not simultaneously model independent variables that were correlated (e.g., Pearson's $r < 0.7$) and removed models with uninformative variables (Burnham and Anderson 2002, Arnold 2010) from the set of candidate models. Uninformative variables were considered as any variable that when added to the model did not reduce AIC values (i.e., AIC values for a model with variables A+B was ≤ AIC values for a model with variables A+B+C, or A+B+D). We used information-theoretic methods (i.e., ΔAIC) to quantify the strength of the remaining models (Burnham and Anderson 2002). We tested quadratic, cubic, and age classes for Dam Age or Sire Age, if retained, because the relationship was considered non-linear a priori. Specifically, young (≤ 3 years of age) and old (≥ 9 years of age) wolves were thought to be less successful than prime-aged (4-8) wolves.

We censored pairs that either bred or produced pups in captivity prior to release into the wild from the dataset. We also censored pairs that did not contain a complete suite of data for both the genetic and environmental variables. The primary reason for incomplete data was because one of the breeding animals was unknown, thus several genetic and environmental variables were unknown. By only using pairs with complete suite of independent variables, direct comparison between models was possible.

Results and Discussion

Because of censoring and restricting the data set, the analyses were conducted on 115 pair years of reproduction. The probability of detecting live pups included zeros in instances when pairs failed to show denning behavior, indicative of no reproduction, and early mortality of the entire litter of pups prior to observation. Overall, 89 pairs were documented with pups and 26 were not (77%), which was proportionally similar to the larger data set that was not restricted due to missing independent variables. The top models included both the age of the dam and the inbreeding coefficient of either the pups or the sire (note: sire and pup inbreeding coefficients were approaching correlation levels of concern, r = 0.658). Categorizing dam age appeared to fit the data the best for the curvilinear relationship (Table B-2). The curvilinear relationship was indicative of younger and older aged dams failed to have pups or the pups failed to survive to an age where they could be documented by field personnel at higher rate than prime age classes (Figure B-1 and B-2). Overall, an increase of 0.1 in the pup inbreeding coefficient resulted in decrease of 0.05 to 0.20 in the probability of detecting pups depending on the age class of the dam (Figure B-3).

Inbreeding may be impacting early survival or production of pups. These analyses may help elucidate the findings of previous analyses (Appendix C) where the impact of including 0's in litter size models tended to result in greater potential impacts of inbreeding on the maximum number of pups documented alive in a pack.

References

Arnold, T. 2010. Uninformative parameters and model selection using Akaike's Information Criteria. *Journal of Wildlife Management* **74**:1175-1178.

Burnham, K. P., and D. Anderson. 2002. Model selection and multi-model inference. Second edition. Spring-Verlag, New York, New York, USA

Table B-1. Description of independent variables used in logistic and generalized linear models for Mexican wolf pup production in Arizona and New Mexico. Classes included demographic variables, genetic, environmental, and structural variables. Structural and demographic variables were included in models initially to control for spurious results from genetic and environmental models. Environmental models include variables that could be associated with a pack of wolves' ability to acquire prey.

Variable Name	Variable Class	Description of Variable (When Necessary)
Count Method	Structural	Dummy variable designed to account for varying counting methodologies during the course of the study. Three time periods were coded (1998 -2004, 2005-2008, and 2009-2014).
Management Actions	Structural	Binomial variable that determined if management actions such a releases, removals, or translocations occurred during the year.
No. Years Pair Produced Pups	Demographic	Number of consecutive years that the same pair had produced pups.
Age of Dam/Sire	Demographic	Age of the breeding female and male within a pack.
Dam/Sire/Pups Inbreeding Coefficient	Genetic	Inbreeding coefficient of the breeding female, breeding male and pups produced within a pack. Based on pedigree analysis.
Dam/Sire/Pups Lineage	Genetic	Categorical variables that describes the lineages present within the breeding female, breeding male, and pups produced within a pack. Categories include MB (McBride lineage), MB-GR (McBride-Ghost Ranch cross), MB-AR (McBride-Aragon cross), and Tri (tri-lineage crosses).
Dam/Sire/Pups Percent McBride	Genetic	Percentage of genetic makeup from the McBride lineage in the breeding female, breeding male, and pups produced within a pack. Percent of other lineages were not included because they were negatively correlated with percent McBride.
Dam/Sire Years in Captivity	Environmental	Number of years that the breeding female and male spent in captivity at the time of whelping.
Dam/Sire Months in the wild	Environmental	Number of months that the breeding female and male spent in the wild at the time of whelping
Dam/Sire Proportion of Life in the Wild	Environmental	Proportion of life that the breeding female and male spent in the wild at the time of whelping
No. of Adults in the Pack	Environmental	Number of adults (including yearlings) present in the pack.

Table B-1. (cont.)

Variable Name	Variable Class	Description of Variable (When Necessary)
Helpers Present	Environmental	Coded as a 1 or 0 based on if non-breeding adult wolves (including yearlings) were present in the pack.
Supplemental Feeding	Environmental	Whether supplemental food was provided or not to a pack to either prevent depredations or assist in the transition of wolves to the wild following an initial release or translocation.
No. Years in Territory	Environmental	Number of continuous years of occupancy of a territory by at least one member of the breeding pair. We maintained time through transition of breeding pairs as long as an individual breeding wolf was with another that had occupied the territory for the previous period of time.

Table B-2. Competing logistic regression models for probability of detecting Mexican wolf pups in New Mexico and Arizona. The sample consisted of 89 pairs that with documented pups (visual observation or howling) and 26 pairs without documented pups. Models with uninformative parameters were excluded from the table. All models included a constant.

Model	AIC_c Value	ΔAIC_c	w_i
CATEGORIZED AGE DAM+INBREEDING COEFFICIENT FOR PUPS	109.565	0	0.536
CATEGORIZED AGE DAM+INBREEDING COEFFICIENT FOR SIRE	110.421	0.856	0.349
CATEGORIZED AGE DAM	112.664	3.099	0.114
AGE DAM	121.959	N/A[1]	N/A[1]
MONTHS IN WILD DAM	123.552	13.987	<0.001
INBREEDING COEFFICIENT FOR PUPS	123.940	14.375	<0.001
MONTHS IN WILD SIRE	124.834	15.269	<0.001
INBREEDING COEFFICIENT FOR SIRE	125.619	16.054	<0.001
CONSTANT ONLY	126.885	17.320	<0.001

[1] We only show the best non-linear form of AGE DAM. We attempted a categorized version for wolves ≤ 3, 4-8, and ≥ 9, AGE DAM SQUARED, AGE DAM + AGE DAM SQUARED, AGE DAM CUBED, and AGE DAM + AGE DAM CUBED. We used AGE DAM CUBED in all subsequent model efforts and only utilized AGE DAM CUBED in calculation of ΔAIC_c and w_i.

Table B-3. Relevant model information for the top model in table 2.

Parameter Estimates						
Parameter	Estimate	Standard Error	Z	p-Value	95% Confidence Interval	
					Lower	Upper
CONSTANT	1.266	0.984	1.287	0.198	-0.662	3.193
GROUPED_AGE_DAM_1	1.819	0.706	2.578	0.010	0.436	3.203
GROUPED_AGE_DAM_2	2.645	0.656	4.034	0.000	1.360	3.930
IC_PUPS	-8.255	3.775	-2.187	0.029	-15.653	-0.857

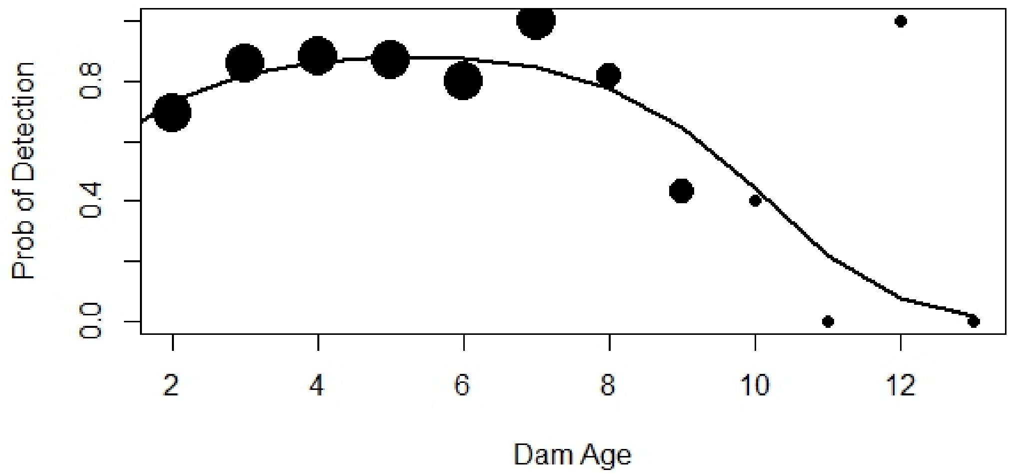


Figure B-1. Model results and data comparing probability of documenting live pups versus dam + dam age squared (the best linear representation of the relationship). Circles are scaled with larger circles representing a larger sample size at a particular age.

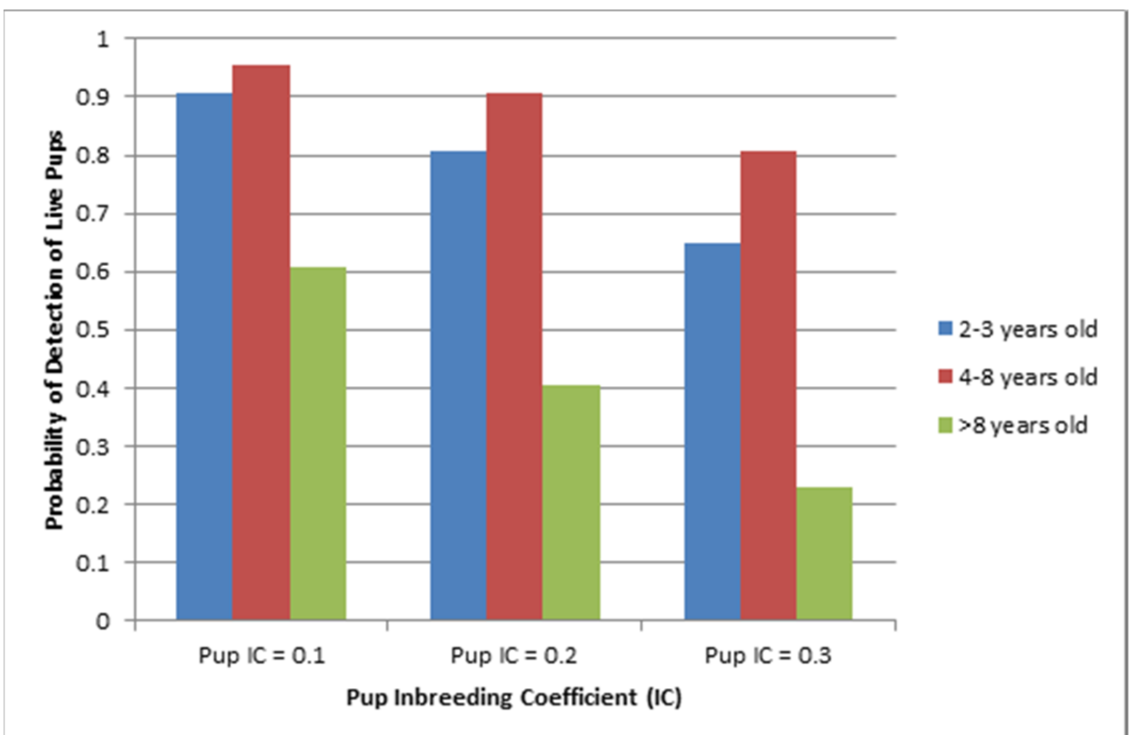


Figure B-2. A comparison of the probability of detection of live pups across the age of the reproducing dam in the pair and various pup inbreeding coefficients, using the regression results from Table B-5.

Appendix C.

Analysis of Inbreeding Effects on Maximum Pup Count in Wild Mexican Wolves[3]

Prepared By: Matthew Clement, Arizona Game and Fish Department (AZGFD) and Mason Cline, New Mexico Department of Game and Fish (NMDGF)

Date: 9 September, 2016

Introduction

Recovery planning for the Mexican wolf has included discussion of the effects of inbreeding depression on demographic parameters such as pup production. An analysis of wild litters produced from 1998 to 2006 indicated a negative association between pup Inbreeding Coefficient (*f*) and Maximum Pup Count (Fredrickson et al. 2007), but analysis of wild litters from 1998 to 2014 found no such relationship (Clement and Cline 2016). Therefore, our goal in this analysis was to revisit the analysis of wild litters, considering the effect of inbreeding in the dam and the pups on Maximum Pup Count.

Methods

We fit several models, described below, in support of our goals. In each case, the response variable was the Maximum Pup Count, as measured by counts of pups in each litter at various times from whelping through December of their birth year. To inform *Vortex* models of Mexican wolf population viability, wolf pairings that did not result in any detected pups were not used in the analysis of inbreeding effects, i.e., only non-zero litter sizes were included in the analysis. The portion of paired wolves that successfully have at least 1 detected pup will be modeled separately in *Vortex*. We analyzed the data with a Poisson-distributed generalized linear mixed-effects model (GLMM, McCulloch et al. 2008). We used mixed-effects models to account for non-independence of litters that come from the same parents. Either Poisson or negative binomial models may be appropriate for non-negative integer data. The negative binomial would be preferred if the variance of Maximum Pup Counts was significantly larger than the mean, but because the variance and mean were similar, we opted for the more parsimonious Poisson distribution.

Our primary research questions focused on the effect of inbreeding, so we initially included pup *f*, dam *f*, and sire *f* as covariates in our models. We also considered additional relevant covariates that might affect reproductive success. For wild populations, these included supplemental feeding, age of the dam, the presence of helpers, and the number of years in a territory. For captive populations, these included whether the dam had prior litters, the number of prior litters, the country of residence, and the age of the dam. We introduced non-correlated covariates (Pearson's $r^2 < 0.5$) sequentially and used Likelihood Ratio Tests (LRT) to determine if they should be retained in the best supported model.

We fit models to different time periods. We analyzed data from the early time period for both captive (1999 to 2005) and wild populations (1998 to 2006) for comparison with Fredrickson et al. (2007). To maximize the size of the data set, we also analyzed the entire time period for both captive (1999 to 2015) and wild (1998 to 2014) populations. For the wild population, we also analyzed subsets of the data that might represent more reliable counts of pups. In particular, as the recovery program matured, survey

[3] Sections of the larger report relevant to model input reproduced here for clarity.

protocols evolved, so that an analysis of counts may partially reflect changes in methodology, rather than the biological process of interest. To deal with this issue, we analyzed wild data from 2009 to 2014, a period with relatively constant survey methods (J. Oakleaf, USFWS, Pers. Comm., 2016). Second, we analyzed counts from 1998 to 2014 that were obtained within six weeks of whelping, which we assumed were closest to the true litter size. These data contained no repeated measures, so we excluded random effects from the model.

Results

As one component of our analysis (full results not shown here), we considered the full time period of data availability (1998 to 2014). In this case, the best supported model included the effects of diversionary feeding, and a quadratic effect of dam age, but no significant inbreeding effects. Maximum Pup Count increased with supplemental feeding, and was highest for dams aged 6.2 years, and lower for younger or older dams. Although the LRT indicated no significant effect of inbreeding, we estimated that increasing pup *f* from 0.1 to 0.2 for six year old dams not receiving diversionary feeding decreased Maximum Pup Count by 0.01 pups (Table C-1, Figure C-1).

References

Clement M, and M. Cline. 2016. Analysis of inbreeding effects on maximum pup count and recruitment in Mexican wolves, unpublished.

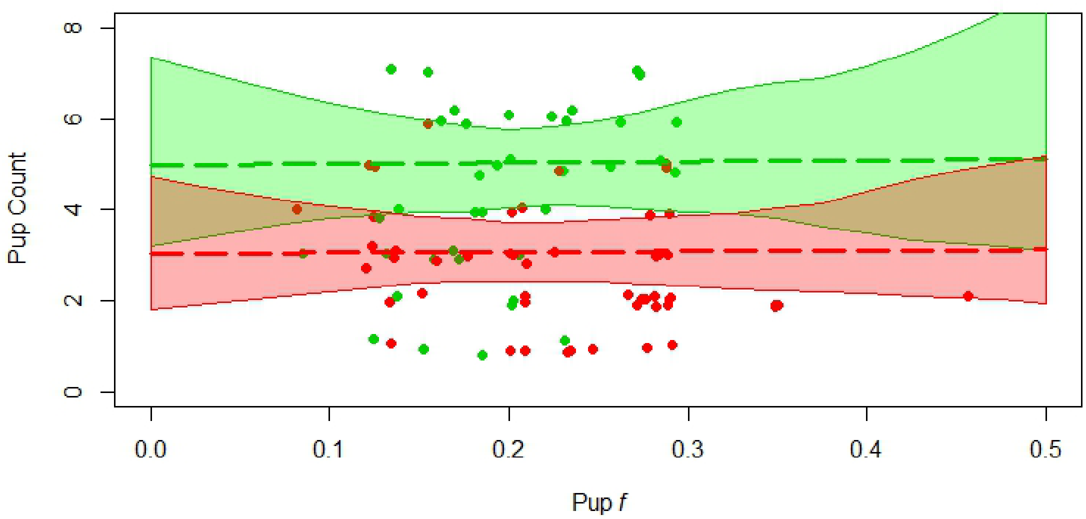
Fredrickson R.J., P. Siminski, M. Woolf, and P.W. Hedrick. 2007 Genetic rescue and inbreeding depression in Mexican wolves. *Proceedings of the Royal Society B* **274**:2365-2371.

McCulloch C.E., S.R. Searle, M. Woolf, and J.M. Neuhaus. 2008. *Generalized, Linear, and Mixed Models*, 2nd ed. John Wiley and Sons, Hoboken, NJ.

Table C-1. Results of Poisson-distributed generalized linear mixed-effects model of litter size in wild Mexican wolves, 1998 – 2014.

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.09370	0.22845	4.787	1.69e-06	***
Ic_Pups	0.05108	0.88744	0.058	0.9541	
Supp_Food1or0	0.49408	0.11908	4.149	3.34e-05	***
Age_Dam.sc	0.09685	0.06474	1.496	0.1347	
Age_Dam2.sc	-0.12114	0.05292	-2.289	0.0221	*

Figure C-1. Relationship between pup inbreeding coefficient and Maximum Pup Count in wild Mexican wolves, 1999 to 2014. Green represents wolves receiving supplemental (diversionary) feeding, red represents wolves not receiving supplemental (diversionary) feeding. Small random noise added to data points to avoid overlap.



Appendix D.

Survival and Related Mexican Wolf Data for Population Model Parameterization[4]

Prepared By: John Oakleaf, U.S. Fish and Wildlife Service

Date: 5 March, 2017

Input Data: Average number of pups born

4.652 ±1.799 ($\mu \pm SD$ for all reported values). Minimum 1, Maximum 7 (does not include 0's). These are litters that were counted in the den (<1 week to 6 weeks post birth).

	EARLY_PUP_COUNT	IC_PUPS	IC_DAM	IC_SIRE
N of Cases	23	22	22	23
Minimum	1.000	0.082	0.059	0.000
Maximum	7.000	0.292	0.289	0.292
Arithmetic Mean	4.652	0.203	0.208	0.187
Standard Error of Arithmetic Mean	0.375	0.014	0.017	0.022
Standard Deviation	1.799	0.066	0.081	0.103

This average covers a variety of inbreeding coefficients for the pups and adults. But average inbreeding is likely higher than the breeding component of the captive community.

Early (< June 30), mid-season counts (July 1 through September 30), and late season counts (October 1 to December 31) are summarized below.

	EARLY_PUP_COUNT	MID_PUP_COUNT	LATE_PUP_COUNT	IC_DAM	IC_SIRE	IC_PUPS
N of Cases	103	98	98	94	99	89
Minimum	1.000	0.000	0.000	0.000	0.000	0.082
Maximum	7.000	7.000	6.000	0.292	0.292	0.457
Arithmetic Mean	3.252	2.699	2.179	0.205	0.189	0.215
Standard Error of Arithmetic Mean	0.172	0.169	0.140	0.009	0.009	0.007
Standard Deviation	1.747	1.670	1.385	0.084	0.087	0.069

Baseline analytical approach

We modified survival analyses to address the current *Vortex* model structure because we utilized a model for first observation as equivalent to pup production (see Clement and Cline 2016). Further, observations of 0 pup counts were included in a probability of producing a detectable litter and thus excluded from these averages. Our approach was similar to previous documents but we utilized confidence intervals and average counts of early pup count for counts vs average pups at the mid-count (<Sept 30th) as a baseline mortality for pups prior to considering survival data from radio collars (which were generally placed on pups). In terms of the average survival this would be 2.699/3.252 = 0.83 survival rate or a corresponding

[4] Sections of the larger report relevant to model input reproduced here for clarity.

0.17 mortality rate among pups during the first 6 months of life for pups. The variability may be difficult in this case, but one may consider that the 95% Confidence interval would be represented by μ ± 1.96 SE in the number of pups counted in the middle pup count/ μ ± 1.96 SE in the number of pups counted in the early pup count). This results in a high survival rate of 3.030/2.915, or 1.0, with a corresponding mortality rate of 0.0. Conversely low survival would be 2.368/3.589, or 0.660 with a corresponding mortality rate of 0.34. A good approximation of this process for modeling purposes would be a survival rate with a mean of 0.83 that is normally distributed between 0.660 and 1.

All other time periods are based on radio collar information from 2009 through 2014 and are summarized below (Table D-1, Table D-2) for three age classes, including: (1) pups (following radio collaring, i.e. after the count time periods above), (2) sub-adults (includes short distance dispersal related mortality), and adults. There are four mortality sources, including: (1) natural (inclusive of unknown cause of death), (2) known human-caused (vehicles, and illegal killings through traps and shooting), (3) cryptic mortality (this represented animals in which circumstances surrounding the disappearance of the collar suggested an illegal mortality [Note: we classified 14 of the 32 missing collars as cryptic mortalities]), and (4) removals (inclusive of depredation and nuisance lethal and non-lethal removals which are classifications of removals that will continue into the future). We pooled mortality and radio days from 2009 to 2014 to represent the average yearly survival or mortality rate across the time period. We utilized methods that accounted for competing risks (Heisey and Fuller 1985).

Cryptic mortality was classified based on the all of the following criteria occurring:

1. Loss of radio contact with no indication of transmitter failure.
2. Subsequent weekly telemetry flights and bi-monthly search flights failed to locate the animal over a large area.
3. The animal failed to be observed for one year through intensive monitoring efforts.

We kept cryptic mortality in the overall survival rates because the data suggest that we were conservative in assessing this source of mortality relative to other authors that suggest it occurs at a similar rate to illegal mortality (Liberg et al. 2012). In addition, numerous collars have been found that have been destroyed, buried, moved, cut off of wolves, put into water, or otherwise tampered with. Although these examples were classified as human-caused mortalities, they provide ample evidence of cryptic mortality within the Mexican wolf population.

Our suggestion on a broad approach to modeling these data is a four stage survival model, as follows:

(1) Survival of pups from the time of first observation to the time of collaring is 0.83 normally distributed from 0.66 to 1.
(2) Survival of pups from time of collaring to 1 year of age is 0.865, distributed as described in Table 2.
(3) Survival from age 1-2 is 0.673, distributed as described in Table D-2.
(4) Survival of Adults is 0.811, distributed as described in Table D-2.

References

Heisey, D.M., and T. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* **49**:668-674.

Liberg, O., G. Chapron, P. Wabakken, H.C. Pedersen, N.T. Hobbs, and H.K. Sand. 2012. Shoot, shovel and shut up: Cryptic poaching slows restoration of a large carnivore in Europe. *Proc. Royal Society Series B* **270**:91-98.

Table D-1. Summary of information used for survival analyses from 2009 to 2014 of Mexican wolves.

Class	Radio Days	No. Natural	No. Human-Caused	No. Cryptic	No. Removed (Nuisance and Livestock)
Adult	46,978	4	14	6	3
Sub-Adult	20,312	2	11	6	4
Pups	8,812	1	4	2	0

Table D-2. Overall survival rates and cause specific mortality rates for Mexican wolves from 2009 to 2014. Pup survival is calculated using a 183-day survival rate, while adult and sub-adult survival is calculated based on a 365-day survival rate. Numbers in parenthesis represent the 95% CI surrounding the estimate.

Class	Survival Rate	Natural Mort Rate	Human-Caused Mort Rate	Cryptic Mort Rate	Removal Rate
Adult	0.811 (0.749, 0.877)	0.028 (0.001, 0.055)	0.098 (0.049, 0.147)	0.042 (0.009, 0.075)	0.021 (0.000, 0.045)
Sub-Adult	0.673 (0.571, 0.794)	0.030 (0.000, 0.070)	0.163 (0.075, 0.251)	0.074 (0.012, 0.137)	0.059 (0.003, 0.116)
Pup	0.865 (0.776, 0.963)	0.019 (0.000, 0.057)	0.0773 (0.005, 0.150)	0.0387 (0.000, 0.0912)	0 (N/A)

Addendum

Two areas of concern arose in subsequent recovery coordination meetings where the survival rates may be overly optimistic, including: (1) Mexican wolves that were recently (<1 year) released from captivity to the wild without wild experience (initial releases); and (2) Mexican wolves that were recently translocated from the wild or captivity with previous wild experience (translocations).

In some of these analyses, we had to acquire information from a larger time frame (1998-2015) to provide inference to the questions, but sources of mortality were classified as described above. The following modifications should be made based on the information below.

1. Based on the information collated as in Table D-3, we originally recommended that Table D-4 (below) should replace Table D-2 for Mexican wolves for the first year after initial release from captivity. We subsequently explored hypotheses that high removals in 2003-2008 biased the results from this analyses or that wolves released in Mexico may have higher survival, but these hypotheses were not supported. Further, the vast majority of the data was acquired during 1998 – 2002. Therefore, the original recommendation (Table D-4 replacing Table D-2) remained after exploration of these data.

Table D-3. Summary of information used for survival analyses of Mexican wolves within one year of initial release from captivity during 1998 - 2015.

Class	Radio Days	No. Natural	No. Human-Caused	No. Cryptic	No. Removed (Nuisance, Livestock)
Adult	7,262	2	7	2	14 (10, 4)
Sub-Adult	3,861	0	7	0	3 (2, 1)
Pups	1,306	1	1	0	3 (1, 2)

Table D-4. Overall survival rates and cause specific mortality rates for Mexican wolves within one year of initial release from captivity during 1998 - 2015. Pup survival is calculated using a 183-day survival rate, while adult and sub-adult survival is calculated based on a 365-day survival rate. Numbers in parenthesis represent the 95% CI surrounding the estimate.

Class	Survival Rate	Natural Mort Rate	Human-Caused Mort Rate	Cryptic Mort Rate	Removal Rate
Adult	0.284 (0.173, 0.465)	0.057 (0.000, 0.134)	0.200 (0.068, 0.332)	0.057 (0.000, 0.134)	0.401 (0.241, 0.561)
Sub-Adult	0.388 (0.216, 0.698)	0.0 (N/A)	0.428 (0.193, 0.664)	0.0 (N/A)	0.184 (0.000, 0.370)
Pup	0.496 (0.268, 0.917)	0.101 (0.000, 0.288)	0.101 (0.000, 0.288)	0.0 (N/A)	0.303 (0.019, 0.586)

Based on the information collated as in Table D-5, we originally recommended that Table D-6 should replace Table D-2 for Mexican wolves for the first year after they were translocated from another population. We subsequently explored a hypothesis that high removals from 2003-2008 biased the results of Table D-6 (note: data on translocations in Mexico was sparse, thus, we could not explore Mexico results relative to translocations). In this case, we found some support that survival could have been negatively impacted by the management strategy from 2003-2008. The general hypothesis is that this level of removal was too aggressive and the project would not return to that level of removal. However, over half of the data on translocations was accumulated during 2003-2008 and removing the data from this time period presents some difficulties relative to sample sizes and inference. Thus, we chose to rarefy depredation related removals by 50% (removal rates were approximately 50% higher for adults (the most robust data) during 2003-2008 relative to other time periods) during 2003 to 2008 to normalize the aspect of the data that was impacted by the management strategy and to redo the analyses with the full complement of other data (mortalities and radio days). This resulted in the reduction of 5 removals from the overall analyses. Thus, we now recommend utilizing Table D-8, based on the data collated as in Table D-7, to replace Table D-2 for Mexican wolves for the first year after translocations.

Table D-5. Summary of information used for survival analyses of Mexican wolves within one year of translocation from captivity or the wild during 1998 - 2015.

Class	Radio Days	No. Natural	No. Human-Caused	No. Cryptic	No. Removed (Nuisance, Livestock)
Adult	13,123	1	9	5	12 (2, 10)
Sub-Adult	3,756	2	3	3	2 (2, 0)
Pups	623	0	1	0	2 (0, 2)

Table D-6. Overall survival rates and cause specific mortality rates for Mexican wolves within one year of translocation from captivity or the wild during 1998 - 2015. Pup survival is calculated using a 183-day survival rate, while adult and sub-adult survival is calculated based on a 365-day survival rate. Numbers in parenthesis represent the 95% CI surrounding the estimate.

Class	Survival Rate	Natural Mort Rate	Human-Caused Mort Rate	Cryptic Mort Rate	Removal Rate
Adult	0.472 (0.355, 0.626)	0.020 (0.000, 0.058)	0.176 (0.072, 0.280)	0.098 (0.017, 0.179)	0.235 (0.119, 0.350)
Sub-Adult	0.378 (0.207, 0.691)	0.124 (0.000, 0.285)	0.187 (0.000, 0.376)	0.187 (0.000, 0.376)	0.124 (0.000, 0.285)
Pup	0.413 (0.152, 1.000)	0.000 (N/A)	0.196 (0.000, 0.537)	0.000 (N/A)	0.391 (0.000, 0.808)

Table D-7. Summary of information used for survival analyses of Mexican wolves within one year of translocation from captivity or the wild during 1998 – 2015. Data was modified to reduce the number of livestock related removals by 50% during 2003-2008. This resulted in 4 fewer adult livestock related removals and 1 fewer pup related removal (see Table 21).

Class	Radio Days	No. Natural	No. Human-Caused	No. Cryptic	No. Removed (Nuisance, Livestock)
Adult	13,123	1	9	5	8 (2, 6)
Sub-Adult	3,756	2	3	3	2 (2, 0)
Pups	623	0	1	0	1 (0, 1)

Table D-8. Survival rates and cause specific mortality rates for Mexican wolves within one year of translocation from captivity or the wild during 1998 - 2015. Pup survival is calculated using a 183-day survival rate, while adult and sub-adult survival is calculated based on a 365-day survival rate. Numbers in parenthesis represent the 95% CI surrounding the estimate.

Class	Survival Rate	Natural Mort Rate	Human-Caused Mort Rate	Cryptic Mort Rate	Removal Rate
Adult	0.527 (0.406, 0.685)	0.021 (0.000, 0.060)	0.185 (0.076, 0.294)	0.103 (0.018, 0.188)	0.164 (0.060, 0.268)
Sub-Adult	0.378 (0.207, 0.691)	0.124 (0.000, 0.285)	0.187 (0.000, 0.376)	0.187 (0.000, 0.376)	0.124 (0.000, 0.285)
Pup	0.555 (0.246, 1.000)	0.000 (N/A)	0.222 (0.000, 0.605)	0.000 (N/A)	0.222 (0.000, 0.605)

Mexican wolf habitat suitability analysis in historical range in the Southwestern US and Mexico

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Summary

In the last three decades, important efforts have been made to evaluate the habitat suitability for the reintroduction and long-term persistence of the Mexican wolf (*Canis lupus baileyi*) both in the US and Mexico. However, such efforts have used different methodological approaches and have covered only some portions of the historical distribution range of this subspecies, making it impossible to have a comprehensive understanding of where and how much habitat is left for maintaining long-term, viable free-ranging populations of the Mexican wolf. This project aims to fill this gap by carrying out a habitat suitability analysis across the whole historical range of the Mexican wolf, from southern Arizona and New Mexico and western Texas, in the US, to central Oaxaca, Mexico, using input information for both countries and under a uniform methodological scheme. We implemented an additive model integrating geographic information of critical environmental variables for the Mexican wolf, including climatic-topographic suitability, land cover use based on frequency of occurrences, ungulate biomass, road density, and human density. Data available for the ungulate biomass index was not robust enough to generate reliable rangewide estimates, so we present a series of maps representing different scenarios depending on the thresholds used in the anthropogenic factors (road and human density) and also with and without the inclusion of the ungulate biomass. We found concordant areas of high suitability irrespective of the scenario, suggesting that such areas are the most favorable to explore for future reintroductions. The largest suitable areas were found both in the US and Mexico, particularly the higher elevation areas of east central Arizona and west central New Mexico in the Mexican Wolf Experimental Populations Area Management (MWEPA) in the US, and in northern Chihuahua-Sonora and Durango in the Sierra Madre Occidental in Mexico. Our results suggest that there is still sufficient suitable habitat for the Mexican wolf both in the US and Mexico, but specific sites for reintroductions in Mexico and estimations of the potential number of wolves need to consider reliable field data of prey density, cattle density, land tenure, natural protected areas, safety to the field team, and acceptability of wolves by local people.

Acknowledgements

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Introduction

The Mexican wolf, *Canis lupus baileyi*, is currently one of the five recognized subspecies of gray wolf (*Canis lupus*) in North America and has been described as the smallest of all gray wolf subspecies in this continent. This subspecies lived in the arid areas and temperate forests of southwestern US and northern and central Mexico, in many different habitats at altitudes higher than 1300 meters above sea level (msl), including areas of chaparral, desert, grasslands, forests and temperate uplands (Gish 1977), but preferring those habitats with high ungulate biomass (McBride 1980).

The history of the extermination of the Mexican gray wolf is inextricably linked to the conquest of the West by the Euroamerican settlers. In the United States, the expansion to the West started in 1804 with the Lewis & Clark expedition (Lavender 1998) and continued throughout the century. Followed by colonization, an ecological catastrophe commenced and reached its climax with the railway construction, between 1863 and 1869. With the railroad, the influx of people and settlements increased all along those routes, and so did the need for goods and supplies. Along with the increase in cattle ranching and settlement (Brown 1983), a depletion of wild animal populations took place, in which the bison (*Bison bison*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and pronghorn (*Antilocapra americana*) experienced an exceptional population decline. These species were hunted for food, leather and fur. Some historians suggest that the amount of carcasses left in this period probably benefited the local predators (coyotes, bears, wolves) due to the increase of food in the form of carrion. As the abundance of wild prey decreased, the increasing human population demanded more food, thus cattle raising expanded and gradually replaced wild herds of bison and other ungulates that comprised the natural prey of wolves, including the elk (*Cervus elaphus*), white-tailed deer and mule deer (Brown 1983). After the short-term availability of meat as carrion for predators in the region, wolf populations may have been elevated and cattle predation increased, triggering the onset of human-predator intense competition.

During the first half of the 20th century, several environmental and political events happened that triggered direct actions against predators, particularly towards the wolf. In the late 19th and early 20th centuries a series of droughts (1880-1902) ended with one of the harshest winters recorded (NOAA 2016). Thousands of cattle were lost and hundreds of villages abandoned; surviving abandoned cattle became feral. Cattle became part of a new source of food for opportunistic predators/scavengers, like the wolf. In 1917, under the pressure from livestock associations in different states incurring the loss of cattle, predator extermination became a central goal and a government branch, the Predator and Rodent Control (PARC), was created to control harmful species; therefore, persecution and extermination of predators took on renewed force and trappers were hired across the United States for a substantial pay, driving the gray wolf to near extinction.

In the southwestern US, history was no different. Settlers in Arizona, New Mexico and Texas used various kinds of methods to eliminate the wolf population, so that by 1950 wolves were scarce. In Cochise Valley, a PARC report from 1926 states that after previous years and less than 50 wolves captured, the county was considered free of wolves. In 1951 another report concluded that the eradication program of wolves took only eight years to achieve the goal of eliminating the Mexican gray wolf, stating that this could be the first "conservation program" completed in Arizona. However, some people in Arizona and New Mexico complained about the constant incursion of gray wolves from Mexico, which did not have a predator control program. In 1949, Mexico and United States signed a binational treaty to control predators –known as the Convention of Nogales–, in which the control scheme was based on the prevention of serious livestock damage and for rabies control (Baker and Villa 1960). By this time sodium fluoroacetate (better known as 1080) was available. Workshops took place in the states of Chihuahua and Sonora to teach Mexican ranchers the adequate and safe use of this chemical. In 1958, a PARC report in Arizona stated that several reliable stockmen in Mexico reported no livestock predation since 1080 was implemented around 1950. The control was absolute, 20 years later, wolves were rarely seen and it was difficult to trap them.

Although it is not clear when the Mexican wolf went extinct in the wild (Hoffmeister 1986; Leopold 1959), by 1976 the USFWS listed the wolf (*C. lupus*) as an endangered species (Parsons 1996). At this time the population of the Mexican wolf in the wild was estimated at less than 50 individuals located in the Sierra Madre Occidental (Brown 1983). This designation encouraged efforts to prevent extinction and favored the creation of a captive breeding program, allocating resources to capture the last wolves in the wild. Between 1977 and 1980, the USFWS hired Roy McBride, an expert in wolf behavior and trapper, in order to capture the last wolves in the wild. McBride caught five wild wolves in the states of Durango and Chihuahua, Mexico. With these individuals (known as the McBride lineage) the US government launched a captive breeding program. Later, with the recognition of another two lineages, Ghost Ranch and Aragón (Hedrick et al. 1997), the captive breeding program became a binational effort. Today, it is considered a successful program having about 240 individuals of the three certified genetic lineages in several institutions both in the US and Mexico (Siminski 2016).

In 1996, the US government started preparations for the release and establishment of a nonessential experimental population of the Mexican wolf in the Blue Range Wolf Recovery Area (BRWRA). The first releases were in Arizona in 1998. The first Mexican Wolf Recovery Plan seeked “to conserve and ensure the survival of *Canis lupus baileyi* by maintaining a captive breeding program and re-establishing a viable, self-sustaining population of at least 100 Mexican wolves in the middle to high elevations of a 5,000-square-mile area within the Mexican wolf's historic range.” (USFWS 1982). Currently, this program has reached this goal by achieving a wild population of at least 113 individuals in the US. Nonetheless, as part of the ecological principles in species’ recovery, ‘redundancy’ (more than one population recovered) is an important element (Wolf et al. 2015), thus the identification of additional release areas was necessary. Therefore, parallel efforts began in Mexico in the early 1980s, with an interdisciplinary group interested in restoring the Mexican wolf in the country, generating different initiatives to determine the best sites in Mexico to establish a Mexican wolf population (CONANP 2009).

In October 2011, after a series of public meetings with ranchers and private owners, the first family group of Mexican wolves was released into the wild in the northern part of the Sierra Madre Occidental (Moctezuma-Orozco 2011). Five wolves (three females and two males) were set free in a private ranch in Sierra San Luis, Sonora. However, within the next two months, four of the wolves were killed, and a lone wolf headed south along the Sierra Madre Occidental in an approximately 400 km dispersing journey to end up in Madera municipality, in the state of Chihuahua. One year after the first release, another pair was released in a private ranch in Chihuahua (López-González et al. 2012), not far from one of the sites that the last single wolf remained for a couple of days during her journey. After another release in the same ranch, the pair produced the first wild litter in Mexico (CONANP 2013). Several other releases have been carried out since 2011, with the support of the private land owner; however, soon after release, the wolves broke apart and wandered away from the release site (CONANP 2014), highlighting the need to define the environmental and social variables that promote territorial pack stability. As many as 31 wolves run free in the mountains of the Sierra Madre Occidental as of April 2017.

Previous habitat suitability analyses for the Mexican wolf

Increasing human pressure constrains remaining habitat for wolves (Thiel 1985), thus an analysis of the available habitat for the reintroduction of the Mexican wolf (*Canis lupus baileyi*) both in Mexico and in the US is a key element for the recovery of the species in the wild. In the last 15 years there has been several efforts to identify suitable areas for the recovery of the Mexican wolf in either the US or Mexico (Araiza 2001; Martínez-Gutiérrez 2007; Araiza et al. 2012; Carroll et al. 2003; 2004, 2013; Hendricks et al. 2016), but only one published study (Hendricks et al. 2016) has attempted an analysis across the historic range of the Mexican wolf. For instance, Araiza et al. (2012) was not intended to be a comprehensive analysis of all potential habitat in Mexico, but rather an exercise to identify the highest priority areas to begin restoration. Others have used the best information available at the time (Carroll et al. 2003; 2004; Martínez-Gutiérrez 2007), but there have been advances in recent years in the type and quality of data available. The most recent analysis (Hendricks et al. 2016) produced an ecological niche model across the whole historical range of the Mexican Wolf and this potential distribution map was then refined with global land cover and human density maps, but the aim of the study was primarily to redefine the historical distribution of the Mexican wolf, rather than a habitat suitability analysis. Thus, there is an opportunity to increase our understanding of available wolf habitat across the historic range of Mexican wolf.

In order to support the recovery of the Mexican wolf it is important to base the geography of recovery on the best science available. With recovery planning currently underway, a habitat analysis becomes an urgent necessity. To fill this gap, we carried out a habitat suitability analysis aiming to identify areas holding favorable conditions for the reintroduction and recovery of the Mexican wolf across its historical range, in order to provide authorities of the two countries with reliable information for decision-making. Thus, the main goals of the present study were:

1) Identify suitable, high-quality habitat areas to carry out recovery actions of Mexican wolf populations in Mexico.

2) Estimate the potential number of wolves in those areas to serve as input for a Population Viability Analysis (PVA).

Methods

Analyses were carried out in six steps: (1) reconstruct the historical distribution of the Mexican wolf via ecological niche modeling; (2) compilation, organization and standardization of compatible environmental and anthropogenic habitat variables for the two countries; (3) estimate ungulate density across the historic range of the Mexican wolf; (4) model the habitat suitability across the historic range of the Mexican wolf; (5) identify the largest, continuous patches through a landscape fragmentation analysis; and (6) estimate the possible number of wolves in those suitable areas. Each phase is described below.

1. Reconstructing the historical distribution of the Mexican wolf

To infer the historical distribution of the Mexican wolf we followed an ecological niche modeling (ENM) approach. The ecological niche of a species is defined by a set of abiotic (e.g., climatic, topographic) and biotic (e.g., food, predators, pathogens) variables that fulfill the ecological requirements of a species (Hutchinson 1957; Soberón & Peterson 2005). However, its modeling and representation in a geographic fashion has often been constrained by our knowledge of the ecological requirements of species and, most importantly, by the available spatial information to construct the niche model. Partial data of ecological requirements or spatial information results in a partial representation of the ecological niche, generally the abiotic portion of it, because information of climatic and topographic features is broadly available worldwide (Soberón 2007).

Ecological niche modeling is a correlative approach between the occurrence records of a species and a set of environmental variables that define the scenopoetic niche of that species (*sensu* Hutchinson 1957). Niche modeling algorithms look for non-random associations between the environmental conditions of a region and the presence of the species; once these conditions are identified (*i.e.*, the scenopoetic niche), similar conditions are searched for across the study region and a map of the potential distribution of the species is produced (Peterson et al. 2011).

For these analyses, the first challenge was to define the historical limits of the Mexican wolf (*Canis lupus baileyi*) in order to select the records to model its niche. In the original description of the gray wolf (*Canis lupus*), 24 subspecies were recognized for North America (Goldman 1944; Hall & Kelson 1959). Further studies considering cranial morphometry and genetic analyses (Nowak 1995, 2003) reduced the number of subspecies to five, namely *C. l. arctos* (Arctic wolf), *C l. lycaon* (Eastern timber wolf), *C. l. nubilus* (Great Plains wolf), *C. l. occidentalis* (Rocky Mountain wolf), and *C. l. baileyi* (Mexican wolf), but all agree that the Mexican wolf is the most differentiated both genetically and morphologically (Heffelfinger et al. 2017).

Participants of the Mexican wolf recovery workshop in April 2016 in Mexico City, agreed the northern extent of the analysis area should include central Arizona-New Mexico up to the I-40 (in order to include all of MWEPA), continuing south to the southernmost occurrence records in Oaxaca, Mexico, and east to include western Texas and the Sierra Madre Oriental in Mexico (Fig 1).

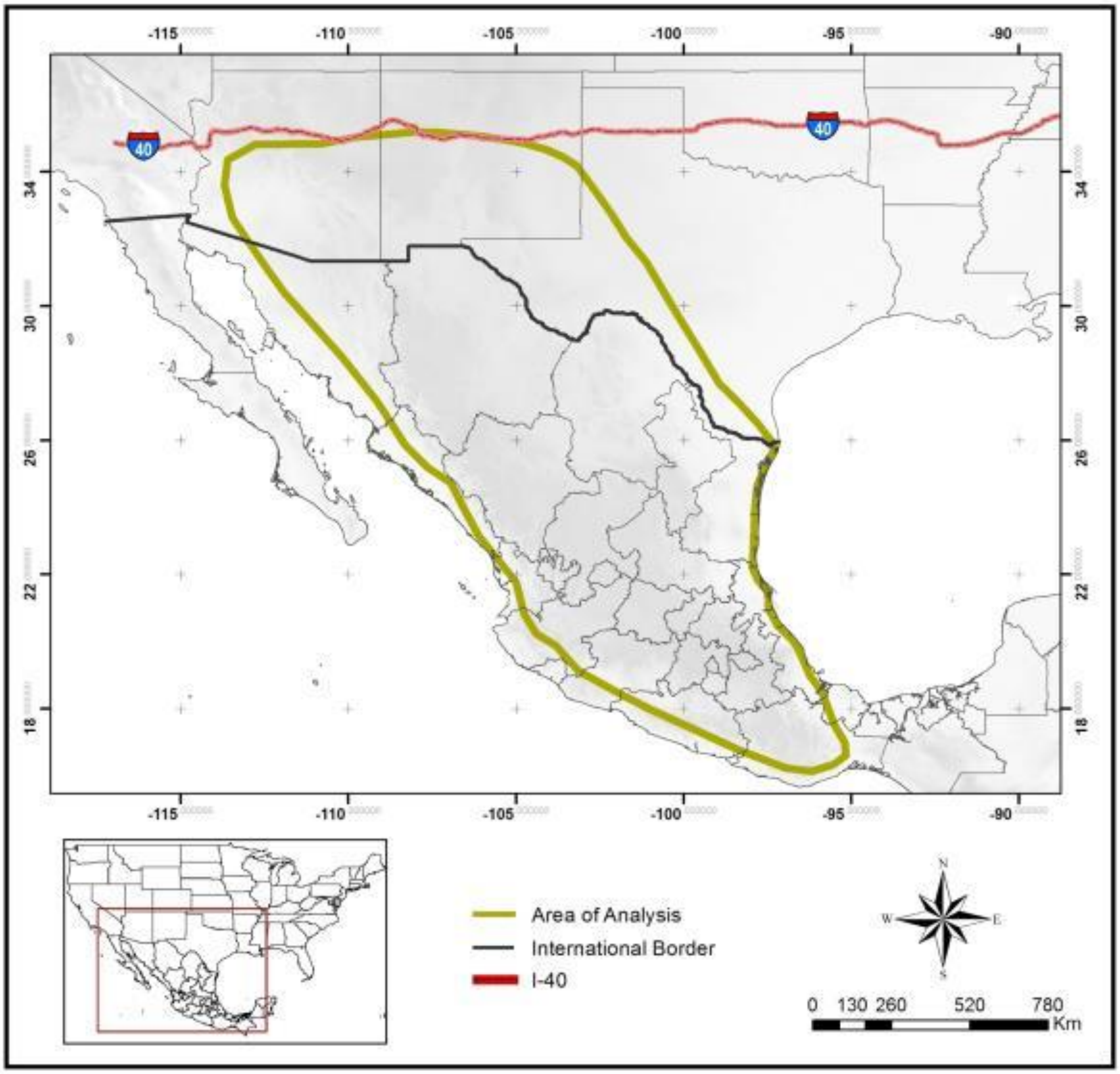

Figure 1. Map depicting the area of analysis.

Occurrence records

We compiled all occurrence records of the gray wolf (*Canis lupus*) available in the literature (Hall 1981, Brown 1983, Nowak 1995, Martínez-Meyer et al. 2006, Araiza et al. 2012), electronic databases (i.e., GBIF, Vertnet) and oral records from local trappers (from Brown 1983 and fieldwork of Jorge Servín), extending from 1848 to 1980. For those records within the polygon of analysis corresponding to the

Mexican wolf (Figure 1), we reviewed each record to accept or discard them based on the georeferencing accuracy. We divided the records according to their reliability into primary (i.e., those with skin or skull specimens preserved in a natural history collection) and secondary (i.e., those from observations or interviews). Only primary records were used to calibrate ecological niche models and secondary records were used for model validation. To avoid over-representation of particular environments due to sample bias that would result in model overfitting and bias, we filtered primary records to ensure a minimum distance of 25 km between each primary record (Boria et al. 2014). Thus, all records used for calibration were separated by a distance of at least 25 km to avoid clusters of points in areas where sampling effort has been higher. Validation records were filtered at a distance of 1 km. Filtering was conducted using the *thin* function in the spThin R package (Aiello-Lammens et al. 2015). Our final dataset to model the geographical distribution of the Mexican wolf consisted of 41 primary occurrences and included all historical records from the Blue Range Wolf Recovery Area (BRWRA) to the south (Fig. 2).

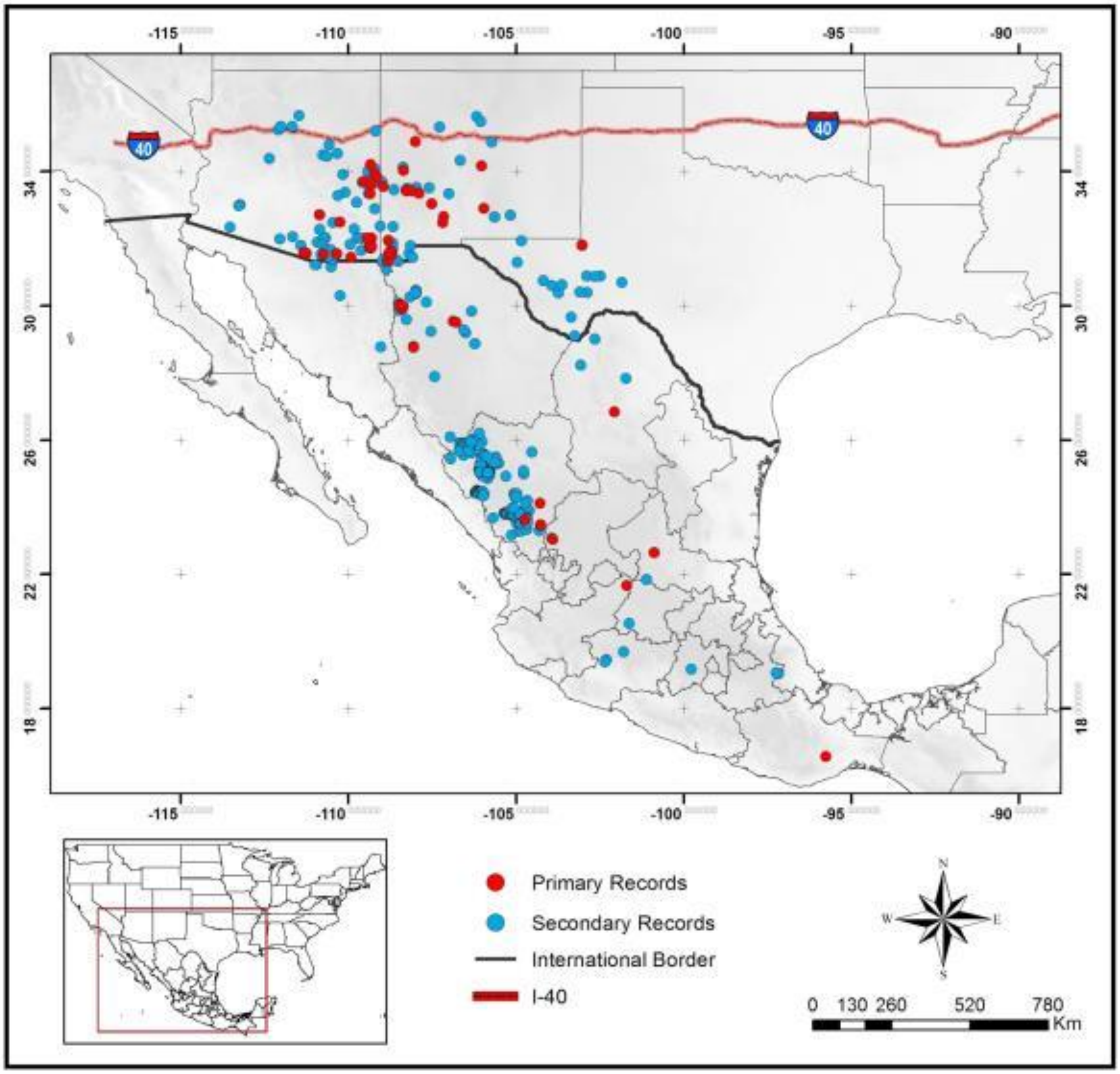

Figure 2. Occurrence records used for the construction of niche models. Primary records (for calibration) are shown in red and secondary records (for validation) are shown in blue. See text for details.

Environmental layers

We used 19 climatic variables obtained from the WorldClim database (Hijmans et al. 2005; Table 1) that have been extensively used in the ecological niche modeling field for thousands of species worldwide, including the Mexican wolf (Hendricks et al. 2016). We also included three topographic variables: elevation, slope and topographic heterogeneity (calculated as the standard deviation of elevation) from the Hydro 1k database (USGS 2008). To avoid model overfitting we used only the most informative variables. We reduced the number of variables using the MaxEnt program, which has implemented a permutation method to identify the relative contribution of all variables to model performance (Phillips et al. 2004; 2006; Searcy & Shaffer 2016). Thus, we selected only those variables with a relative contribution to model performance >1% (Table 1). The resolution of all variables was set to 0.008333 decimal degrees, which corresponds approximately to 1 km^2.

Table 1. Environmental abiotic variables selected (X) for building ecological niche models for the extended and restricted sets of occurrence data.

Variable	**Selected**
Elevation	X
Slope	X
Topographic Index	X
bio 1: Annual Mean Temperature	X
bio 2: Mean Diurnal Range	X
bio 3: Isothermality	X
bio 4: Temperature Seasonality	
bio 5: Max Temperature of Warmest Month	
bio 6: Min Temperature of Coldest Month	X
bio 7: Temperature Annual Range	X
bio 8: Mean Temperature of Wettest Quarter	X
bio 9: Mean Temperature of Driest Quarter	X
bio 10: Mean Temperature of Warmest Quarter	
bio 11: Mean Temperature of Coldest Quarter	X
bio 12: Annual Precipitation	
bio 13: Precipitation of Wettest Month	X
bio 14: Precipitation of Driest Month	X

bio 15: Precipitation Seasonality	X
bio 16: Precipitation of Wettest Quarter	
bio 17: Precipitation of Driest Quarter	
bio 18: Precipitation of Warmest Quarter	
bio 19: Precipitation of Coldest Quarter	X

Ecological niche and distribution modeling

Niche modeling algorithms perform differently depending on the type (i.e., presence-only, presence-absence, presence-pseudoabsence, or presence-background), amount and spatial structure (e.g., aggregated, biased) of occurrence data (Elith et al. 2006). There is not a single algorithm that performs best under any condition (*i.e.*, Qiao et al. 2015); therefore, it is advisable to test more than one algorithm and evaluate the results to select one or more with the best performance (Peterson et al. 2011). Hence, to model the ecological niche and potential distribution of the Mexican wolf we used the following algorithms: Bioclim, Boosted Regression Trees (BRT), Classification and Regression Trees (CART), Generalized Additive Model (GAM), Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MaxEnt), Random Forest (RF), and Support Vector Machine (SVM). These models were implemented using the R packages *sdm* (Naimi & Araújo 2016) and *dismo* (Hijmans et al. 2005), and MaxEnt was used in its own interface (Phillips et al. 2006). For those algorithms based on presence and absence data (e.g., GLM, GAM, MARS), we generated pseudo-absences randomly across the geographical region with the same minimum distance as presences (*i.e.*, 25 km). The number of pseudo-absences used was based on the prevalence, i.e., the proportion of sites in which the species was recorded as present (Allouche et al. 2006; Peterson et al. 2011); however, prevalence usually is unknown and depends on the size of the analysis area (Peterson et al. 2011). We defined prevalence based on the results of the first niche model performed in MaxEnt, where it was of 0.3.

Thus, we multiplied the number of calibration and validation presences by three to get the number of absences according to prevalence (Table 2).

Table 2. Number of presences and pseudo-absences for calibration and validation used for ecological niche modeling.

Calibration		**Validation**	
Presences	**Pseudo-absences**	**Presences**	**Pseudo-absences**
41	123	296	888

We used calibration data to produce niche models for each algorithm under default settings. Potential distribution maps produced with these algorithms represent either an estimation of the probability of presence of the species or a suitability score, both in a continuous scale from 0-1. To make them comparable, we converted continuous maps into binary (presence-absence) based on a 10-percentile threshold value (i.e., we allowed 10% of the presence records fall outside the prediction map). We chose a 10-percent threshold value to account for some inaccuracy in the original collection locations (*e.g*., locality description: “Chiricahua Mountains”).

Model validation

We validated each model using a set of metrics based on the models performance in correctly predicting presences and absences (Fielding & Bell 1997; Allouche et al. 2006). We selected the best models according to a combination of four metrics: omission and commission errors (i.e., the number of presences predicted as absences and vice versa), True Skill Statistic (TSS), and chi-squared values.

Niche models produced results with large variation. BRT and GLM produced overpredicted distributions (Fig. 3); according to the validation metrics, the algorithms that performed better were MaxEnt, RF, CART, and GAM (Table 3).

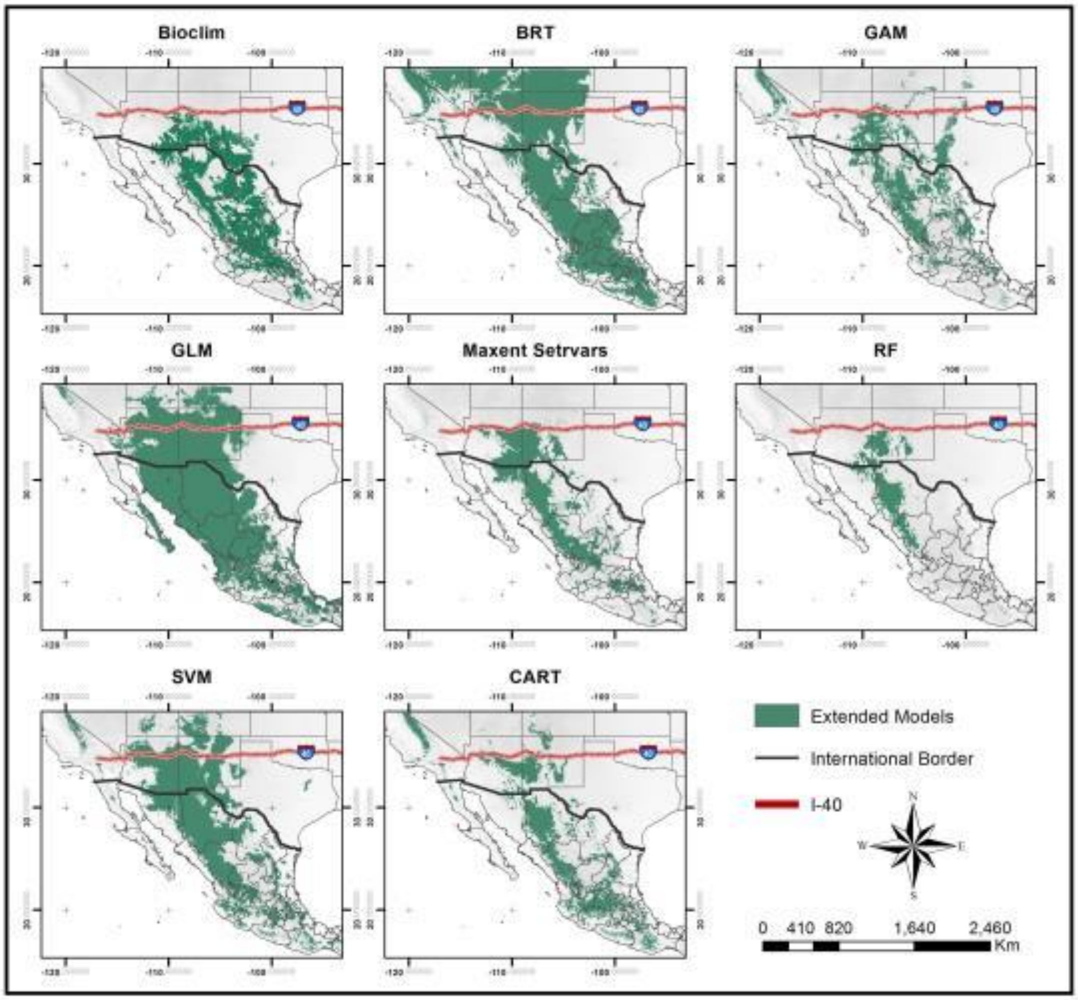

Figure 3. Binary maps of the potential geographical distribution of the Mexican wolf (*Canis lupus baileyi*) for each ecological niche modeling algorithm. Bioclim; BRT: Booted Regression Trees; GAM: Generalized Additive Model; GLM: Generalized Linear Model; Maxent: Maximum Entropy; RF: Random Forest; SVM: Support Vector Machines; CART: Classification and Regression Trees.

Table 3. Model performance metrics for binary predictions generated by each ecological niche modeling algorithm. In bold the selected binary predictions.

Metrics	Bioclim	BRT	CART	GAM	GLM	Maxent	RF	SVM
Omission error rate	0.23	0.06	**0.15**	**0.13**	0.02	**0.07**	**0.19**	0.03
Commission error rate	0.18	0.38	**0.14**	**0.13**	0.42	**0.12**	**0.04**	0.27
TSS	0.60	0.56	**0.72**	**0.74**	0.55	**0.81**	**0.77**	0.70
Chi-squared	928.88	402.05	**1513.69**	**1312.72**	352.03	**1768.84**	**4091.42**	753.43
p-value	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001

TSS: True Skill Statistic

Model assembling

We generated a consensus map with the four algorithms that performed better by summing each binary map. A consensus map expresses the areas where one, two, three, or four algorithms predicted the presence of appropriate abiotic conditions for the Mexican wolf. We selected the areas where two or more models coincided to predict the presence of the Mexican wolf and converted that in a binary map, representing the potential distribution of the subspecies. To approximate the historical distribution of the Mexican wolf from the potential distribution map, we discarded those climatically suitable areas within biogeographic regions that do not contain historical occurrence records of the species (e.g., Baja California), assuming that those regions have not been inhabited by Mexican wolves at least in the last two-hundred years (Anderson & Martínez-Meyer 2004) (Fig. 4).

The model shows that suitable climatic niche conditions for the Mexican wolf exist in central Arizona and New Mexico, The Sky Islands in southwestern US and northwestern Mexico, central-south New Mexico and western Texas in the US, and in the Sierra Madre Occidental, scattered mountain ranges in the Sierra Madre Oriental, along the Transvolcanic Belt in Mexico, and in the higher sierras of Oaxaca

(Fig. 4). This geographic description of the historical range of the Mexican wolf shows strong phylogeographic concordance with the distribution of the Madrean pine-oak woodlands and other endemic subspecies concomitant with this vegetation association, such as Mearns' quail (*Cyrtonyx montezumae mearnsi*), Coues' white-tailed deer (*Odocoileus virginianus couesi*), Gould's turkey (*Meleagris gallopavo mexicana*) and several others (Brown 1982; Heffelfinger et al. 2017).

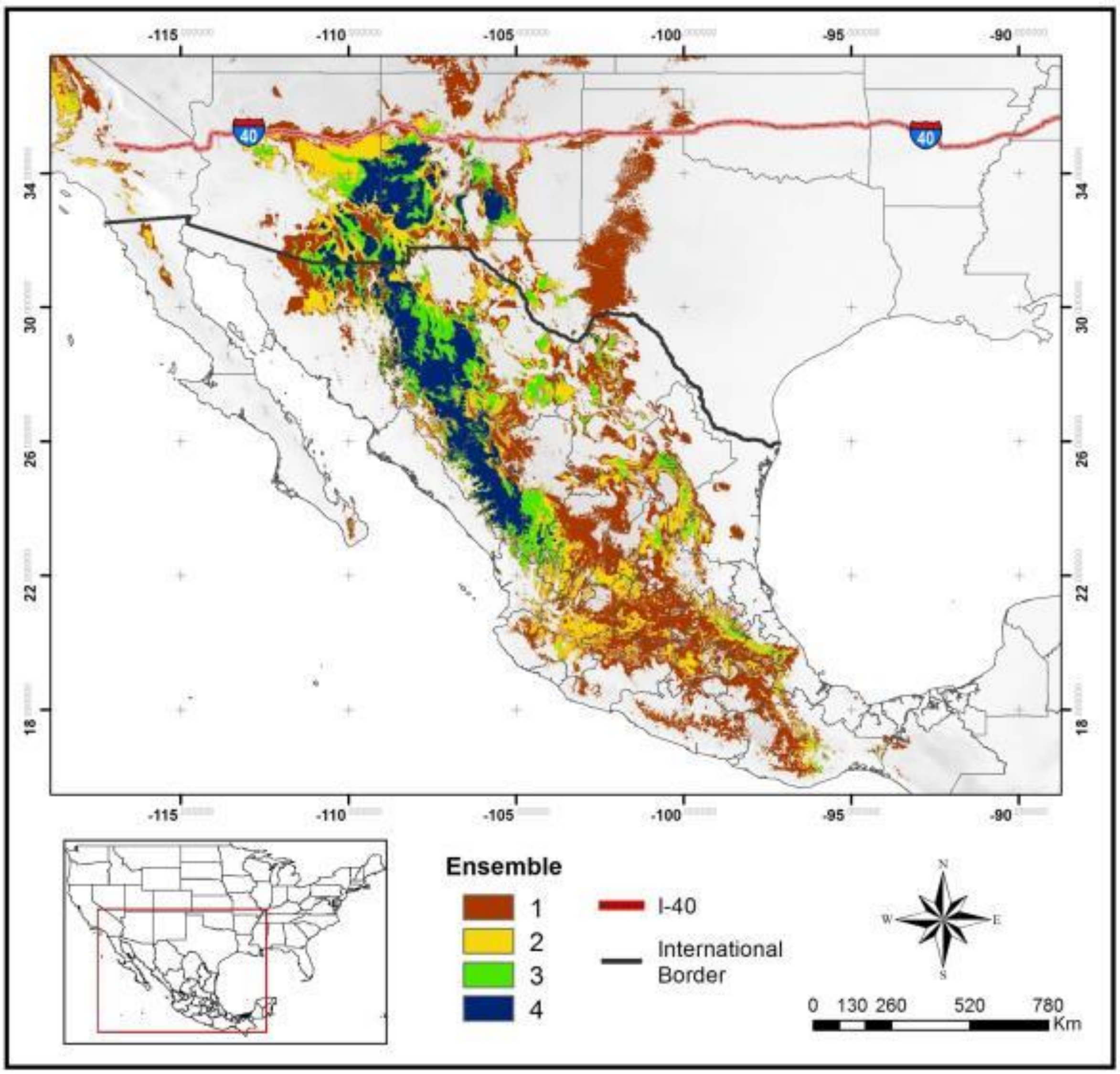

Figure 4. Consensus map representing the ensemble of four individual best models (see text for

details).

Climatic suitability

Based on the final ensemble, we characterized the climatic suitability across the geographical distribution based on the notion that optimal conditions for a species is towards the ecological centroid of its niche in multidimensional space (Hutchinson 1957; Maguire 1973). We followed the methodological approach proposed by Martínez-Meyer et al. (2013) to estimate the distance to the ecological niche centroid as an estimation of environmental suitability. To do so, for all grid cells defined as presence, we extracted the climatic values of the bioclimatic variables used in the modeling (Table 1), we *z*-standardized the values in a way that mean is 0 and standard deviation 1. For each pixel, we calculated the Euclidean distance to the multidimensional mean and finally rescaled these distances from 0-1, where 0 corresponds to the least climatically suitable areas (*i.e.*, farther away from the niche centroid) and values near 1 correspond to pixels with the highest suitable climates.

The resulting map indicates that the highest values of climatic suitability are in the western portion of the distribution (the Sky Islands, southwestern Texas, Sierra Madre Occidental [including western Sonora, Chihuahua, Durango, and Zacatecas]). In the eastern portion of the distribution there are scattered areas in Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí. Interestingly, there are three connections between the two Sierras Madre, one is from Chihuahua-Coahuila to Nuevo León, the other from the middle of the Sierra Madre Occidental via Durango-Zacatecas-Coahuila to Nuevo León, and finally, from Zacatecas-San Luis Potosí to Tamaulipas (Fig. 5).

In contrast, the least suitable niche conditions for the Mexican wolf are at the northern, southern and western edges of the distribution, as well as in the eastern edge of southern Sierra Madre Oriental (Fig. 5). The MWEPA generally resulted climatically-lower suitability, presumably because it is less like the conditions in the core of Mexican wolf historical range.

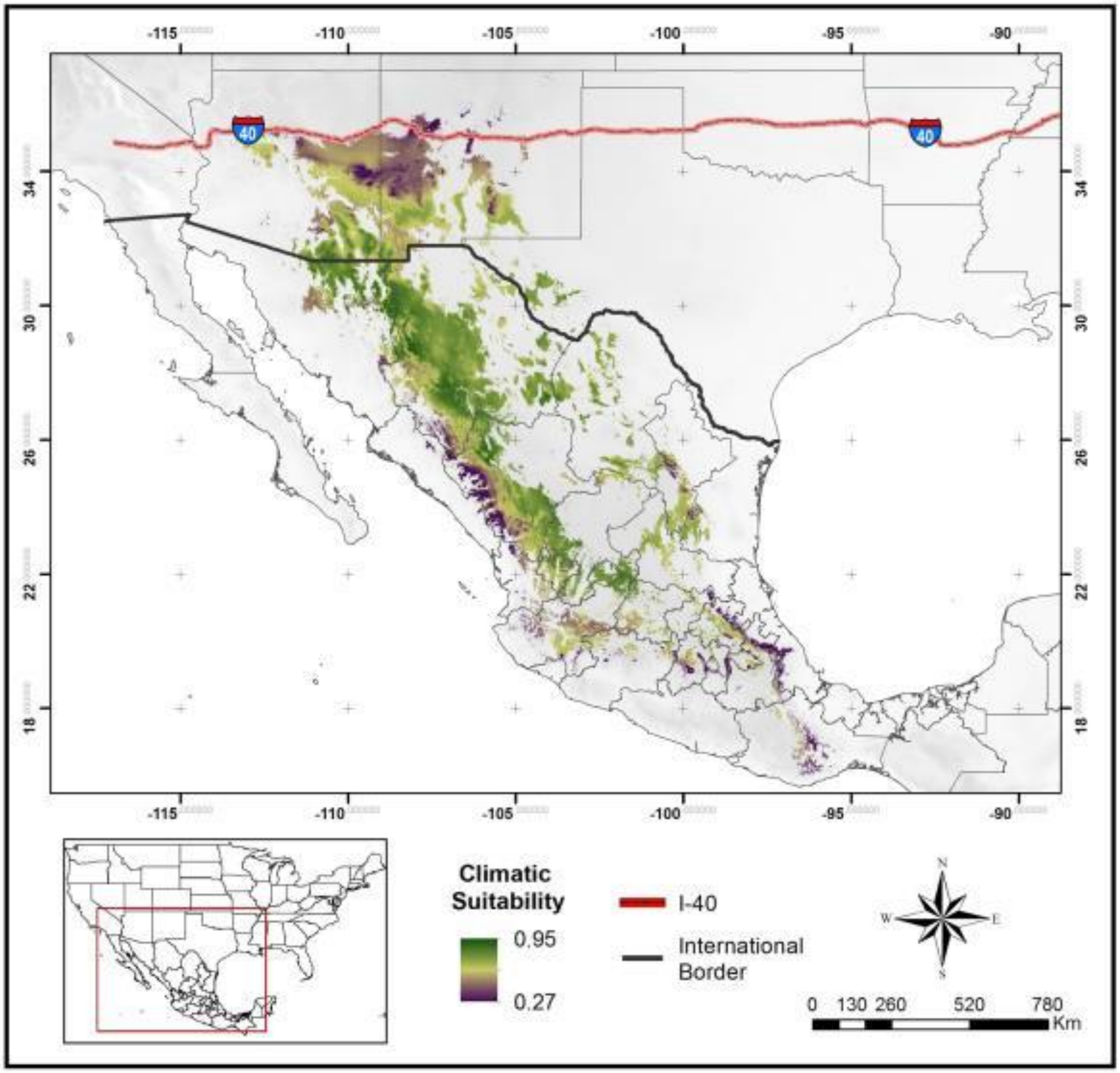

Figure 5. Climatic suitability map of the Mexican wolf based on the distance to the niche centroid approach (Martínez-Meyer et al. 2013) (see text for details). This map represents the historical distribution of the Mexican wolf.

2. Environmental and anthropogenic habitat variables

One of the main limitations of habitat analyses for the Mexican wolf in the past has been the asymmetry of environmental and anthropogenic variables between the

US and Mexico, thus concordant information of critical habitat variables for the two countries is necessary. Natural factors, including vegetation and prey density (Chambers et al. 2012), and anthropogenic factors, such as human population density, infrastructure (e.g., roads, settlements), land tenure and protection are key factors to consider relative to wolf population establishment (Jedrzejewski et al. 2004; Oakleaf et al. 2006; Carroll et al. 2013). In the US, high-quality or high-resolution information exists for all of these factors. Mexico information is quite reliable for some factors (e.g., land cover or population density), but is low-quality or lacking for many regions within the distribution of the Mexican wolf for other factors (e.g., prey density). An additional problem has been the difference in the classification scheme of the vegetation types in the two countries that makes it difficult to homogenize.

To overcome this limitation, we utilized regional or global information produced under the same criteria and methodological approach that covers the two countries. For the habitat model we considered the following natural variables: (1) the abiotic niche model expressed as the suitability score described above, (2) land cover and vegetation types and (3) ungulate biomass. The anthropogenic variables considered were: (1) human population density and (2) road density. All variables were clipped to the potential distribution map of the Mexican wolf (Fig. 5) and resampled from their native spatial resolution to 1 km pixel size. These methodologies allowed all maps to have the same extent and spatial resolution for further analysis. The ecological niche model was described above; below is a description of the remaining variables.

Land cover and vegetation types

Wolves are generalist and use a great variety of land cover and vegetation types. Preference for certain types of vegetation varies across areas and regions as a response to local differences in prey density and/or human tolerance levels (Oakleaf et al. 2006). Land cover has been used for suitability analysis in several studies (Mladenoff et al. 1995; Gehring & Potter 2005; Oakleaf et al. 2006; Carnes 2011; Fechter & Storch 2014; García-Lozano et al. 2015), mainly because it has proven important in different aspects of the ecology of wolves and a good predictor of wolf habitat (Mladenoff et al. 1995; Oakleaf et al. 2006). Vegetation types have also been considered an important factor in permeability for dispersing individuals (Geffen et al. 2004) and for predation (Kunkel et al. 2013). For instance, in reproduction periods, vegetation cover has been associated with the selection of denning sites (Kaartinen et al. 2010). For the Mexican wolf, previous studies have shown that it prefers certain types of vegetation cover, like Madrean evergreen and pine forests at altitudes above 1370 m, where they can find timber and bush cover (McBride 1980). Also, certain types of vegetation present barriers for dispersal. Historical reports indicate that Mexican wolves rarely denned or established a territory in desert-scrub habitats or below 1000 m elevation (Gish 1977) and were absent from desert and grasslands, except when dispersing (Brown 1983). Vegetation cover has also been used in other habitat analyses for the recovery of the species (Carroll et al. 2004, Araiza et al. 2012).

For these analyses, we used the land cover information for the entire study region (southern US and Mexico) provided by the European Spatial Agency (http://maps.elie.ucl.ac.be/CCI/viewer/). This map represents the major land cover and vegetation types of the world produced in 2010 at a spatial resolution of 300 m. We clipped the land cover layer to our study region (Fig. 7) and performed a use/availability analysis as follows: we used all available records of the Mexican wolf (primary and secondary) and also included records from free-ranging individuals in the US. GPS records from free-ranging individuals in the US wild population were generously provided by the Fish and Wildlife Service, which were selected randomly (one location/pack/month) since 1998, totaling 2190 records. In order to avoid over-representation of certain types of vegetation due to the large amount of records in the US, we reduced the number of records by selecting only those from 2011-2013 and only one record per year per pack, resulting in a total of 45 records. The final database for the use/availability analysis consisted of 421 occurrences including historical and GPS records. This database was transformed to a GIS shapefile and used ArcMap 10.0 to extract the cover type for each point record. We considered the vegetation cover from a surrounding area to each point equal to the average home range size of wolves in the US wild population (ca. 462 km^2) and extracted the vegetation types within this buffer area. We summed all areas of the same land cover class to obtain the proportional area available of each class and contrasted that information with the frequency of records in each land cover class, obtaining a score of frequency/availability, and a chi-squared test was performed (Araiza et al. 2012).

However, there is an effect of overestimating the importance of those cover classes that have a reduced distribution and very few occurrences (Table 4). Therefore, to obtain the relative importance of each land cover class we simply obtained the proportional number of records in each class (no. of records in class x / no. of records outside class x). Most records were in the ‘needleleaf evergreen closed to open forest’ class, followed by ‘shrublands’ (Table 4). However, shrublands apparently is a vegetation type that wolves do not prefer (Gish 1977; McBride 1980), but is so extensive in the area that wolves necessarily use it, mainly for dispersal (Brown 1983).

Finally, the land cover layer was standardized based on the proportional occurrence using the following conditional formula in the raster calculator of ArcGIS 10.1:

Con(**"x"**<=**a**,(1*((**"x"** - **a**)/**a**)),(1*(**"x"/b**))) Equation 1;

where ***x*** refers to the land cover layer; ***a*** is the threshold value which was defined based on the ‘Proportion In’ column (Table 3) and ***b*** refers to the maximum value of the land cover layer **x**. Values greater than ***a*** were considered classes positively used by wolves and values lower than ***a*** were classes not used or avoided by wolves. The threshold value (***a***) corresponded to the shrubland, thus its value was 0. The only land cover class above zero was needleleaf forest, so its rescaled value was 1 and the remaining classes had values below 0 (Table 4; Fig. 7). The land cover classes “Urban areas” and “Water bodies” were manually set to -1.

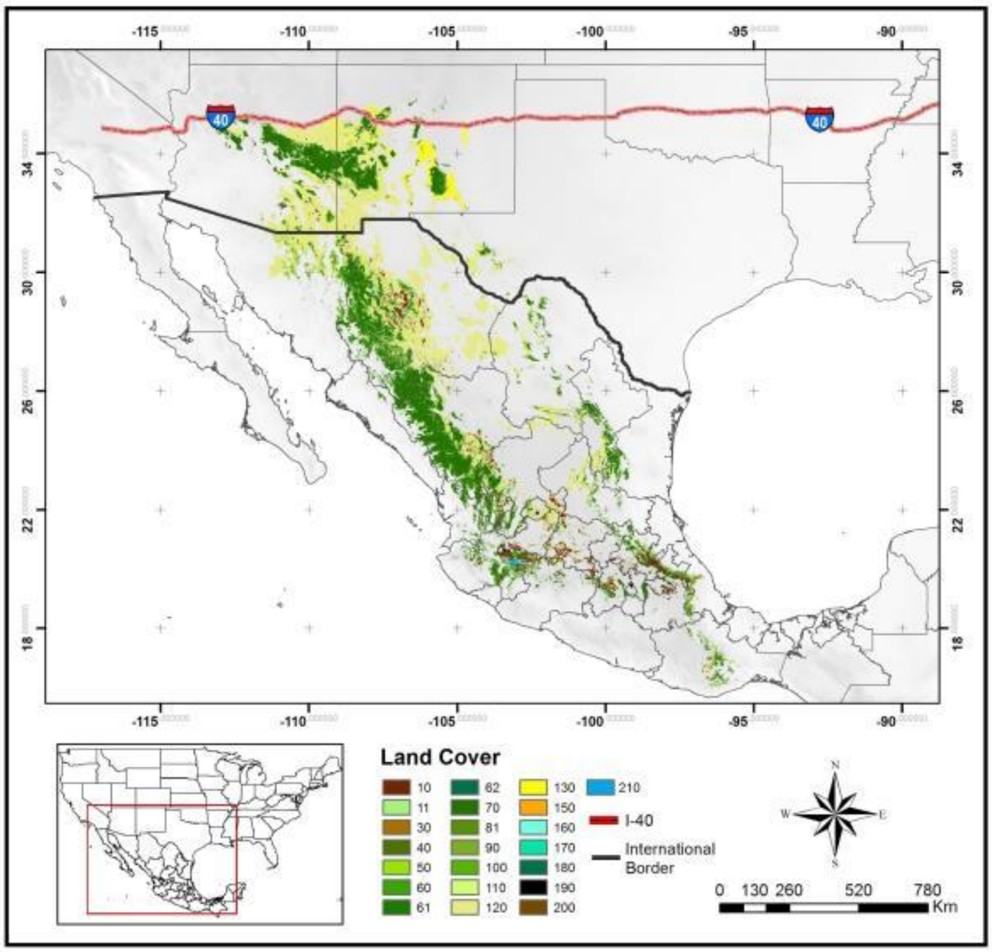

Figure 6. Landcover map for the study region from the European Spatial Agency (http://maps.elie.ucl.ac.be/CCI/viewer/). Codes are as follows: (10): Cropland rainfed, (11) Herbaceous cover; (30) Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous); (40) Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%); (50) Tree cover, broadleaved, evergreen, closed to open (>15%); (60) Tree cover, broadleaved, deciduous, closed to open (>15%); (61) Tree cover, broadleaved, deciduous, closed (>40%); (62) Tree cover, broadleaved, deciduous, open (15-40%); (70) Tree cover, needleleaved, evergreen, closed to open (>15%); (81) Tree cover, needleleaved, deciduous, closed (>40%); (90) Tree cover, mixed leaf type (broadleaved and needleleaved); (100) Mosaic tree and shrub (>50%) / herbaceous cover (<50%); (110) Mosaic herbaceous cover (>50%) / tree and shrub (<50%); (120) Shrubland; 130) Grassland; (150) Sparse vegetation (tree, shrub, herbaceous cover) (<15%); (160) Tree cover, flooded, fresh or brakish water; (170) Tree cover, flooded, saline water; (180) Shrub or herbaceous cover, flooded, fresh/saline/brakish water; (190) Urban areas; (200) Bare areas; (210) Water bodies.

Table 4. Frequency of Mexican wolf occurrences in land cover classes. The ‘Proportion In’ column was used to produce the rescaled values. Codes are as follows: (10): Cropland rainfed, (11) Herbaceous cover; (30) Mosaic cropland (>50%) / natural vegetation; (40) Mosaic natural vegetation (>50%); (50) Tree cover, broadleaved, evergreen, closed to open (>15%); (60) Tree cover, broadleaved, deciduous, closed to open (>15%); (61) Tree cover, broadleaved, deciduous, closed (>40%); (62) Tree cover, broadleaved, deciduous, open (15-40%); (70) Tree cover, needleleaved, evergreen, closed to open (>15%); (81) Tree cover, needleleaved, deciduous, closed (>40%); (90) Tree cover, mixed leaf type; (100) Mosaic tree and shrub (>50%) / herbaceous cover (<50%); (110) Mosaic herbaceous cover (>50%)/tree and shrub (<50%); (120) Shrubland; 130) Grassland; (160) Tree cover, flooded, fresh or brakish water; (170) Tree cover, flooded, saline water; (180) Shrub or herbaceous cover, flooded, fresh/saline/brakish water; (190) Urban; (200) Bare areas; (210) Water bodies.

Land cover	#Rec In	#Rec Out	Area (km^2)	Expected In	Expected Out	Proportion In	Chi^2	*P*-value	Rescaled value
10	3	418	17313	7.71	413.29	0.01	2.34	0.13	-0.98
11	1	420	956	0.43	420.57	0.00	0.01	0.91	-0.99
30	0	421	1032	0.46	420.54	0.00	0.00	0.95	-1.00
40	1	420	6105	2.72	418.28	0.00	0.55	0.46	-0.99
50	0	421	204	0.09	420.91	0.00	1.84	0.17	-1.00
60	1	420	4847	2.16	418.84	0.00	0.20	0.65	-0.99
61	0	421	286	0.13	420.87	0.00	1.09	0.30	-1.00
62	0	421	49	0.02	420.98	0.00	10.47	0.00	-1.00
70	290	131	405105	180.50	240.50	2.21	116.29	0.00	1.00
81	0	421	35	0.02	420.98	0.00	15.05	0.00	-1.00
90	0	421	96	0.04	420.96	0.00	4.89	0.03	-1.00
100	13	408	29834	13.29	407.71	0.03	0.01	0.94	-0.90
110	0	421	1590	0.71	420.29	0.00	0.06	0.80	-1.00
120	100	321	394987	175.99	245.01	0.31	56.38	0.00	0.00
130	7	414	20143	8.97	412.03	0.02	0.44	0.51	-0.95
160	0	421	29	0.01	420.99	0.00	18.36	0.00	-1.00
170	0	421	2	0.00	421.00	0.00	279.55	0.00	-1.00
180	0	421	89	0.04	420.96	0.00	5.34	0.02	-1.00
190	4	417	6392	2.85	418.15	0.01	0.15	0.70	-0.97
200	0	421	247	0.11	420.89	0.00	1.38	0.24	-1.00
210	1	420	237	0.11	420.89	0.00	1.47	0.22	-0.99

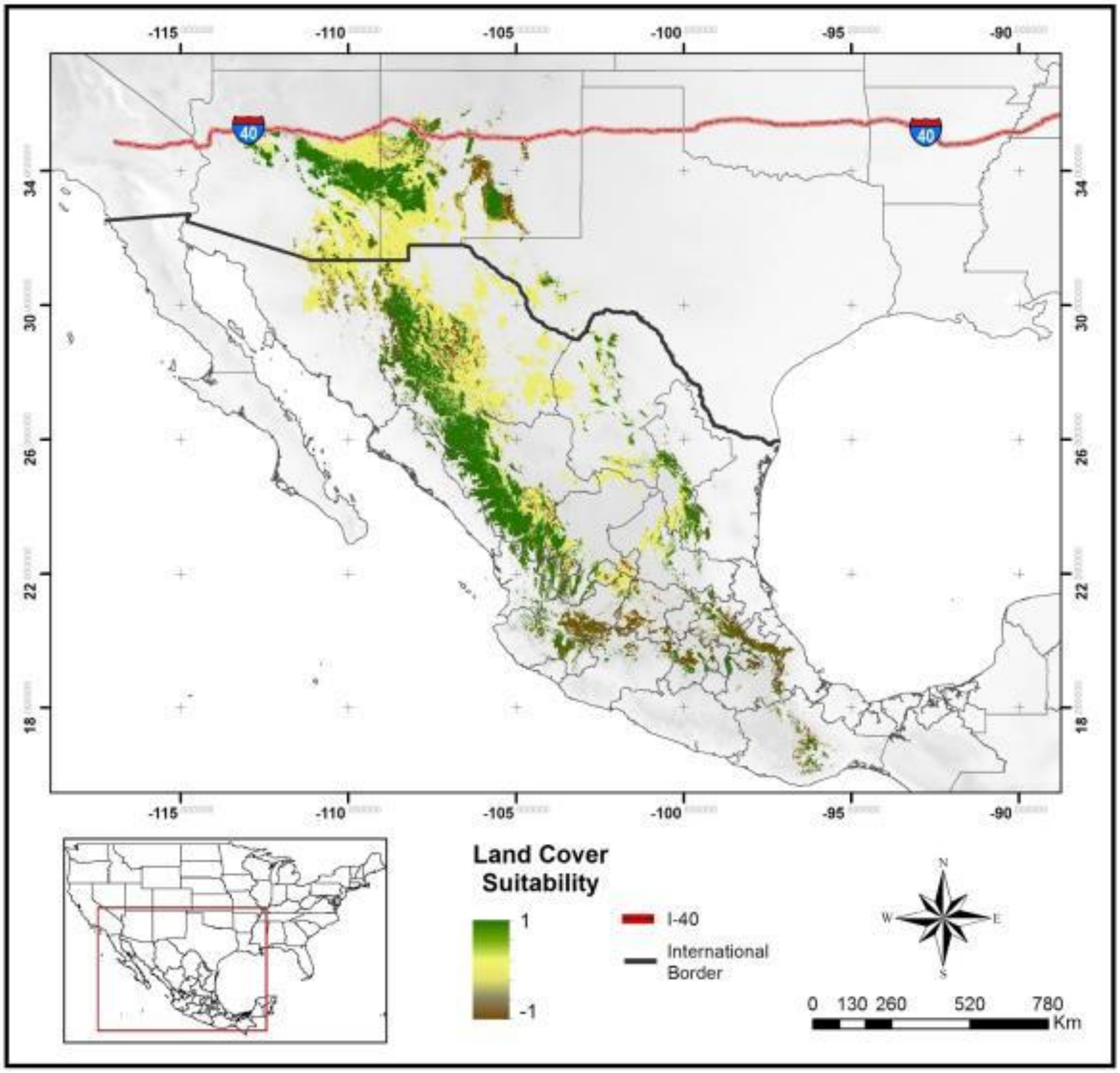

Figure 7. Standardized land cover map according to the habitat use/availability ratio (see text for details).

Human population density

The conflicts between humans and wildlife are one of the leading factors encroaching populations of large mammals (MacDonald et al. 2013), especially carnivores (Dickman et al. 2013). Particularly for wolves, previous studies have found that humans can have a strong influence in wolf ecology, behavior and mortality rates (Creel & Rotella 2010). For instance, human disturbance influence wolves' den selection and home range establishment (Mladenoff et al. 1995; Sazatornil et al. 2016). As well, a negative relationship between density of humans with wolf abundance has been documented, detecting critical thresholds of wolf tolerance to human presence, ranging from 0.4 to1.52 humans/km^2 (Mladenoff et al. 1995; Jedrzejewski et al. 2004; Oakleaf et al. 2006, Carroll et al. 2013). Therefore, human density is one of the key aspects to be considered for an analysis of suitable habitat for the wolf (Mladenoff et al. 1995; Kuzyk et al. 2004; Gehring & Potter 2005; Larsen & Ripple 2006; Belongie 2008; Jędrzejewski et al. 2008; Houle et al. 2009; Carnes 2011; Araiza et al. 2012; Fechter & Storch 2014; Bassi et al. 2015).

For this analysis we obtained a global human population density (individuals/km^2) raster map sampled at 1 km resolution from the Gridded Population of the World, version 4 (GPWv4) web page (CIESIN-FAO-CIAT 2005): http://sedac.ciesin.columbia.edu/data/collection/gpw-v4 and clipped to our study region (Fig. 9). Then, the original values of the raster were rescaled from -1 to 1 using the following conditional formula in the raster calculator of ArcGIS 10.1:

Con(**"x"**<=**a**,(-1*((**"x"** - **a**)/**a**)),(-1*(**"x"/b**))) Equation 2;

where ***x*** refers to the human population density layer; ***a*** is the threshold value and ***b*** refers to the maximum value of layer **x**. In this scale negative values represent human population densities unfavorable for the wolf and positive values favorable under three scenarios (optimistic, intermediate and pessimistic). Threshold values were defined at the Wolf Recovery Workshop in April 2016 based on Mladenoff (1995), who reports a value of 1.52 humans/km^2 (1.61 SE). We established that value for the pessimistic scenario, thus pixel values below this density were rescaled from 0 to 1 and above this value were rescaled from 0 to -1. We calculated 2 SE above the pessimistic threshold for the optimistic scenario, resulting in a human population density of 4.74 humans/km^2, which was used to rescale the map in the same way as in the previous map. Finally, for the intermediate scenario we simply averaged these two values, resulting in 3.13 humans/km^2 and then rescaled (Figs. 8 and 9).

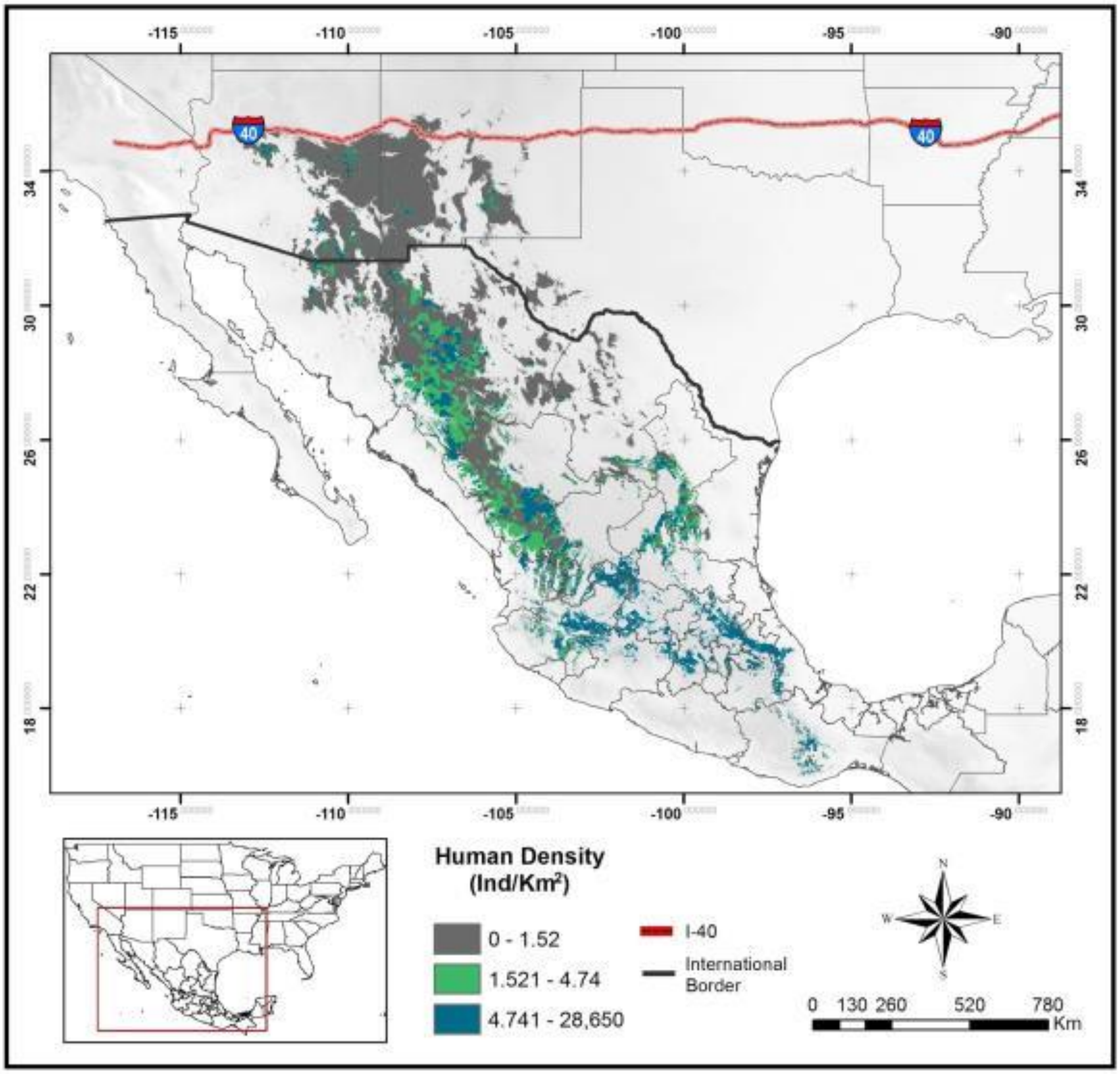

Figure 8. Human population density map in the inferred historic distribution of the Mexican wolf obtained from the Gridded Population of the World, version 4 (GPWv4).

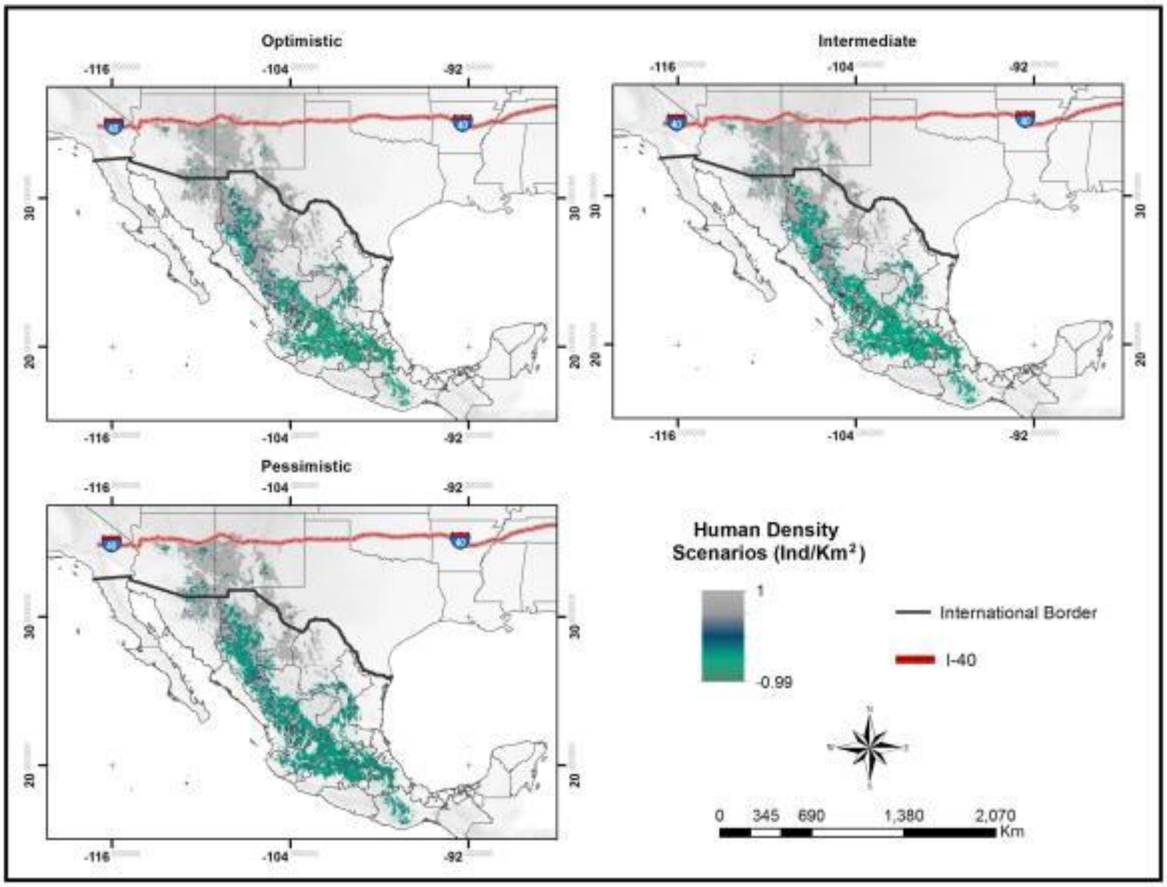

Figure 9. Rescaled human population density scenarios in the historic distribution of the Mexican wolf.

Road density

Road density has been recognized by several authors as one of the limiting factors in habitat suitability of carnivores, specially for wolves (Mladenoff et al. 1995; Jedrzejewski et al. 2004; Oakleaf et al. 2006; Basille et al. 2013; Dickson et al. 2013; Bassi et al. 2015; Angelieri et al. 2016). Different studies have found that wolves can persist in human-dominated landscapes with road density thresholds varying from 0.15 to 0.74 km/km^2, preventing colonization, den establishment and intensive use of the habitat, showing that wolves preferably select areas isolated from human influence, including roads (Thiel 1985; Fuller et al. 1992; Mladenoff et al. 1995; Vickery et al. 2001; Mladenoff et al. 2009; Sazatornil et al. 2016). It has been advised that road density should be monitored in wild areas to prevent exceeding limiting thresholds (Fuller et al. 1992). Several studies have included this variable in habitat suitability analysis for the wolf (Mladenoff et al 1995; Gehring & Potter 2005; Larsen & Ripple 2006; Mladenoff et al 2009; Carnes 2011; Carroll et al. 2013).

For this analysis we used two data sources for roads: OpenStreetMap (http://www.openstreetmap.org/), downloaded from Geofabrik (http://download.geofabrik.de/), which is a vector map of the roads of the world at a maximum scale of 1:1,000 in urban areas, and because the roads from Mexico in this database were not complete we complemented the information with a road map for Mexico at a scale of 1:250,000 (INEGI 2000). From these two maps we selected paved roads and dirt roads suitable for two-wheel drive vehicles. From the unified map we calculated road density (linear km/km^2) using the Line Density function in ArcGis 10.0 (Fig. 10).

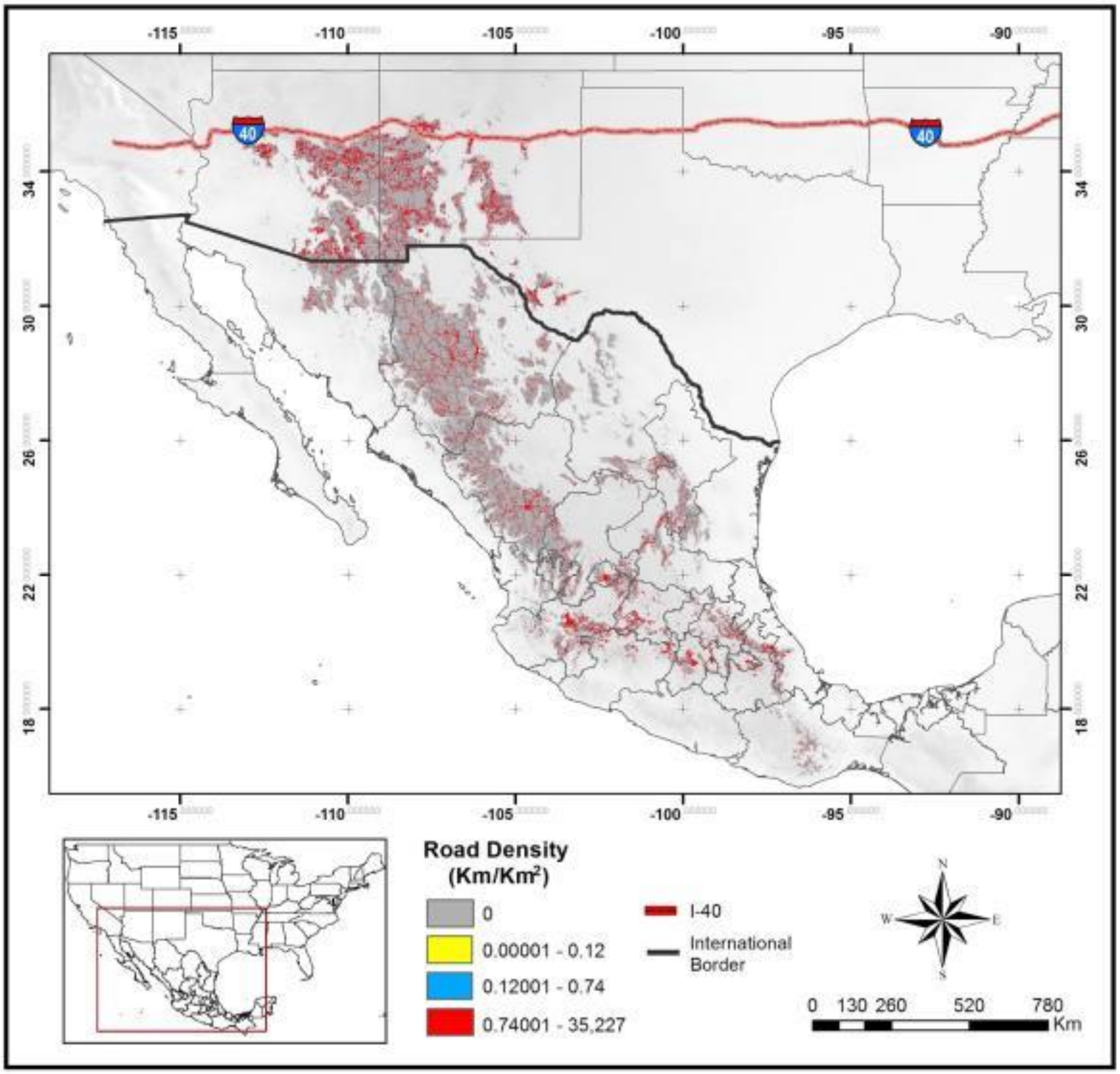

Figure 10. Road density map in the historic distribution of the Mexican wolf obtained from a combination of the OpenStreetMap database and INEGI (2000).

Road density values were rescaled to -1 to 1 using Equation 1 in the same way as we did with the human density map to construct the pessimistic, optimistic and intermediate scenarios, using the following threshold values: for the optimistic scenario it was 0.74 km/km^2, for the pessimistic 0.15 km/km^2, and for the intermediate 0.445 km/km^2 (Fig. 11).

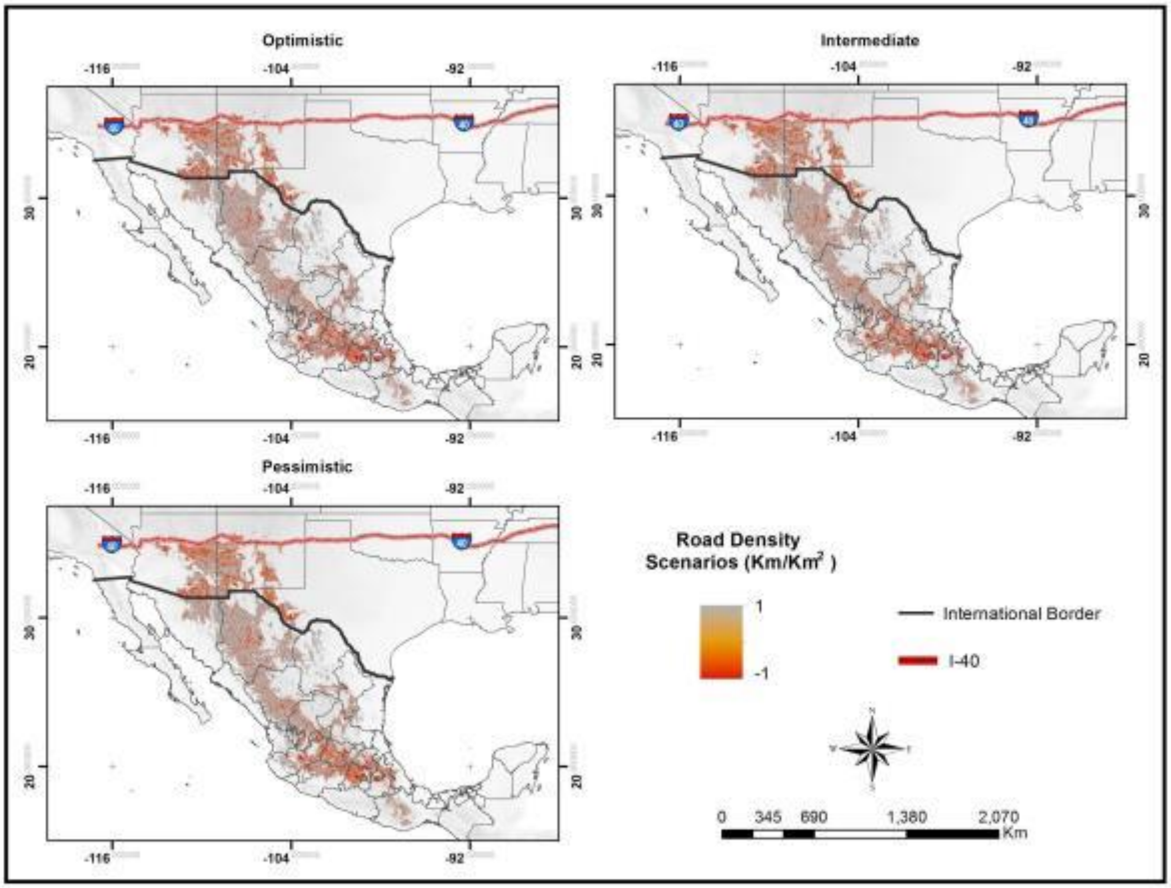

Figure 11. Rescaled road density scenarios in the historic distribution of the Mexican wolf.

3. Ungulate density estimation

Demography of wolves, as many other carnivores, strongly depends on the availability of their prey (Fuller et al. 1992). For instance, density of primary prey species has been identified as an important factor promoting wolf survival, recruitment and habitat use (Oakleaf et al. 2006). In contrast, the effect of wolf predation on wild prey largely depends on the number of wolves, kill rates and the response of prey to other predators (Seip 1995). For these reasons, prey densities have been used as a key predictor of wolf population and for habitat analysis (Fuller et al. 1992, 2003; Oakleaf et al. 2006; Belongie 2008; Moctezuma-Orozco et al.

2010). Based on this knowledge, we used ungulate field density estimations in the US and Mexico to calculate an ungulate biomass index (UBI) (Fuller et al. 2003) across wolf historical distribution (according to Fig. 5).

Ungulate field density estimates in the US come from aerial counts of elk, mule deer and white-tailed deer at 23 Game Management Units (GMUs) in Arizona and 7 in New Mexico. In the case of New Mexico, counts for mule and white-tailed deer were aggregated, so it was not possible to estimate an UBI value for each species thus this information was not used. For Mexico, we had two sets of white-tailed deer density estimates: (1) from wildlife surveys carried out in 2009 by Carlos López and his team using 30 sites with camera-traps (around 30 camera traps per site) across the state of Chihuahua. Details on the sampling scheme and density estimations can be found in Lara-Díaz et al. (2011). (2) White-tailed deer density from 193 Unidades de Manejo para la Conservación de la Vida Silvestre (UMAs) in four states of Mexico: Sonora, Chihuahua, Durango, and Sinaloa from 1999 to 2010 (Fig. 13). UMA data were gathered and organized by Jorge Servín, but the original source came from UMAs' field technicians that estimated deer density under different sampling techniques (e.g., direct, tracks and fecal pellets counts), but reliability has not been thoroughly evaluated, thus there is some uncertainty in these estimates. Importantly, all these data do not account for the high frequency (annual to semi-decadal) changes in ungulate populations that are influenced by a myriad of factors including prior harvest, drought, disease, or habitat degradation. Ideally, we would use a long-term average which would indicate the central tendency for the UMA or GMU areas.

After preliminary analyses to model the UBI across the Mexican wolf range we made several decisions for each species. For elk, we used the 30 available density data obtained from the GMUs (23 from Arizona and 7 from New Mexico) because elk do not occur in Mexico. The New Mexico data for elk are at a large regional GMU level. This leads to two results: (1) the variability in the environmental signatures is very small, and (2) the non-linearity in habitat quality may be hidden;

however, the estimates were very similar to the Arizona GMU data in most cases. For mule deer we used survey data for the Arizona GMUs, Mexican UMAs and camera trap data from Chihuahua. We discarded the UMA data from the UBI modeling because values reported in the Sonora and Chihuahua UMAs were up to 10 times greater than the average values in Arizona and New Mexico. Therefore, for this analysis we used 67 point estimates of density data from GMU and camera-trap surveys. For the analysis we initially split the data into two subspecies of mule deer (Desert and Rocky Mountain), but this proved uninformative so we combined both types into a single UBI model. Finally, for the white-tailed deer, we decided to use only density data from within the historical range of the wolf in the Sierra Madre thus excluding several UMAs located in the desert lowlands in western Sonora. This resulted in 90 point estimates of whitetail density data to build the UBI model.

Methodological differences between sources of data had an effect on density estimation. UMA data come from the annual reports of management units which, in turn, also have different methodologies to estimate densities. Also, UMAs primary source of income come from hunting tags, thus different management practiced in ranches caused important variability in the data. Aerial counts for ungulates in Arizona may be more accurate in open areas, but in dense forested areas –where white-tailed deer usually prefer– counts may be less reliable. All these factors contributed to differences in density estimations from the three sources.

Rangewide density estimations for the three ungulate species were explored under a Generalized Linear Model (GLM) and Random Forest (RF) modeling. The last approach was also implemented for the mule deer and elk. The GLM/RF approach was implemented to establish the critical parameters for the best estimate of the Ungulate Biomass Index (UBI) (Fuller et al. 2003).

UBI modeling

The Ungulate Biomass Index (UBI) (Fuller et al. 2003) is a standardized value which uses a weighting factor based on mean animal biomass (Table 6) to make body mass of different ungulate species comparable. For the purpose of the habitat model, we used the density estimates described above to build a UBI model across the historical range of the Mexican wolf under the GLM/RF approach. The UBI model was then included in some habitat suitability scenarios.

Table 6. Description of the Ungulate Biomass Index (UBI) factor for white-tailed deer, mule deer and elk.

Dependent parameter	ID	Units	UBI factor	Density data source
White-tailed deer density	WT	Individuals/km^2	0.6	GMU, CAMSURV, UMA
Mule deer density	MD	Individuals/km^2	1	GMU, CAMSURV
Elk density	ELK	Individuals/km^2	3	GMU

In general, ensemble modelling using machine learning and data-driven tools, such as RF, use non-linear and non-parametric data with numerous hidden interactions, thus, they are likely to violate most statistical assumptions and traditional parametric statistical approaches. RF can be used for prediction, bagging (decision-trees) can be used for assessing stability, and a single decision tree is used for interpreting results if stability is proven. The RF model helps to establish which model parameters are useful. In our case, we used RF with the density data from GMU, CAMSURV and UMA for regression modelling. We also used climatic, topographic, and ecological variables available for calibrating models. Reliability of individual species' models were measured via r^2 and the Akaike Information Criterion (AIC).

For the analyses we compared the response of ungulate density to 15 variables selected from an initial set of 27 based on their levels of significance versus the UBI: (1) monthly climate data archive (DAYMET v2, Thornton et al. 2014); (2) NASA SRTM (90m) digital elevation model and derivative products including the topographic wetness index and slope; (3) EarthEnv.org suite of habitat types (Tuanmu & Jetz 2014); (4) global cloud cover layers from MODIS (Wilson & Jetz 2016); and population density (CIESIN-FAO-CIAT 2005) (Table 7).

Table 7. Independent parameters used for the GLM/RF modeling.

Independent Parameters	ID	Units	Scale	Source
Slope	SLP	radians	90 m	Calculated using the patched SRTM DEM with SAGA-GIS
Mean Annual Precipitation	MAP	millimeters (cm)	1 km^2	DAYMET v2
Mean Annual Temperature	MAT	degrees Celsius (C)	1 km^2	DAYMET v2
Net Primary Productivity	NPP	kg C m2	1 km^2	MODIS MOD17A3
Forest Canopy Cover	FORCOVER	%	1 km^2	NASA (Hansen et al. 2013)
Forest Canopy Height Model	CHM	meter	1 km^2	NASA (Simard et al. 2011)
Topographic Wetness Index	TWI	index (unitless)	90 m	NASA SRTM, TauDEM (OpenTopo metadata job 1, job 2)
Digital Elevation Model	DEM	meters (m)	90 m	NASA SRTM, TauDEM (OpenTopo metadata job 1 , job 2)
Vegetation Types:		%	1 km^2	Tuanmu & Jetz 2014.

Herbaceous; Cultivated; Evergreen-deciduous-needleleaf	HERB CULTIV EVDECNEED			Data available on-line at http://www.earthenv.org/.
Population Density	POPDENS	Individuals/ km^2	1 km^2	CIESIN-FAO-CIAT 2005. Data available on-line at http://dx.doi.org/10.7927/H4639MPP.
MODIS Cloudiness: Mean annual; Inter-annual SD; Intra-annual SD	CLDANN CLDINTER CLINTRA	Mean, Inter-annual Standard Deviation,	1 km^2	Wilson & Jetz 2016. http://www.earthenv.org/cloud

We used the shapefiles for the current distribution of white-tailed deer, mule deer, and elk for Arizona in each GMU and the perimeter boundaries of the UMAs to calculate the mean value for each species habitat distribution area with the QGIS Raster Zonal Statistics. The input variable for ungulates was the Ungulate Biomass Index (UBI). To calculate the UBI within the total suitable habitat area we used the following function:

UBI = n * B / area   Equation 3;

where n is the observed number of individuals in the GMU, B (beta) is a weighting factor, and area is square kilometers of suitable habitat in the GMU or UMA.

For the UMAs we had the total number of individuals per km only, so we weighted this using the B factor to derive the UBI for Mexico, as follows:

UBI = (n / area) * B   Equation 4;

All calculations were made in RStudio (Rstudio Team 2016). The script loads the data, calculates a series of GLM models, and then produces variable importance models and figures of the Random Forest outputs.

In general, for elk, the variance explained with the RF regression models was relatively good, but low for the mule deer and white-tailed deer (Table 8). Low R^2, particularly for deer data, is a consequence of the large dispersion of density data values, where wide variability exists within and amongst identical climate and topographic areas. Despite this, a relationship with predictor variables exists, which suggests that the model conservatively estimates the central tendency for the broader landscape.

Table 8. Percentage of the UBI variance explained and Mean of Squared Residuals of the GLM/RF models for the three ungulates.

Species	% of variance explained (R^2)	Mean of Squared Residuals
Elk	43.5	9.33
Mule deer	25.49	0.2
White-tailed deer	9.39	1.94

Rangewide UBI map

UBI distribution maps of each species across the whole study area were built in a GIS using the best fit GLM/RF models. Then, the UBI map of each species was clipped to its known distribution using the IUCN polygon maps (IUCN 2016) (Fig. 12). Finally, the three individual UBI maps were summed together in a GIS to produce a combined UBI map, which was clipped to match the historical distribution of the Mexican wolf (Fig. 13). This map represents the estimated ungulate biomass available for Mexican wolf populations. Finally, the UBI map was rescaled from 0-1 to match the other layers for the habitat suitability model (Fig. 14).

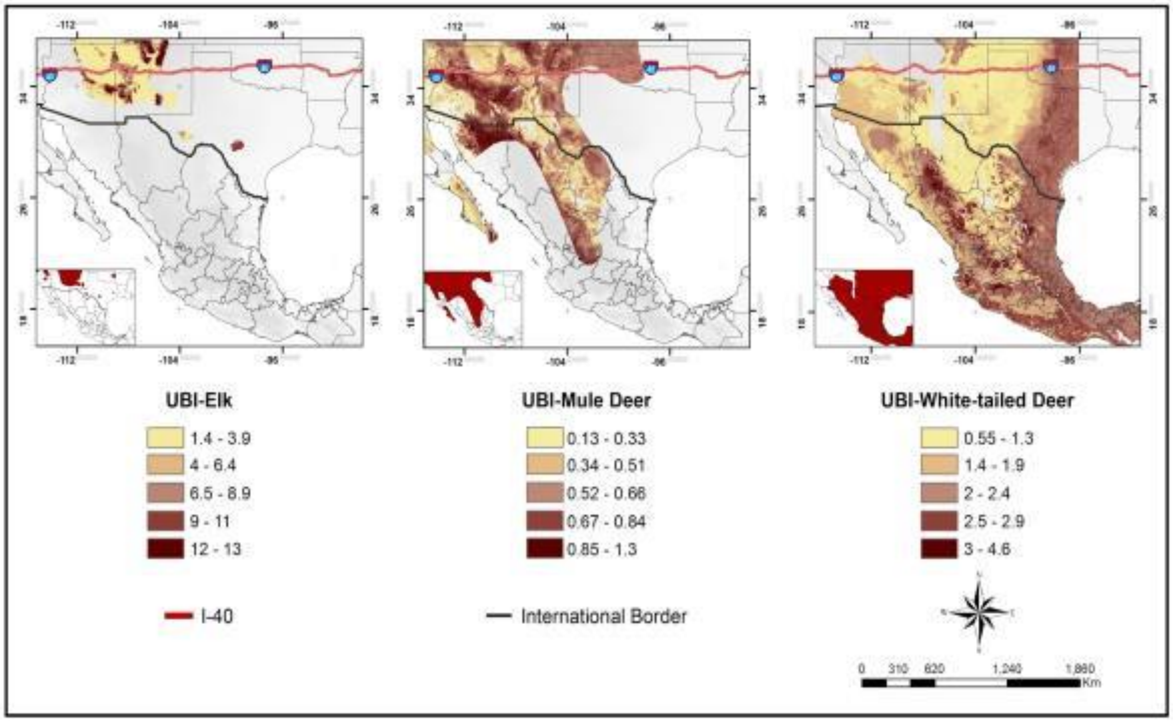

Figure 12. Ungulate Biomass Index (UBI) map for the elk, mule deer and white-tailed deer. Inset images represent the known distribution of species according to IUCN (2016).

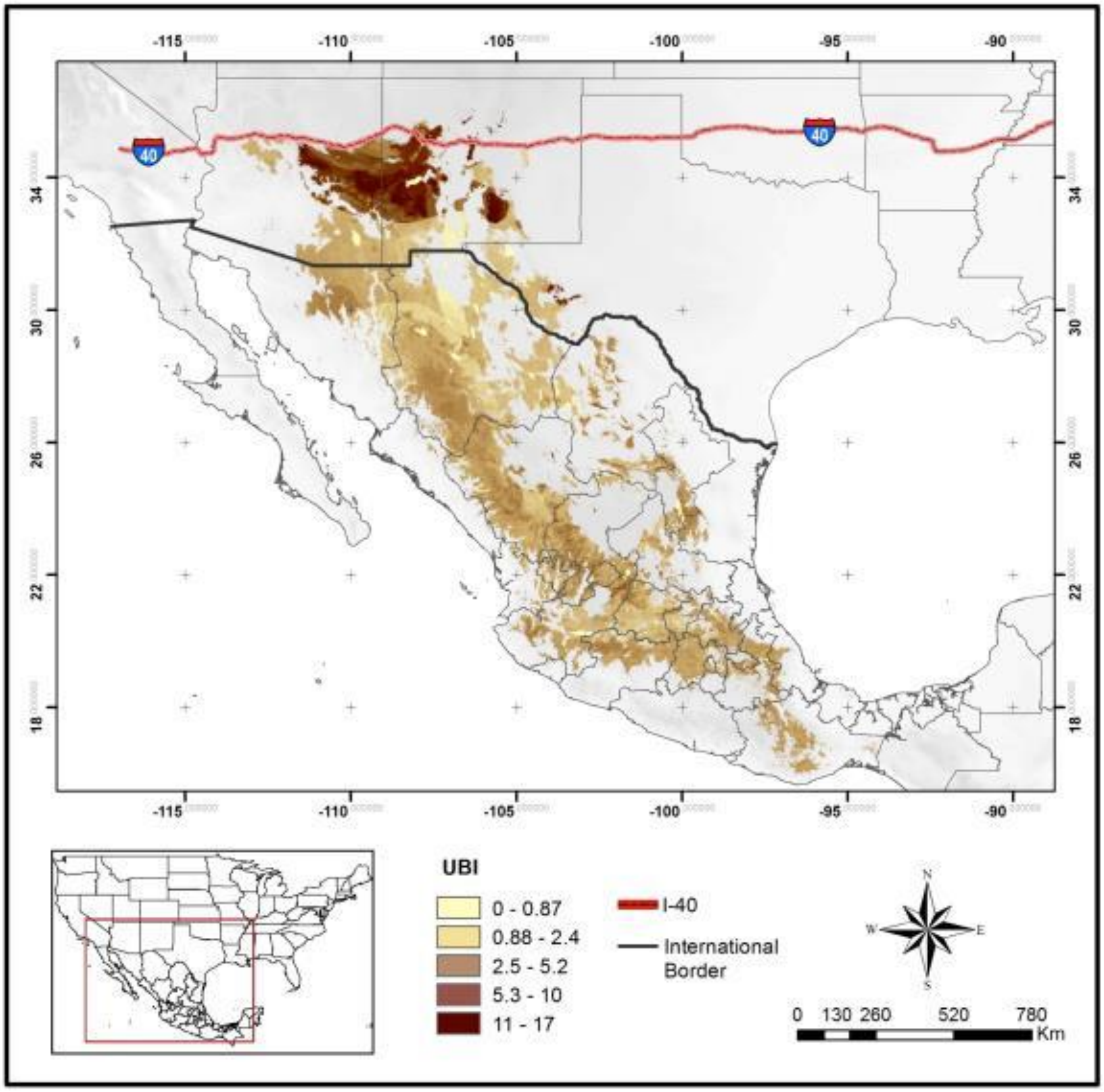

Figure 13. Combined Ungulate Biomass Index (UBI) map for the elk, mule deer and white-tailed deer across the Mexican wolf historical range.

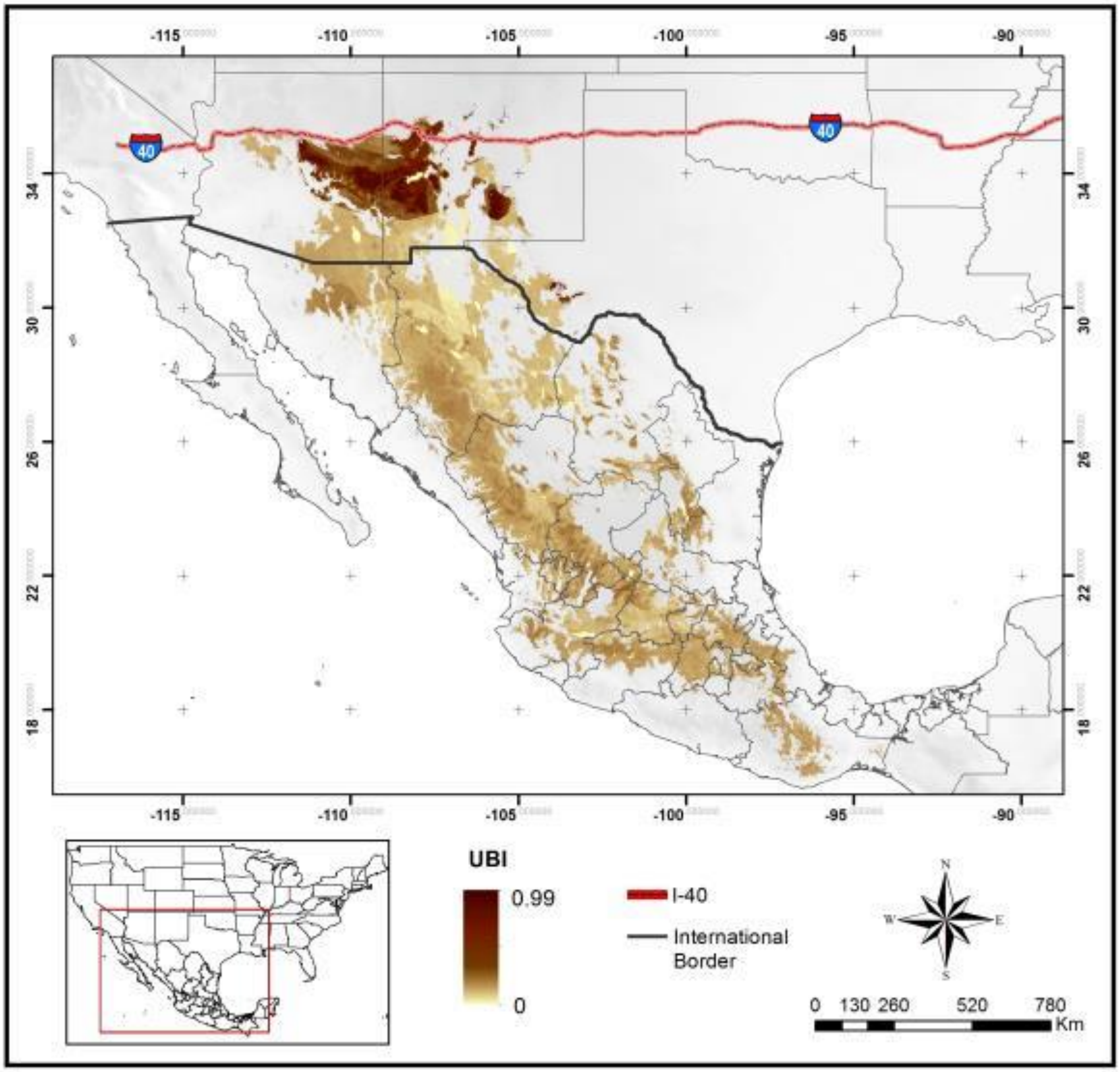

Figure 14. Rescaled Ungulate biomass index (UBI) map.

4. Habitat suitability modeling

We produced two sets of habitat suitability scenarios, with and without the Ungulate Biomass Index (UBI) map. This is because our geographic estimations of the UBI are less reliable than the other habitat variables, therefore its inclusion may mislead the habitat models.

To produce all habitat suitability scenarios for the Mexican wolf we implemented an additive model with the rescaled variables. For the set of scenarios without UBI information we summed: the niche model (with values from 0-1) + land cover + human density + road density maps (all with a scale from -1 to 1) using the raster calculator in ArcGis 10.0; hence, the resulting map may have values ranging from -3 to 4. For the set of scenarios including the UBI variable (with values from 0-1) we simply summed this variable to the rest as described above, thus potentially holding values of -3 to 5. The niche model and land cover were fixed factors for all scenarios (pessimistic, intermediate and optimistic), whereas human and road densities varied depending on the scenario: in the pessimistic scenario habitat suitability is more strongly impacted by anthropogenic variables (human and road densities), whereas for the optimistic scenario wolves tolerate higher values of these two variables. The intermediate scenario is simply the mean value of the two anthropogenic variables between these two extremes.

In order to identify the areas of the highest habitat quality for the wolf, we reclassified each scenario as follows: for the set of scenarios without UBI, values lower than zero were coded as unsuitable, values between 0-3 were coded as low quality, and values >3 were coded as high quality. Therefore, pixels classified as high quality corresponded to areas with a combination of high climatic suitability, in needleleaf forests and with low human impact. For the set of scenarios with UBI, unsuitable areas corresponded to values lower than 0; values between 0-3.2 were considered low quality; pixel values between 3.2-3.95 were classified as high quality and pixels >3.95 were coded as highest quality, indicating that ungulate density in those areas is highest.

5. Identification of suitable areas for future recovery actions

High-quality pixels in each scenario were converted to vector format to carry out a connectivity analysis using Fragstats ver. 4 (McGarigal et al. 2012), in order to identify continuous or aggregated patches across the geographic distribution of the Mexican wolf. Then, we identified geographical units in the US and Mexico containing these habitat clusters. Finally, polygons representing the protected areas of the US and Mexico were overlaid on the habitat suitability scenarios and high-quality patches, as well as the map of the municipalities of Mexico to identify potential areas for future releases.

6. Estimation of Mexican wolf population size in suitable areas

There are two fundamental approaches that have been previously used to estimate wolf population size: (a) based on home range size of wolf packs and calculate the number of wolves in the available area, and (b) based on the relationship of prey density with wolf density and then extrapolate to the available area (Bednarz 1988; Fuller 1989; Messier 1995; Mladenoff 1997; Paquet et al. 2001; Table 10). Despite the fact that all of them estimate the number of wolves per 1000 km^2, not all of the formulas use the same input units. For instance, Bednarz (1988) uses number of prey per 100 km^2, Fuller (1989) and Messier (1995) use units of prey (equivalent to 1 white-tailed deer), whereas Paquet (2001) uses average biomass.

Mladenoff et al. (1997) used the Fuller (1989) model and a home range-based model to estimate eventual wolf populations for Wisconsin and Michigan about 20 years ago, when about 99 wolves existed in Wisconsin (Wydeven et al. 2009), and 116 in Michigan (Beyer et al. 2009). The Fuller (1989) model estimated an eventual population of 462 for Wisconsin (90% confidence interval [CI]: 262-662), and 969 for Michigan (90% CI: 581-1357). A home range/habitat area-based model estimated potential population of 380 for Wisconsin (90% CI: 324-461) and 751 for Michigan (90% CI: 641-911). In recent years, the maximum population count achieved in Michigan was 687 in 2011, 71% of estimate by Fuller (1989) model and 91% of home range model estimate, and both estimates were within 90 CI of both models. The maximum count in Wisconsin was 866 in 2016, 187% of the Fuller (1989) model estimate and 228% of the home range model, and the recent count excedes the 90% CI of both methods. Thus, these two methods made reasonable estimates of potential wolf population for Michigan, but underestimated wolf numbers for Wisconsin, suggesting that the methods are reliable but somewhat conservative.

For this analysis we used and compared available methods to estimate wolf numbers (Table 9). In all cases, an estimation of the available suitable area was necessary, so for the scenarios not including the UBI layer, we used the high-quality patches and calculated their areas, and for the scenarios with the UBI layer we used the high- and highest-quality patches to obtain area calculations, and from these calculations we estimated wolf numbers.

Table 9. Equation and it author to estimate wolf numbers. y= number of wolves /1000km2; x= number of prey/biomass.

Author	**Formula**
Bednarz 1988	$y = 14.48 + 0.03952x$
Fuller 1989	$y = 3.34 + 3.71x$
Messier 1995	$y = 4.19x$
Paquet 2001	$y = 0.041x$
Home-range-based	764 km^2 / pack (4.19 wolves)

For estimations of wolf numbers based on the home range size, we used the average size reported for the wolf packs in the US for the last two years of 764 km^2 and an average of 4.19 wolves per pack (USFWS 2014, 2015). For wolf numbers estimations based on deer density, we obtained UBI values directly from the ungulate density map (see 'Ungulate density estimation' section) and averaged all pixel values from the same geographic unit (e.g., Arizona-New Mexico, Northern Sierra Madre Occidental, etc.), and finally those values were used in the equations of Table 9.

In sum, we generated two sets of wolf population size estimations for each scenario: (1) using the habitat suitability map with the UBI in the additive model and UBI averaged across geographic units from the GLM/RF model; and (2) using the habitat suitability map without the UBI in the additive model and UBI was also averaged across geographic units from the GLM/RF model.

Results and Discussion

Habitat suitability scenarios without the Ungulate Biomass Index (UBI) map

Results of the additive habitat suitability models excluding the Ungulate Biomass Index (UBI) map indicate that relatively large areas of high-quality habitat exist for the Mexican wolf in southwestern US, Sierra Madre Occidental and Sierra Madre Oriental even under the pessimistic scenario (Fig. 15). Although high-quality patches still remain in the Mexican Transvolcanic Belt and southwards, these are not large enough by themselves or are not connected to form continuous areas, thus they are unsuitable to maintain a large population of wolves, even in the intermediate (Fig. 16) and optimistic (Fig. 17) scenarios.

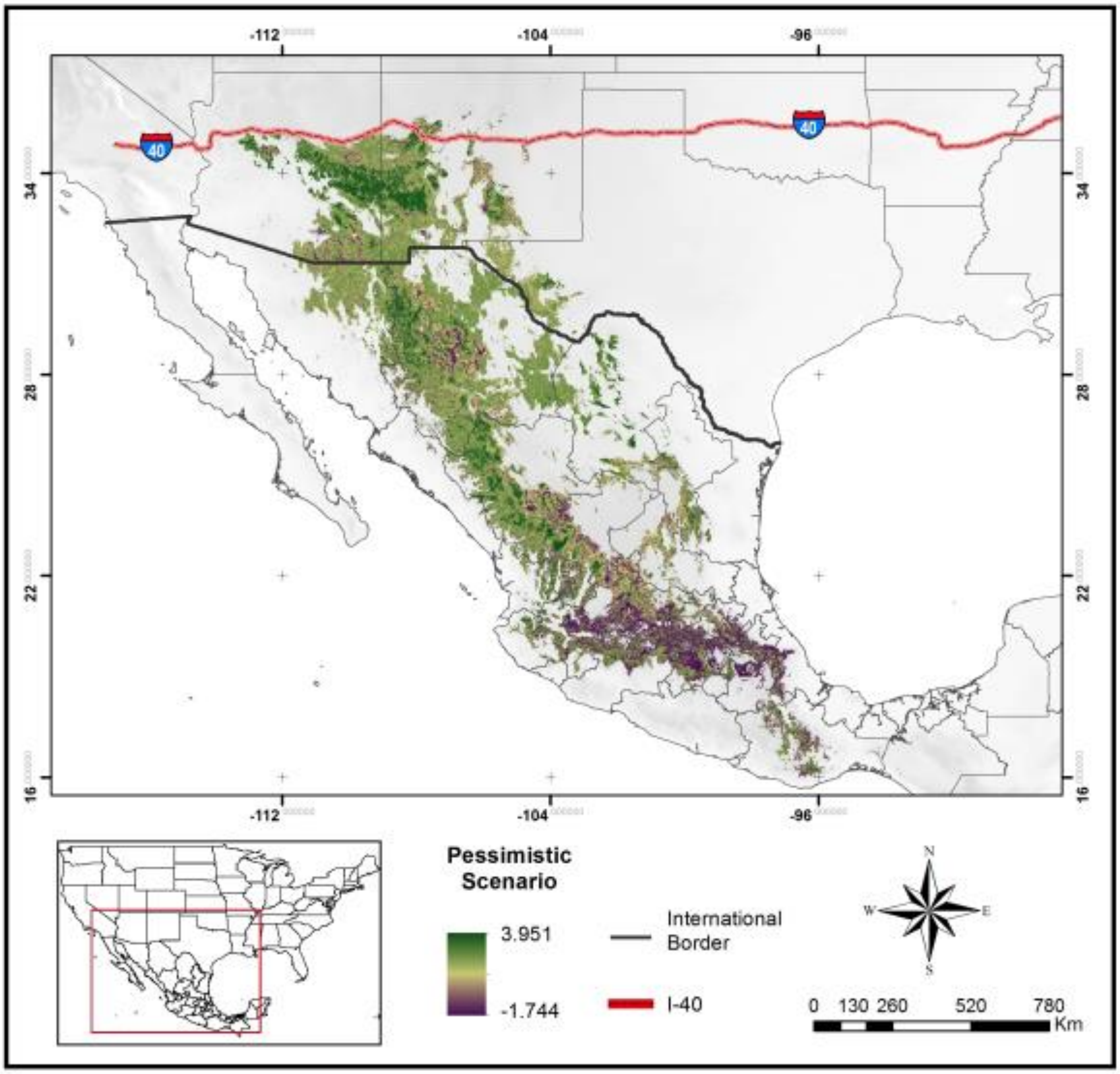

Figure 15. Pessimistic habitat suitability scenario (continuous) for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

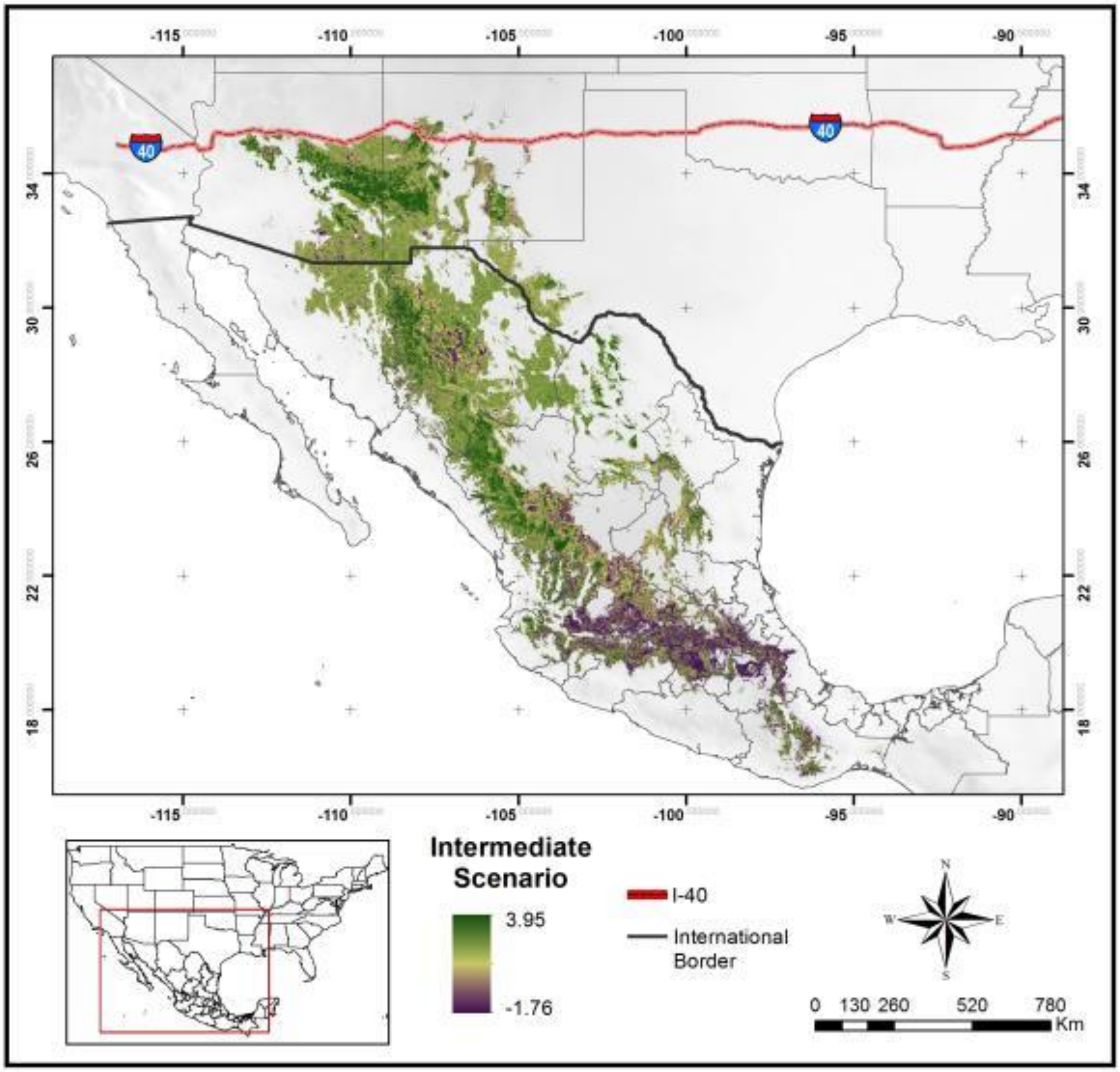

Figure 16. Intermediate habitat suitability scenario (continuous) for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

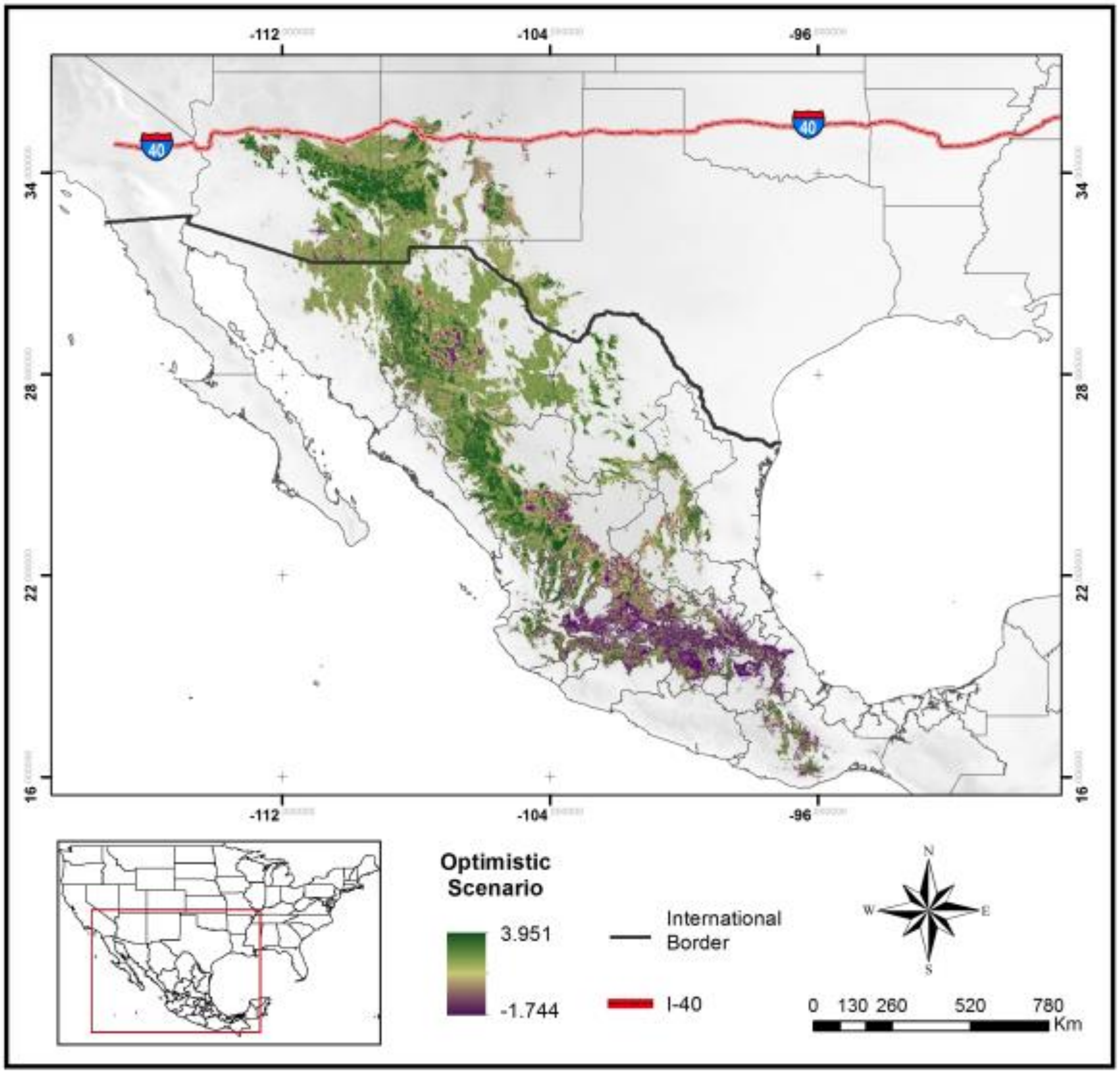

Figure 17. Optimistic habitat suitability scenario (continuous) for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

Reclassified continuous maps into unsuitable, low-quality and high-quality habitat indicate that remaining high-quality areas exist in the two countries. In the US, highest-quality areas are located in and around the MWEPA and in southern New Mexico in the three scenarios (Figs. 19-21). In Mexico, the Sierra Madre Occidental holds large areas of high-quality habitat concentrated in two main areas, one in northern Chihuahua running along the border with Sonora, and the other one in Durango down to western Zacatecas and northern Jalisco. The Sierra Madre Oriental holds significant high-quality areas in Tamaulipas, Nuevo León and Coahuila, but mountain ranges in that region are naturally more fragmented than in the Sierra Madre Occidental (Figs. 18-20).

Potential connectivity between the two Sierras Madre mountain ranges is detected in at least three regions: at the north via eastern Chihuahua and Coahuila; in the center, from Durango to Nuevo León crossing through southern Coahuila, and in the south from Durango-Zacatecas to Tamaulipas via San Luis Potosí (Figs. 18-20).

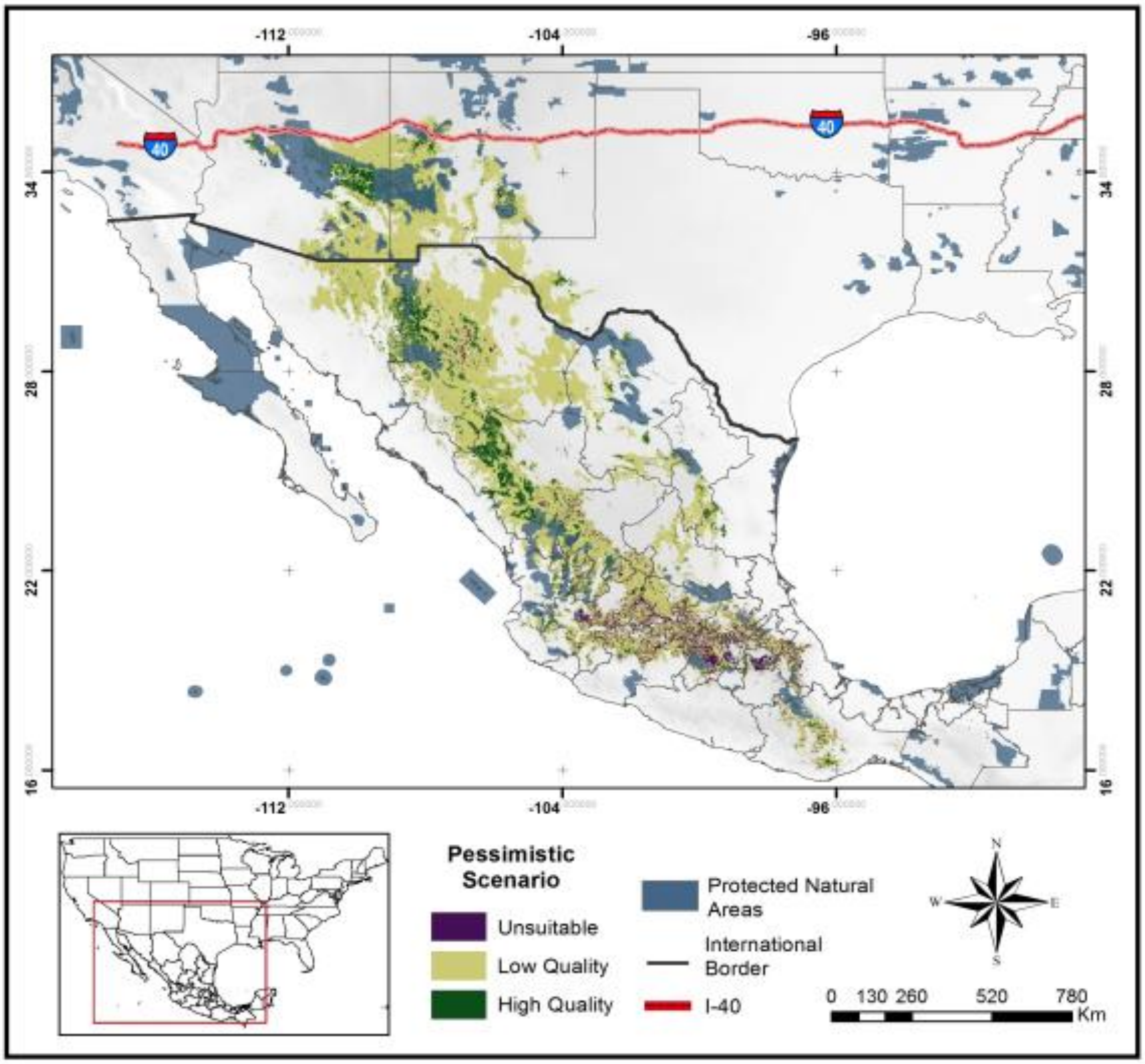

Figure 18. Reclassified pessimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3, High Quality > 3.

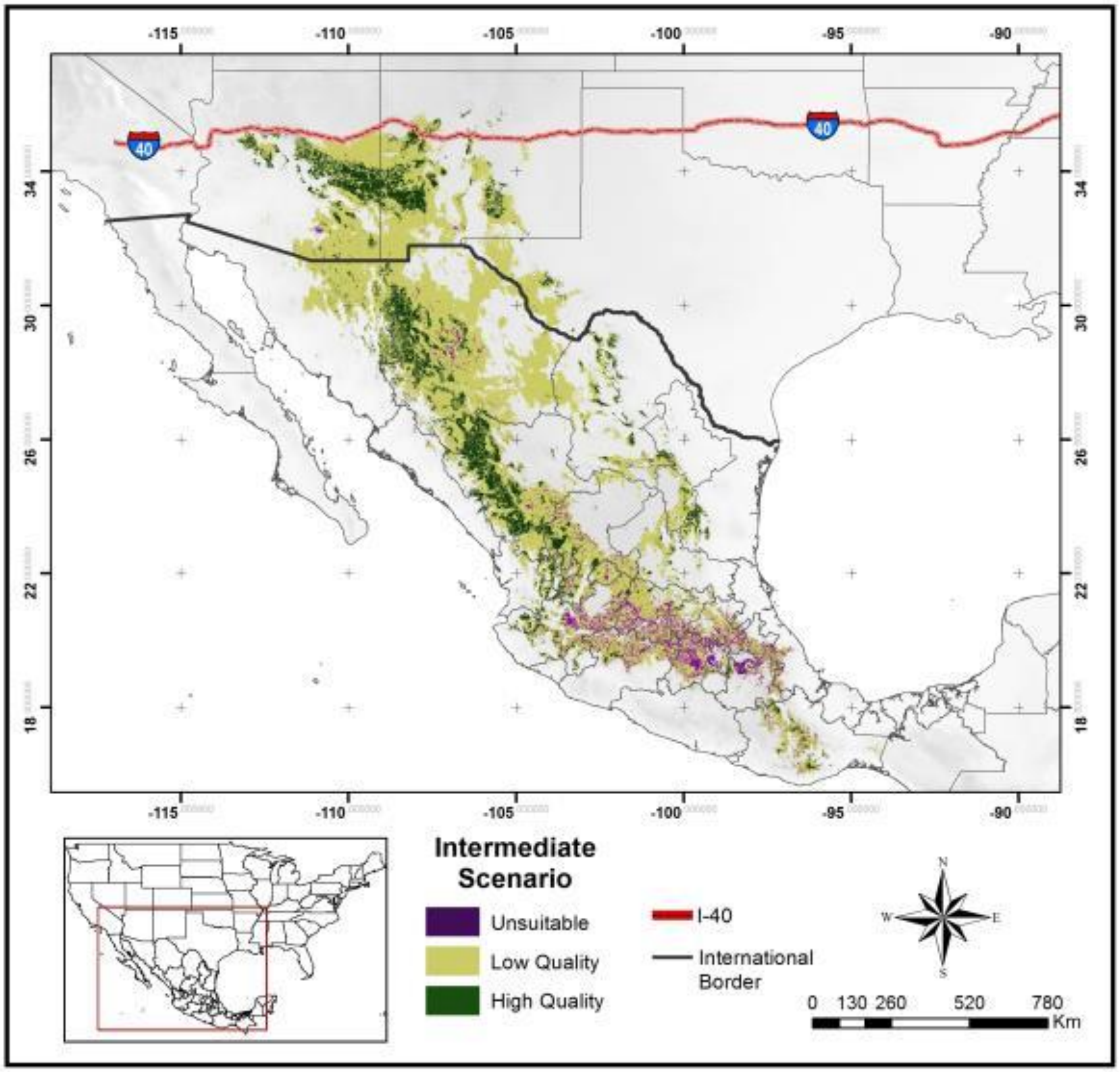

Figure 19. Reclassified intermediate habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3, High Quality > 3.

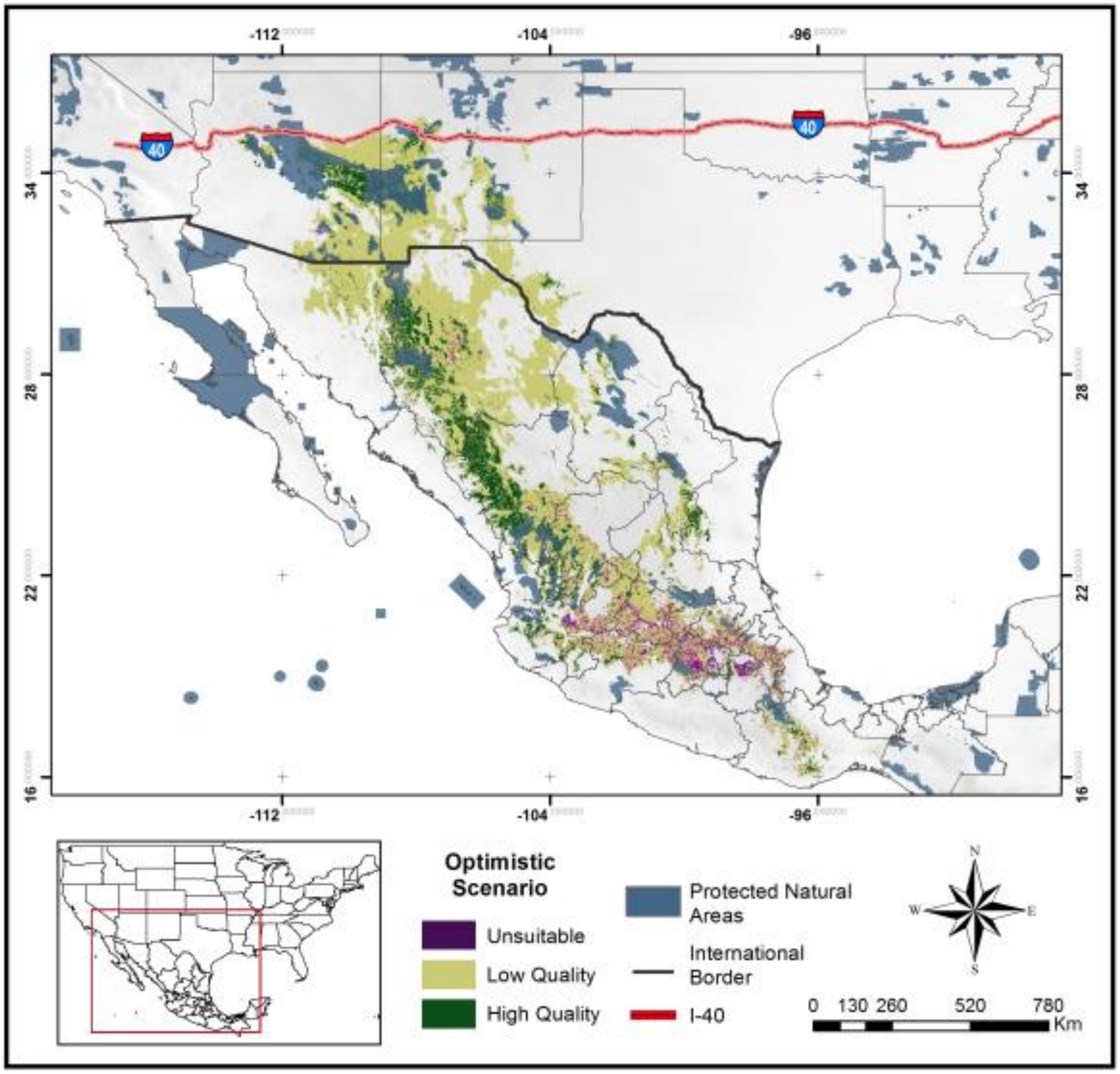

Figure 20. Reclassified optimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3, High Quality > 3.

We calculated the area of all high-quality habitat patches for the reclassified maps for each scenario (Figs. 18-20) in the four regions with largest continuous areas: (1) Arizona-New Mexico, (2) Northern Sierra Madre Occidental, (3) Southern Sierra Madre Occidental, and (4) Sierra Madre Oriental. Individually, the Arizona-New Mexico area holds the largest amount of high-quality habitat in the intermediate, followed by Northern Sierra Madre Occidental, Southern Sierra Madre Occidental, and Sierra Madre Oriental (Table 10). However, the two large areas of habitat of the Sierra Madre Occidental are not completely isolated, they are extensively connected by suitable habitat of variable quality, even in the pessimistic scenario, conforming the largest continuum of habitat for the Mexican wolf (Fig. 18).

Table 10. Area estimates of high-quality patches for the intermediate scenario without UBI.

Intermediate Scenario	***Area (Km2)***
Region	**108,522**
1. Arizona-New Mexico	44,477
2. Northern Sierra Madre Occidental	21,538
3. Southern Sierra Madre Occidental	34,540
4. Sierra Madre Oriental	7,967

Habitat suitability scenarios with the Ungulate Biomass Index (UBI) map

When the UBI layer was added to the habitat suitability model, an additional quality category was included (highest quality) to identify the areas with highest prey density. Comparing the two habitat models (with and without the UBI information), we observe that geographic patterns of the highest quality areas are maintained: Arizona-New Mexico, Sierra Madre Occidental and Sierra Madre Oriental regions hold large high-suitable areas in the three scenarios (Figs 21-23). However, the highest-quality areas were found in large patches only in the Arizona-New Mexico and in a much lesser extent in the two Sierras Madre (Figs 21-23); this is particularly conspicuous in the pessimistic scenario (Fig. 21). This is an expected result as the Arizona-New Mexico area holds the highest UBI (Fig. 14) due to the presence of the three ungulate species, whereas in most of the Mexican portion of the wolf distribution, there is only white-tailed deer and smaller mammals (Fig. 13). Examining the intermediate scenario, the extent of habitat increases dramatically on the Mexican side of the distribution when the high- and highest-quality patches are combined (Table 11). This is not so dramatic for the Arizona-New Mexico region because most of the habitat of this area is of the highest quality (Fig. 22).

Table 11. Area estimates of the highest-quality patches and high- and highest-quality patches combined for the intermediate scenario with UBI.

Intermediate Scenario	***High and Highest quality patches (Km^2)***	***Highest quality patches (Km^2)***
Region	**108,722**	**51,829**
1. Arizona-New Mexico	44,477	30,255
2. Northern Sierra Madre Occidental	21,538	8,073
3. Southern Sierra Madre Occidental	34,540	8,689
4. Sierra Madre Oriental	7,967	4,782

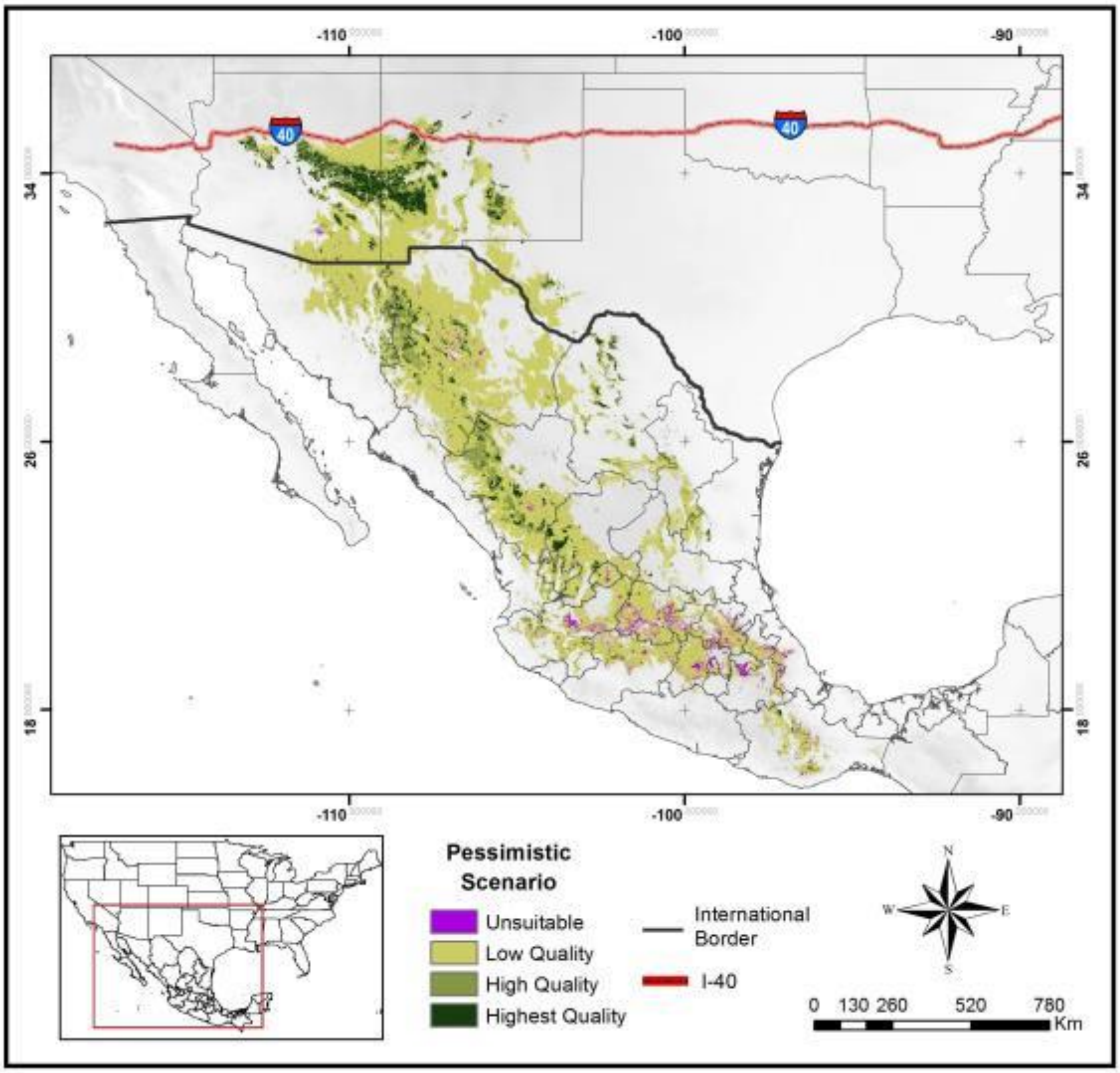

Figure 21. Rescaled pessimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, road density, and UBI. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3.2, High Quality = 3.2-3.95, Highest Quality > 3.95.

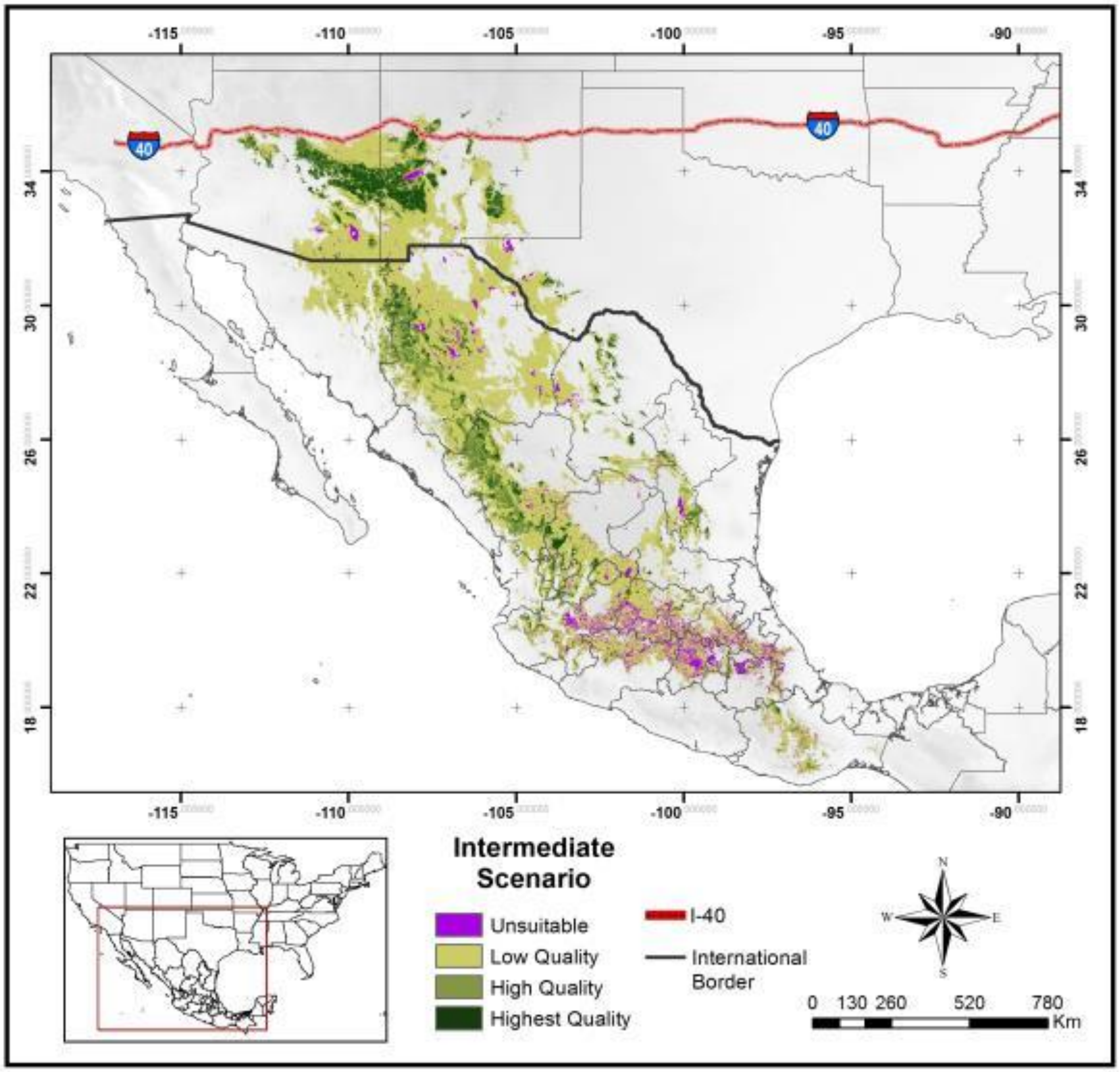

Figure 22. Rescaled intermediate habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, road density, and UBI. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3.2, High Quality = 3.2-3.95, Highest Quality > 3.95.

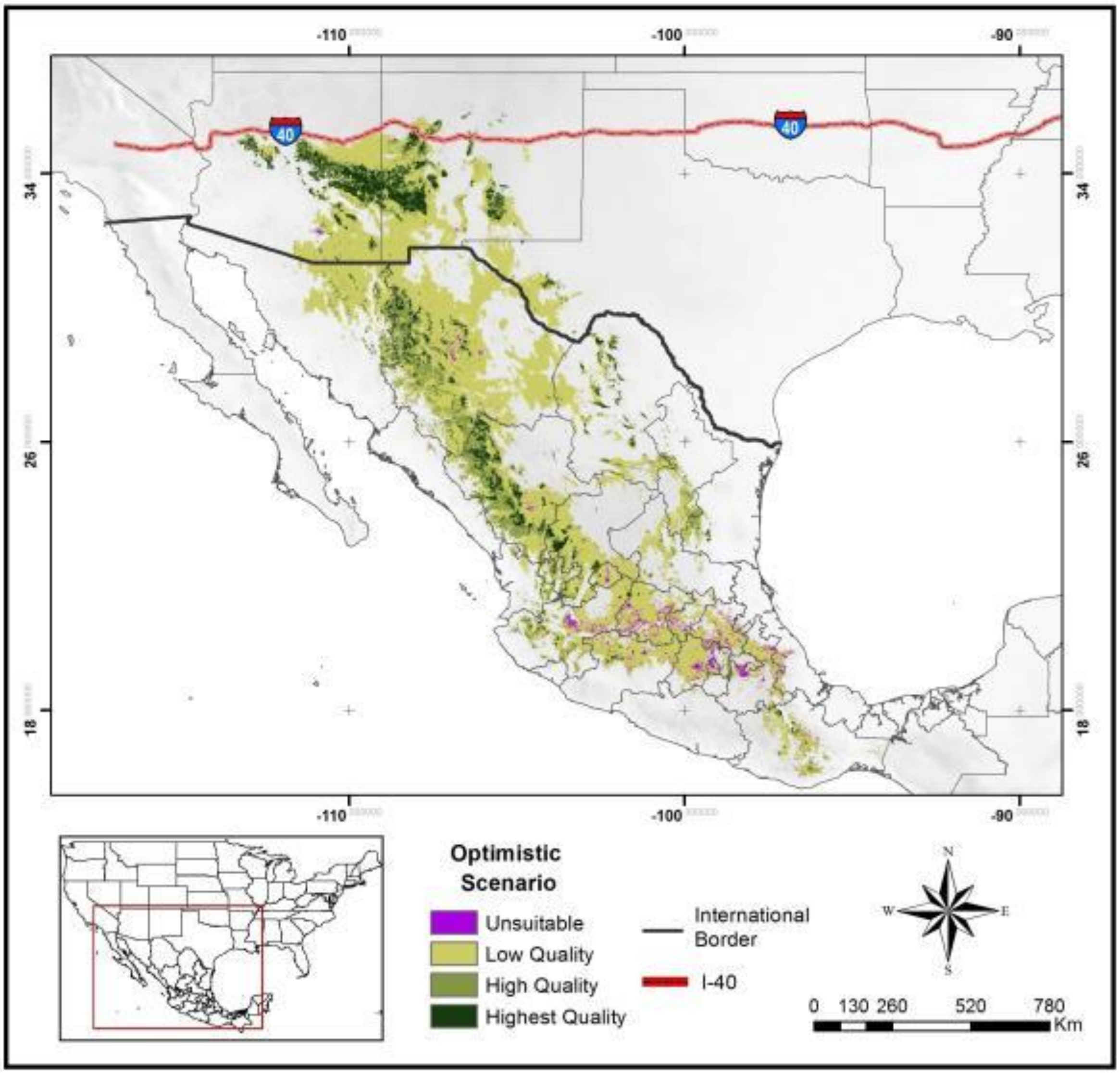

Figure 23. Rescaled optimistic habitat suitability scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, road density, and UBI. Habitat model values for reclassification were: Unsuitable < 0, Low Quality = 0-3.2, High Quality = 3.2-3.95, Highest Quality > 3.95.

Goal 1: Potential areas for undertaking recovery actions in Mexico

We consider that recovery efforts should focus in areas where conditions – both environmental and social– are favorable. This habitat suitability analysis is only the first of a series of steps that should be considered to select specific sites for further releases. Therefore, the scope of this study is to identify those areas in which suitable habitat conditions prevail and thus fieldwork should be initiated to evaluate environmental parameters like prey and cattle density, habitat condition, and social aspects such as land tenure, attitude towards the presence of wolves, and safety conditions for field teams, among others.

To be conservative, we carried out this analysis for the scenarios obtained from the habitat model without UBI information, as we are concerned about the reliability of this map. From the patch analysis and for each scenario we identified the largest, continuous patches. In the intermediate scenario, the largest patch was located in the Arizona-New Mexico region with an extension of 33,674 km^2. The other two were located in the Sierra Madre Occidental, one in the north, in Chihuahua-Sonora covering 25,311 km^2 and the other one in Durango with an expanse of 39,610 km^2 (Table 10). No continuous patches larger than 1,500 km^2 were identified in the Sierra Madre Oriental, suggesting that forests in this area are fragmented and connectivity is probably lower than in the Sierra Madre Occidental; nonetheless, scattered patches combined cover 9,259 km^2. Several small patches exist along and between the two Sierras Madre, in Coahuila and San Luis Potosí, and also between the Northern Sierra Madre Occidental and the MWEPA, in the Sky Islands, that might serve as stepping-stones for dispersing individuals across big patches (Fig. 25). It is important to highlight that as we move towards optimistic scenarios, change in total suitable area, especially in the south of the Sierra Madre, increases disproportionately compared to other areas, including those in the United States (Figs. 24-26). This suggests that if conditions in the field are more similar to optimistic scenarios, available area for the wolves will be much higher. Also, with habitat restoration and appropriate social conservation programs, the potential for wolf recovery in Mexico greatly increases.

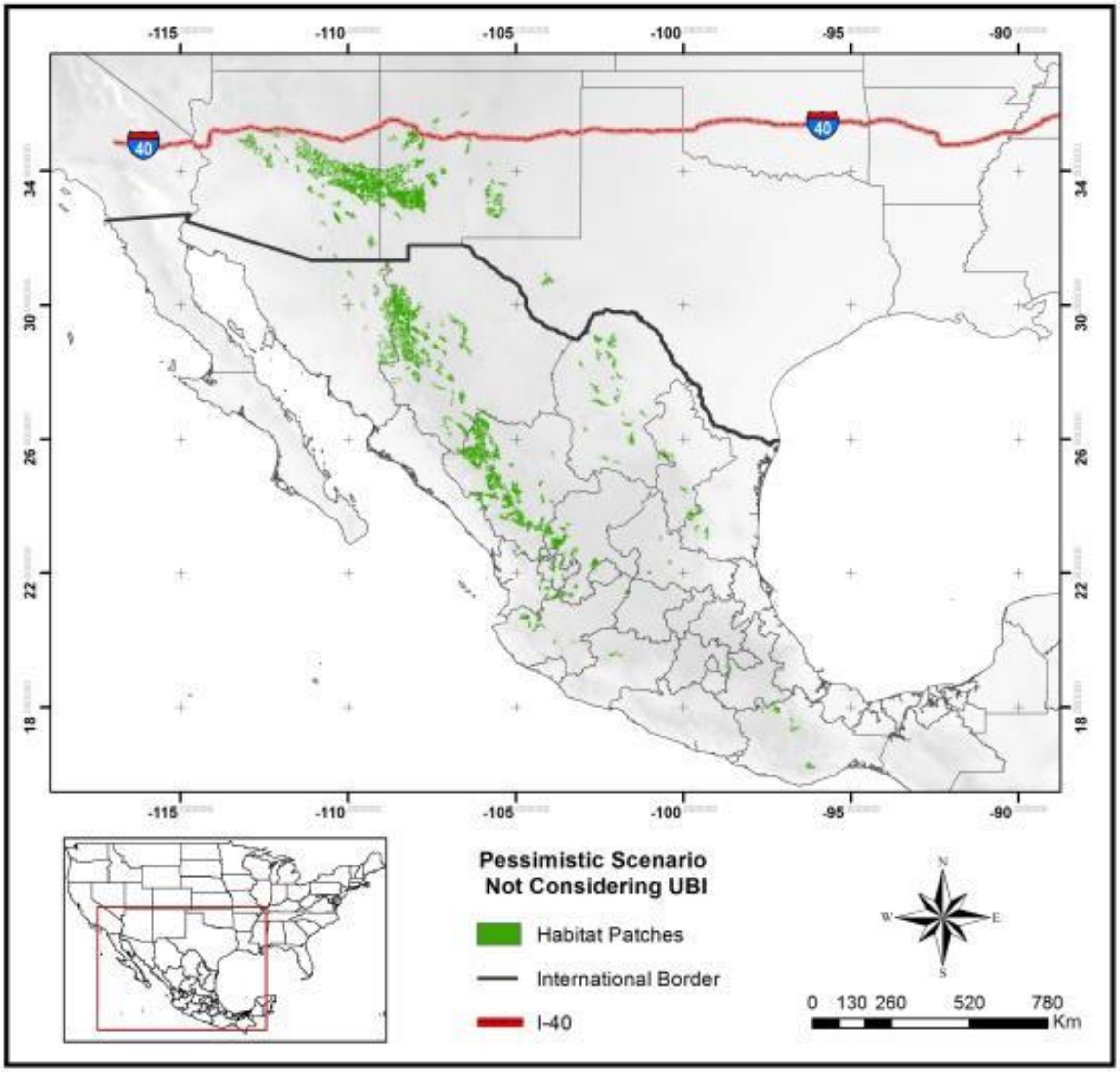

Figure 24. Depiction of only the contiguous patches of high-quality habitat under the pessimistic scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

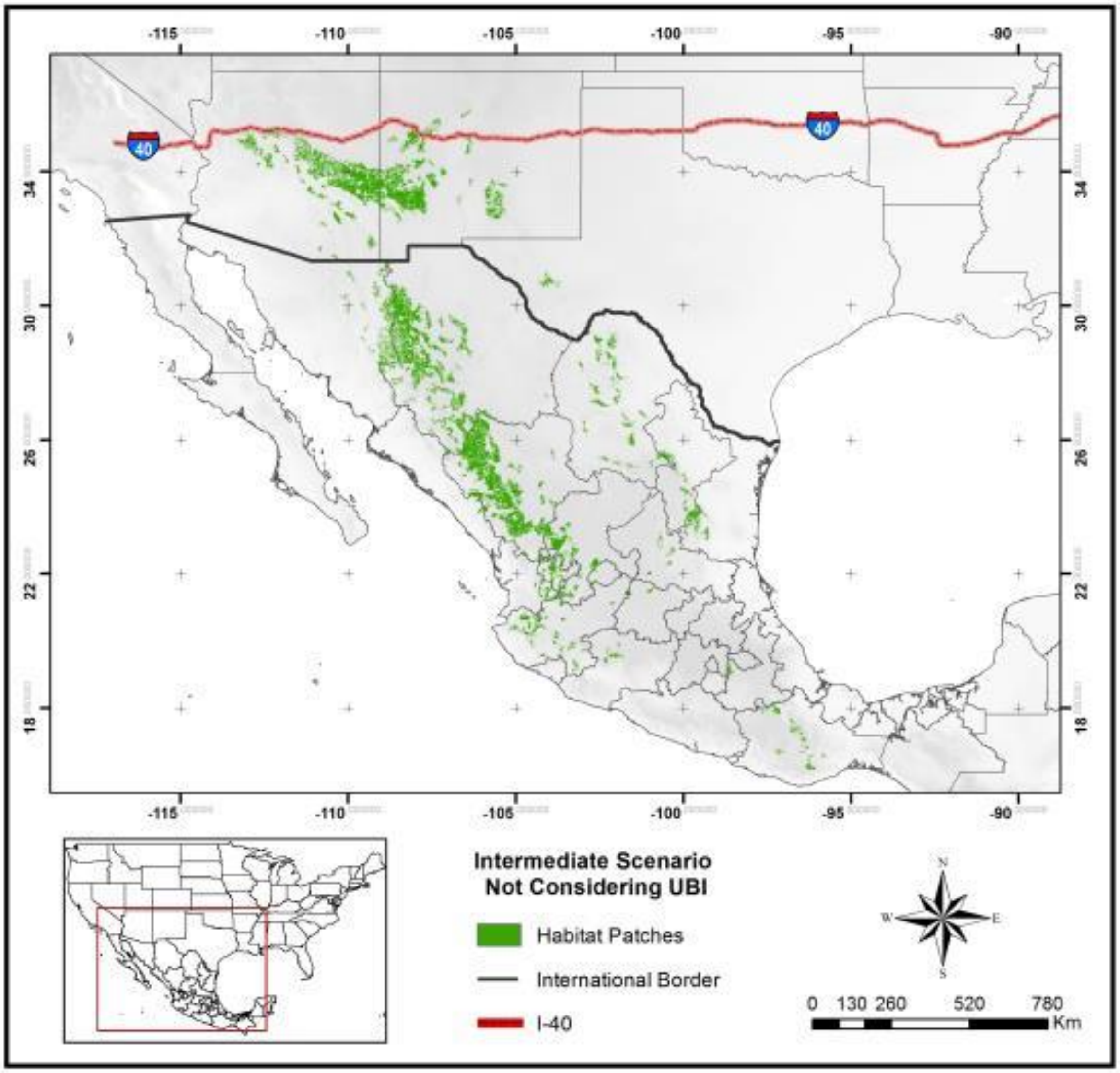

Figure 25. Depiction of only the contiguous patches of high-quality habitat under the intermediate scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

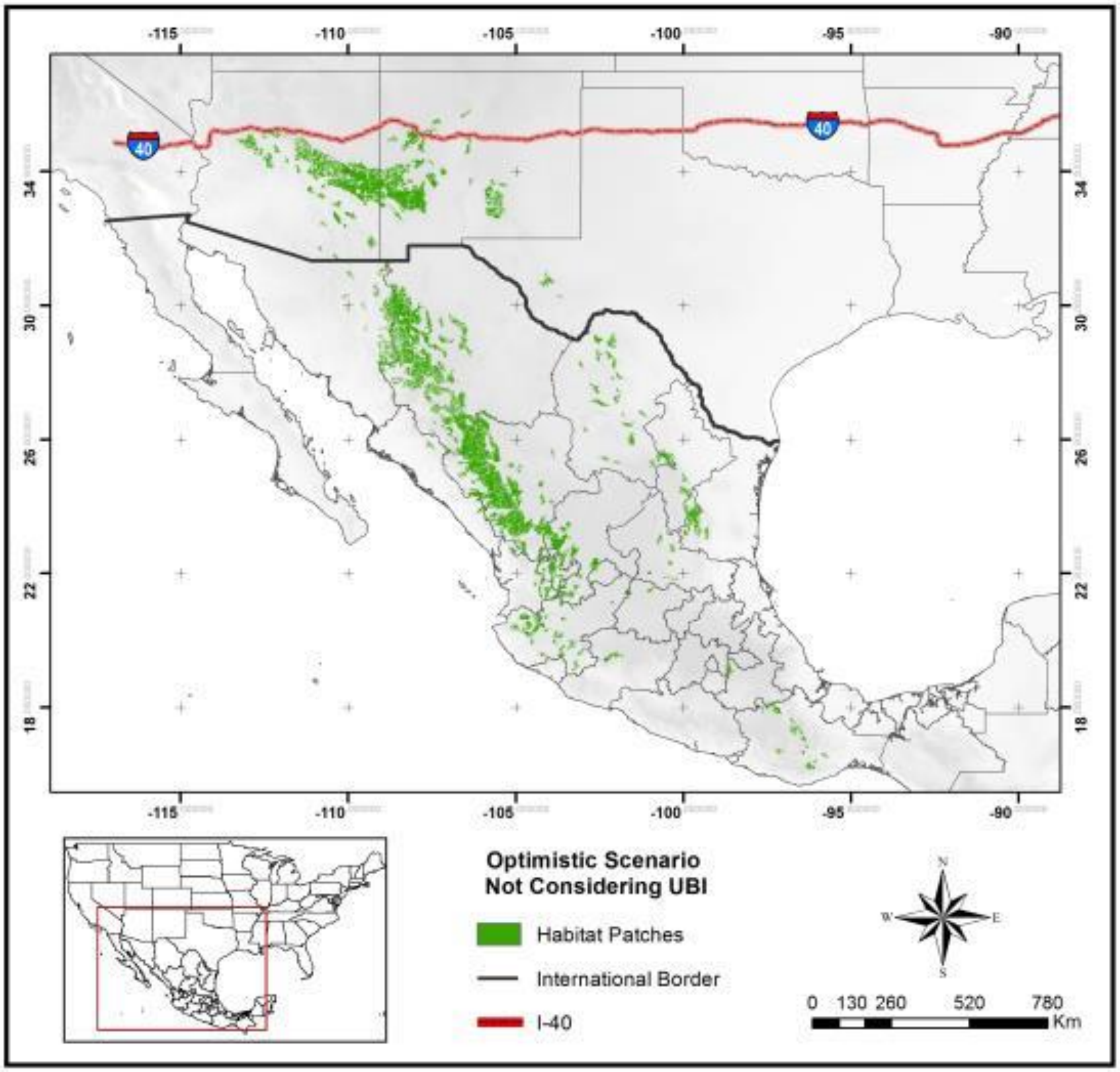

Figure 26. Depiction of only the contiguous patches of high-quality habitat under the optimistic scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

Three natural protected areas in Chihuahua (Tutuaca-Papigochi, Campo Verde and Janos), one in Sonora (Ajos-Bavispe) and one in Durango (La Michilía, as well as the proposed protected area Sierra Tarahumara) cover part of the largest high-quality habitat patches in the Sierra Madre Occidental, as exemplified with the intermediate scenario (Fig. 27). In the Sierra Madre Oriental, Maderas del Carmen in Coahuila and Cumbres de Monterrey in Nuevo León are two federal protected areas that hold wolf high-quality habitat (Fig. 27). Hence, an opportunity to merge efforts among authorities from different government agencies at the federal and state levels seems feasible.

Regarding the results in the United States, we obtained several patches including the largest one in Arizona-New Mexico (in the MWEPA and surrounding area), which comprises several national forests parks that combined reaches ~33,000 km^2. This includes areas located in Lincoln National Forest and along the Cibola National Forest, in New Mexico (Figs. 27).

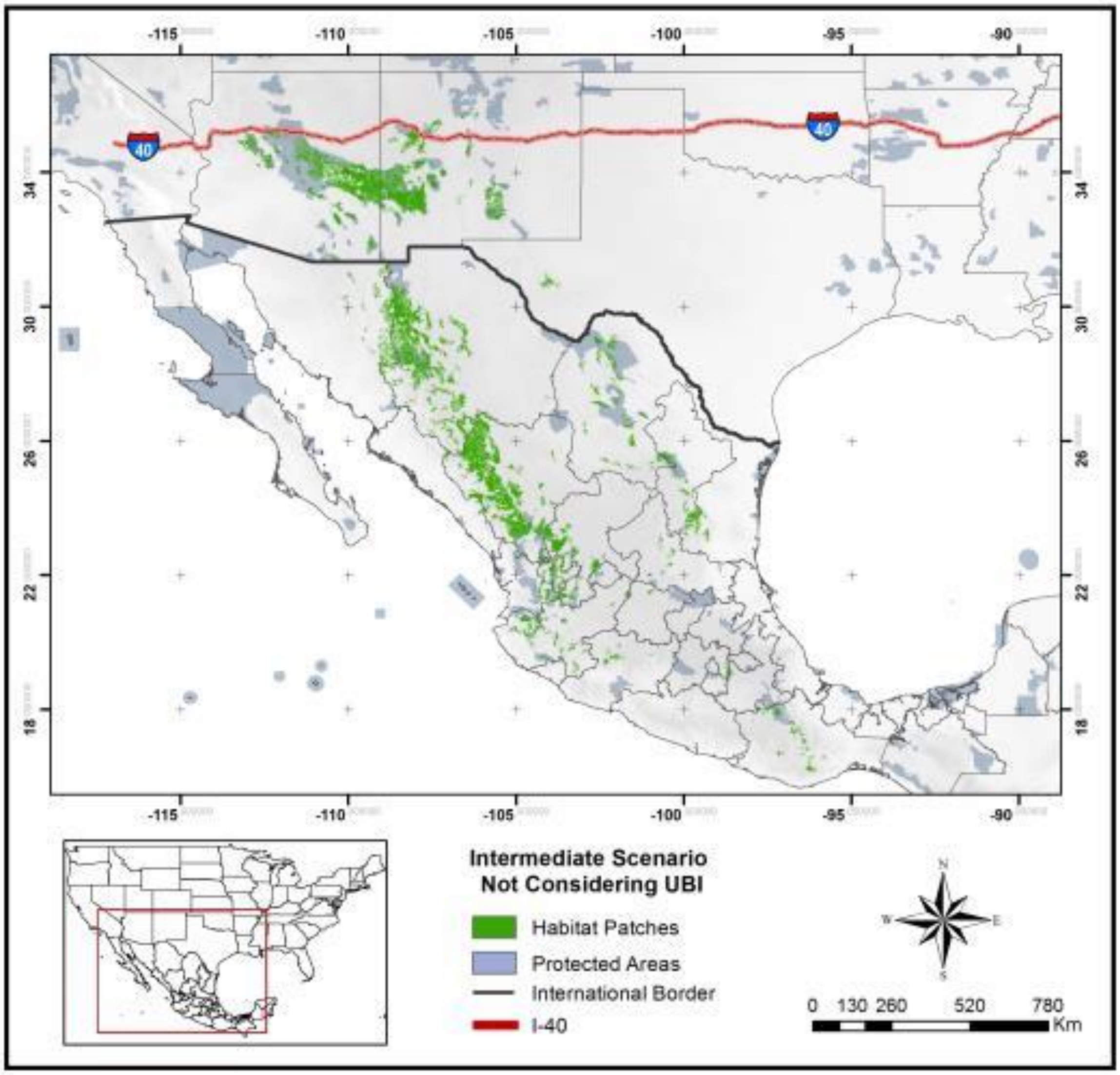

Figure 27. High-quality habitat patches and protected areas in the intermediate scenario for the Mexican wolf based on the combination of climatic suitability, land cover use, human population density, and road density.

Finally, we overlaid the municipal boundaries map of Mexico on the intermediate scenario to identify the municipalities that hold significant area of high-quality habitat. In the northern Sierra Madre Occidental, 13 municipalities were identified, 15 in southern Sierra Madre Occidental 15, and 9 in the Sierra Madre Oriental (Table 12).

Table 12. Municipalities with high-quality habitat under the intermediate scenario for the Mexican wolf.

State	Municipality
Sierra Madre Occidental North	
Chihuahua	Carichi
Chihuahua	Casas Grandes
Chihuahua	Guerrero
Chihuahua	Ignacio Zaragoza
Chihuahua	Janos
Chihuahua	Madera
Chihuahua	Maguarichi
Chihuahua	Temosachi
Sonora	Bacerac
Sonora	Huachinera
Sonora	Nacori Chico
Sonora	Sahuaripa
Sonora	Yécora
Sierra Madre Occidental South	
Chihuahua	Balleza
Chihuahua	Guadalupe y Calvo
Durango	Canatlan
Durango	Durango
Durango	Guanacevi
Durango	Mezquital
Durango	Ocampo
Durango	Otaez

Durango	San Bernardo
Durango	San Dimas
Durango	Santiago Papasquiaro
Durango	Suchil
Durango	Tepehuanes
Zacatecas	Jimenez del Teul
Zacatecas	Valparaiso
Sierra Madre Oriental	
Coahuila	Acuña
Coahuila	Múzquiz
Coahuila	Ocampo
Coahuila	San Buenaventura
Nuevo León	Doctor Arroyo
Nuevo León	General Zaragoza
Tamaulipas	Jaumave
Tamaulipas	Miquihuana
Tamaulipas	Palmillas

Goal 2: Estimates of Mexican wolf population sizes

There are at least five methods to infer the potential number of wolves in an area (Bednarz 1988, Fuller 1989, Messier 1995, Paquet 2001, and based on average home range). The first four methods rely directly on the estimation of prey abundance or biomass in a simple multiplication with a constant factor (i.e., Paquet 2001) or in a regression equation (i.e., Bednarz 1988, Fuller 1989, Messier 1995). The home-range-based method is an extrapolation of the home range size and the mean number of wolves in the packs of a site or region to a given area. This method also relies, but indirectly, to prey density, because the home range and pack sizes depend on availability of prey (Fuller et al. 1992; Oakleaf et al. 2006; Belongie 2008).

Our estimates of prey density and UBI come with significant uncertainty, mainly for the Mexican portion of the distribution of the wolf. In Mexico the only wild ungulate that is a primary prey for the Mexican wolf is the Coues white-tailed deer and our analysis revealed the density modeling for this species is the weakest. The difficulty in modeling prey density and an Ungulate Biomass Index across a broad landscape is due to the large range of variation in estimated ungulate densities among sample points with similar environmental conditions. Also, in some cases there is wide environmental variation among ungulate management areas with similar ungulate densities. Trying to model these conflicting parameters resulted in poor model fit. Nonetheless, it is important to note that our relative ungulate density results for this species do capture the general geographic patterns of density known for this species in the US (J. Heffelfinger [AZGFD] and S. Liley (NMDGF]) Despite this general agreement with known variations in elk, mule deer, and white-tailed density, the UBI values for any given pixel may not accurately represent the actual biomass at that location.

Currently, there is no better information available on prey density, so it is clear that an urgent next step is to carry out a coordinated effort to gather updated, systematic field data that fulfills the needs for robust rangewide ungulate density estimations. In the meantime, we present biological carrying capacity estimations for the Mexican wolf in the different areas where suitable habitat exists, according to our geographical analyses.

We observed large variations in the wolf numbers depending on the method; estimations under Paquet (2001) and Bednarz (1988) methods were consistently higher, and the home-range-based approach is consistently lower –as much as one order of magnitude– than Fuller's (1989) and Messier (1995) methods, irrespective of the scenario analyzed (Tables 13-14). For instance, in the intermediate scenario of the habitat model for which the UBI layer was not included, the number of wolves estimated under Paquet's (2001) method is 1925, and with the home-range-based method is 184 (Table 13).

Another general result is that the largest estimated wolf population sizes were consistently from the Arizona-New Mexico region, in the MWEPA area; at least two or three times larger than Southern Sierra Madre Occidental, the next region in carrying capacity, again, irrespectively of the scenario (Tables 13-14). In turn, the Northern and Southern Sierra Madre regions have more similar numbers between them than to the other areas, and Sierra Madre Oriental always showed the lowest numbers. This relationship among regions seems very reasonable, since the MWEPA and surrounding areas holds the largest areas of highest quality habitat, according to our models, due to the high availability of ungulates, particularly elk (Figs. 22-24).

Table 13. Mexican wolf carrying capacity estimates in high-quality patches under the intermediate scenario for the habitat suitability model without the UBI layer. Deer densities were obtained from the GLM/RF model. In parenthesis are the estimates under the pessimistic and optimistic scenarios, respectively.

Intermediate (Pessimistic-Optimistic) scenarios without the UBI layer				
Carrying capacity estimation method	**Region**			
	Arizona-New Mexico	*SMOcc North*	*SMOcc South*	*SM Oriental*
Bednarz 1988	1798 (1624-1818)	579 (444-762)	982 (584-1072)	248 (159-256)
Fuller 1989	1343 (1217-1361)	284 (216-387)	516 (308-562)	138 (88-141)
Messier 1995	1390 (1261-1913)	225 (171-317)	433 (260-471)	121 (83-123)
Paquet 2001	1925 (1747- 1954)	312 (236-439)	600 (361-653)	168 (115-171)

Home range-based	184 (164-186)	138 (107-165)	217 (128-237)	50 (34-52)

Interestingly, there is not much variation in the carrying capacity between scenarios. Numbers remain relatively constant in the optimistic, intermediate and pessimistic scenarios for the habitat model with (Table 13) and without (Table 14) the UBI layer. Furthermore, it is important to emphasize that although we treated here the four regions as independent units to facilitate calculations, these areas may not be isolated from each other. Actually, there is extensive connection between the northern and southern portions of the Sierra Madre Occidental (Fig. 28), which may, in effect, be a single unit. Likewise, movements between the existing US wild population and Northern Sierra Madre Occidental are very possible due to the high mobility of wolves as evidenced by exploratory travels of US wolves and the released wolves in Mexico (Carlos López, pers. obs.).

Table 14. Mexican wolf carrying capacity estimates in high- and highest-quality patches under the intermediate scenario for the habitat suitability model including the UBI layer. Deer densities were obtained from the GLM/RF model. In parenthesis are the estimates under the pessimistic and optimistic scenarios, respectively.

Intermediate (Pessimistic-Optimistic) scenarios with the UBI layer				
Carrying capacity estimation method	**Region**			
	Arizona-New Mexico	*SMOcc North*	*SMOcc South*	*SM Oriental*
Bednarz 1988	2487 (2427-2534)	495 (443-672)	858 (547-1024)	222 (190-240)
Fuller 1989	1880 (1836-1911)	244 (195-337)	452 (290-538)	127 (97-136)
Messier 1995	1954 (1910-1986)	194 (171-272)	380 (245-452)	113 (88-121)

Paquet 2001	2708 (2646-2752)	269 (236-377)	527 (340-626)	157 (121-168)
Home range-based	243 (236-250)	122 (106-157)	212 (128-237)	50 (34-53)

The question that arises is, which of all these estimations is reliable? Unfortunately, the wolf-ungulate system in the Southwest has never been studied and all these methods based on ungulate biomass use formulas developed with data from northern ecosystems with different assemblages of ungulate and non-ungulate prey. These methods were also merely descriptive, that is they were published to describe the density of wolves experienced throughout a range of ungulate biomass indices. None were intended to predict the number of wolves one could expect when recovering a population from extirpation (especially not in the Southwestern US). The only reference point we have for comparison is the number of wolves in the US population which in 2016 was estimated to have a minimum of 113 individuals (J. Oakleaf, pers. comm.). However, we do not know the number of wolves that this area can actually support because the current population is growing.

In the Mexican side of the border, numbers are more uncertain. Currently, there are around 31 wolves distributed in three packs, but the level of human intervention is quite high, supplementing at least two of the packs (C. Lopez, pers. comm.). The reintroduction efforts are still in an early stage making it impossible to draw any conclusions regarding the potential carrying capacity in Mexico. The Mexican wolf is widely assumed to have evolved on a more diverse diet of smaller prey items in addition to white-tailed deer, indicating these estimates based solely on ungulate biomass may be biased somewhat lower if smaller prey items contributed substantially to maintaining wolves and increasing wolf densities.

Conclusions

The analyses presented here allow drawing some preliminary conclusions. First, under any scenario generated, results suggest that there is still sufficient habitat remaining in the US and Mexico to support viable populations of the Mexican wolf in the wild. Large, relatively continuous extensions of high-quality habitat remain mainly in the areas within and around the MWEPA and in Sierra Madre Occidental. High-quality habitat exists in Sierra Madre Oriental, but is naturally more fragmented than in Sierra Madre Occidental. Nonetheless, suboptimal habitat exists between high-quality patches within and between the two Sierras Madre, suggesting that dispersion of individuals is possible.

Second, information on ungulate density in Mexico is still poor. It is necessary to carry out systematic, extensive field surveys to produce reliable density estimates and rangewide models to be incorporated in the habitat suitability analysis.

Third, four natural protected areas cover portions of high-quality patches identified in the Sierra Madre Occidental. Most of high-suitable areas for wolves are under private lands, thus diversified conservation strategies are needed.

Finally, wolf number estimations showed a variation up to one order of magnitude, due to the estimation methods, input data and habitat scenario. The MWEPA region is the area overall with the highest-quality habitat due to the high availability of ungulate, particularly elk and therefore, with the highest estimation of Mexican wolf carrying capacity under any scenario. The Sierra Madre Occidental, both north and south, is the area with the potential to hold the largest number of wolves in Mexico.

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