Draft Mexican Wolf Revised Recovery Plan

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DRAFT

U.S. Fish and Wildlife Service
Southwest Region (Region 2)
Albuquerque, New Mexico
20xx
The purpose of a recovery plan is to provide a scientifically based, logical, and effective roadmap for the recovery of a species. It explains what is needed for species recovery and how to get there. Recovery plans are advisory documents, not regulatory documents. A recovery plan does not commit any entity to implement the recommended strategies or actions contained within it for a particular species, but rather provides guidance for ameliorating threats and implementing proactive conservation measures, as well as providing context for implementation of other sections of the ESA, such as section 7(a)(2) consultations on Federal agency activities, development of Habitat Conservation Plans, or the creation of experimental populations under section 10(j).
DISCLAIMER
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Recovery plans delineate reasonable actions believed to be required to recover and/or protect listed species. Plans published by the U.S. Fish and Wildlife Service (FWS), are sometimes prepared with the assistance of recovery teams, contractors, state agencies, and other affected and interested parties. Recovery teams serve as independent advisors to FWS. Plans are reviewed by the public and submitted to additional peer review before they are adopted by FWS. Objectives of the plan will be attained and any necessary funds made available subject to budgetary and other constraints affecting the parties involved, as well as the need to address other priorities. Recovery plans do not obligate other parties to undertake specific tasks and may not represent the views nor the official positions or approval of any individuals or agencies involved in the plan formulation, other than FWS. They represent the official position of FWS only after they have been signed by the Regional Director as approved. Approved recovery plans are subject to modification as dictated by new findings, changes in species status, and the completion of recovery tasks.

By approving this document, the Regional Director will certify that the data used in its development represent the best scientific and commercial data available at the time it was written. Copies of all documents reviewed in development of the plan are available in the administrative record located at New Mexico Ecological Services Field Office, U.S. Fish and Wildlife Service, 2105 Osuna Dr., NE, Albuquerque, NM, 87113, #505-346-2525 or 1-800-299-0196.
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LITERATURE CITATION AND AVAILABILITY

Literature citation should read as follows:

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U.S. Fish and Wildlife Service
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EXECUTIVE SUMMARY
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I. BACKGROUND

A. Brief Overview

(Note to Reviewer: This section should orient the reader to the situation.)

Recovery Planning

The Mexican Wolf Revised Recovery Plan (Plan) is the first recovery plan developed for the Mexican wolf that contains the required recovery plan elements specified by the Endangered Species Act (ESA, or Act) (section 4(f)(1)):

i) a description of such site-specific management actions as may be necessary to achieve the plan’s goal for the conservation and survival of the species;

ii) objective, measurable criteria which, when met, would result in a determination, in accordance with the provisions of this section, that the species be removed from the list; and

iii) 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.

Two other recovery plans have been written for the Mexican wolf: the 1982 Mexican Wolf Recovery Plan, which was written by a recovery team established by the Service and signed by the Service and the Dirección General de la Fauna Silvestre in Mexico; and the Programa de Recuperación del Lobo Mexicano (Programa de Recuperacion), written by a team of scientists in Mexico, in 1999 (SEMARNAT 2000). Both of these plans acknowledge the binational historical range of the Mexican wolf within the United States and Mexico, but each plan was written within the context of the federal laws governing its content: the 1982 Mexican Wolf Recovery Plan was written pursuant to the Service’s obligation to develop recovery plans for species protected by the Act, whereas Mexico’s plan was written pursuant to the Mexican federal law protecting wildlife, Norma Oficial Mexicana NOM-059-ECOL-1994.

The 1982 Mexican Wolf Recovery Plan did not contain all three of the recovery plan elements specified in section 4(f)(1) of the Act. The recovery team could not foresee full recovery and
eventual delisting of the Mexican wolf due to its dire status in the wild and the lack of suitable habitat within the historical range due to anthropogenic activities. Therefore, they stopped short of providing the objective and measurable recovery criteria required by the Act. Instead, the recovery team laid out a “prime objective”:

“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 1982:23).”

The recovery actions and attending time and cost estimates in the 1982 Recovery Plan focused on information gathering and management recommendations in support of this prime objective. The Service initiated revision to the 1982 Mexican Wolf Recovery Plan in the mid-1990s and early 2000’s. These revisions were not finalized due to logistical issues, including litigation related to gray wolf reclassifications (see National Gray Wolf Recovery, below).

Mexico’s 1999 Programa Recuperacion was not required by law to set a numeric goal for recovery. It did, however, establish an objective to reach population levels that would ensure long-term viability by reintroducing Mexican wolves into several areas in Mexico (V: Objectives, VI: Strategies, Projects, and Actions) (SEMARNAT 2000). The document explained that Mexico supported reintroduction on both sides of the Mexico-United States border, and stated that it would be difficult to find appropriate habitat for reintroduction in Mexico. The plan suggested that the best habitat may exist within the Sierra Madre Occidental and the Sierra Madre Oriental mountain ranges (SEMARNAT 2000).

The 201x Mexican Wolf Revised Recovery Plan replaces and supersedes the Service’s 1982 Mexican Wolf Recovery Plan, but it does not replace, supersede, or otherwise affect Mexico’s Programa de Recuperacion. [More here as necessary to broadly describe national/bi-national aspects of this plan.]

*Recovery Implementation in the United States and Mexico*

Recovery efforts for the Mexican wolf have been underway in the United States and Mexico for several decades. Both countries have adopted a two-pronged approach to recovery: maintaining
a captive population of Mexican wolves, and re-establishing wild populations by releasing
captive wolves into designated reintroduction areas to establish viable populations that count
toward recovery..

The Mexican wolf captive breeding program established in the late 1970’s saved the Mexican
wolf from extinction. The breeding program was founded by three of the last six Mexican
wolves removed from the wild in Mexico. The first Mexican wolf pups were conceived and born
in captivity in the United States in 1981 (Parsons 1996, Hedrick et al. 1997, Lindsey and
Siminski 2007). Mexico formally joined the captive breeding effort in 1987 (SEMARNAT
2000), and by 1994, the binational breeding program had produced a captive population of 92
wolves. These founding wolves and their offspring were initially referred to as the Certified
lineage, later renamed the McBride lineage. In 1995, two additional lineages of pure Mexican
wolves, the Ghost Ranch lineage, founded by two wolves, and the Aragon lineage, founded by
two wolves, were integrated into the captive breeding program to increase the genetic diversity
of the founder population and reduce the potential for inbreeding depression to hinder recovery
(Parsons 1996, Hedrick et al. 1997). Ultimately then the founding base of the captive population
included only seven pure Mexican wolves (Hedrick et al. 1997).

Today, the binational captive breeding program continues to conserve the subspecies’ genome
and provide healthy offspring for release to the wild (Parsons 1996, Lindsey and Siminski 2007).
The program has been managed pursuant to breeding protocols and genetic and demographic
goals established by the Association of Zoos and Aquariums’ Species Survival Plan (AZA
Mexican Wolf SSP) since 1994 (Siminski and Spevak 2011). The captive breeding program
currently houses 283 wolves in 52 facilities, 34 of which are in the United States and 18 of which
are in Mexico (Siminski and Spevak 2011). In an analysis of the captive population in 2011, the
calculated retention of the original gene diversity of the founding seven wolves was 83.3 percent
(Siminski and Spevak 2011). However, even with optimal management the genetic diversity in
the captive population will continue to decline and could eventually compromise the Mexicna
wolf’s ability to survive in the wild (cite).
The United States and Mexico have both initiated re-establishment of the Mexican wolf in the wild by releasing captive-bred wolves into areas of suitable habitat in each country. In the United States, Mexican wolves were reintroduced to the wild in 1998 (cite annual report); as of December 31, 2011, a population of approximately 58 wild Mexican wolves inhabits the southwestern United States (update, cite). Mexico reintroduced Mexican wolves to the wild in 2011; as of MONTH, 2012 x wild Mexican wolves inhabit Mexico (update, cite). These reintroduction efforts are independent of the captive breeding program, although closely coordinated. The United States and Mexico also communicate their reintroduction plans with one another, share equipment, and transfer information and technology through staff visits to each country. Implementation of reintroductions occurs according to the legal frameworks and management provisions relevant to each country.

In the United States, plans for the reintroduction of the Mexican wolf to the wild began to develop in the early-1990s, stimulated in part by a suit filed against the Service by seven environmental organizations for failure to implement provisions of the ESA (Wolf Action Group, et al. vs. United States, Civil Action CIV-90-0390-HB, U.S. District Court, New Mexico). During this time, the Service formed a new recovery team to revise the 1982 Mexican Wolf Recovery Plan with updated scientific information and recovery criteria. The draft recovery plan developed by the new recovery team was not finalized. The prime objective of the 1982 recovery plan to establish a population of at least 100 wolves in the wild was maintained as a guiding recommendation for the reintroduction. Several analyses were conducted to assess locations for the reintroduction (Johnson et al. 1992, USFWS 1993), culminating with the Final Environmental Impact Statement, “Reintroduction of the Mexican Wolf within its Historic Range in the Southwestern United States,” (FEIS) (USFWS 1996).

By 1998, the plans for the reintroduction were solidified in the final rule, “Establishment of a Nonessential Experimental Population of the Mexican Gray Wolf in Arizona and New Mexico” (Final Rule) (63 FR 1752-1772, January 12, 1998), and in March of that year, 11 Mexican wolves from the captive breeding program were released to the wild. The Final Rule established the Mexican Wolf Experimental Population Area (MWEPA) in central Arizona and New Mexico, and designated the reintroduced population as a non-essential experimental population
under section 10(j) of the ESA (Figure x). This designation was justified because wolves
released to the wild would be genetically redundant to the captive breeding program and because
it allowed for regulatory flexibility in managing released wolves and their progeny, an important
consideration at the time for gaining public support (63 FR 1752-1772, January 12, 1998; Brown
and Parsons 2001). The rule stipulated that the reintroduction of wolves would take place within
the Blue Range Wolf Recovery Area, a 17,775 km² (6,845 mi²) area within the MWEPA that
included the Apache National Forest in east-central Arizona and the Gila National Forest in
west-central New Mexico. The remainder of the MWEPA outside of the BRWRA was
considered recovery habitat for the Mexican wolf and provided a transition zone between the
non-essential experimental designation of the BRWRA to the endangered designation that
applied to Mexican wolves elsewhere (i.e., wolves outside of the MWEPA have full endangered
status under the classification provided by the 1978 gray wolf listing) (63 FR 1752-1772,
January 12, 1998).

The strategy for the reintroduction was to release 14 family groups of wolves into the Blue
Range Wolf Recovery Area over a period of five years in order to establish the population (63 FR
1752-1772, January 12, 1998). The FEIS projected that the population target of at least 100 wild
wolves and 18 breeding pairs would be reached in 2006 (USFWS 1996). Because a source
population of Mexican wolves did not exist in the wild, the reintroduction would be initially
dependent on captive-bred wolves. As of December 31, 2011, the minimum estimate for the
BRWRA population is 58 wolves, about half of the minimum population objective (USFWS
2011).

In 2000, the White Mountain Apache Tribe (WMAT) agreed to allow wolves to inhabit Fort
Apache Indian Reservation (FAIR), and in 2002 signed an agreement allowing direct release of
wolves onto the reservation providing an additional 500 mi² (6,475 km²) of wolf habitat.

In October 2011, Mexico released five captive wolves to the wild in Sonora (Araiza et al. in
press). Four of these wolves were illegally killed by poison within several months of release.
Mexico plans on releasing additional wolves in this area, and in other areas targeted for
reintroduction, in the near future. Since Mexico developed its Programa de Recuperacion,
Researchers in Mexico have conducted several habitat analyses to identify areas of suitable
habitat for the establishment of wild wolf populations (see Section I.H. and Modeling Appendix
Section 5.B.).

With the recent release of wolves in Mexico close to the United States-Mexico border, there is
potential for wolves from Mexico to disperse into the United States. Based on the current Code
of Federal Regulations (cite), such wolves would be considered “endangered” anywhere in the
Southwest other than within the boundaries of the Mexican wolf non-essential experimental
population (see Figure x). Wolves entering into this zone from Mexico will be managed
pursuant to a management plan developed by the Service, in coordination with the states of
Arizona, New Mexico, and Texas, and Mexico (cite).

National Gray Wolf Recovery

Since the Service’s listing of the gray wolf in the coterminous United States in 1978 (43 FR
9607-9615, March 9, 1978), the Service has implemented three gray wolf recovery programs in
different regions of the country: the Western Great Lakes (Minnesota, Michigan, and Wisconsin,
administered by the Service’s Great Lakes, Big Rivers Region), the Northern Rocky Mountains
(Idaho, Montana, and Wyoming, administered by the Service’s Mountain-Prairie Region and
Pacific Region), and the Southwest (Arizona, New Mexico, Texas, Oklahoma, Mexico,
administered by the Service’s Southwest Region). Recovery plans were developed in each of
these areas to organize and prioritize recovery criteria and actions appropriate to the unique local
circumstances of the gray wolf. As such, the three gray wolf recovery programs have functioned
independently from one another since their inceptions. The Service also initiated a red wolf
(Canis rufus) recovery program in 1982 in the eastern United States that it continues to
implement today.

Progress toward recovery of gray wolves in the Western Great Lakes, Northern Rocky
Mountains, and Southwest has differed substantially between the regions over the last four
decades.
B. Status of the Species

(Note to Reviewer: This section should provide the species’ federal and state status, and FWS recovery priority status; the rest of the section should note things of importance related to species status.)

The gray wolf, *Canis lupus*, is currently listed as endangered with a recovery priority number of (X) (cite 1978 FR or update with reclassification if applicable). The Service originally listed the Mexican wolf subspecies in 1976 (41 FR 17736-17740, April 28, 1976). In 1978, this and several other gray wolf subspecies-level listings were subsumed into a species-level listing to protect the gray wolf species throughout its range in the coterminous United States and Mexico (43 FR 9607-9615, March 9, 1978). This reclassification provided a commitment that the Service would maintain a conservation focus on recognized gray wolf subspecies. The Service’s Mexican wolf program is conducted as a component of the agency’s gray wolf recovery obligations under the ESA.

In addition to its listed status under the ESA, the gray wolf is also protected under State wildlife statutes in the Southwest. The gray wolf is managed as a species of Special Concern and is identified as a Species of Greatest Conservation Need (endangered) in Arizona (Wildlife of Special Concern in Arizona 1996), and listed as state endangered in New Mexico (Wildlife Conservation Act, 17-2-37 through 17-2-46 NMSA 1978) and Texas (Texas Statute 31 T.A.P). Wolves are considered “protected wildlife” in Utah; they cannot be harvested unless the Wildlife Board establishes an open season for harvest (Utah Code Annotated, Title 23). The gray wolf is not included on Utah’s Sensitive Species List, as the species is not considered a resident in Utah at this time and because the ESA provides protection. Wolves are listed as endangered by Colorado (Colorado Revised Statues 33-2-105, “Nongame, Endangered, or Threatened Species Conservation Act”, Title 33). The gray wolf is not listed or protected by State law in Oklahoma.

C. Description

(Note to Reviewer: )

The gray wolf, *Canis lupus*, is a 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, Chambers et al. 20xx). The Mexican wolf, *C. l. baileyi*, is a subspecies of gray wolf (Nelson and Goldman 1929). Type localities of previously recognized subspecies are documented in Young and Goldman (1944). The type locality of *Canis lupus 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 (*Canis lupus baileyi*) (Nelson and Goldman 1929).

Gray wolves often vary considerably in size, although males typically weigh between 36-55 kg (80-120 lbs), are 1.5 to 2 m (5-6.5 ft) long from tip of nose to tip of tail, and 66 to 81 cm (26-32 in) high at the shoulder. Females are typically 15-20 percent smaller than males in weight and length (Mech 1970). The Mexican wolf is the smallest extant gray wolf in North America; adults weigh 23-41 kg (50-90 lbs) with a length of 1.5-1.8 m (5-6 ft) and height at shoulder of 63-81 cm (25-32 in) (Young and Goldman 1944, Brown 1983). Gray wolves exhibit significant variety in pelt color; the most commonly observed pelt is a mottled charcoal gray, but pelt color can range from white, cream, brown and red, to dark gray and black (Mech 1970). Individual wolves may exhibit any or all of these colors (Fuller 2004). Mexican wolves are typically a patchy black, brown to cinnamon, and cream color, with primarily light underparts (Brown 1983); solid black or white Mexican wolves do not exist as seen in other North American gray wolves (USFWS 2008).
D. Taxonomy and Distribution

Taxonomy

It is likely that all gray wolves evolved from the small, early canids that were widespread in North America and the Old World during the Pliocene, some 2 to 4.5 million years ago (Nowak 2003). The modern gray wolf, with the possible exception of the wolves of southeastern Canada and northeastern United States (Wilson et al. 2003), likely evolved in Eurasia from wolves that crossed into Eurasia from North America. A branch of these wolves (i.e., *Canis lupus*) then reinvaded North America during the middle Pleistocene (around 300,000 years ago) via the Bering Strait land bridge (Wayne et al. 1992, Brewster and Fritts 1995, Nowak 1995, Parsons 1996, Nowak 2003: Table 9.2). It is hypothesized that there were at least three waves of colonization from Eurasia each from different wolf lineages in response to changing glacial ice patterns and openings in the Bering Sea (Nowak 1995, Nowak 2003, Wayne and Vilá 2003). The Mexican wolf may represent the last surviving remnant of the initial wave of gray wolf migration (vonHoldt et al. 2011). Once in North America, wolves dispersed southward and eastward, gradually spreading across most of North America and Mexico (Nowak 2003).

*C. l. baileyi* has been recognized as a subspecies of gray wolf since its description by Nelson and Goldman (1929; Goldman 1937). Goldman (1944, pp. 389-636), provided the first comprehensive treatment of North American wolves; this gray wolf classification scheme was subsequently followed by Hall and Kelson (1959, Hall 1981). Since that time, gray wolf taxonomy has undergone substantial revision, including a major taxonomic revision in which the number of recognized gray wolf subspecies was reduced from 24 to 5 (Nowak 1995). However, the distinctiveness of *C. l. baileyi* and its recognition as a subspecies continues to be supported by both morphometric and genetic evidence. The Mexican wolf’s uniqueness is due at least in some part to its long term isolation in Mexico. What is not know is if the uniqueness was brought about by selective pressures related to ecological conditions or arose as a result of random genetic drift or both.
Three published studies of morphometric variation conclude that \textit{C. l. baileyi} is a morphologically distinct and valid subspecies. Bogan and Mehlhop (1983) analyzed 253 gray wolf skulls from southwestern North America using principal components analysis and discriminant function analysis. They found that \textit{C. l. baileyi} was one of the most distinct of the five subspecies of gray wolves in the Southwest recognized at that time. Hoffmeister (1986) conducted principal component analysis of 28 skulls, also recognizing \textit{C. l. baileyi} as a distinct southwestern subspecies. Nowak (1995) analyzed 580 skulls from across North America using discriminant function analysis. He concluded that \textit{C. l. baileyi} was one of only five distinct North American gray wolf subspecies that should continue to be recognized.

Genetic research provides additional validation of the recognition of \textit{C. l. baileyi} as a subspecies. Three studies demonstrate that Mexican wolves have unique genetic markers that distinguish them from other North American gray wolves. Hedrick et al. (1997; see also Garcia-Moreno et al. 1996; Wayne 19995) examined data for 20 microsatellite loci, from samples of Mexican wolves (N=38), northern gray wolves (N=55), coyotes (N=39), and dogs (N=27). They concluded that Mexican wolves were divergent and distinct from other sampled northern gray wolves, coyotes and dogs. They also determined that data from two captive groups of putative Mexican wolves were consistent with the conclusion that these animals were in fact Mexican wolves, and that these groups should be interbred with the captive certified lineage of Mexican wolves (now known as the McBride lineage) that had founded the captive breeding program. Leonard et al. (2005) examined mitochondrial DNA sequence data from 34 pre-extinction wolves collected from 1856 to 1916 from the historic ranges of \textit{C. l. baileyi} and \textit{C.l. nubilus}. They compared these data with sequence data collected from 96 wolves in North America and 303 wolves from Eurasia. They found that the historic wolves had the twice the diversity of modern wolves, and that two-thirds of the haplotypes were unique. They also found that haplotypes associated with Mexican wolves formed a unique southern clade distinct from that of other North American wolves. A clade is a taxonomic group that includes all individuals (in this case DNA haplotypes) that have descended from a common ancestor. VonHoldt et al. 2011 investigated the taxonomy of wolves and coyotes world-wide using 48,000 single nucleotide polymorphisms (SNPs) and found Mexican wolves to be the most genetically distinct group of New World gray wolves, again supporting the validity of the subspecies.
Most recently, Chambers et al. (2012, in review) reviewed the scientific literature related to *C. l. baileyi*’s classification as a subspecies and concluded that this subspecies’ recognition remains well-supported.

**Distribution**

Gray wolves were once abundant and widespread in North America. Before European settlement, the gray wolf ranged from the Canadian high arctic through the United States to central Mexico (Mech 1970, Wayne and Vilá 2003), with the exception of the southeastern United States which was occupied by the red wolf (U.S. Fish and Wildlife Service 1989). The scientific literature contains several descriptions of Mexican wolf historical range in Mexico and the United States that generally concur with one another but vary in their interpretation of the northern boundary of historical range.

Based on morphology (mostly skull and pelage characteristics) 24 subspecies of gray wolf have been described in North America (Hall and Kelson 1959). Five of these subspecies occurred in the southwestern United States and Mexico: *C. l. baileyi*, *C. l. mogollonensis*, *C. l. monstrabilis*, *C. l. nubilus*, and *C. l. youngi*. Original descriptions of Mexican wolf range by Young and Goldman (1944) and Hall and Kelson (1959) delineated range for each of *C. l. baileyi*, *C.l. monstrabilis*, and *C.l. mogollonensis* (Figure ). Hall (1981) described the range of *C. l. baileyi* as including only a small portion of extreme southwestern New Mexico and southeastern Arizona. Bogan and Mehlhop (1980, 1983) generally combined *C. l. mogollonensis* and *C. l. monstrabilis* with *C. l. baileyi*, thereby extending *C. l. baileyi*’s range north to central Arizona and central New Mexico (Figure ) through the area that Goldman had identified as an intergrade zone with an abrupt transition from *baileyi* to *mogollensis*. Bogan and Mehlup’s analysis did not indicate a sharp transition zone between *baileyi* and *mogollensis*, rather the wide overlap between the two subspecies led them to synonymize *baileyi* and *mogollensis*. The Service adopted the findings of Bogan and Mehlhop in the 1982 Mexican Wolf Recovery Plan, thus supporting reintroduction of *C. l. baileyi* north of *C. l. baileyi*’s range as originally conceived by Young and Goldman (1944) and Hall and Kelson (1959). Subsequently, Hoffmeister (1986) added to the taxonomic confusion by regarding *C. l. mogollonensis* as a synonym of *C. l. youngi* rather than as a synonym of *C. l. baileyi*. 
Brown (1983) stated that in southern Arizona, Mexican wolves inhabited the Santa Rita, Tumacacori, Atascosa-Pajarito, Patagonia, Chiricahua, Huachuca, Pinaleno, and Catalina mountains, west to the Baboquivaris and east into New Mexico in the late 19th and early 20th centuries. In central Arizona, he described a mixing ground where Mexican wolves and several formerly recognized subspecies of gray wolf were interspersed (Brown 1983). He also stated that Mexican wolves and up to four formerly recognized subspecies were present throughout New Mexico, with the exception of low desert areas, and were documented as numerous or persisting in areas including the Mogollon, Elk, Tularosa, Diablo and Pinos Altos mountains, the Black Range, Datil, Gallinas, San Mateo, Mount Taylor, Animas, and Sacramento mountains (Brown 1983). Brown (1983) described Mexican wolves frequenting the borderlands between Mexico and the US, and claimed that they were abundant in the Sierra Madre and the altiplano (high plains) of Mexico.

In 1995, Nowak proposed a major shift from the identification of 24 subspecies of North American gray wolves to only 5 subspecies (1995), recognizing *C. l. baileyi* as a subspecies, but grouping *C. l. mogollonensis* and *C. l. monstrabilis* with *C. l. nubilus*, providing a more restrictive range for *C. l. baileyi* than Bogan and Mehlhop (Figure 1). It is important to note that Nowak (1995) agreed with Bogan and Mehlhop (1983) that the range of *C. l. mogollonensis* in Arizona was a transition zone where *C. l. baileyi* intergraded with more northern *C. lupus*. Parsons (1996) added knowledge of dispersal patterns to the historic range of *C. l. baileyi* proposed by Nowak (1995) and concluded that historically Mexican wolves ranged as far north as central New Mexico and east-central Arizona (Figure 1). In 1996, the Service adopted the historical range proposed by Parsons (1996) and included it in the final EIS for the reintroduction of Mexican wolves into the BRWRA (SUFWS 1996). This version of historical range was more restrictive than that defined by Bogan and Mehlhop (1908, 1983) but more expansive than that defined by Nowak (1995) due to the inclusion of a 200-mile northward extension of Nowak’s (1995) range to account for contemporary knowledge of wolf movements (USFWS 1996). After conducting an exhaustive review of molecular genetics and morphological data, Chambers et al. (200xx) supported the Service’s decision to adopt the findings of Bogsan and Mehlhop (1980, 1983) in the 1982 Mexican wolf recovery plan.
Evidence of historical gene flow across the various surmised boundaries of *C. l. baileyi* suggests that Mexican wolves likely intergraded with other gray wolves in a wide zone at the northern extent of their range. Wolves’ dispersal behavior as revealed by numerous telemetric studies (Mech and Biotani 2003) has long led to the contemporary conclusion that there were large zones of intergradation across the North American landscape (Young and Goldman 1944, Mech 1970, Brewster and Fritts 1995) and indicates that the periphery of Mexican wolf historical range occurred somewhere within such a zone in the southwestern U.S. These zones of intergradation allowed for considerable genetic exchange between wolf subspecies (Leonard et al. 2005, Chambers et al. 20xx). On this matter Mech (1970) wrote: “Wherever subspecies meet, their characters tend to blend as a result of interbreeding, or intergradation …”. Analyses of historic specimens (Leonard et al. 2004) demonstrate that the gray wolves that inhabited northern Arizona, Utah, northern New Mexico, and southern and central Colorado had genetic markers associated with the Mexican wolf. This research shows that within the time period that the historic specimens were collected (1856-1916) a mitochondrial DNA haplotype characteristic of northern wolves was found as far south as Arizona, and individuals with southern clade haplotypes (associated with the Mexican wolf) occurred as far north as northern Utah and Nebraska (Leonard et al. 2005).

A few historical reports of Mexican wolf locations indicate that wolves from one area began to occupy habitat recently vacated due to predator eradication efforts. Scudder (1977) reported on two male Mexican wolves collected in 1970 in Brewster County, Texas and concluded that *C. l. baileyi* “was a late comer to Texas, probably moving in as *C. l. monstrabilis* was eliminated in the Trans-Pecos region.” Gish (1977) thought that *C. l. baileyi* increasingly moved into Arizona from Mexico and southwestern New Mexico as other subspecies were eliminated in Arizona. Nowak (1995) noted that a male Mexican wolf taken in 1957 near Concho, Arizona, was well within the original range of *C. l. mogollonensis* (subsequently synomized by Nowak with *nubilis*). By 2002, Nowak (personal communication with Mike Phillips) had concluded that the two animals collected from Brewster County, Texas and the one animal collected near Concho, Arizona represented a 160 km northward extension of the historical range that he had recommended for the subspecies in 1995.
E. Historical Population Trends

Population estimates of gray wolves, and specifically Mexican wolves, prior to the advent of extermination efforts in the late 1800s and early to mid-1900s are not available for the Southwest or Mexico. This is due primarily to a lack of available data on wolf abundance, but also in some part to difficulty in interpreting anecdotal accounts of wolf abundance. Brown (1983) summarized historical distribution records for the wolf from McBride (1980) and other sources that repeatedly indicated, at least for the southwestern United States, that wolves were common. His map (Brown 1983: 10) shows most records in the southwestern United States as being from the Blue Range and the Animas region of New Mexico. The high number of wolf bounties collected in southern Colorado and northern New Mexico suggest that wolves were abundant in that area as well (Robinson 2005). Wolves appear to have been less numerous in northern Arizona during this time period, with only 30 wolves reported killed on or near the North Kaibab between 1907 and 1926 (Russo 1964). Young and Goldman (1944) stated that in 1916-1918 the wolf was fairly numerous in Sonora, Chihuahua, and Coahuila. Brown (1983) described the Sierra Madre Occidental in the Mexican states of Sonora, Chihuahua, and Durango as a stronghold for the Mexican wolf. Leonard et al. (2005) analyzed mitochondrial DNA sequences of 34 pre-extermination wolves and found that they had more than twice the diversity of their modern conspecifics, implying a historic population of several hundred thousand wolves in the western U.S. and Mexico.

The status of the Mexican wolf declined rapidly to near extinction during the 1900’s. The intensification of human settlement, agriculture, and livestock operations in the Southwest in the 1800’s led to human persecution of wolves due to wolf depredation of livestock (Brown 1983, Robinson 2005). Federal control programs and extermination campaigns, coupled with habitat alteration resulting from settlement patterns, led to the near extinction of the gray wolf in the Southwest by the early 1900s (Brown 1983). By 1925, poisoning, hunting, and trapping efforts had drastically reduced wolf populations in all but a few remote areas of the southwestern United States, and control efforts shifted to wolves in the borderlands between the United States and Mexico (Brown 1983). Bednarz (1988) estimated that breeding populations of Mexican wolves were extirpated from the United States by 1942. The use of increasingly effective poisons and
trapping techniques during the 1950s and 1960s eliminated remaining wolves north of the border, although occasional reports of wolves crossing into the United States from Mexico persisted into the 1960s. By the time of Leopold (1959), the formerly continuous wolf distribution in northern Mexico had contracted to encompass the Sierra Madre Occidental in Chihuahua, Sonora, and Durango, as well as a disjunct population in western Coahuila (from the Sierra del Carmen westward). Leopold (1959) found conflicting reports on the status of the Coahuila population and stated that wolves were likely less abundant there than in the Sierra Madre Occidental. McBride (1980) surveyed the distribution of the last wild populations of Mexican wolves. He mapped three general areas where wolves were recorded as still present in the Sierra Madre Occidental: 1) northern Chihuahua/Sonora border (at least eight wolves); 2) western Durango (at least 20 wolves in two areas); and 3) a small area in southern Zacatecas. McBride (1980) believed that wolves did not occur in northern and eastern Coahuila despite the existence of what he judged to be excellent wolf habitat there. Although occasional anecdotal reports have been made during the last three decades that a few wild wolves still inhabit forested areas in Mexico, no publicly available documented verification exists.
F. Current Population Trends and Distribution

(Note to Reviewer: The text below has been adapted from the CA. Entire section needs to be updated through 2012 annual reports as available. Needs graphs/visuals.)

United States

The population trends and distribution of the current wild nonessential experimental Mexican wolf population in the BRWRA are well documented, as monitoring of the population has been ongoing since its inception in 1998. Between one and 21 wolves have been released into the the BRWRA every year since 1998, with the exception of 2005, 2007, 2009, 2010 (update with 2011-2012) in which no wolves were released (cite online stats or 2011 annual report). As of December 31, 2012, the Blue Range population consisted of a minimum of xx wolves and xx breeding pairs (cite end of year count/annual report). The growth of the population from its initial end-of-year count of four wolves in 1998 to a minimum of xx wolves today is attributed to continued releases and to natural reproduction (AMOC and IFT: TC-11).

The growth of the Blue Range population has been more modest than expected based on the agency’s initial predictions (cite FEIS). Between 1998 and 2003, the Blue Range population tracked fairly closely to FEIS projections for population count, reaching (a minimum of) 55 wolves in 2003, but was consistently below the FEIS’s estimated number of breeding pairs. The population decreased significantly in 2004-2005 and then rebounded to a high of 59 wolves in 2006, the year in which the FEIS projected the population target of 100 would be met. Between 2007-2011, the population has fluctuated between a minimum count of 42-xx wolves and two (2011?) to four breeding pairs. Thus, the population has remained around the halfway point of the population target since 2003, with fewer breeding pairs than estimated (cite USFWS: Mexican Wolf Blue Range Reintroduction Project Statistics or 2011 annual report) (Figure/s).

BRWRA Project Evaluation
Evaluation of the BRWRA reintroduction project has been on-going since its inception to identify biological and regulatory issues affecting its progress. Initial observation of the population from 1998-2000 documented that most of the captive-bred wolves that were released into the BRWRA were successfully establishing home ranges, breeding, and killing native prey, alleviating some apprehension over the use of captive born wolves (Brown and Parsons 2001). Challenges for the reintroduction, as seen after its first few years, included the intense management response necessary to address wolves dispersing outside of the BRWRA (which necessitated their removal due to the regulations established in the 1998 Final Rule), wolf-livestock interactions, the possible consequences of limited genetic diversity, and sociopolitical acceptance of the reintroduction (Brown and Parsons 2001), as evidenced by a very high level of illegal killing.

Two formal agency reviews of the reintroduction project were conducted at three and five years after its inception to determine whether the reintroduction should continue, or be modified or terminated, as stipulated in the Final Rule (63 FR 1752-1772, January 12, 1998). The technical component of the 3-Year Review, commonly referred to as the Paquet Report, assessed the progress of the reintroduction from its inception to 2001. The review was conducted by four independent researchers under contract to the Service: Paul Paquet, John Vucetich, Leah Vucetich, and Michael Phillips. Paquet et al. (2001) found that continuation of the population’s documented reproduction and survival rates would result in slower progress achieving the population target of at least 100 wolves than estimated during the planning of the reintroduction. They concluded that several factors were ultimately hindering the biological success of the project: 1) the small size of the Primary Recovery Zone of the BRWRA, which limited the establishment phase of the project by constraining the number and location of wolves that could be released; 2) the requirement that wolves stay within the BRWRA, which did not allow for natural dispersal movements; and, 3) the Service’s objective to establish a population of at least 100 wolves, which was not deemed an adequate size for long-term viability (Paquet et al. 2001:60-61). To address these issues, Paquet et al. (2001) recommended the Service initiate a recovery team to revise the 1982 Mexican Wolf Recovery Plan, modify the Final Rule to allow initial releases into the Gila National Forest, allow wolves to establish territories outside of the BRWRA, and require livestock operators on public lands to take some responsibility for managing/Removing carcasses to reduce the likelihood of wolves becoming habituated to feeding on livestock.
The 5-Year Review evaluated the reintroduction from 1998 to 2003, but also included analysis of some aspects of the project through 2005. This review was conducted by the Mexican Wolf Adaptive Management Oversight Committee (AMOC) and the Interagency Field Team, the multi-agency group leading the project and the multi-agency staff in charge of day to day operations, respectively. In the Technical Component of the Review, which addressed the biological progress of the project, AMOC concluded that at least until 2003, progress toward establishment of a population of at least 100 wolves had generally proceeded in line with projections from the FEIS. However, they also recognized that guidelines in the Final Rule requiring removal of wolves that establish home ranges outside of the BRWRA, or at landowner’s request, are contrary to normal wolf movements, resulting in higher levels of wolf releases and removals than projected in the FEIS. Further, they found that wolves spending a greater proportion of their lives in the wild are more likely to be successful, and therefore wolves ought to be translocated, rather than permanently removed, after their first removal event except in extreme situations (AMOC and IFT: TC-24). The review recommended further analysis of potential modification of the Final Rule, including expansion of external boundaries, expansion of a recovery zone designated for release of wolves, additional provisions for harassment and take of wolves, creation of an incentives program to mitigate wolf nuisance and livestock issues, analysis of social and economic impacts associated with any MWEPA modifications under consideration, and provisions for another review of the reintroduction project in 2009-2010 (AMOC and IFT: ARC). Following the completion of the 5-Year Review in 2005, the Service determined that the reintroduction should continue, and acknowledged that modifications to the Final Rule were necessary (USFWS 2006b).

The status of the reintroduction project is also documented and evaluated in annual Interagency Field team reports. Since the 5-Year Review, FWS and partner agencies have acknowledged in these reports that the population is lagging behind the projections of the FEIS, citing the high mortality and removal rates of the population as responsible for this trend (USFWS 2005:27) and concluding that changes in management are needed to support population growth (AGFD et al. 2007:13, AGFD et al. 2008).
In 2010, the Service contracted with a former employee, Tracy Melbihess, to develop an assessment of the reintroduction project within the context of gray wolf recovery. The Mexican Wolf Conservation Assessment found that (…wild population faces a number of challenges; risk of extinction averted due to captive breeding program but wild population is susceptible to failure due to small size, lack of redundancy, cumulative effect of stressors/threats, etc.).

Mexico

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. Officials released five captive-bred Mexican wolves into the San Luis Mountains in Sonora just south of the US-Mexico border (SEMARNAT e-press release, 2011). As of February 2012, four of the five released animals were confirmed dead due to ingestion of illegal poison (USFWS, our files). One wolf remains near the area in which it was released (USFWS, our files). Additional releases are tentatively planned for 2012-2013 to continue efforts to establish a wild population.
G. Life History

(Note to Reviewer: This section is copied directly from CA. Needs updating with 2009/2010/2011 annual reports.)

Basic descriptive life history information is well documented for gray wolves, although less so for the Mexican wolf since the subspecies had been extirpated before useful studies could be conducted. What we have learned in the recent past from captive breeding programs and the BRWRA project is that the Mexican wolf does not manifest any particularly unique life history strategies compared to other gray wolf subspecies.

In the wild, gray wolves typically live 4 to 5 years, although they can reach 13 years (Mech 1988). They reach sexual maturity at two years of age (Mech 1970). Wolves have one reproductive cycle per year, and females are capable of producing a litter of pups, usually four to six, each year (Mech 1970). Litters are born in spring in a den or burrow that the pack digs (Mech 1970, Packard 2003). Pups weigh about one pound (0.5 kg) at birth (Mech 1991), and remain inside the den for at least four weeks, during which time their eyes open and the animals learn to walk (Packard 2003). Pup mortality during the denning period is difficult to document due to lack of access to den sites (Fuller et al. 2003).

Documentation in the BRWRA of wild-born wolves breeding and raising pups has been made for 11 years in a row (2001-2012), and in 2012 approximately x percent of wolves in the Blue Range population were wild-born (cite). In the wild, Mexican wolf pups are generally born between early April and early May (AMOC and IFT 2005: TC-6). Pup counts are conducted opportunistically after the denning period, but prior to October, at which point Mexican wolf pups are difficult to distinguish from adults (AMOC and IFT 2005: TC-6). Average litter size has been estimated at 3.26 (n = 95) pups in the reintroduced population (USFWS files), which is noticeably smaller than Mexican wolf litters in captivity (4.6 pups/litter) (AMOC and IFT: TC-17-18), gray wolf litters elsewhere (AMOC and IFT: TC-12, see Fuller et al. 2003), or the historical litter sizes of wild Mexican wolves reported by McBride (4.5 pups) (1980). Pup counts, however, are documented at some substantial time from whelping (post den emergence), thus some mortality would be expected prior to initial wild counts, and may explain the difference between the...
number of pups counted in the wild and captivity. Note that red wolf litter sizes (2.8 pups/litter) during their initial restoration were similar (Phillips et al. 2003).

Recent analyses of the captive and reintroduced populations suggest the low litter sizes observed in the reintroduced population may be influenced by the level of inbreeding (Fredrickson et al. 2007). In the Blue Range population, the number of pups observed in packs producing cross-lineage pups (those descended from outbred F1 wolves created by the merging of the founding lineages) was 52 percent greater than packs producing pure McBride wolves, indicating that inbreeding may be negatively affecting litter sizes because fitness was greatest in the less-inbred cross-lineage wolves (Fredrickson et al. 2007). Several other factors may also explain small litter sizes in the reintroduced population due to early pup mortality: 1) wolves may be limited seasonally by the amount of vulnerable prey; 2) litter sizes may be an historical adaptation to the environment; or, 3) wolves released from captivity may be less capable of exploiting vulnerable prey, potentially further affected by frequent management that decreases their ability to fully exploit their home ranges (AMOC and IFT: TC-18). Additionally, cryptic poaching of pups may be occurring before litters are censused (Liberg et al. 2012). Mexican wolf females from the wild population brought into captivity before or shortly after whelping pups had an average litter size matching that of the captive population (4.6 pups/litter, n = 6), suggesting that more Mexican wolf pups are born than are observed in the wild. Since litter size at birth and early pup mortality are unknown (AMOC and IFT 2005: TC-18), either could explain the small number of pups observed during pup counts.

During the first few months of life, gray wolf pups are gradually weaned from their parents, transitioning from nursing to feeding on semi-liquid regurgitated food provided by adult wolves at the den site, to consuming solid food. During this period, pups grow rapidly, likely due to high prey availability during summer months and pup survival is typically highest in those areas of high prey availability (Fuller et al. 2003). Wolves are referred to as pups up to one year of age and yearlings when between one and two years of age (Packard 2003).

Pups begin hunting with adults when 4 to 10 months old (Packard 2003), remaining with their family until they disperse to establish a new territory. Wolves exploit their prey by hunting in
Adult wolves typically experience a feast or famine existence, gorging on freshly killed prey after successful hunts and subsequently able to survive for days with low food intake (Peterson and Ciucci 2003). Wolves buffer these extremes of food availability by burying food for later consumption, scavenging carcasses, and have the ability to use a variety of prey and habitat types (Peterson and Ciucci 2003, Mech 1991, Weaver et al. 1996).

Wolf survival rates vary seasonally, as shifts in prey availability occur (Fuller et al. 2003). Annual survival rate of yearling and adult gray wolves is estimated at 0.55 to 0.86 (Fuller et al. 2003: table 6.6). Documented causes of death include starvation, disease, human-caused mortality, and interactions with other wolves or predators (Ballard et al. 2003, Fuller et al. 2003). In the Blue Range population, causes of mortality have been largely human-related, including vehicle collision, illegal gunshot, lethal control, and capture complications, although dehydration, brain tumor, infection, snakebite, disease, mountain lion attack, and unknown causes have also been documented (AMOC and IFT 2005: TC-12). Between 1998 and December 31, 2011, illegal gunshot (43 of 88 deaths) and vehicle collision (14 of 68 deaths) were the two most prevalent causes of death (USFWS 2012: Population Statistics). Wolf population can compensate to a degree for relatively high mortality rates by means of increased reproduction, but current mortality rates in the Blue Range may exceed this level (Weaver et al. 1996, Oakleaf in prep., Vucetich et al. in review). The average annual survival rate of the Blue Range population between YEAR-YEAR is xx (or a corresponding failure rate of xx, which includes both mortality and management removal of wolves), a rate considered too low for natural population growth (cite).

Wolves are social animals that live in hierarchical families, referred to as packs. Wolf packs consist of a breeding pair (formerly “alpha” (Packard 2003)) and their subordinate pup and yearling offspring (Mech 1970) although many variations of this typical pack structure have been observed (Mech and Boitani 2003). The minimum number of breeding pairs observed in the Blue Range population is documented by the IFT in the annual end-of-year population count. “Breeding pair” as defined in the Final Rule as, “…an adult male and an adult female wolf that have produced at least two pups during the previous breeding season that survived until December 31 of the year of their birth” (50 CFR 17.84(k)(15). Over the span of the
reintroduction, the number of breeding pairs meeting the Final Rule definition has ranged from zero to seven pairs (USFWS 2012: Population Statistics). During two years, the Service interpreted the Final Rule to include any adult male and adult female associated with any two surviving pups at the end of the year, even if the adult pair did not breed (e.g., one member of a breeding pair is replaced by a new wolf that raises pups born to the former pair). This interpretation resulted in the number of breeding pairs counted being higher than if only the pairs that produced pups that survived until the end of the year were counted (AGFD et al. 2006, AGFD et al. 2007). Additional breeding events occur within the population, but do not meet the Final Rule definition for a breeding pair, making the original definition of “breeding pair” conservative. For example, in 2008, wild-born, wild-conceived pups were produced by seven packs (AGFD et al. 2008), but only XX of these packs had at least two surviving pups, and their biological parents, at the end of the year. Pack size in the Blue Range population between 1998 and 2012 ranged from 2 to x (mean = x) wolves ( ). Bednarz (1988) estimated historic Mexican wolf pack size as two to eight animals. Brown (1983) reported that Mexican wolf packs typically included fewer than 6 wolves. A wolf pack is typically some variation on a mated pair and offspring, sometimes of varying ages (Mech and Boitani 2003).

To secure food, water, and shelter, a pack establishes an area, or territory, that is maintained through scent-marking (Peters and Mech 1975), howling (Harrington and Mech 1983), and direct defense (Mech and Boitani 2003). Wolf packs move within their respective territories as they forage and defend their territories (Mech and Boitani 2003). Wolves’ daily movements vary in response to the distribution, abundance, and availability of prey. Seasonal movements vary as well: while rearing pups, adult wolves leave the den, returning throughout the day to care for their young. When pups are old enough to travel with adults, packs become nomadic, traveling throughout the territory, sometimes returning to rendezvous sites (Mech and Boitani 2003). Daily pack movements of less than 10 miles per day to over 40 miles in a 24-hour period have been documented in different wolf populations in different seasons (see Mech and Boitani 2003).

In addition to movements within territories, wolf travels typically include dispersal movements (Mech and Boitani 2003). An individual wolf, or rarely a group, will disperse from its natal pack in search of vacant habitat or a mate; dispersers are typically younger wolves of 9 to 36 months
of age (Packard 2003). A yearling might make several dispersal forays before completely
disassociating from the family (Messier 1985). These dispersals may be short trips to a
neighboring territory, or may be a long journey to find a mate and establish a territory. Dispersal
of more than 655 mi (1092 km) has been documented in northern populations (Wabakken et al.
movements) were documented in the Blue Range population, with an average distance of xx mi
+/- x mi (x km +/- x km). This is likely an under-representation of true movement distances, due
to management response required by the nonessential experimental-population designation when
wolves disperse outside of the BRWRA. Wolves in the BRWRA primarily dispersed
northwestward or southeastward, in the direction that mountain ranges lie within the area
(AMOC and IFT 2005: TC-13).

Dispersing gray wolves usually travel alone and tend to have a high risk of mortality (Fuller et al.
2003). In the Blue Range population, x known mortalities were documented in association with
dispersal between 1998-2012 (including natural dispersal and movements directly after release to
the wild) (USFWS our files). Wolves that disperse and locate a mate and an unoccupied patch of
Wolves, historically the most widely distributed large terrestrial mammal, can be found throughout much of the Northern Hemisphere where sufficient ungulate prey exists and the risk of being killed by humans is not excessive (Fuller et al. 2003). These two factors, prey biomass and human-associated mortality risk (and the resultant variation in wolf fecundity rate and survival rate, respectively) define the extent of suitable habitat for the Mexican wolf and other wolf subspecies (Fuller et al. 2003, Carroll et al. 2006, Mladenoff et al. 2009).

The gray wolf hunts in packs, primarily pursuing medium to large hoofed mammals, potentially supplementing its diet with small mammals (Mech 1970). Wolf density is positively correlated to the amount of ungulate biomass available and the vulnerability of ungulates to predation (Fuller et al. 2003).

Although vegetation and climate vary greatly across the range of the Mexican wolf, the region as a whole is generally more arid than regions of North America such as the Northern Rocky Mountains (NRM) and the western Great Lakes states to which wolves have previously been recovered (Brown 1983). Because of the semi-arid climate, primary productivity in the southwest is generally lower than in these areas (Carroll et al. 2006). In consequence, prey species available to Mexican wolves may be smaller in size, have lower population growth rates, exist at lower densities, and exhibit patchy distributions.

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 1219-1524 m (4,500-5,000 ft) (Brown 1983). 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 1983). Wolves traveled between suitable habitats using riparian corridors, and later, roads or trails (Brown 1983). Elevation in the BRWRA ranges from 1219-3353 m (4,000-11,000 ft), ranging from semi-desert grasslands to conifer forests, with ponderosa forests dominating the area in between (USFWS 1996).

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 (mi²) (200-400 square kilometers (km²), 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 (that is, mountainous terrain that included areas of unsuitable lowland habitat) and lower prey densities associated with the arid environment. Between 1998 and 2010, home range size of 80 denning packs in the Blue Range population averaged 182 mi² +/- 24 mi² (464 km² +/- 298 km² (179 mi² +/- 115 mi²) (John Oakleaf, pers. comm., 2012). The average home range size for 22 non-denning packs during the same time period was 330 mi² +/- 272 mi² (855 km² +/- 704 km²). Pack home range size for denning packs has remained remarkably consistent since the beginning of this wolf recovery effort.

Wolves and Prey

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. 1993, Messier 1994, Ballard et al. 2001). Ungulates employ a variety of defenses against predation (e.g., aggression, altered habitat use, gregariousness, migration) (MacNulty et al. 2007), and wolves are frequently unsuccessful in their attempts to capture prey (Mech and Peterson 2003, Smith et al. 2004). Generally, wolves tend to kill less-fit prey (e.g., young, old, injured) that are predisposed to predation (Mech and Peterson 2003, Smith and Bangs 2009). Wolves may reduce prey density, especially during periods of adverse weather or habitat conditions, but only in extreme circumstances have they
been documented exterminating a prey population, and then only in a relatively small area (Mech and Peterson 2003).

Historically, Mexican wolves were believed to have preyed upon white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), collared peccaries (javelina) (*Pecari tajacu*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), jackrabbits (*Lepus spp.*), cottontails (*Sylvilagus spp.*), and small rodents (Parsons and Nicholoupoulos 1995). White-tailed deer and mule deer were believed to be the primary sources of prey (Brown 1983, Bednarz 1988, Bailey 1931, Leopold 1959), but Mexican wolves may have consumed more vegetative material (Brown 1983:134) and smaller animals as do coyotes in southern latitudes (Hidalgo-Mihart et al. 2001).

Wolves are highly-adaptable prey generalists and available evidence suggests that Mexican wolves can efficiently capture a range of ungulate prey species of widely varying size. Elk have comprised the bulk of the biomass in the diet of wolves reintroduced to the Blue Range area of Arizona (Paquet et al. 2001, Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009a), and elk kill rates by Mexican wolves are similar to those for northern wolf subspecies (Oakleaf et al. in prep.). Data from the Blue Range indicate that elk are the preferred prey (Brown and Parsons 2001, Reed et al. 2006, Merkle et al. 2009a), with wolves showing a preference for calf elk over adult elk (AMOC and IFT 2005: TC-14). AMOC and IFT (2005) reported that wolf activity in the BRWRA appears to be located in areas of high elk density. Mexican wolves are also feeding on adult and fawn deer, cattle, small mammals, and occasionally birds (Reed et al. 2006). The difference between historical versus current prey preference is probably due to the lack of elk in historical Mexican wolf range except for very low densities at the northern periphery in central Arizona and New Mexico and yet elk are very common in the current Mexican wolf range in the BRWRA (AMOC and IFT: TC-1). Although white-tailed and mule deer are present, the Mexican wolves' preference for elk may be related to the gregariousness, relative abundance, naïveté, and consistent habitat use by elk. There is also a possibility some of the dominance of elk in their diet was skewed by data collection methods of analyzing only large scats in order to minimize the probability of including coyote scat (Reed et al. 2006, Carrera et al. 2008).
Mexican wolf predation rates are well within the range of other wolf populations (Mech and Peterson 2003) suggesting no unusual difficulty killing elk. Given that wolves often hunt in groups, multiple wolves can be involved in attacks on elk (MacNulty et al. 2012) which ameliorates the effect of the elk’s large size. Further, the size ratio of wolf to elk in the Blue Range (1:11) is no greater than wolves preying on bull bison in Yellowstone National Park (1:20) and wolves preying on bull moose (1:10) on Isle Royale suggesting that size of prey is not a good predictor of hunting success. Considering all the prey of Mexican wolves, they are less variable in size compared to other multi-prey wolf systems in North America (Mech and Peterson 2003). Studies of wolf hunting behavior in Yellowstone National Park also indicate that wolf hunting strategy is plastic and capable of adjusting for variously sized prey (MacNulty 2007). In fact, virtually all wolves in a particular location (e.g. population) prey on more than one species of prey and wolf hunting strategies reflect this variability. For example, in Yellowstone one pack successfully preys on a range of species from deer to bison (Smith et al. 2004). Wolves have adapted their hunting strategy by varying age, size (males vs. females), behavior, and hunting group size all within one pack depending on the situation (Kaffmann et al. 2007) and species of prey indicating a wide adaptability to successfully capture a range of prey types (MacNulty et al. 2009a, MacNulty et al. 2009b, MacNulty et al. 2012). Deer and elk typically flee in the presence of a large predator, whereas bison typically stand their ground causing wolves to respond differently. For Mexican wolves, their primary prey, deer and elk, behave similarly making adjustment to each easier compared to other wolf populations with diverse prey. In short, while the historical literature indicates that Mexican wolves preyed primarily on deer (USFWS 1982, Brown 1983, USFWS 1996), current research shows successful adaptation to elk with normal to high consumption rates and even a preference for elk when they are sympatric with deer.

Kill rates of individual 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). Prior to the Blue Range reintroduction, it was estimated that Mexican wolves would need to kill 1 mule deer every 12-13 days (29/year) or 1 white-tailed deer every 8-9 days (43/year, Johnson et al. 1992). Stark et al. (in prep) used clusters of wolf GPS locations to estimate kill rates of Mexican wolves in the BRWRA and estimated a kill rate of 6.53 kg/wolf/day in early winter (assuming 68% of an elk is edible biomass), and a 9.42 kg/wolf/day consumption rate in late winter (March), for an overall winter estimate of 8.59 kg/wolf/day. Most studies in other wolf/ungulate systems show a lower kill rate in the summer (perhaps only 70% of winter kill rates) due to a higher diversity of food items available at that time (Messier 1994, Metz et al. 2012). Using kill rates from Stark et al. (in prep.), an independent analysis by the SPS estimated each Mexican wolf would kill 19.9 elk per year if feeding on only elk. Assuming elk comprise 80% of the biomass consumed and deer comprise 8%, each wolf would annually kill approximately 16 and 6.5-11 elk and deer (both species), respectively.

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). Vegetative communities in the arid southwestern forests are not as lush and productive as similar-looking communities in the Rocky Mountains. The lower productivity of the vegetative community influences productivity upwards through several trophic levels resulting in lower inherent herbivore reproductive rates in the Southwest than in their northern counterparts (Heffelfinger 2006:156). In addition, recruitment differs between southwestern and northern ungulate populations because winter precipitation comes as rain rather than snow. Lack of widespread winterkill of ungulates means that lower recruitment is needed to sustain a stable population compared to northern ungulate populations. Southwestern deer herds require 35-50 fawns per 100 does to remain stable (Heffelfinger 2006:158), while those in the northern Rocky Mountains require 66: fawns 100 does for population maintenance (Unsworth et al. 1999). As in deer, southwestern elk seem to have adopted a life history strategy of lower overall recruitment and higher survival.

Similarly, predator-prey dynamics may differ in the Southwest compared to other systems… 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 kept mostly below a fluctuating carrying capacity via chronically low recruitment. 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). However, Heffelfinger (1999) pointed out that “… time and time again, deer research in Arizona has found that habitat conditions are what primarily drive deer populations up and down, with other factors like overgrazing, habitat change, predation, poaching, and human encroachment playing secondary roles.” As in deer, southwestern elk have a similar life history strategy of lower overall recruitment and higher survival. With a high adult cow elk survival (90-97%, Ballard et al. 2000), there is little room for existing sources of mortality to compensate for additional sources of mortality, except for those herd units and time periods that female elk are being harvested to manage the population.

Wolves may also impact 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. In the Southwest, one should expect that increasing numbers of wolves as a result of recovery, along with other carnivores, could have impacts on biodiversity and ecosystem processes. This may occur through two mechanisms: a behavioral mediated or numeric response on prey – or both (Terbough et al. 1999). Such 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, Ripple and Beschta 2011). Such a trophic cascade was caused by wolf effects on elk (numeric/behavioral or both is yet to be determined) which caused a response in willow which in turn created habitat and forage for songbirds and beavers (Hebblewhite and Smith 2010, Baril et al. 2011). Impacts like this may be an outcome of wolf recovery in the Southwest. However, wolves have yet to have a demonstrable trophic cascade effect in the BRWRA likely due to the low densities of Mexican wolves in the area (Beschta and Ripple 2010).

Livestock are another widely available potential source of prey for Mexican wolves in the BRWRA. Historically, records of Mexican wolf exploitation of livestock were prominent (Young and Goldman 1944, McBride 1980, Brown 1983, Bednarz 1988); this is not surprising

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given that such reports were made by government and private wolf control agents whose jobs focused on depredating animals (and see Gipson and Ballard 1998, Gipson et al. 1998). When the reintroduction began, sheep and cattle grazing were permitted on approximately 69 percent of the BRWRA, with about half of the allotments being grazed year-round (USFWS 1996). Program projections predicted that at the population objective of at least 100 Mexican wolves, depredation levels of 1-34 cattle per year would occur (USFWS 1996). Between 1998 and 2012, x confirmed cattle depredations were documented, or an average depredation rate of x cattle per 100 wolves per year. This depredation rate may represent an underestimate due to incomplete detection of wolf-killed cattle, which has been demonstrated in XXXX(Oakleaf et al. 2003, Breck et al. 2011). Between 1998 and 2012, xx wolves were removed as a result of xxx confirmed depredations (xxx cattle, xx sheep, and x horses) (USFWS our files), or one wolf removal per xx confirmed depredations.

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, wolves may interact with other wolves, coyotes, mountain lions (Puma concolor), and black bears (Ursus americanus) (AMOC and IFT 2005: TC-3). Aggression among wolves is typically associated with food shortages as wolves venture into neighboring territories to locate prey (Mech and Boitani 2003). Observations of wolf and coyote interactions in other regions have documented decreased coyote density in areas of high wolf density and that wolves occasionally kill or eliminate coyotes (Ballard et al. 2003, Merke et al. 2009). A current study of Mexican wolf and coyote diets in the BRWRA shows that wolves and coyotes have similar diets consisting mainly of elk (Carrera et al. 2008). It is not known whether coyotes are scavenging elk carcasses from wolf kills (cite?) or preying on elk directly (Gese et al. 1994), although both behaviors have been documented in other areas. It is hypothesized that this shared source of prey may cause competition between wolves and coyotes that will result in wolves killing coyotes when coyotes visit wolf kills to scavenge (Carrera et al. 2008), as has been documented in Yellowstone National Park (Merkle et al. 2009b).
Bednarz (1988) hypothesized that wolves and mountain lions interacted historically, given their overlapping habitats and shared prey source of deer, but suggested that wolves may have exploited gentler sloping terrain, with mountain lions hunting in steeper craggy mountainous terrain. The potential for competition between wolves and lions certainly exists in areas where spatial overlap is extensive and prey selection patterns are similar (see Kunkel et al. 1999), although differences in hunting behavior and prey vulnerability to wolves and mountain lions have been observed (see Husseman et al. 2003). One Mexican wolf death from a mountain lion attack has been recorded in the BRWRA (AMOC and IFT 2005: TC-12). Gray wolves have been known to kill black bears near their dens and to take over kill sites occupied by black bears (Ballard and Gipson 2000, Ballard et al. 2003), but interactions between Mexican wolves and black bears have not been documented. Two other Mexican wolf deaths have been attributed to predators, but identification of specific predators was not provided (USFWS 2004, USFWS 2006a, USFWS 2009: Population Statistics).

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 fearless 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) and are less so (as measured by the number of attacks/carnivore species) that other carnivores that are currently common in the western U.S. and Mexico (citation). An inquest jury has attributed one recent human death in Canada to wolves, although a number of wildlife experts disagree whether wolves or a black bear were responsible for the death (Paquet and Walker 2006). During March 2010, a women jogging alone in rural Alaska was killed by wolves (Butler et al. 2011).

In the BRWRA, wolf-human interactions have been documented. For example, between 1998 and 2012, xx cases of wolf-human interactions were documented in the BRWRA. The majority
of these incidents (xx percent) were considered investigative searches in which wolves ignored human presence. In several cases (xx percent), wolves approached humans in a non-threatening manner, and in x reports wolves displayed aggressive behavior (charging) toward humans (USFWS our files). A majority of the interactions involved wolves recently released from captivity, suggesting that wolves released from captivity may be prone to initial tolerance of humans, despite appropriate captive management techniques and selection criteria for release candidates that promote and select for intolerance (shyness), respectively (AMOC and IFT 2005: TC-22).

Wolves are known to kill dogs virtually everywhere the two coexist (Fritts et al. 2003), thus the presence of dogs may provoke investigative or aggressive behavior. Dogs were present in many of the cases above (including xx charges) in which the aggression appeared to focus on the dogs rather than the humans (USFWS our files). Aversive conditioning (rubber bullets, cracker shells) or translocation or removal of the wolf was applied in response.

Humans also 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 illegal shooting or poisoning. 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). Past recommendations estimated suitable Mexican wolf habitat to occur where human density is less than 12 people per square mile (2.56 km²), with an optimum density of less than 6 people per square mile (Johnson et al. 1992). In keeping with these guidelines, the BRWRA was selected in part due to its low human population density (estimated at 0.31/km² or 0.8/mi² prior to the reintroduction) (USFWS 1996: Table 3-3). In the BRWRA, illegal shooting is the biggest mortality source for Mexican wolves (USFWS 2009: Population Statistics) (and see “Physical Description and Life History”, and factor (E) in “5-factor analysis”).
I. The Geography of Recovery

(IMPORTANT Note to Reviewer: This subsection is not standard in a recovery plan. I have swapped out the “Critical Habitat” section that typically occurs here in the recovery plan with this one, based on the FWS recovery planning guidance, “If important habitat has been identified as needed for recovery but has not been designated as critical habitat, be sure to note this in this section and include the necessary management of the habitat in the recovery actions section.” We can/will make clear that the areas discussed here are NOT being recommended for critical habitat / that critical habitat cannot be designated for 10j species. Rather, this subsection provides an opportunity to broadly explain what the Southwestern landscape looks like from the perspective of the wolf recovery effort. Thus at minimum it should contain a description of ecologically suitable habitat; it could also include an overview of non-ecological factors that the team wants acknowledged, such as land ownership (including tribal lands), land use, binational aspects, etc. We need additional team discussion about what might be useful and appropriate in this section, but this may be the place to address some of the non-biological concerns raised at our August and November 2011 meetings. As I think about this section more, it may be better placed AFTER the recovery criteria…we need to flesh it out and see where it fits the best.)

Because Mexican wolf recovery will require reintroduction projects to restore populations it is essential to define the region where such efforts would be scientifically sound and ecologically feasible. It is also important to carefully assess the major social, cultural, political, and economic characteristics of the region that may influence implementation of Mexican wolf recovery activities. Defining the ecological basis for Mexican wolf recovery includes consideration of historical range and current range, and current and future habitat conditions, including, most importantly, prey availability and conflicts with humans. This information is given context by the policy framework created by applicable federal, state, and international laws and regulations, as well as by social aspects of this region pertinent to Mexican wolf recovery such as land ownership, tribal boundaries, international relations with Mexico, and ranching and other economically and culturally significant land uses that have potential to conflict with wolf recovery. This subsection of the plan provides a holistic description of the landscape within which Mexican wolf recovery is ecologically appropriate and biologically feasible.
We first describe initial analyses of potential Mexican wolf habitat that occurred prior to the widespread availability of digital data on habitat attributes. We then discuss how the two factors limiting wolf distribution (prey abundance and human-caused mortality) have been evaluated in more recent studies using geographic information systems (GIS) (below and Appendix X).

Because of the contrasts in available digital data between the US and Mexico, we review habitat distribution in each nation separately. The available digital data in the two nations allows us to make quantitative comparisons between sites within each nation, but only qualitative comparisons of sites between nations.

*Initial Analyses of Habitat Suitability in the United States*

In the course of planning for Mexican wolf recovery in the 1990s, the FWS evaluated the habitat suitability of five potential core areas in Arizona and New Mexico (with those within each of the two states being evaluated separately). Bednarz (1989) evaluated the suitability of the White Sands Missile Range (WSMR, see Figure 1 for this and other locations) in central New Mexico, finding it suitable in terms of habitat security but marginal in habitat productivity (prey abundance). A later assessment concluded that the area could only support 20 to 30 wolves (Green-Hammond 1994). Johnson et al. (1992) evaluated four areas in Arizona: the Blue, Galiuro-Pinaleno, Chiracahua, and Atascosa-Patagonia ranges (Figure 1). The New Mexico portion of the current Blue Range Wolf Recovery Area (BRWRA) was not considered in either Johnson et al. (1992) or Bednarz (1989). The Arizona portion of the BRWRA was scored by Johnson et al. (1992, see also Groebner et al. 1995) as highest in 7 of 13 habitat factors. The Atascosa/Patagonia ranges were the only one of the remaining three areas to approach the BRWRA in quality (highest in 5 of 13 habitat factors). Parsons (1995) produced a comprehensive reassessment of all 5 of the proposed sites in Arizona and New Mexico. He found that, based on the sum of scores for seven factors affecting wolf habitat suitability (habitat area, ungulate density, water availability, livestock density, human density, road density, and effects on threatened species), WSMR scored highest, followed by the Blue Range, and more distantly, the Atascosa/Patagonia Mountains. The contrast between these results and those of others who discount the potential of the WSMR (e.g., Paquet et al. 2001, Carroll et al. 2005), is due to the fact that habitat area, for which WSMR scores very low, is only one of seven factors given equal weight in Parsons (1995). USFWS (1996) evaluated four alternatives for Mexican wolf restoration and chose a preferred alternative involving reintroduction to the BRWRA, with potential use of WSMR as a second core area if necessary.
The preferred alternative notwithstanding, given the lack of robust prey populations the WSMR offers little actual support for Mexican wolf recovery. Sneed (2001) evaluated suitability of wolf habitat in the Grand Canyon and Mogollon Rim region in northern and central Arizona. While this area includes some habitat with relatively low ungulate density due to the arid climate, other portions of the area such as the Kaibab Plateau support ungulate densities comparable to mesic forest ecosystems of the NRM (> 8 deer/km²). Sneed (2001) concluded that the North Kaibab and South Colorado Plateau could support between 115 and 187 wolves.

GIS Assessment of Habitat Suitability in the US: Factors Associated with Wolf Fecundity

A large body of literature links wolf redundancy (productivity) with ungulate biomass available per wolf (Fuller et al. 2003). Consequently, estimates of potential wolf fecundity can be based on surveys of abundance of prey species. However, these data are challenging to assemble across a multi-state region because methods for estimating ungulate abundance vary between jurisdictions. A comprehensive survey of available data on prey abundance in the US was developed as part of this recovery plan, and is discussed below.

Because best available data on prey abundance is inconsistent between areas due to differences in collection methods and resolution, it is also useful to evaluate potential wolf fecundity based on surrogate variables for prey productivity that are consistently measured for the areas in question. Past studies have found good concurrence between such surrogate variables and actual prey abundance in Colorado and Utah (Carroll et al. 2003a, Carroll 2003). The drawbacks of using surrogate variables (e.g., vegetation patterns) for estimating prey abundance are countered by the benefits of obtaining consistent and comparable data across a wide region. This, of course, facilitates comparison of areas within the wide region. Facilitated comparisons notwithstanding it is true that ungulate abundance may differ between two areas with similar vegetation due to contrasting levels of hunting pressure by humans. Although prey species in the US are often managed near carrying capacity, in some areas of Mexico prey abundance may be locally depleted by heavy hunting pressure, lowering the match between vegetation productivity and prey abundance (i.e., wolf habitat)(Lara-Diaz et al. 2011).
Carroll et al. (2005, 2006) developed a binational evaluation of habitat for the Mexican wolf using predicted prey abundance based on vegetation data, with a focus on 13 evaluation areas (Figure 1). The National Land Cover Dataset (NLCD) was used for the United States. NLCD data were derived from Landsat TM imagery at a resolution of 30 m, and contains 21 landcover classes. Landcover types from both the US and Mexican data sets were ranked as to their value as wolf habitat (see Tables 4 and 5 in Carroll et al. 2005) based on expert opinion and historical records (Brown 1983, C. Lopez-Gonzalez pers. comm.).

Because ungulate prey density may vary greatly within a particular vegetation type due to variation in primary productivity and other factors, Carroll et al. (2005, 2006) augmented the vegetation data with a satellite imagery-derived metric, tasseled-cap greenness (Crist and Cicone 1984). Variables such as greenness that are derived directly from unclassified satellite imagery are correlated to varying degrees with ecological factors such as net primary productivity and green phytomass that influence the abundance of ungulates (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997). Summer greenness values were found to be strongly correlated with ungulate density in the northern Rocky Mountains and Pacific Northwest (Carroll et al. 2001b, 2003a). Carroll et al. (2005, 2006) combined greenness levels with ranking of vegetation types to produce a composite ranking (Figure 2). This prey productivity or potential fecundity layer also incorporated the negative effect of terrain (slope) on prey availability to wolves (Paquet et al. 1996). Because the season of maximum productivity varies across the region, Carroll et al. (2005, 2006) used the maximum greenness level found in either March or July (2001) MODIS imagery.

GIS Assessment of Habitat Suitability in the US: Factors Associated with Wolf Survival

As with fecundity estimates, wolf survival estimates in different habitat types would ideally be based on models of the relationship of habitat variables to wolf survival from other recovery areas such as the NRM. However, although analysis of NRM survival data has occurred (e.g., Murray et al. 2010), these studies have not yet produced models of the relationship between survival and habitat variables as has been done for other carnivore species (e.g., grizzly bears; Schwartz et al. 2010). However, a large body
of literature links wolf survival with surrogates for human caused mortality such as roads and population (reviewed in Fuller et al. 2003).

Previous studies have incorporated “habitat effectiveness” as a composite metric for relative mortality risk to large carnivores based on roads and human population (Figure 3). This has proven to be a useful surrogate for wolf mortality risk in the northern Rocky Mountains (Merrill et al. 1999, Carroll et al. 2003a, 2003b). In the analysis of Carroll et al. (2005, 2006), roads data for the US were derived from USGS Digital Line Graphs (DLG) coverage at 1:100,000 scale (USGS, unpublished data) (Figure 3).

Population data for the US was derived from 1990 and 2000 censuses (US Census Bureau 2001) at the census block scale. Human population growth from 2000 to 2025 was predicted based on growth rates from 1990 to 2000. Road density was predicted to increase at 1% per year (Theobald et al. 1996).

Because much of the data relating human population and roads to wolf mortality come from areas without the public lands grazing patterns found in the western US, less is known about the quantitative effects of livestock density, and resulting depredation-related removals, on wolf survival (but see Treves et al. 2011 for an example from the Great Lakes states). For this document data on livestock abundance for the US was derived from the 1997 US Census of Agriculture at the county level (Figure 4). Livestock data are therefore at a substantially coarser scale than available human population data.

Identification of Potential Core Areas of Suitable Habitat within the US

Once data on both potential wolf fecundity and survival is collected, one is faced with the challenge of estimating the relative influence of habitat factors related to fecundity and survival in determining persistence of wolf populations. For example, habitat suitability for southwestern Colorado which has very high prey abundance and likely moderate human impacts to any wolf population (i.e., those anthropogenic activities that might affect wolf fecundity and survival by altering habitats needed by prey and providing increased access that might lead to elevated levels of human-caused mortality) may be contrasted with habitat suitability for the Grand Canyon region and western Texas both of which have lower prey abundance and but likely lower human impacts as well. Similarly, arid ecosystems in many areas of the southwestern US likely have relatively low human impacts but also support prey abundance near the lower threshold for wolf
persistence. Because previous reintroductions in the western US were to sites in the Greater Yellowstone Ecosystem and central Idaho which have both high prey abundance and low human impacts, they do not provide detailed guidance as to the relative strength of these two factors.

An effective strategy for wolf recovery involves establishing well-distributed source populations in core areas of highly suitable habitat and then allowing natural dispersal to re-establish a regional metapopulation. For a core area of suitable habitat to include potential reintroduction sites it would need to contain areas of highly secure habitat that are well situated to facilitate growth of the regional wolf metapopulation. The several habitat suitability assessments that have been conducted over the last 20 years indicate that only three major core areas of suitable habitat exist in the area encompassing the Mexican wolf’s historical range and adjacent areas in Arizona, New Mexico, southern Colorado and southern Utah that are capable of supporting Mexican wolf populations of sufficient size to contribute to recovery. The three core areas of suitable habitat are 1) the Blue Range Wolf Recovery Area and adjacent public lands, 2) the Grand Canyon and adjacent public lands in northern Arizona and southern Utah (as circumscribed by interstate highways 15 and 70), and 3) Carson National Forest/San Juan National Forest and other connected areas of public lands and private lands with conservation management in northern New Mexico and southern Colorado (as circumscribed by interstate highways 70 and 25) (Table 1). We describe these areas using regional-scale habitat data, but a more detailed evaluation of local land ownership, land use, and prey abundance patterns would be necessary in subsequent stages of recovery (e.g., development of an Environmental Impact Statement before conducting reintroductions to restore populations that count toward recovery). An additional area in western Texas which has some attributes of suitable habitat is also described here.

Although some areas which are not currently suitable habitat might become so in future decades due to recovery actions, this plan's recovery strategy focuses primarily on the three areas identified above because they are currently capable of expeditiously advancing wolf recovery. Expeditious recovery (i.e., consistent with the timeline set forth in this plan) is necessary to fulfill recovery objectives because any additional time that captive and wild Mexican wolf populations remain at their current low levels accentuates genetic threats and reduces recovery
potential. The accumulating genetic effects of the current population bottleneck lend urgency to recovery and require a focus on areas that currently could support relatively rapid growth of Mexican wolf populations due to high survival rates and abundant prey.

The three major core areas of suitable habitat are each projected to become more distinct and separated as landscape change factors such as exurbanization continue (Carroll et al. 2006). All areas except western Texas include large tracts of public lands subject to conservation mandates (National Park, wilderness) where wolves are predicted to experience the lowest human-induced mortality. While the Grand Canyon and northern Arizona and southern Utah core area and northern New Mexico/southern Colorado core area are both located north of the Mexican wolf’s historical range, in the recent past they each supported a closely related subspecies (C. l. nubilus) that has for over half a century been restricted to the western Great Lakes states and Canada (Nowak 1995) due to 20th century extermination campaigns (Robinson 2005). The two areas are proximate to (Brown 1983, Bogan and Mehlhop 1983, Hoffmeister 1986, Nowak 1995) or well within (Leonard et al. 2005) the zone of gray wolf subspecies intergradation that characterized the southwest historically. For these reasons and others to be discussed, northern Arizona/southern Utah and northern New Mexico/southern Colorado are appropriate for inclusion in the Mexican wolf recovery program.
Table 1. Ecological attributes of core areas of suitable Mexican wolf habitat. All metrics are expressed as per km² unless noted. Isolation is center-to-center distance from nearest neighboring potential core area. Wolves per 1000 km² is based on the model of Fuller et al. (2003). ‘Total wolves’ indicates estimates of potential population size based on previously-published studies and the analysis in this document.

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<td></td>
</tr>
<tr>
<td>1. Sierra San Luis/Ajos-Bavispe</td>
<td>25,900</td>
<td>15,700</td>
<td>300</td>
<td>5</td>
<td>1-2</td>
<td>2.41</td>
</tr>
<tr>
<td>2. Tutuaca/Sierra Tarahumara</td>
<td>21,200</td>
<td>300</td>
<td>4</td>
<td>1-2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>3. Chihuahua/Durango</td>
<td>29,975</td>
<td>8,300</td>
<td>350</td>
<td>7</td>
<td>1-2</td>
<td>3.6</td>
</tr>
<tr>
<td>4. Sierra de Valparaiso/Sierra de Urica/Mezquital</td>
<td>12,667</td>
<td>60</td>
<td>1-2</td>
<td>0.68</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Maderas del Carmen/Serranias de Burro</td>
<td>19,564</td>
<td>250</td>
<td>6</td>
<td>1-2</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>6. Sierra Plegada</td>
<td>17,968</td>
<td>450</td>
<td>7</td>
<td>1-2</td>
<td>0.23</td>
<td></td>
</tr>
</tbody>
</table>
Description of Core Areas of Suitable Habitat in the US

1. Blue Range: The Blue Range Wolf Recovery Area (BRWRA) covers 17,545 km² and is located on the Apache-Sitgreaves and Gila National Forests (NFs) along the Arizona/New Mexico border. Since 1998 the FWS has released Mexican wolves into this area. The Mogollon Rim area lies along a block of forested public lands (e.g. Tonto NF) stretching between the Blue Range and Grand Canyon sites. The two areas (Blue Range and the Mogollon Rim) would likely function as a semi-continuous block of suitable wolf habitat in the absence of management actions to limit wolf populations or movement. However, Carroll et al. (2006) concluded that the wolf survival would be lower in the Mogollon Rim area than in the Blue Range due to greater levels of threat factors (primarily roads) in the former area. We do not identify the Mogollon Rim as a separate core area of suitable habitat both because of its greater threat levels and because it does not represent a geographically disjunct block of potential wolf habitat that would support a spatially and demographically distinct population.

2. Grand Canyon (Northern Arizona/Southern Utah as circumscribed by interstate highways 15 and 70): This core area encompasses the Grand Canyon and adjacent public lands in northern Arizona and southern Utah. The area is centered on the Grand Canyon National Park (4900 km²) and adjacent of Kaibab and Coconino NF lands (13,300 km²). The Grand Canyon National Park is not predominantly highly productive wolf habitat, although wolves within its boundaries would likely benefit from low rates of human-caused mortality. Adjacent public lands on the Kaibab Plateau, other portions of the Kaibab National Forest, and areas in southern Utah such as the Paunsaugunt Plateau are more mesic with greater prey densities as described below.

With the exception of the Blue Range, the Northern Arizona/Southern Utah core area may have the highest probability of enhancing regional wolf populations through dispersal (Carroll et al. 2005, 2006). This is due to both a large area of public lands with low mortality risk for wolves, and substantial connectivity from that habitat southward through the Mogollon Rim towards the Blue Range and northward to the public lands of the mountains of southern and central Utah and north to Wyoming and Idaho.
3. Carson National Forest/San Juan National Forest (Northern New Mexico/Southern Colorado as circumscribed by interstate highways 70 and 25): This core area of suitable habitat encompasses connected areas of extensive public lands and private lands with conservation management in northern New Mexico and southern Colorado. The New Mexico portion of this area includes sections of the Carson National Forest (6,000 km²), Santa Fe National Forest (6,400 km²), Vermejo Park Ranch (2,300 km²), 268 km² of additional private lands protected under conservation easements, and the Taos Pueblo (391 km²) of which 230 km² are managed as wilderness by the tribe. The Valle Vidal Unit of the Carson National Forest (407 km²) is managed with special emphasis on wildlife and fisheries resources. For example, 88% of the roads present in 1982 have since been closed or removed to enhance wildlife and fisheries habitat. Given tightly restricted access to Vermejo Park Ranch and careful monitoring of traffic and road use that is allowed, when considering human-caused mortality of wolves the ranch is functionally roadless.

The Colorado portion of this area extends across portions of the San Juan National Forest (8,345 km²), Rio Grande National Forests (7,440 km²), and Grand Mesa, Uncompahgre, and Gunnison National Forests (12,600 km²). The San Juan Mountains contain 4,000 km² of Wilderness Areas and 4,000 km² roadless areas including significant lower-elevation ecosystems. Relatively low levels of livestock grazing occur public land and private conservation land throughout the area (Bennett 1994).

Similarly to the Grand Canyon, the northern New Mexico/southern Colorado core area would aid the reestablishment of well-distributed wolf populations northward to the public lands in western Colorado. However, these sites appear to have somewhat higher vulnerability to habitat reduction or isolation by landscape change than does the Grand Canyon region (Carroll et al. 2005). This is due to a higher proportion of private lands in lower elevation valleys, as well as the generally higher predicted rate of landscape change in Colorado and New Mexico (Carroll et al. 2005).

4. Western Texas: Approximately 24,000 km² of potentially suitable habitat occurs in western Texas (Carroll et al. 2006). This area is assessed as suitable in the model of Carroll et al. (2005)
due primarily to low numbers of roads and human settlements. Potential prey productivity is low but likely sufficient to support low densities of wolves (Table 1). This area lies between the Davis Mountains and the Pecos River watershed in Jeff Davis, Brewster, Pecos, Terrell and Val Verde Counties, from approximately State Route 385 on the west to State Route 163 on the east. The few public landholdings (Davis Mountains State Park, Seminole Canyon State Park) in this area are relatively small in size. Private lands under conservation easements total approximately 270 km². Big Bend National Park, while large in size, lies to the south of this area and does not offer extensive suitable habitat due to its aridity. The area of suitable habitat in western Texas is distant (700 km) from the nearest core area of suitable habitat in New Mexico, but relatively near (250 km) the potential reintroduction area in the northern Coahuila identified by Araiza et al. (2006).

Other Areas of Arizona and New Mexico
The US/Mexico border region is likely to serve as sink habitat for wolves under current conditions (Carroll et al. 2006) despite the presence of some potentially suitable habitat such as the 305 km² Galiuro Wilderness. Sites in this area that have previously been proposed as reintroduction locations (e.g., Galiuro/Pinaleno, Chiricahua Mountains, and Atascosa/Patagonia Mountains [Johnson et al. 1992]) appear, based on the model of Carroll et al. (2005), to be poor choices for such efforts. However, the area’s key role in facilitating dispersal between US and Mexican wolf populations suggests that it be given significant attention in recovery planning, through recovery actions which increase the likelihood of these sites being naturally recolonized by dispersers from the Blue Range or Mexican populations. The importance of binational population connectivity is further highlighted by the recent release of Mexican wolves in northern Sonora ~100 km south of the Arizona/New Mexico border.

Data on Prey Distribution and Abundance in the US
Carroll et al. (2003a, 2005, 2006) used spatially explicit population models (SEPM) to assess the potential of prey populations to support wolf populations in the southwestern US with differential emphasis on the three core areas of suitable habitat. Abundance estimates of ungulate prey are not collected in some areas of the western US and where they do exist they show strong inconsistencies across state boundaries. Therefore, as a surrogate for ungulate
abundance they used tasseled-cap greenness (Crist and Cicone 1984), a metric derived from MODIS (Moderate Resolution Imaging Spectroradiometer) satellite imagery from mid-July 2003 and 2004 (Wharton and Myers 1997). “Pseudo-habitat” variables such as greenness are correlated to ecological factors like net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997) and thus with ungulate abundance (Carroll et al., 2001b, 2003a). Furthermore, the large body of published research on relationships between wolf demographics and habitat (as reviewed by Fuller et al. 2003) strengthens the power of conceptual models such SEPM. SEPM for the Blue Range, Grand Canyon, and northern New Mexico/southern Colorado core areas indicated that prey populations in each were sufficient to support > 250 wolves (Table 1) (Carroll et al. 2005, 2006).

As a validation of the GIS modeling that used a surrogate variables to estimate prey populations (as described above), J. Heffelfinger (while a member of the Science and Planning Subgroup) assembled ungulate abundance estimates from game surveys for selected areas in the US portion of the region. These data were provided primarily by the state game departments of Arizona, New Mexico, Utah, and Colorado. Survey and population estimation methodology varied between jurisdictions but data were reduced to animal density as a common denominator. Survey data were summarized at the spatial resolution of game management units (GMU), with the exception that New Mexico summarized data over general regions. Members of the SPS calculated a standard Ungulate Biomass Index (UBI) for several areas of interest (Fuller et al. 2003). Using estimated densities of elk, white-tailed deer, and mule deer from several areas considered in this document as potential recovery areas, the resultant UBI was calculated and compared to a regression equation showing the relationship between UBI and wolf density in 31 studies throughout North America (Fuller et al. 2003, fig. 6.2). Based on this regression equation, wolf density would be estimated at 21 wolves/1000 km² for the Blue Range/Mogollon Rim, 17 wolves/1000 km² for the Grand Canyon area, and 28 wolves/1000 km² for Carson/San Juan (J. Heffelfinger, unpublished data assembled while a member of the Science and Planning Subgroup). Since elk make up a majority of the Mexican wolf diet, the same exercise was conducted for elk alone yielding wolf density estimates of 18, 12, and 25 wolves/1000 km² for the Blue Range/Mogollon Rim, Grand Canyon area, and Northern New Mexico/Southern Colorado areas, respectively.
These predicted wolf densities were extrapolated to previously identified core areas using hexagons of >60% predicted wolf occupancy from spatially explicit models (Carroll et al. 2006). Respective wolf densities for the core areas were applied to the number of 500 km² hexagons with at least 60% probability of occupancy to estimate the total number of wolves that could be supported in these areas. These calculations indicate each of the three core areas identified are of sufficient size and currently support ungulate biomass sufficient to support > 250 wolves (Table 2).

Before wolves were reintroduced to the BRWRA, in the FEIS it was estimated that the area contained adequate prey to support a population of at least 100 wolves (USFWS 1996). Prior to the outset of reintroductions a population of 15,800 elk (average density 3.7 elk/km²) and 57,170 deer (average density 13.4 deer/km²) were estimated to inhabit the BRWRA. The 3-year review of the reintroduction project indicated that elk in the area could support about 213 wolves and when combined with deer could support about 255 wolves, based on calculations of standing biomass and estimated consumption rates (Paquet et al. 2001:47). This estimate was solely for the BRWRA and did not include the capacity of the FAIR and other areas of Mogollon Rim to support wolves. Data collected since the BRWRA project began indicate that the wolf population there is not limited by food (see *BRWRA Project Evaluation*).

All estimates of wolf densities and corresponding estimates of population size that can be expected to persist in the US core areas should be viewed cautiously. Game management units and occupancy polygon boundaries did not correspond exactly to the potential core areas of suitable habitat, so predicted densities and numerical values are approximations. Additionally, it is uncertain to what extent the regression equation of Fuller et al. (2003) applies to less productive arid southwestern environments where ungulate population dynamics may differ to a degree from those in mesic ecosystems. Seasonality of prey availability and vulnerability may also affect wolf carrying capacity differently in areas where altitudinal migration of ungulates occurs, versus areas that receive little or no snow. These shortcomings notwithstanding, extrapolating each density estimate across the respective core areas affirmed that the US portion
of the Mexican wolf recovery region that extended into Utah and Colorado could potentially support > 900 wolves (Table 2).

Table 2. Based on ungulate biomass and their areal extent each of the three core areas identified are expected to support > 250 wolves.

<table>
<thead>
<tr>
<th>Core Area</th>
<th>Area (km²) with 60%+ Predicted Wolf Occupancy</th>
<th>UBI based on all Deer &amp; Elk</th>
<th>Predicted wolf density (/1000km² based on Deer &amp; Elk)</th>
<th>Predicted No. of Wolves (based on Deer &amp; Elk)</th>
<th>UBI based on Elk only</th>
<th>Predicted wolf density (/1000km² based on Elk only)</th>
<th>Predicted No. of Wolves (based on Elk only)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carson/San Juan (northern New Mexico/southern Colorado)</td>
<td>11,500</td>
<td>7.6</td>
<td>28</td>
<td>322</td>
<td>6.5</td>
<td>25</td>
<td>288</td>
</tr>
<tr>
<td>Grand Canyon (northern Arizona/southern Utah)</td>
<td>23,000</td>
<td>4.1</td>
<td>17</td>
<td>391</td>
<td>2.6</td>
<td>12</td>
<td>276</td>
</tr>
<tr>
<td>BRWRA/Mogollon Rim</td>
<td>20,500</td>
<td>5.6</td>
<td>22</td>
<td>442</td>
<td>4.5</td>
<td>18</td>
<td>369</td>
</tr>
</tbody>
</table>

Effects of Future Landscape Change on Habitat in the US

Potential effects of landscape change on wolf habitat are summarized based on the results of Carroll et al. (2006). That study estimated potential change in human-associated impact factors (i.e., roads and human population) by proportionately increasing road density and by increasing human population on the basis of current trends derived from a time series of human census data. The study predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 2000, but adjusted the predicted 2025 population to match state-level predictions based on more complex socioeconomic models. Road density projections incorporated an increase of 1% per year (proportional to the current road density at the 1-km² scale), a rate half of that seen
in the most rapidly growing portions of our study region (e.g., western Colorado; Theobald et al. 1996).

Wolf habitat in New Mexico and Colorado are most vulnerable to landscape change because habitat in those states is relatively more fragmented than in Arizona and is experiencing more rapid development. Outside of those two states, the US southwest shows vulnerability levels similar to those in the US Northern Rockies - about a 25% decline in wolf carrying capacity over 25 years (Carroll et al. 2003, 2006). Carroll et al. (2005, 2006) predicted that, absent management actions to mitigate threat factors, future wolf populations in the southwestern US may be primarily confined to the highest quality habitat in the core areas previously discussed. Future landscape change would also compromise the already modest connectivity between the Blue Range and the Sierra Madre Occidental (Sonora/Chihuahua) via occupied habitat along the Arizona/New Mexico border.

Connectivity between US core areas
Earlier studies concluded that potential wolf population connectivity between the Blue Range and Grand Canyon core areas is greater than between the Blue Range and the Carson/San Juan core area (Carroll et al. 2005, 2006). We analyzed potential connectivity in more detail using the Connectivity Analysis Toolkit software (Carroll et al. 2011). We used a habitat model based on data used in previous studies (Carroll et al. 2006) as input to an analysis of shortest-path betweenness centrality (BC) and current-flow BC (Carroll et al. 2011). Shortest-path BC identifies the single best linkage between each pair of core areas, whereas areas of high current flow BC reveal connectivity 'pinchpoints' where much potential dispersal flow is being routed through relatively limited habitat. Results indicate that the best linkage in the southwestern US corresponds to a rate intermediate between the well-connected populations in the northern Rocky Mountains (i.e., Greater Yellowstone to central Idaho and central Idaho to northwestern Montana) and the poorly connected populations (i.e., Greater Yellowstone to northwestern Montana). Recovery actions designed to facilitate dispersal between populations in the southwestern US (especially those that reduce or eliminate human-caused mortality) will be critically important to recovery and may focus on the most important shortest-path linkages while giving additional attention to areas with high current flow as well. Such recovery actions may be essential in ensuring that connectivity-related recovery criteria are achieved.
Results of Previous GIS Analyses of Habitat Suitability in Mexico

In Mexico, several previous analyses have evaluated the extent of potential habitat. Araiza et al. (2002) evaluated GIS data from Sonora, Chihuahua, and Coahuila and identified an area in the northern Sierra Madre Occidental with relatively high levels of habitat security (low road density and human settlement). However, field measurements of prey abundance indicated deer densities in this area were near the lower limit for wolf population persistence. This suggested that augmentation of deer herds through revised grazing techniques and reduced hunting might be necessary before the area could support wolves (Araiza 2002).

Sanchez and Guevera (2006) examined habitat potential in Coahuila and Nuevo Leon and identified areas of as potential habitat in northern Coahuila (Sierra del Carmen) and central Nuevo Leon (Sierra Plegada). Servín et al. (2007) analyzed historic wolf distribution records using the Genetic Algorithm for Rule-Set Prediction (GARP) method and regional-scale GIS data on vegetation type, elevation, temperature, and precipitation to define the probable historic distribution and ecological niche of the Mexican wolf. Areas with land use unsuitable for current occupation by wolves (human-altered habitats) were then excluded from the historic distribution to produce an estimate of the area of remaining suitable habitat. A large portion of the Sierra Madre Occidental (90,000 km²) was predicted to be suitable for wolves under these assumptions, whereas little habitat remained in other areas such as Nuevo Leon and Tamaulipas (Servín et al. 2007).

Carroll et al. (2005) identified and compared four potential core areas of suitable habitat in Mexico: the Sierra San Luis (northern Chihuahua/Sonora), Maderas del Carmen (northern Coahuila), an area in northwestern Durango near the Chihuahua border, and the Tutuaca reserve area (west-central Chihuahua near the Sonora border). Of the four, the Durango site contained the most productive habitat for wolves, but the Tutuaca and Maderas del Carmen sites appeared to have lower risk of conflict with livestock production.

Martinez Meyer et al. (2006) developed a habitat model based on climate, vegetation, and human impacts (Figure 5). The study predicted that only 2% of the area with suitable climate and
vegetation also showed low human impacts (i.e., those anthropogenic activities that might affect wolf fecundity and survival by altering habitats needed by prey and providing increased access that might lead to elevated levels of human-caused mortality). These core areas of potential habitat were found widely distributed across northern Mexico in small patches (<100km² in size). Of the 7,265 km² of currently suitable habitat with low human impacts, 2,284 km² was predicted to retain suitability under future climate.

Martinez-Gutierrez (2007) identified two areas of >600 km² in size in the northern Sierra Madre Occidental (western Chihuahua near the border with Sonora) with habitat suitability and low human-associated mortality risk (Figure 6). The more southerly of these areas falls within the Tutuaca core area (see below). Additionally, several additional areas of between 200 and 500 km² in size were identified in the same region of northern Sierra Madre Occidental as well as in western Durango.

**Habitat Factors Associated with Wolf Fecundity: Vegetation Data for Mexico**

Several studies, including Carroll et al. (2005, 2006), have used vegetation data from the 2000 National Forest Inventory (Palacio-Prieto et al. 2000). This inventory mapped land cover across Mexico at a scale of 1:250,000 based on Landsat TM imagery. Land cover was assigned to one of 75 classes, with a minimum mapping unit (MMU) of approximately 1 km². The vegetation data (Palacio-Prieto et al. 2000) for Mexico is the first detailed national vegetation data set for the area and provides a more accurate record of human-altered land cover types than did the Mexican roads data described below.

**Habitat Factors Associated with Wolf Fecundity: Climate Data for Mexico**

Species distribution models based on climate data are termed “climatic niche” models. These models are most commonly applied to allow first approximations of potential effects of global climate change on large suites of taxa (Thomas et al. 2004). Because many of these species are poorly-known, and relevant non-climatic environmental variables may be unavailable over the global or continental extent of analysis, more detailed and biologically-informed models may not be feasible. Servin et al. (2007) and Martinez Meyer et al. (2006) used the Genetic Algorithm for Rule-set Prediction (GARP) to predict the potential distribution of the Mexican wolf. Stockwell
and Peters (1999) proposed that the GARP method they developed identifies the ecological niche of a species, defined as the multi-dimensional environmental space which contains those ecological conditions under which the species can maintain populations without immigration (Grinnell 1917, MacArthur, 1972). As climatic niche models are increasingly applied to inform single-species conservation strategies, the assumption that such models adequately describe a species “fundamental niche” have been questioned, particularly when the mechanisms by which climate influences physiology and demography of the species of interest are unknown (Elith and Leathwick 2009). Although climatic niche models might be expected to suggest overarching limiting factors within which finer-scale habitat relationships operate, results may be misleading in the absence of relevant finer-scale habitat variables (Pearson and Dawson 2003, Carroll 2010).

To develop input data for GARP, available occurrence points are divided evenly into training and extrinsic test data sets; the former set is again divided evenly into true training data (for model rule development) and intrinsic test data sets (for model rule evaluation and refinement). Although input data was derived from historical records, GARP projects results onto current landscapes to estimate the current geographical distributions of suitable areas. GARP is designed to work based on presence-only data; absence information is included via sampling of pseudo-absence points from those pixels where the species has not been detected. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection: firstly, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules), and is then applied to the training data and a rule developed; rules may evolve by several means (truncation, point changes, crossing-over among rules) to maximize predictivity. Predictive accuracy (for intrinsic use in model refinement) is then evaluated based on 1,250 points re-sampled from the intrinsic test data and 1,250 pseudo-absence points. Change in predictive accuracy between iterations is used to evaluate whether particular rules should be incorporated into the model, and the algorithm runs either 1,000 iterations or until convergence.

Martinez Meyer et al. (2006) predicted Mexican wolf distribution based on a niche model developed with data on topography (elevation, slope, aspect, topographic index) and annual means of climate variables (diurnal temperature range, precipitation, maximum, minimum, and mean temperatures, solar radiation, wet days, and vapor pressure) (Figure 5). Martínez-Gutiérrez
(2007) used 14 climatic variables (average annual temperature, mean diurnal range, seasonal temperature, annual temperature range, average temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, seasonal rainfall (coefficient of variation), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter) and three topographic variables (elevation, slope and topographic index) (Figure 6). Both studies subsequently filtered suitable areas based on data on human-associated threats (e.g., roads) and other factors.

Habitat Factors Associated with Wolf Fecundity: Prey Data for Mexico

Estimates of prey abundance in Mexico are limited in spatial extent in comparison to those collected by state game agencies within the US. For this reason, the most comprehensive evaluation of potential wolf reintroduction areas in Mexico (Araiza et al. 2006) relied on expert-based estimates of prey abundance within core areas of suitable habitat. Estimates for all of the six areas were between 2 and 4 deer per km², which would correspond to densities of 10-17 wolves/1000 km² based on the model of Fuller et al. (2003). Subsequent studies (Arellano et al. 2009, Lara-Díaz 2011) using standardized survey methods have found similarly low prey densities within potential wolf habitat in northern Mexico. Another potential source of prey abundance data derives from information collected by Game Management Areas (UMA). UMA are required to base the number of hunting permits sold on estimates of prey abundance. Although these estimates are often greater than 2-4 deer per km², the lack of standardized methodology, limited area sampled, and financial motivation to inflate estimates cause these data to be of limited relevance to recovery planning.

The diversity of prey available to Mexican wolves in ecosystems of the Sierra Madre Occidental in Mexico may be higher than in the United States, which might partially compensate for the low abundance of wild ungulates. In a prey survey in Sierra Madre Occidental, Servín et al. (2007) found that ungulates (deer) constituted 84% of total wild prey biomass (1.92 of 2.28 kg/ha), whereas medium-sized and small prey (i.e., rabbits, hares, and rodents) constituted approximately 16%.
Habitat Factors Associated with Wolf Survival: Available Data for Mexico

The relative proportion of private to public lands is higher in northern Mexico than in the southwestern US. Privately owned land makes up a majority of the states of Northern Mexico: Chihuahua 84.9%, Sonora 76.8%, Coahuila 73.9%, Nuevo Leon 69.4%, Zacatecas 59.3%, and Durango 54.7%. Remaining lands are typically held in communal (ejidal) rather than public ownership. Public lands cover less than 10% of northern Mexico. State and federal nature reserves cover approximately 4.4% of Nuevo Leon and 2.8% of Tamualipas (Cantu et al. 2001). Consequently, most wolves would have to inhabit private lands in Mexico, although some of these large landholdings are well protected against trespass and deer populations are well-managed for commercial hunting operations. As a consequence, some large ranches might play a role in lowering the extinction risk of reintroduced wolves.

Transportation infrastructure (e.g. roads) data for Mexico, as used in several studies including Carroll et al. (2005, 2006), are derived from the Inventario Nacional de Infraestructura para el Transporte (INIT), a national database created from state and local level roads data sources at 1:50,000 or coarser scales (Backhoff Pohls et al. 2000). Due to its coarse-scale source, the INIT data potentially excludes a large proportion of the unpaved roads within northern Mexico (Figure 3). To compensate for this omission in areas of Mexico that showed human-altered land cover types but no roads (at a resolution of 1 ha), Carroll et al. (2005, 2006) set minimum road densities of 1.24 km/km² for pasture and 2.0 km/km² for other human-altered lands, based on an evaluation of road densities in similar land cover types in the US.

Population data for Mexico is typically derived from census databases at the locality scale (INEGI 2000). The locality is the finest scale of census data collected in Mexico, and thus approximately corresponds to the census block in the United States. However, locality data is available as point locations rather than the polygons used to delineate US census blocks. Livestock data for Mexico may be derived from the Census of Agriculture at the municipality level (Census of Agriculture 1991). Because available data on human settlement patterns and roads is relatively sparse in Mexico, data on livestock density may allow more realistic evaluation of potential wolf survival in remote areas.
Potential Core Areas of Suitable Habitat in Mexico

Potential core areas of suitable habitat in Mexico are found along the mid to higher elevations (2400 – 3200 m) of the Sierra Madre Occidental, as well as in two smaller mountain ranges located in Coahuila (Maderas del Carmen) and Nuevo Leon (Sierra Plegada) (Figures 7 and 8). Due to the continuous band of forest habitat at higher elevations of the Sierra Madre Occidental, wolves historically may have been widely distributed through this region. In contrast, the Maderas del Carmen and Sierra Plegada are relatively isolated from other areas of temperate forest habitat (Araiza et al. 2006, in press) (Figures 7 and 8).

In 2006, a workshop convened researchers involved with several of the studies described above, in order to derive a consensus opinion of which areas held potential for wolf reintroduction in Mexico (Araiza et al. 2006, in press). Because these six areas have subsequently formed the focus of recovery planning in Mexico, we describe them in detail here. Araiza et al. (in press) subsequently analyzed habitat suitability and human-associated mortality risk within each of the six larger areas to identify optimal sites in which to focus recovery efforts. Using historical occurrence records, Araiza et al. (in press) ranked vegetation types as to suitability. The study then developed three alternate scenarios for human-associated risk (low, intermediate, and high risk) that made alternate assumptions as to the extent of the zone around roads and human settlements in which wolves would experience increased mortality. Although the expert’s workshop (Araiza et al. 2006) had concluded that patches of suitable habitat larger than 10,000 km² were most suitable for reintroductions, no single patch in any of the six areas met that criterion (Araiza et al. in press). However, the largest clusters of suitable patches were found in Sonora-Chihuahua (area 1) and Chihuahua-Durango (area 3) (15,705 and 8,344 km² in area, respectively - Figure 7; under the intermediate risk assumptions - Figure 8).

The six potential core areas of suitable habitat identified by Araiza et al. (2006, in press) (Table 1, Figure 7) generally correspond with core areas identified in the various habitat models cited above. Many of these areas are not under legal protection, because past conservation efforts in Mexico have primarily focused on Desert and Tropical Forest biomes. The Mexican wolf
conservation program thus has stimulated broader awareness by the Mexican federal government of the need to protect areas of temperate forests in northern Mexico.

Description of six candidate core areas of suitable habitat in Mexico (numbering as shown in Table 1 and Figure 7)

1. Sierra San Luis/ Ajos-Bavispe (Sonora/Chihuahua): This area, of 10-15,000 km² in extent, lies in the northern portion of the states of Chihuahua and Sonora, abutting the US border and the northern end of the Sierra Madre Occidental. Vegetation ranges from lower elevation desert grassland to montane forest. The area is estimated to support 2-4 deer/ km². Livestock density is approximately 5 cattle/ km². In October 2011, five wolves were released in this area. Araiza et al. (2006) estimated that the area could support 80 wolves.

2. Tutuaca/Sierra Tarahumara (Chihuahua): This area, of 10,000 km² in extent, lies in the Sierra Madre Occidental in the central and southern portions of the state of Chihuahua. Vegetation is primarily montane pine and pine-oak forest and grassland. A protected area of the same name (Refugio de la Fauna Silvestre Tutuaca) lies within this area. The area is estimated to support 2-4 deer/ km² (Araiza et al. 2006) and may range up to 6 deer/ km² in some areas (J. Servín, unpubl. data). Livestock density is about 4 cattle/ km². It is estimated the area could support 80 wolves (Araiza et al. 2006).

3. Chihuahua/Durango: This area, of 15,000 km² in extent, lies in the central Sierra Madre Occidental on the border of the states of Chihuahua and Durango. Vegetation is montane pine, pine-oak, and oak forest and grassland. The area is estimated to support 2-4 deer/ km² (Araiza et al. 2006) and may range up to 7 deer/ km² in some areas (J. Servín, unpubl. data). Livestock density is about 7 cattle/ km². Road density is less than 0.23 km/km². It is estimated the area could support 60 wolves (Araiza et al. 2006).

4. Sierra de Valparaiso/Sierra de Urica/Mezquital (Zacatecas/Durango): This area, of 6,000 km² in extent, lies in the southern Sierra Madre Occidental on the border of the states of Durango, San Luis Potosi and Zacatecas. Vegetation is montane pine, pine-oak, and oak forest, grasslands, and mesquite shrublands. The area is estimated to support 2-4 deer/ km² (Araiza et al. 2006) and
may range up to 6 deer/km² in some areas (J. Servín, unpubl. data). Livestock density is about 6 cattle/km². Road density is low at approximately 0.08 km/km². It is estimated the area could support 24 wolves (Araiza et al. 2006).

5. Maderas del Carmen/Serranias de Burro (Northern Coahuila): The area of the Sierra del Carmen in northern Coahuila, of 13,000 km² in extent, is characterized by pine-oak and oak forest, grassland and mesquite shrubland vegetation. The area is estimated to support 2-4 deer/km². Livestock density is about 6 cattle/km². Road density is less than 0.23 km/km². It is estimated the area could support 85-100 wolves (Araiza et al. 2006).

6. Sierra Plegada (Nuevo Leon/Tamaulipas): This mountain range, of 17,000 km² in extent, lies primarily in the state of Nuevo Leon. Vegetation is primarily montane pine-oak and oak forest, grassland, and mesquite shrubland, with a sub-tropical forest influence in the eastern portion of the area. The area is estimated to support 2-4 deer/km². Livestock density is about 7 cattle/km². Road density, although averaging less than 0.23 km/km², is somewhat higher than in the Sierra Madre Occidental. It is estimated the area could support 60-140 wolves (Araiza et al. 2006).
reveal important patterns to the suitability of habitat between the six potential reintroduction areas in Mexico. For example, the southern boundary of the Sierra San Luis/Ajos-Bavispe reintroduction area (area 1, Figure 7) was defined by the presence of the logging town of Madera, which itself is surrounded by a heavily roaded and logged landscape.

To ensure detection of such patterns within the potential reintroduction areas Araiza et al (in press) performed a detailed modeling of risk under alternate assumptions of risk levels (i.e., high, intermediate, and low) associated with human population centers and road. Their analysis revealed that within the core areas of suitable habitat (i.e., areas 1 through 6, Figure 7) the most suitable areas for reintroductions are somewhat fragmented (Figure 10). It follows logically from their work that areas of low risk and preferred habitat are even more uncommon and fragmented between the six core areas of suitable habitat. The Mexican wolf recovery plan for Mexico that was written by a team of scientists in Mexico also concluded that it would be difficult to find appropriate habitat for wolves (SEMARNAT 2000).

Servín et al. (2007) proposed that the six Mexican core areas of suitable habitat in Mexico might form two disjunct metapopulations. The larger metapopulation would include the four areas in the Sierra Madre Occidental (i.e., areas 1 though 4, Figure 7), with interchange of dispersers along the Sierra Madre Occidental from Sonora to Zacatecas, with potentially connections with the Blue Range Wolf Reintroduction Area in Arizona and New Mexico. The two areas in eastern Mexico (Coahuila and Nuevo Leon, areas 5 and 6, Figure 7) could potentially exchange dispersers with Mexican wolf populations in Texas and New Mexico.

We considered the relative distance between the various Mexican core areas and with the US core areas to qualitatively evaluate the connectivity between sites (Table 1). Areas in eastern Mexico (Sierra Plegada and Maderas del Carmen) are qualitatively better connected to each other than to the other 4 potential core areas in western Mexico. This is due to barriers created by large areas of unsuitable low-elevation habitat and the human population between these areas. However, higher-elevation areas may offer some potential for connectivity between the Sierra Plegada core area (6 in Figure 7) and areas 3 and 4 in the states of Durango and Zacatecas (J. Servin, pers. comm.). The four areas in the Sierra Madre Occidental are largely connected with
each other and to a lesser degree, through the Sierra San Luis Complex, to the Blue Range core area in the US.

Comparing potential core areas of suitable habitat in Mexico

Araiza et al. (2006) estimated potential size of wolf populations in the six core areas of suitable habitat in Mexico (Table 1). These estimates indicate that the areas have varying potential to contribute to recovery. Areas in the Sierra Madre Occidental are more likely to form part of a connected metapopulation than are the two eastern areas. Additionally, the two areas in the northern Sierra Madre Occidental are predicted to support larger wolf populations (80 wolves each) than are the two areas in the southern Sierra Madre Occidental (60 and 24 wolves). However, the relative potential for successful reintroductions within each of these areas may also depend on public attitudes and details of land use that are not quantifiable using available data (Servín et al. 2007).

Comparing potential core areas of suitable habitat between the US and Mexico

Although we sought to use the best available data in both the US and Mexico, we encountered inconsistencies in the resolution and completeness of data between the two nations. This inconsistency was greatest for the roads data, as the mapped roads network in Mexico was quite sparse when compared to the relatively complete mapping of four-wheel drive routes in the US (INIT, USGS)(Figure 4). In contrast, human population data was relatively consistent in scale between the two nations. Carroll et al. (2005, 2006) concluded that the sparseness of the available data on mapped human impacts (roads and altered habitat types) in remote areas of the Sierra Madre Occidental strongly affected estimates of potential wolf habitat. The authors therefore concluded that their model results for the Sierra Madre Occidental (cores areas 1 through 4, Figure 7) should be used only as an initial comparison of habitat suitability among sites within Mexico to be followed by local surveys of land use and prey abundance.

Available vegetation data also differed between the two nations. Such data was available at a finer spatial scale in the US than Mexico. Conversely, thematic detail (floristic types) was greater for the Mexican data. However, due to the generalized nature of the rankings of vegetation by wolf habitat value (both due to generalist nature of wolf habitat associations and lack of detailed
data on Mexican wolf natural history) and the large extent of wolf territories, both the thematic and spatial detail of the vegetation data is sufficient for the recovery planning.

These bi-national contrasts in the data used in the studies reviewed above limit quantitative comparison of habitat suitability between US and Mexican potential core areas of suitable habitat. For example, Carroll et al. (2005) concluded that “the resolution of the habitat data was still inconsistent between US and Mexico to an extent that significantly limits comparability between Mexican and US reintroduction sites.”

Implications of comparison of core areas of suitable habitat

Despite the challenges arising from bi-national contrasts in available data, we conclude based on qualitative comparisons that potential core areas in the US are likely to support larger wolf populations than potential core areas in Mexico (Table 1). The Mexican wolf recovery plan developed by a team of scientists in Mexico similarly concluded that it would be difficult to find appropriate habitat for reintroduction to Mexico (SEMARNAT 2000). The core areas identified in the US are 24,000-25,000 km² in extent. Core areas identified by Araiza et al. (2006) in Mexico were 6,000-17,000 km² in extent. Although the subsequent analysis by Araiza et al. (in review) expanded the potential recovery areas to encompass areas of 12,000 to 30,000 km² in extent, they noted that areas of low or moderate mortality risk formed no more than half of these expanded areas (e.g., 10,500 of the total 30,000 km² comprising the Chihuahua/Durango potential recovery area). Notably, the core areas in the US are defined by large tracts of federal land managed per longstanding, legally mandated conservation prescriptions that ensure that the risk to wolves from human-caused mortality is relatively low. Such public land is absent in the core areas in Mexico.

In addition to the contrast in patterns of land ownership between the US and Mexico that would affect wolf survival, contrast in prey density between the US and Mexico core areas results in a sharply different estimates of the number of wolves that could be potentially supported in each of the core areas. Ungulate biomass in US core areas (with the exception of western Texas, where prey density is likely low) was 4.1-7.6 deer equivalents (UBI)/km² vs. 2-4 deer/km² in Mexico. Although habitat exists in the in the U.S./Mexico border area, the area would likely serve as a
mortality sink for wolves (Carroll et al. 2005). The Service concluded that other than the
BRWRA, since other reintroduction sites in the border country were isolated and could each
support only 5 to 30 wolves that they offered little support to Mexican wolf recovery (U.S. Fish
and Wildlife Service 1996). This is consistent with Service findings that the small isolated gray
wolf population that inhabits Isle Royale National Park (Peterson et al. 1998) does not contribute
to gray wolf recovery in the Western Great Lakes states (U.S. Fish and Wildlife Service 1992,

Recommended Recovery Region for the Mexican Wolf
Studies of Mexican wolf habitat suitability in the US and Mexico as summarized above and
Appendix 1 indicate that the most feasible and expeditious recovery strategy will require a
recovery region that includes Mexico, extreme western Texas, Arizona, New Mexico, southern
Utah (as circumscribed by interstate highways 15 and 70), and southern Colorado (as
circumscribed by interstate highways 70 and 25) (Figure 11). Three core areas of suitable habitat
exist within this recovery region and include: 1) the BRWRA and adjacent public lands, 2) the
Grand Canyon and adjacent public lands in northern Arizona and southern Utah (circumscribed
by interstate highways 15 and 70), and 3) Carson and San Juan National Forests and other
connected areas of public lands and private lands with conservation management in northern
New Mexico and southern Colorado (circumscribed by interstate highways 70 and 25). Primary
reintroduction sites could be found within each of these core areas since they all include large
patches of high quality habitat on public or private lands subject to conservation mandates
(National Park, wilderness, conservation easements) where wolves would experience relatively
low human-caused mortality. The uncertainty introduced by climate change notwithstanding,
these core areas of suitable habitat are projected to persist under potential future landscape
changes (Carroll et al. 2006). Based on GIS modeling of current habitat conditions it is
estimated that these three core areas in the US could support > 250 wolves (Table 1) and the
entire US portion of the recovery region could support > 1,000 wolves (Carroll et al., 2003,
2006). In an independent assessment of standing ungulate biomass Heffelfinger (unpublished
data assembled while serving on the Science and Planning Subgroup) used ungulate density
estimates and concluded that current abundance levels in the entire US portion of the recovery region could support > 900 wolves.

Although some areas which are not currently suitable habitat might become suitable in future decades due to recovery actions, this plan's recovery strategy focuses primarily on areas that are currently among the most highly secure and productive areas for wolf recovery. Expeditious recovery (that is, consistent with the timeline set forth in this plan) is necessary to fulfill recovery objectives because any additional time that captive and wild Mexican wolf populations remain at their current low population size accentuates genetic threats and reduces future recovery potential. In other words, the accumulating genetic effects of the current population bottleneck lend urgency to recovery, and require a focus on areas where growth of Mexican wolf populations will be relatively rapid due to high survival rates and adequate prey abundance.

Relevance to Historical Range

Two of the core areas of suitable habitat, the Grand Canyon and adjacent public lands in northern Arizona and southern Utah (as circumscribed by interstate highways 15 and 70), and the Carson and San Juan National Forests and other connected areas of public lands and private lands with conservation management in northern New Mexico and southern Colorado (as circumscribed by interstate highways 70 and 25) are located north of the Mexican wolf’s historical range. For the following reasons it is appropriate to include both areas in the Mexican wolf recovery region.

- The Mexican wolf is a close living relative to the gray wolf subspecies that occupied the areas historically.
- The Mexican wolf is the closest geographic source of wolves to the areas.
- The Mexican wolf is capable of surviving and thriving in the areas.
- Of all gray wolf subspecies, the Mexican wolf is in greatest need of conservation assistance.
- Including areas in Mexican wolf recovery region that are located outside the subspecies’ historical range is consistent with the best available science.
- The Mexican wolf is not recoverable unless the areas are included in the recovery region.
Each of these reasons is discussed below.

The Mexican Wolf is a Close Living Relative to the Gray Wolf Subspecies That Occupied the Areas Historically.

The Mexican wolf is a close living relative to the gray wolf subspecies that occupied the areas historically. These two core areas are proximate to (Brown 1983, Bogan and Mehlhop 1983, Hoffmeister 1986, Nowak 1995) or well within (Leonard et al. 2005) the large zone of gray wolf genetic intergradation that characterized the southwest historically (see Taxonomy). Leonard et al. (2005) interpret the geographic distribution of genetic markers as evidence that historical gene flow among the Mexican wolf and other wolf “subspecies” was extensive in time and space and supports an area for recovery of the Mexican wolf that extends well beyond the subspecies historical range.

The Mexican Wolf is the Closest Geographic Source of Wolves to the Areas.

The Minnesota wolf (C. l. nubilus), a close relative of the Mexican wolf, was probably widespread throughout the southwestern US historically (Nowak 1995) until it was extirpated from the region over 50 years ago (Brown 1983, Robinson 2005). In response, at least a few Mexican wolves moved north to occupy the vacated habitat in New Mexico and Arizona (Gish 1977, Scudday 1977, Nowak 1995). Nowak (1986:1-2) considered the relevance of the shifting range when he endorsed the reintroduction of the Mexican wolf “beyond its designated range on the grounds that it could have occupied such sites naturally, if other wolves had not already been there, and indeed, may have been attempting to do so after the other wolves had been extirpated... Suppose, however, that there had been no gray wolves to the immediate north of the range of baileyi. In that case, there is no reason to think that baileyi would not have kept right on going to eventually occupy a large part of the western United States... The genus Canis is remarkably adaptable to a variety of conditions. The main factor limiting the distribution of a particular species or subspecies seems not to be different habitat conditions, but rather the presence of another kind of Canis. It has not been unusual for one subspecies of gray wolf to invade and establish itself in the range of another subspecies that had disappeared.”
After conducting an exhaustive review of molecular genetics and morphological data (Chambers et al. 20xx) the senior author concluded: “I think drawing a line to represent the geographical limits of the taxon C. l. baileyi (its boundary if you will) will always be problematical (I dislike that term, but it actually fits this situation).... I am fearful that in defining a subspecies range, that some may try to manage to maintain that boundary. A lesson from our range-wide review of North American wolves is that there are genetic lineages of wolves that correspond to some subspecies groupings, but the geographical relationships of these lineages has been dynamic over time. Even if one maps a range for a subspecies for any given time, it would be a mistake both biologically and in terms of management to treat a boundary as a static line. They never have been static."

Wide-ranging wolves from the BRWRA affirm Nowak’s expectation about range expansion and indicate that the subspecies’ current range extends north of the historical range proposed by Parsons (1996). Two wolves from the BRWR traveled to the edge of the historical range and two beyond that range (see Life History). The wolf’s ability to colonize distant, unoccupied habitat is well known (Mech and Boitani 2003) and is one reason why the USFWS recognizes the importance of long distance movements by gray wolves for defining the boundaries of recovery areas (U.S. Fish and Wildlife Service 2009:15126 – 15127). It is quite possible that the four wolves that traveled considerable distances from the BRWRA could have survived and reproduced (assuming the presence of other Mexican wolves) in areas well outside the historical range if they had not been captured and returned to the BRWRA. The proximity of the BRWRA population and the wide-ranging capabilities of wolves combine to indicate that northern Arizona/southern Utah and northern New Mexico/southern Colorado will be part of the subspecies’ future range due to similar forays by other young dispersing wolves.

The Mexican Wolf is Capable of Surviving and Thriving in the Areas.

Data collected from the BRWRA, especially those concerning food habitats (see Wolves and Prey), indicate that Mexican wolves are capable of living as far north as southern Utah and southern Colorado. This is not surprising given the broad ecological abilities of gray wolves.

Of All Gray Wolf Subspecies, the Mexican Wolf is in Greatest Need of Conservation Assistance.
As noted previously (see Taxonomy and Distribution) early taxonomists identified five gray wolf subspecies that inhabited the southwestern US including three (C. l. mogollonensis, C. l. monstrabilis, C. l. youngi) that have been have been extinct for decades and a fourth (C. l. nubilus) that is represented in the wild by a robust population in the western Great Lakes states and eastern Canada. This subspecies was extirpated from the southwestern US over 50 years ago (Brown 1983, Robinson 2005). The fifth southwestern subspecies, C. l. baileyi, is represented in the wild by only one small population in the BRWRA (see Current Population and Trends).

Given its precarious status in the wild, the Mexican wolf is the most endangered gray wolf subspecies (Phillips et al. 2000) and has been targeted as a conservation priority by the Wolf Specialist Group for the International Union for the Conservation of Nature (IUCN) (L.D. Mech, pers. comm.). Including northern Arizona/southern Utah and northern New Mexico/southern Colorado in the Mexican wolf recovery region is strongly indicated from a conservation perspective.

Including Areas in the Mexican Wolf Recovery Region That Are Located Outside the Subspecies’ Historical Range is Consistent With the Best Available Science.

Defining a Mexican wolf recovery region that extends outside the historical range for the subspecies is consistent with the conclusion reached by the IUCN Conservation Breeding Specialist Group and other experts involved in a comprehensive wolf population and habitat viability analysis (Phillips et al. 2000). Additionally, it is consistent with the findings of the science and planning subgroup of the recovery team that was assembled to develop a recovery plan for the gray wolf southwestern distinct population segment (DPS) that was adopted by the USFWS in 2003 and included the southern half of Utah and Colorado (Federal Register 68:15804 – 15875). Members of that subgroup concluded that C. l. baileyi was the most appropriate source stock for recovering the DPS (U.S. Fish and Wildlife Service 2003).

More broadly, defining a recovery region that extends outside a species or subspecies historical range following a comprehensive assessment of historical, contemporary, and future conditions is supported by leading ecological research (Lomolino 2006, Caro 2007, McLachlan et al. 2007, Davis et al. 2011). In an increasingly dynamic and uncertain world (Dimento and Doughman 2007, Brown 2011, Orr 2010), recovering taxa outside purported historical ranges (assisted
Migration) based on diligently assembled scholarship from the best available science may become increasingly common (Lomolino 2006, Caro 2007, Hunter 2007, McLachlan et al. 2007, Hayward 2008, Davis et al. 2011, Marris 2011). While this approach is not without risk (Rubenstein et al. 2006, Ricciardi and Simberloff 2009, Marris 2011:111-132), it seems environmentally benign when it involves species that are defined by ecologically similar subspecies with historical distributions that included extensive zones of intergradation. Such an approach to recovery will allow such species (or subspecies) to experience greater security than a more conservative approach based on an exclusive focus on subspecies’ historical ranges. The Mexican wolf is one such subspecies: it arises from a species that is defined by many subspecies all of which were ecological generalists with historical ranges that included wide zones of ecologic and genetic integration (Brewster and Fritts 1995, Mech and Boitani 2003:11-17, Von Holdt et al. 2011, Chambers et al. submitted).

The Mexican Wolf is Not Recoverable Unless the Areas are Included in the Recovery Region. Due to alteration of the historic habitat inhabited by Mexican wolves from human development and resource use, defining a recovery region for the Mexican wolf that focused solely on historical range would preclude recovery (see Geography of Recovery). The authors of the 1982 Mexican Wolf Recovery Plan concluded the same and commented: “In formulating a recovery plan objective for any subspecies of *C. lupus*, one must realistically view, not only the causes of the wolf’s past endangerment, but also present trends toward ever-increasing human needs – whether real or perceived – for space and for the renewable and nonrenewable resources present or producible in wolf habitat” (USFWS 1982:23). The tension between recovery and habitat availability within historical range led them to conclude that recovery of the Mexican wolf was not possible. That conclusion remains valid. This problem is remedied by including areas outside the Mexican wolf’s historical range in the recommended recovery region.

**Land Ownership Status and Use in the US and Mexico**

Recovery plans in the United States for wide-ranging species such as the wolf typically assume that the primary responsibility for species conservation will fall on federal lands, with additional activities potentially occurring on private and other non-federal lands when these actions are also necessary for recovery. A mixed pattern of land ownership characterizes that portion of the
Mexican wolf recovery region in Utah, New Mexico, and Arizona (Figure 9, Table 3). In contrast western Texas is nearly all privately owned which seriously compromising the usefulness of otherwise suitable wolf habitat there to serve as a primary reintroduction area. Regulations limiting wolf mortality in western Texas (e.g., limitations on hunting of wolves) could, however, allow a population of wolves to become established there due to natural dispersal from either the Blue Range or any wolf populations resulting from future reintroductions in the northern portion of Coahuila state (Mexico).

Table 3*. Land ownership in the Mexican wolf recovery area.

<table>
<thead>
<tr>
<th>Category of Land Type (Landownership)</th>
<th>Amount of land type found within the Recommended Mexican Wolf Recovery Region in the U.S. (percentage)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Federal Land</td>
<td>36.6%</td>
</tr>
<tr>
<td>Native American Land</td>
<td>12.8%</td>
</tr>
<tr>
<td>Private Land</td>
<td>41.7%</td>
</tr>
<tr>
<td>State Land</td>
<td>8.6%</td>
</tr>
<tr>
<td>Other Land (Local Govt. Unknown, Joint Ownership)</td>
<td>.3%</td>
</tr>
</tbody>
</table>

*Note: We are still waiting on data layers to be able to map/calculate land ownership for Mexico.

Mexico
Ejidos and communities

Policy-Related Considerations

ESA
An exclusive focus on historical range is not mandated in the ESA or related USFWS policies. There is no direct reference to historical range in the ESA, and only one ESA related policy makes reference to it [50 CFR 17.81(a)]: “The Secretary may designate as an experimental population a population of endangered or threatened species that has been or will be released into suitable natural habitat outside the species current range (but within its probable historic range).
The Mexican wolf recovery region recommend in this plan is similar to the area delineated for southwestern gray wolf (*Canis lupus*) distinct population segment (DPS) that was adopted by the USFWS in 2003 (Federal Register 68:15804 – 15875). While the language authorizing the DPS was silent on the topic of gray wolf subspecies, the science and planning subgroup of the team that was assembled to develop a recovery plan for the DPS concluded that *C. I. baileyi* was the most appropriate source stock for recovering the DPS (USFWS 2003).
Describe state game commissions, state laws/regulations/commission policies/rules, management plans, etc. related to wolves.

Binational US-Mexico Policy Coordination

As previously described (see Background), Mexico and the United States have worked independently yet collaboratively on Mexican wolf recovery for over three decades. Today, both countries are actively engaged in the binational captive breeding program and in efforts to re-establish the Mexican wolf in the wild. Recognition of the historical cross-border distribution of the Mexican wolf paired with recognition that the two countries’ legal frameworks for species protection differ, leads both countries to desire the establishment of a bi-national collaborative framework that is mutually supportive yet respectful of each country’s autonomy.

Smaller populations in Mexico as well as in the US (e.g., Texas) could be critically important for ensuring connectivity between larger core areas in each country, as well as meeting representation goals (Shaffer and Stein 2000). The modest potential for connectivity between US and Mexican wolf populations suggests that recovery planning would benefit from a binational coordination. However, determining the appropriate degree of coordination, and the respective roles of actions in US and Mexico, is difficult given contrasting policy contexts and biological realities in the two nations.

There are many similarities between Mexico and the United States in the regulatory context of Mexican wolf conservation. Both have federal legal frameworks for recovery: Mexico's Ley General de Vida Silvestre (2000), NOM 059 ECOL 2001 (2002), and the United States' ESA ofBoth nations have developed recovery plans for the Mexican wolf. Mexico's Programa de Recuperacion del Lobo Mexicano was published in 1999; the United States' Mexican Wolf Recovery Plan was published in 1982, and was co-signed by Mexico's Direcccion General de la Fauna Silvestre. In both nations, Federal agencies lead the recovery efforts: Mexico's Direcccion General de Vida Silvestre (DGVS) and the US Fish and Wildlife Service (FWS). Both nations have comparable advisory committees for recovery: Mexico's Subcomite Technico Consultivo Nacional para la Recuperacion del Lobo Mexicano (STCN RLM); the United States' Mexican Wolf Recovery Team. In both nations, the parties interested in and affected by wolf recovery
actions include state and local governments, as well as non-governmental organizations and private property owners.

There are, however, also significant differences in the regulatory context between Mexico and the United States. Whereas the US ESA mandates development of species-specific recovery criteria, Mexico's red list of endangered species (NOM 059 ECOL 2001) has downlisting criteria that apply to broad categories of species, one of which includes the Mexican wolf.

Local and Regional Culture

Etc...

Summary Description of Recovery Area
J. Reasons for Listing/Threats Assessment

(Note to Reviewer: I have provided an explanation of what this subsection of the plan should provide directly from the Service’s recovery planning guidance: “This subsection should include an overview of the species’ decline, and its causes of decline (to the extent they can be determined). The causes of decline, or threats, may be past, continuing from the past into the future, newly identified, and reasonably anticipated in the future (including, but not limited to, those that have been temporarily curtailed but are likely to recur). Where possible, this subsection should also identify the source of threats, e.g., if the threat is siltation in a stream, the source could be urban runoff, watering cattle, removal of riparian vegetation, recreational uses, etc. Noting the source helps tailor the recovery action(s) needed. When discussing each threat and its source(s), the geographic scope, severity, and frequency of the various threats should be indicated, noting those that present greater or lesser threats to the species. Uncertainties with respect to threats to the species should be identified as well…To provide continuity among the listing package, this section and the recovery criteria, threats that were listed in the final rule should be addressed in this section and discussed in terms of the five listing factors. If the species was recently listed, much of this information can be taken from the “Factors Affecting the Species” section of the listing rule. Plans should assess any new threats, changes in severity of threats, and threats that have been reduced or removed since publication of the final listing rule.”)

The ESA defines an “endangered species” as “any species which is in danger of extinction throughout all or a significant portion of its range” 16 U.S.C 1532(6). Similarly, a “threatened species” is “any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range” 16 U.S.C 1532(20). A species is listed as threatened or endangered if one or more of the following five factors in section 4(a)(1) of the ESA are determined to be responsible for its condition (a process referred to as a 5-factor analysis):

(A) the present or threatened destruction, modification, or curtailment of its habitat or range;

(B) overutilization for commercial, recreational, scientific, or educational purposes;

(C) disease or predation;
the inadequacy of existing regulatory mechanisms; or,

(E) other natural or manmade factors affecting its continued existence.

Subsequent 5-factor analyses are conducted while a species is listed to periodically assess its status and ensure that conservation actions are addressing current threats. Finally, a 5-factor analysis is conducted when a species is proposed for delisting due to recovery to ensure that none of the factors continue to threaten or endanger the species.

Several 5-factor analyses have been conducted for the Mexican wolf. In the initial proposal to list the Mexican wolf as endangered in 1975, the Service found that threats from habitat loss (factor (A)), sport hunting (factor (B)), and inadequate regulatory protection from human persecution (factor (D)) were responsible for the subspecies’ decline and near extinction (40 FR 17590-17591, April 21, 1975). In the 1978 listing of the entire gray wolf species as endangered throughout the coterminous United States and Mexico (except for Minnesota, where it was classified as threatened), the Service identified the same threats (43 FR 9607-9615, March 9, 1978).

In 2003, when the Service reclassified the gray wolf into three distinct population segments, the agency conducted a 5-factor analysis of the Mexican wolf as a part of the SWDPS (68 FR 15804-15875, April 1, 2003). The reclassification rule stated that habitat destruction or modification (factor (A)) was not currently considered a threat or deterrent for restoration of southwestern (Mexican) gray wolves based on the 1982 Mexican Wolf Recovery Plan which stated that sufficient habitat existed at that time to support current reintroduction objectives. “Take” for commercial or recreational purposes (factor (B)) was not considered a threat. 16 U.S.C 1532(19). Diseases and parasites (factor (C)), which are known to be an important consideration in wolf conservation, were not known to be significant factors in the decline of the Mexican wolf, and there was no reason to believe they would hinder recovery. Illegal killing (“human predation”, considered factor (C) in the rule) was recognized as a factor that may slow, but not likely preclude, recovery in the Southwest. Regulatory protection of reintroduced Mexican wolves was deemed adequate (factor (D)). Finally, public attitudes toward gray wolves were cited as a primary determinant in the long-term recovery status of
wolves (factor (E)), and the rule anticipated that the potential for human-wolf interactions would increase as the number of wolves increased.  

The Mexican Wolf Conservation Assessment (USFWS 2010 add cite) contained an updated 5-factor analysis specific to the Blue Range population (…summarize findings…). The draft reclassification….

The following 5-factor analysis identifies current and anticipated threats throughout the entire area considered potentially suitable recovery habitat for the Mexican wolf (see Geography of Recovery), thus the geographic scope of this assessment is larger than that in the Conservation Assessment or the draft rule to reclassify….

When available, information on the source, geographic scope, severity, frequency, and overall known or perceived magnitude of each threat is provided.
(This table is a result of team brainstorm at February 2012 meeting; we will continue to revise it…)

<table>
<thead>
<tr>
<th>Factor A: Habitat Attribute</th>
<th>Stressor</th>
<th>Geographic Scope</th>
<th>Severity / Intensity</th>
<th>Occurrence (Past/present/future; single episode vs. continuous; regular vs. sporadic; likelihood)</th>
<th>Overall Magnitude</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey Availability / Biomass</td>
<td>Forage production</td>
<td></td>
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<tr>
<td></td>
<td>Competition between livestock and other prey for forage</td>
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<tr>
<td></td>
<td>Spread of non-native vegetation (inedible? lower nutrition?)</td>
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<tr>
<td></td>
<td>Change in vegetation due to livestock grazing (inedible? lower nutrition?)</td>
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<tr>
<td></td>
<td>Wolf predation</td>
<td></td>
<td></td>
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<td></td>
<td>Ungulate mortality</td>
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<tr>
<td></td>
<td>Ungulate Disease (See Factor C.)</td>
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<td></td>
<td></td>
<td></td>
<td>Ungulate mortality; ___ in wolves</td>
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<tr>
<td>Habitat Quantity to Support Core Populations</td>
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<tr>
<td>Increasing urbanization</td>
<td>Decreased ability for natural wolf range expansion; decreasing habitat availability over time in areas of low human inhabitance; increased likelihood of wolf-human interactions</td>
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<tr>
<td>Increasing road density / traffic</td>
<td>Mortality from vehicular collision; behavior modification? (denning, dispersal)</td>
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<td>Quantity of public land</td>
<td>Private lands have a greater potential for human-wolf interactions</td>
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<td>Wildfire</td>
<td>Mortality; prey availability?</td>
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<tr>
<td>Climate Change</td>
<td>Regional Drought Cycles</td>
<td>Mortality? Prey availability?</td>
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<tr>
<td>Habitat Connectivity to Support Migration Between Subpopulations</td>
<td>Increasing urbanization in US and Mexico</td>
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<td>Increasing road density / traffic in US and Mexico</td>
<td>Borderlands activities and infrastructure</td>
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<td>Habitat Quality</td>
<td>Increasing urbanization in US and Mexico</td>
<td>Behavior disturbance (</td>
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<td>Regional Drought</td>
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<td><strong>Cycles</strong></td>
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<td><strong>Climate Change</strong></td>
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<td><strong>Wildfire</strong></td>
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<tr>
<td><strong>Factor B. Overutilization</strong></td>
<td>Vaccinations and medical treatment; capture and control actions</td>
<td>Mortality</td>
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<tr>
<td>Incidental take by FWS and partner agencies</td>
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<td><strong>Factor C. Disease</strong></td>
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<td><strong>Rabies</strong></td>
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<tr>
<td>Transmission by domestic canids</td>
<td>Mortality</td>
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<tr>
<td>Transmission by wild canids or other animals</td>
<td>Mortality</td>
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<tr>
<td>Lack of labeled vaccines for wolves</td>
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<td><strong>Parvovirus</strong></td>
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<td>Transmission by domestic canids</td>
<td>Mortality</td>
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<td>Transmission by wild canids or other animals</td>
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<td><strong>Distemper</strong></td>
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<td>Transmission by domestic canids</td>
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<td>Transmission by wild canids</td>
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<tr>
<td>Corona virus</td>
<td>Chronic wasting disease</td>
<td>Mortality to ungulates;</td>
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<tr>
<td>Predation (on wolf by other predators)</td>
<td>Competition between predators</td>
<td>Mortality</td>
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**Factor D. Regulatory Mechanisms**

<table>
<thead>
<tr>
<th>Legislative efforts to delist wolves in UT, AZ, NM</th>
<th>Public opinion</th>
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</thead>
<tbody>
<tr>
<td>Illegal / accidental take of Mexican wolves</td>
<td>McKittrick policy / difficulty successfully prosecuting offenders</td>
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<tr>
<td></td>
<td>Nighttime spotlight hunting</td>
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<td></td>
<td>Misidentification</td>
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<td></td>
<td>Lack of law enforcement capacity</td>
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| Progress / status of BRWRA | |

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<table>
<thead>
<tr>
<th>reintroduction</th>
<th>BRWRA Regulations BRWRA boundary, SRZ/PRZ. Removals due to depredations, boundary removals, etc.</th>
</tr>
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<tbody>
<tr>
<td>Funding mechanisms to support reintroduction and recovery</td>
<td></td>
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<tr>
<td>Mechanisms to regulate hybrids</td>
<td></td>
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<tr>
<td>Mechanisms that reduce forage (repetitive with factor A?)</td>
<td>Competing management regimes stemming from single species management focus (e.g., MSO vs MW?)</td>
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<tr>
<td>Insufficient 7(a)(1)(A)</td>
<td>Budgetary and staffing constraints of federal agencies</td>
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<tr>
<td>Management by litigation</td>
<td>Public opinion; lack of policy direction from USFWS (SPR, use of DPS policy, etc).</td>
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<tr>
<td>Lack of a (binational)</td>
<td>FWS priorities, US-Mexico coordination</td>
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<tr>
<td>recovery plan</td>
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<tr>
<td><strong>Factor E. Other</strong></td>
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<tr>
<td>Tribal participation in recovery</td>
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<tr>
<td>Lack of funding, economic impacts</td>
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<tr>
<td>Competing land uses</td>
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<td>Cultural values</td>
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<td>Stakeholder participation in recovery</td>
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<td>Inadequate public education</td>
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<tr>
<td>Social and economic impacts</td>
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<tr>
<td>USFWS intolerance of local communities, culture</td>
<td></td>
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<tr>
<td>Lack of funding to support recovery implementation</td>
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<tr>
<td>Political support</td>
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<td>Interagency coordination to support recovery</td>
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<tr>
<td>Foothold traps</td>
<td>Release sites too close to human inhabitance</td>
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<tr>
<td>Human tolerance</td>
<td>Fear of wolves, negative perceptions of wolves</td>
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<td></td>
<td>Dislike of federal government</td>
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<td></td>
<td>Economic impacts of reintroduction</td>
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<td>Wolf habituation to humans</td>
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<tr>
<td>Progress of BRWRA</td>
<td>Lack of response to 3 year and 5 reviews</td>
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<td></td>
<td>Depredation and boundary related removals</td>
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<td></td>
<td>Human-caused mortality (all sources; poisoning, road kill, other)</td>
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<td></td>
<td>Lack of incentives, funding, resources to support implementation, esp. in local communities to reduce interactions,</td>
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<tr>
<td>Genetic health</td>
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<tr>
<td>Lack of gene flow</td>
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<td>Hybridization with dogs and coyotes</td>
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<td>Genetic swamping by northern wolves</td>
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<tr>
<td>Low levels of genetic variation, lack of robustness</td>
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<tr>
<td>Limited capacity of captive breeding program</td>
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<th>Use of livestock protection collars</th>
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especially depredation;
management of human habituated wolves, aversive conditioning
communication with affected parties
monitoring of uncollared wolves
Lack of trust (of USFWS) due to failure to live up to commitments
K. Conservation Efforts

(Note to Reviewer: This section is not intended to be a laundry list of all conservation efforts, rather it is a concise list of those efforts that most contribute to recovery. Due to the specific situation with the Mexican wolf, i.e., that it is contained within the BRWRA, I’m not sure this section is terribly relevant. We may just want to reiterate the reintroduction projects and captive breeding program with some mention of important partners, etc. Perhaps also the Interdiction Council?)
L. Biological Constraints and Needs

(Note to Reviewer: Recovery planning guidance says, “Based on all of the above, identify any biological constraints or needs of the species that need to be considered in planning and management. The purpose of this section is to state up front any known limiting factors that are biologically inherent in the species and non-modifiable, and which must be honored when designing any management/recovery program for that species. Examples might include extremely delayed maturity which requires unusually high annual survival in juvenile stages; needs for a particular and rare habitat for one or another life history stage; or a need for a minimum population size for successful breeding behavior.”

Perhaps we focus here on the “basic three”, prey, large area, and security from humans? Whatever constraints we list, this section will not provide new information; rather it will refer back to where the constraints are initially discussed (probably in the Background or Threats Assessment) and reemphasize them as critical considerations for the recovery effort. This section should be just a few pages or less in length.)

Large Area with Security from Human Exploitation

Prey

Historical data indicate that Mexican wolves preyed extensively on the diminutive Coues white tailed deer (*Odocoileus virginianus couesi*) prompting some to suggest that the subspecies was an ecological or habitat specialist (Brown 1983:6 12). An early assessment of Mexican wolf ecology was completed by McBride (1980). On the notion that the Mexican wolf was a habitat specialist fine tuned to the Madrean montane forests, evergreen woodlands, and adjacent grasslands in Mexico, extreme southeast Arizona, and southwest New Mexico (Brown 1983:7), McBride (1980:13) wrote: "While it might appear that wolves
Historically Mexican wolves in Mexico probably preyed differentially on Coues white tailed deer simply because of its relative abundance. Supporting this notion are studies that indicate that elk (*Cervus elaphus*), the most abundant wild ungulate in the BRWRA, is the primary prey of Mexican wolves there despite an abundance of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) (Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009a). Consequently, this recovery plan is based on the expectation that the Mexican wolf is an ecological generalist, like all other gray wolf subspecies, and can successfully subsist on both small and large ungulates. This expectation does not detract from the Mexican wolf’s genetic uniqueness. It is, however, impossible to know if this uniqueness resulted from selective pressures brought about by the specific ecological conditions of the southwestern US and Mexico or a result of random genetic drift that attends any sexually reproducing organism.
M. Tribal Perspectives on Mexican Wolf Recovery

(Note to Reviewer: This subsection under development by Tribal Subgroup, 6-2012.)
N. Binational Coordination for Mexican Wolf Recovery

(Note to Reviewer: The 3 paragraphs below were developed by the 2002 DPS team; perhaps they can serve as a model for us? Also, Carlos has drafted some text that for now I placed in Section III Recovery Actions as a placeholder to develop a US-Mexico MOU.)

“Despite their independent authorities, the two countries are similar in many ways regarding gray wolf conservation. Both have legal frameworks for recovery: Mexico’s Ley General de Vida Silvestre (2000), NOM-059-ECOL-2001 (2002) and the Endangered Species Act of 1983. Both countries have developed recovery plans for the Mexican wolf – Mexico’s Programa de Recuperacion del Lobo Mexicano was published in 1999; the United States’ Mexican Wolf Recovery Plan was published in 1982, and was co-signed by Mexico’s Direcion General de Vida de la Fauna Silvestre. In both countries, Federal agencies lead the recovery efforts: Mexico’s Direcion General de Vida Silvestre (DGVS) and the U.S. Fish and Wildlife Service. Both countries have comparable advisory committees for recovery: Mexico’s Subcomite Technico Consultivo Nacional para la Recuperacion del Lobo Mexicano (STCN-RLM); the Service’s Mexican wolf recovery team. In both countries, the parties interested in and affected by wolf recovery actions include State and local governments, as well as nongovernmental organizations and private property owners.

There are, however, significant differences between Mexico and the United States in approaches and limitations to Mexican wolf recovery. The listed entity in Mexico is the subspecies, Canis lupus baileyi; it is listed as extinct in the wild. In the United States, the gray wolf species, Canis lupus, is listed [UPDATE as necessary], with a suggested focus on the subspecies. Mexico’s red list of endangered species (NOM-059-ECOL-2001) has down-listing criteria that apply to broad categories of species, one of which includes the Mexican wolf. The United States’ recovery plan does not include downlisting or delisting criteria [UPDATE!]. Once a Federal recovery plan has been approved, Mexico has fewer legal mechanisms by which non-federal entities can constrain or advocate implementation of recovery actions than does the United States.
Clearly, the SWDPS Recovery Plan, when approved, will have legal standing in guiding recovery actions in the United States. It may also provide recommendations useful to recovery efforts in Mexico. Thus, the recovery plan can be an invaluable resource for complementary efforts in Mexico. However, Mexico is singularly responsible for enacting and implementing recovery regulations, plans, and approaches in Mexico. Its authorities and decisions are not subject to U.S. approval. Conversely, the recovery program in Mexico in terms of law, policy, and activity may provide insights for and be useful to complementary efforts in the United States, but decision made by Mexico for Mexico are not binding on the United States. Also, by necessity and force of law, each country must respect the other’s independent authority for law enforcement, i.e., Mexico cannot address law enforcement within the MOU proposed below” (excerpted from a white paper drafted by members of the 2003 SWDPS recovery team)
II. RECOVERY STRATEGY, GOALS, OBJECTIVES, AND CRITERIA

(A Note to Reviewer: )

A. Recovery Strategy

The ultimate goal of this Recovery Plan is to recover the Mexican wolf so that protections afforded by the ESA are no longer necessary, thus allowing for delisting. The objectives of the Recovery Plan describe a scenario in which the Mexican wolf’s population is stable or increasing, well distributed, and affected only by manageable threats. This Recovery Plan was developed using the best scientific information available and a “step-down” approach of objectives, criteria, and actions. As part of this approach, we have developed a state-of-the-science modeling framework that can provide information for numerous Mexican wolf recovery actions and management decisions. This modeling effort is described in detail in Appendix [ ].

Recovery criteria are specific statements that describe the conditions under which the Service would consider the Mexican wolf to be recovered. Recovery criteria aim to establish wild, self-sustaining populations of Mexican wolves which show attributes that demonstrate that threats have been ameliorated and, consequently, serve as objective, measurable guidelines to assist in determining when an endangered species has recovered to the point that it may be downlisted to threatened, or that the protections afforded by the ESA are no longer necessary and the species may be delisted. Recovery actions are those activities that are needed to accomplish the recovery criteria by addressing the specific threats that threaten or endanger the Mexican wolf. Implementation of the full suite of recovery actions to achieve this will involve participation from the States, Federal agencies, non-federal landowners, and the public.

Currently the most important biological threats to the Mexican wolf are 1) excessive mortality due to human-associated factors, 2) overall small population size due to the existence of only one wild population, that is itself small and exhibits a low rate of growth, and 3) continuing loss of genetic diversity in both the captive and wild populations. To address these threats, a successful recovery strategy must:
1. Manage the captive population to produce reintroduction stock with an optimal genetic composition and prospects for survival in the wild;
2. Reduce mortality of wild wolves so that multiple populations restored via reintroductions can quickly grow to a sufficient size and persist with minimal management to minimize further loss of genetic diversity;
3. Maintain habitat connectivity to ensure that these restored populations are effectively connected by dispersing wolves.

B. Recovery Goals, Objectives and Criteria

Recovery Goals

The goal of the Mexican wolf recovery plan is to improve the status of the species so it can be removed from protection under the ESA (i.e., delist the species). The interim goal is to downlist the Mexican wolf to threatened status under the ESA. This recovery plan was developed using the best scientific information available and a “step-down” approach of objectives, criteria, and actions. As part of this approach we developed a state-of-the-art modeling framework that provided insight into numerous recovery actions and related management options.

Recovery Objectives

The objectives of this recovery plan are:

1. To establish a sufficient number of Mexican wolf populations that each are sufficiently large and distributed such that the subspecies no longer requires listing under the ESA; and

2. To ensure that threats have been reduced or eliminated such that the requisite Mexican wolf populations are stable or increasing.

Recovery Criteria

There are five recovery criteria in this recovery plan that are discussed below. Recovery criteria are achievable targets that we believe can result from implementation of the
recovery actions in this recovery plan. Recovery criteria serve as objective, measurable
guidelines to assist in determining when an endangered species has recovered to the point
that it may be downlisted to threatened, or that the protections afforded by the ESA are no
longer necessary and the species may be delisted. Achievement of these criteria will take
time and is intended to be measured over the life of the plan, not on a short-term basis.
Consequently, recovery criteria should not simply be considered near-term
recommendations. The recovery criteria in this recovery plan represent the best
assessment of the conditions that should result in a determination that delisting the
Mexican wolf is warranted. Once the criteria are achieved the Service should complete a
formal regulatory rule-making process to delist the species.

Recovery Actions
Recovery actions are activities (both field-based and administrative) that need to be
implemented to achieve Mexican wolf recovery. Based on the statutory criteria for
determining whether a species should be listed [16 U.S.C. § 1533(a)(1)], not all recovery
actions need to be implemented for the Service to consider initiating the delisting
process. A change in status (downlisting or delisting) requires a separate rule-making
process based on an analysis of the same five factors (referred to as the listing factors)
considered in the listing of a species, as described in section 4(a)(1) of the ESA. These
include:

A. The present or threatened destruction, modification, or curtailment of its habitat or range;
B. Overutilization for commercial, recreational, scientific, or educational purposes;
C. Disease or predation;
D. The inadequacy of existing regulatory mechanisms; and
E. Other natural or manmade factors affecting its continued existence.

3.1 Reclassification to Threatened Under the ESA (downlisted)
The Mexican wolf can be reclassified to threatened when the following two criteria are met:
Criterion 1 – Adequate population size for a sufficient period of time: Three populations, with a census population of \( \geq 100 \) wolves each, have simultaneously been maintained in the wild for 8 successive years (2 successive generations).

Criterion 2 – Stable or increasing population trend: The trend for each of the three populations has been stable or increasing over 8 years (2 generations), as measured by a statistically reliable monitoring effort.

3.2 Reclassification to Unprotected Under the ESA (delisted)

The Mexican wolf can be delisted when the following five criteria are met:

Criterion 1 – Adequate Population Size for a Sufficient Period of Time:

Option 1: A metapopulation of \( \geq 850 \) wolves distributed among 4 populations in the wild that have simultaneously persisted for 8 successive years (2 successive generations) at or above the following sizes: three primary core populations with a census population of \( \geq 200 \) wolves each and a total population size of at least 750 wolves, and a secondary core population with a census population of \( \geq 100 \) wolves.

Option 2: A metapopulation of \( \geq 750 \) wolves distributed among 3 populations in the wild that have simultaneously persisted for 8 successive years (2 successive generations) with a census population of \( \geq 200 \) wolves each. Wolves in excess of the minimum number required for the 3 populations must occur as part of one or more of the 3 populations.

Option 3: A metapopulation of \( \geq 750 \) wolves distributed among 3 populations in the wild that have simultaneously persisted for 8 successive years (2 successive generations) with a census population of \( \geq 250 \) wolves each.

Criterion 2 – Adequate Population Connectivity: Immigration into each of the 3 populations via natural dispersal at a rate not less than 0.5 genetically effective migrants per generation (4 years), averaged over a period of 2 successive generations (8 successive years), as measured by
a statistically reliable monitoring effort. If the metapopulation includes ≥ 850 wolves then immigration into one of the 3 populations may be less than 0.5 genetically effective migrants per generation.

**Criterion 3 – Stable Population Trend:** The overall population trend of Mexican wolves throughout the range is stable or increasing over 8 years, as measured by a statistically reliable monitoring effort.

**Criterion 4 – Post-delisting Monitoring:** To monitor the continued stability of the recovered Mexican wolf, a post-delisting monitoring plan has been developed and is ready for implementation within the States of Arizona, Colorado, New Mexico, and Utah, as required in section 4(g)(1) of the ESA.

**Criterion 5 - Regulatory Mechanisms:** State management plans and adequate post-delisting regulatory protection are available.

* A "wolf population" is defined as a group of wolf packs that are relatively spatially contiguous and demographically connected by typical dispersal events, and are relatively spatially and demographically disjunct from other wolf populations, except for long distance dispersal events as specified above.

### 3.3 Justification for Recovery Criteria

This section explains the rationale for the recovery criteria.

**Guiding Principles for Mexican Wolf Recovery**

To identify appropriate criteria for recovery of the Mexican wolf, the Service used four Biological Indicators (abundance, redundancy, connectivity, and trend) and six “Guiding Principles” to help ensure recovery of Mexican wolf.

**Four Biological Indicators**
Six Guiding Principles:

1. Ensure sufficient abundance and trend indices to support population viability;
2. Ensure sufficient redundancy in populations;
3. Ensure sufficient connectivity among populations;
4. Ensure distribution of populations across representative habitats;
5. Ensure future adaptive potential by reducing the loss of genetic diversity.
6. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, and other factors;

Rationale for Delisting Criteria

Four categories of threats compromise the future of the Mexican wolf: reduced genetic diversity (due to inbreeding and genetic drift), demographic viability, environmental stochasticity, and catastrophes (disease outbreaks, etc.). Loss of genetic diversity is an inevitable consequence of small finite population size for any sexually reproducing organism like the Mexican wolf. However, if small, relatively genetically compromised populations are connected by immigration, the genetic diversity
maintained by the meta-population approaches that of one population as large as the sum of the connected populations. Thus, sufficient connectivity among Mexican wolf populations can help maintain genetic diversity, the viability of each of the small populations, and the long-term adaptive potential of the subspecies. Genetic threats are greater for the Mexican wolf than for other wolf subspecies because only 7 wolves were available as founders for the captive population which is the source of all Mexican wolves alive today. Effects of demographic viability and environmental stochasticity on population persistence also generally diminish as the size and connectivity of populations within a metapopulation increases.

Loss of genetic diversity, due to the pronounced population bottleneck that the Mexican wolf experienced, is a function of both small population size and the length of time that the population remains at a small size. Thus recovery criteria and associated recovery actions that are projected to result in rapid population growth and expeditious recovery are strongly preferred over those that would require more time. For example, an area that could support a core population under current habitat conditions should be strongly favored over an area that would require time consuming habitat restoration. Reintroductions projects should be designed to effect rapid population growth. A tepid or modest approach to population restoration will not serve Mexican wolf recovery well.

Environmental stochasticity generated by variation in environmental conditions (e.g., drought, fire, prey fluctuations) and catastrophes (episodic threats like disease outbreaks) challenge wild populations of most species, including wolves. In the case of the Mexican wolf, these “background” threats are especially problematic because of the subspecies’ eroded genetic diversity which has and will continue to compromise its adaptive potential. If a wolf population experienced no unfavorable variation in environmental conditions or disease occurrence, a small, genetically compromised population would probably be able to persist with greater certainty. Conversely, if the wolf population was genetically robust then it would have sufficient resilience (greater adaptive potential) to withstand the impact of these background threats. To achieve the same level of resiliency, a population derived from inbred and interrelated founders must be larger than a population derived from outbred and unrelated individuals, in order to...
avoid the genetic damage that occurs in a small inbred population during demographic
downturns associated with background threats.
We used the 3-stage modeling framework to evaluate what level of population
size, abundance, persistence, and connectivity are necessary for the Mexican wolf to be
likely able to withstand the threats described above in the presence of minimal
management. The criteria detailed below are appropriate because they serve as effective
redress of the general threats that compromise the Mexican wolf’s future in a manner
that ensures that the subspecies no longer fits the ESA’s definition of threatened or
endangered. Restoration of smaller populations than those recommended below would
be too small to withstand threats unique to each with a sufficient degree of certainty, and
would also result in a metapopulation with an insufficient level of connectivity to
withstand threats common to all. The several components of the recovery criteria are
thus interrelated and mutually supporting in ensuring recovery of the Mexican wolf in a
manner that comports with the spirit and intent of the ESA.

Criterion 1 – Adequate Population Size for a Sufficient Period of Time. A
metapopulation size of 750 wolves distributed among three populations ≥ of 200 wolves
each that have simultaneously persisted for 8 successive years (2 generations), is
considered highly robust to threats from environmental stochasticity as well as
inbreeding and demographic stochasticity (see Modeling Appendix). Populations of this
size and base persistence (i.e. 8 successive years), when connected within a
metapopulation, are resistant to threats to viability arising from loss of genetic variation.
Three populations are designated because 1) this number allows a metapopulation of
sufficient size and maximizes redundancy given the configuration of suitable habitat; and
2) arrangement of the three populations facilitates natural dispersal among populations
and thus retention of genetic variability. Any secondary core population(s) would help to
ensure distribution of populations across representative habitats. Two generations (8
successive years) was designated because it is a meaningful biological period of time
that is of sufficient duration to allow reliability in trend data that would indicate that
threats to population persistence have been reduced. Underlying these conclusions are
several themes emerging from the results of the 3-stage modeling framework (see Modeling Appendix):

1) Multiple large populations are necessary for Mexican wolf recovery.

2) Smaller secondary core populations, with the possible exception of the Sonora-Sky Island population, will likely contribute minimally to sustaining a viable regional wolf metapopulation.

3) Due to its poor genetic composition, the Blue Range population (BRP) in isolation underperforms the other two requisite populations. However, when three populations are present, the BRP’s central location allows it to receive dispersal from the two other populations, making its performance comparable to theirs.

The criterion for metapopulation size (750) is larger than the numeric recovery criterion for the Northern Rocky Mountains (450 wolves) and smaller than that for wolves in the Great Lakes states (1,350 to 1,450 wolves). The extent of genetic threats to Mexican wolves make recovery for this subspecies qualitatively different than for recovery of the metapopulation in the Northern Rocky Mountains that was established from outbred, unrelated individuals translocated from two disparate and naturally populations in Canada. Concerning the Great Lakes states, wolves there also were genetically diverse having arose from a large historic population that extended into Canada. Additionally, the extant population in the region included about 1,000 wolves at the time it was listed under the ESA. Recovery criteria were, therefore, developed that called for at least a modest increase in population size (35% to 45%).

**Criterion 2 – Adequate Population Connectivity.** A rate of natural dispersal, between three populations of the size specified above, of 0.5 genetically effective migrants per generation, is sufficient to alleviate threats to viability arising from loss of genetic variation. This rate of natural dispersal was also feasible given rates observed in other regions, and taking into account the lower levels of habitat connectivity evident between the three core areas of suitable habitat in the US portion of the recommended Mexican wolf recovery region.
Recovery Criterion 3 – Stable Population Trend. A stable or increasing population trend over 8 successive years (2 generations) supports the conclusion that threats have been adequately alleviated.

Recovery Criterion 4 – Post-delisting Monitoring. Continued population monitoring is necessary to ensure that the subspecies does not again fall to threatened or endangered status.

Recovery Criterion 5 - Regulatory Mechanisms: Adequate state management plans and other regulatory protection indicate that threats arising from inadequacy of regulatory mechanisms have been remedied.

Rationale for Downlisting Criteria

Recovery Criterion 1 – Adequate Population Size. The establishment of three primary core populations of 100 individuals each indicate reduction in threats to viability arising from loss of genetic variation and other factors.

Recovery Criterion 2 – Stable Population Trend. A stable or increasing population trend over 8 successive years (2 successive generations) supports the conclusion that threats to population persistence have been reduced.

Modeling Approach

Several modeling tools are available to inform development of recovery criteria based on best available science. It is important to acknowledge the strengths and weaknesses of each type of model and to consider information from multiple models in an appropriate decision-support context. We employed state-of-the-art modeling tools in a multi-step analysis for evaluating alternative recovery criteria. Collectively, these modeling tools allow comparison of estimated population viability (probability of population recovery)
and distribution among alternative recovery scenarios under a variety of potential conditions. The modeling approach consisted of three main steps:

**Step 1 Population Simulation Model** - Because of the magnitude of genetic threats to the Mexican wolf, we selected a population simulation model (Vortex; Lacy et al. 2010) with the capability to explore how genetic threat factors vary with population size, population growth rate, and metapopulation structure. This informs development of criteria for the size, number, and connectivity of subpopulations required to reduce the loss of genetic diversity to ensure the Mexican wolf’s long-term adaptive potential.

**Step 2 Habitat-based Model** – The Vortex model lacks sophisticated treatment of spatial dynamics or habitat. Once Step 1 of criteria development was completed, a second stage of the process was used to determine where on the landscape the requisite populations could be restored given the distribution of suitable habitat. Information sources for this step in modeling included results from a spatially-explicit population model (PATCH; Carroll et al. 2006).

**Step 3 Connectivity Model** - The Vortex analysis suggested that population connectivity was especially beneficial for persistence in Mexican wolves due the subspecies being derived from inbred and interrelated founders. We therefore examined what rate of natural dispersal between primary core populations was sufficient for population persistence and could be achieved given the distribution of suitable habitat. We did this by relating observed connectivity rates in other regions to relative habitat connectivity between primary core populations in those regions, and extrapolating to evaluate rates expected given habitat connectivity between potential primary core populations of Mexican wolves.
III. RECOVERY PROGRAM
(Note to Reviewer:)

A. Recovery Action Outline

Recovery actions are near-term recommendations to guide the activities needed to accomplish the recovery objectives and achieve the recovery criteria. This Recovery Plan presents actions that address overall recovery. These actions are organized following the five listing factors described earlier.

A. The present or threatened destruction, modification, or curtailment of its habitat or range;

B. Overutilization for commercial, recreational, scientific, or educational purposes;

C. Disease or predation;

D. The inadequacy of existing regulatory mechanisms; and

E. Other natural or manmade factors affecting its continued existence
B. Recovery Narrative
C. Threats Tracking Table

This table demonstrates how the recovery criteria and/or recovery actions ameliorate threats to the Mexican wolf.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Threat</th>
<th>Criteria</th>
<th>Recovery Action</th>
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IV. IMPLEMENTATION SCHEDULE
V. LITERATURE CITED

LITERATURE CITED (MASTER LIST – 4/21/2012)


Araiza Ortiz, M. A. 2002. Determinación de sitios potenciales para la reintroducción del lobo mexicano (Canis lupus baileyi) en Sonora, Chihuahua y Coahuila, México.


Arizona Game and Fish Department [AGFD], and New Mexico Department of Game and Fish [NMDGF]. 2002. Arizona-New Mexico review of the U.S. Fish and Wildlife Service’s 3-year review of the Mexican wolf reintroduction project. Final, September 30, 2002.


Association of Zoos and Aquariums [AZA]. 2008a. Letter to Benjamin Tuggle, USFWS Regional Director, Region 2, Duane Shroufe, AGFD Director, Bruce Thompson, NMDFG Director. Re: A request for a moratorium on lethal control and permanent removal (rescind or suspend SOP13) of Mexican wolves in the Blue Range Wolf Recovery Area until an expert taskforce on genetic issues can be convened to provide guidance to these actions. January 2, 2008.


Foley, P. (1994) Predicting extinction times from environmental stochasticity and carrying-capacity. Conservation Biology 8, 124-137


Boitani, editors. Wolves: behavior, ecology, and conservation. The University of Chicago
Press, Chicago, Illinois, USA.

restoration: where to from here? Pages 410?421 in V. M. Temperton, R. J. Hobbs, T. Nuttle,
and S. Halle (eds.), Assembly rules and restoration ecology: bridging the gap between theory


of Science 36:101?123.

2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild
populations. Biological Conservation 133:42-51.

Mech, L.D. and L. Boitani, editors. Wolves: behavior, ecology, and conservation. The
University of Chicago Press, Chicago, Illinois, USA.

wolves. Pages 78-85 in Carbyn, L.N., S.H. Fritts, and D.R. Seip, editors. Ecology and
conservation of wolves in a changing world. Occasional Publication No. 35. Canadian
Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada.

Palacio-Prieto, J. L., G. Bocco, and 14 others. 2000. La condición actual de los recursos
Geográficas (UNAM) 43:183-203.

population size: what can they tell us about the importance of genetic stochasticity for wild
population persistence? Molecular Ecology 17:3428–3447.

Paquet, P. C. and E. G. Walker. 2006. Review of investigative findings relating to the death
of Kenton Carnegie At Points North, Saskatchewan. Prepared for and submitted to Office of
the Chief Coroner Saskatchewan Justice #920, 1801 Hamilton Street Regina, Saskatchewan
S4P 4B4.  32 pp.


SEMARNAT. 2000. Mexican wolf (Canis lupus baileyi) recovery project (Proyecto de recuperación del Lobo Mexicano). SEMARNAT, Mexico, D.F.


Siminski, D. P. 2005. Mexican wolf, Canis lupus baileyi, international studbook. The Living Desert, Palm Desert, California, USA.


Mountain wolf recovery 2007 annual report. U.S. Fish and Wildlife Service, Region 6, Helena, Montana, USA.


U.S. Fish and Wildlife Service [USFWS]. 2000. Environmental Assessment for the translocation of Mexican wolves throughout the Blue Range Wolf Recovery Area in Arizona and New Mexico. Region 2, Albuquerque, New Mexico, USA.


U.S. Fish and Wildlife Service [USFWS]. 2011. Proposed rule to revise the list of endangered and threatened wildlife for the gray wolf (Canis lupus) in the eastern United States, initiation of status reviews for the gray wolf and the eastern wolf (Canis lycaon). Federal Register 76:26086-26145.


structure and gene flow in grey wolf populations of the Northern Rocky Mountains of the United States. Molecular Ecology 19:4412–4427.


Wiersma, Y. F., and J. Sandlos. 2011. Once there were so many: animals as ecological baselines. Environmental History 16:400?407.


INCOMPLETE CITATIONS


### APPENDIX A. GLOSSARY AND LIST OF ABBREVIATIONS

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<th>Page</th>
<th>GLOSSARY AND LIST OF ABBREVIATIONS</th>
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<tr>
<td>4497</td>
<td><strong>3-Year Review</strong> Mexican Wolf Recovery: Three Year Program Review and Assessment</td>
</tr>
<tr>
<td>4499</td>
<td><strong>5-Year Review</strong> Mexican Wolf Blue Range Reintroduction Project 5-Year Review</td>
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<tr>
<td>4500</td>
<td><strong>AGFD</strong> Arizona Game and Fish Department</td>
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<tr>
<td>4501</td>
<td><strong>AMOC</strong> Adaptive Management Oversight Committee</td>
</tr>
<tr>
<td>4502</td>
<td><strong>AMOC and IFT</strong> Adaptive Management Oversight Committee and Interagency Field Team, commonly used as a literature citation referencing these committees as authors of sections of the 5-Year Review, including the Technical Component (TC), Administrative Component (AC), or AMOC Recommendations Component (ARC)</td>
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<tr>
<td>4503</td>
<td><strong>AMWG</strong> Adaptive Management Working Group</td>
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<td>4504</td>
<td><strong>APA</strong> Administrative Procedures Act of 1946</td>
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<tr>
<td>4505</td>
<td><strong>AZA</strong> Association of Zoos and Aquariums</td>
</tr>
<tr>
<td>4506</td>
<td><strong>Blue Range population</strong> Wolves in the BRWRA, FAIR, and surrounding areas</td>
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<tr>
<td>4507</td>
<td><strong>BRWRA</strong> Blue Range Wolf Recovery Area, as designated by the Final Rule (50 CFR 17.84(k))</td>
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<td>4508</td>
<td><strong>DPS</strong> Distinct Population Segment</td>
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<tr>
<td>4509</td>
<td><strong>EIS</strong> Environmental Impact Statement</td>
</tr>
<tr>
<td>4510</td>
<td><strong>ESA</strong> Endangered Species Act of 1973, as amended</td>
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<tr>
<td>4511</td>
<td><strong>FAIR</strong> Fort Apache Indian Reservation of the White Mountain Apache Tribe</td>
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<tr>
<td>4512</td>
<td><strong>FEIS</strong> Final Environmental Impact Statement of 1996 (for proposed reintroduction of Mexican wolves)</td>
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<tr>
<td>4513</td>
<td><strong>Final Rule</strong> Final “nonessential experimental population” or “10(j)” rule of 1998 for Mexican wolf reintroduction in Arizona and New Mexico, 50 CFR 17.84(k)</td>
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<tr>
<td>4514</td>
<td><strong>Great Lakes</strong> USFWS gray wolf recovery program administered out of the Great Lakes, Big Rivers Region (Region 3)</td>
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<td>4515</td>
<td><strong>IFT</strong> Interagency Field Team (for the Reintroduction Project, see below)</td>
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<td>4516</td>
<td><strong>MVP</strong> Minimum Viable Population</td>
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<td>4517</td>
<td><strong>MWEPA</strong> Mexican Wolf Experimental Population Area</td>
</tr>
<tr>
<td>4518</td>
<td><strong>NEPA</strong> National Environmental Policy Act of 1969</td>
</tr>
<tr>
<td>4519</td>
<td><strong>NMDGF</strong> New Mexico Department of Game and Fish</td>
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<tr>
<td>4520</td>
<td><strong>Northern Rockies</strong> USFWS gray wolf recovery program administered out of the Mountain-Prairie Region (Region 6) and Pacific Region (Region 1)</td>
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<tr>
<td>4521</td>
<td><strong>PVA</strong> Population Viability Analysis</td>
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<tr>
<td>4522</td>
<td><strong>SOP</strong> Standard Operating Procedure for the Reintroduction Project</td>
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<tr>
<td>4523</td>
<td><strong>SSP</strong> Species Survival Program</td>
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<tr>
<td>4524</td>
<td><strong>SWDPS</strong> Southwestern Gray Wolf Distinct Population Segment</td>
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<tr>
<td>Code</td>
<td>Description</td>
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<tr>
<td>SWDPS Recovery Team</td>
<td>Southwestern Gray Wolf Distinct Population Segment (with emphasis on the Mexican gray wolf, <em>Canis lupus baileyi</em>)</td>
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<tr>
<td>USDA-WS</td>
<td>Recovery Team</td>
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<td>USFS</td>
<td>USDA Forest Service</td>
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</table>
Appendix 1. Modeling and analysis procedures used to evaluate recovery criteria for the Mexican wolf

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I. INTRODUCTION

This document provides a description of the modeling process used by the U.S. Fish and Wildlife Service (Service) to identify and evaluate appropriate recovery criteria for the Mexican wolf (*Canis lupus baileyi*). We consistently based our evaluations on the best scientific information available, while acknowledging that this information is incomplete. We do our best to recognize and articulate uncertainties, and the relative strength of evidence for information versus our use of professional judgment or other sources of information for making recommendations. The approach we have adopted makes use of the best available quantitative modeling tools, and is designed to be thorough, transparent, and repeatable.

Our criteria development process began with the statutory definition of recovery, which is aimed at ameliorating threats to an extent that the species no longer requires listing under the ESA. This would occur at the point at which Mexican wolf populations are stable or increasing and distributed such that the Mexican wolf is unlikely to become threatened again in the foreseeable future. Based on this definition, as well as precedent set by other recovery plans and principles from the field of conservation biology, we developed a set of Guiding Principles that generally identified what is essential for recovering the Mexican wolf.

Recovery criteria should be objective and measurable, and comprehensively address all aspects of the definitions of endangered and threatened species contained in the Endangered Species Act (ESA). To identify appropriate criteria for recovery of the Mexican wolf, the Service used four Biological Indicators (abundance, redundancy, connectivity, and trend) and six Guiding Principles:

1. Ensure sufficient abundance and trend indices to support population viability;

2. Ensure sufficient redundancy in populations;

3. Ensure sufficient connectivity among populations;

4. Ensure distribution of populations across representative habitats;

5. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, demographic stochasticity, and other factors;

II. JUSTIFICATION FOR GUIDING PRINCIPLES

A. THE THREE RS: RESILIENCY, REDUNDANCY AND REPRESENTATION

Guiding Principles:
Ensure sufficient redundancy in populations;
Ensure distribution of populations across representative habitats;
Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, and other factors.

The conservation principles of resiliency, redundancy and representation (the ‘3R’ criteria) developed by Shaffer and Stein (2000) are widely applied in recovery planning (USFWS 2009, 2011). In essence, the 3R framework states that, to be considered recovered, a species should be present in many large populations arrayed across a range of ecological settings. The 3R framework parallels the intent of the ESA in that it links the concepts of geography and viability by combining protection of representative examples of ecosystem types or species’ populations with two additional factors typically associated with population viability. First, resiliency may be associated with factors such as population size that describe a single subpopulation and its ability to persist (Shaffer & Stein 2000). Second, redundancy of such subpopulations in a metapopulation enhances the viability of each and provides a margin of safety for the species (DenBoer 1968).

The concept of redundancy acknowledges that demographic persistence is enhanced by creation of a metapopulation, in which multiple subpopulations are linked by dispersal. This is in part due to “spreading of risk”, since episodic threats such as disease outbreaks may not affect all subpopulations simultaneously (DenBoer 1968). A comprehensive set of demographic recovery criteria should include criteria on the size of individual subpopulations, the number of subpopulations, and the degree of metapopulation connectivity. The status of two populations of the same size would differ if one was stable while the other was declining. Demographic recovery criteria should thus specify both the required state or status and trend over time in population size and demographic rates.

Recovery criteria that explicitly address the geographic distribution of recovered populations should also typically be present in recovery plans. For example, the recently revised Recovery Plan for the Northern Spotted Owl (Strix occidentalis caurina) requires demographically stable populations in each of eleven recovery units (USFWS 2011). Such criteria help fulfill the ESA’s mandate (contained in the preamble of the Act) to conserve the ecosystems on which species depend. Fulfillment of geographic criteria promotes recovery of ecological-effective populations (Soule et al. 2005), and help increase resilience of populations to climate change (Carroll et al. 2010).
Geographic criteria are complementary to genetic and demographic criteria in that a species that meets geographic criteria is also more likely to be considered recovered in terms of the other types of criteria (Carroll et al. 2010). Conservation planners have frequently proposed representation as an important complement to viability-related goals because it allows consideration of biological diversity at multiple scales (e.g., populations, ecotypes, and species)(Shaffer & Stein 2000).

**B. POPULATION VIABILITY ANALYSIS (PVA) AS A TOOL FOR ADDRESSING RESILIENCY AND REDUNDANCY IN RECOVERY PLANNING**

**Guiding principles:**
*Ensure sufficient abundance and trend indices to support population viability;*
*Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, demographic stochasticity, and other factors.*

Recovery criteria appropriately focus on addressing factors that affect the demographic status and trends of the population (Caughley 1994) and its geographic distribution. In terms of population status, recovery criteria are typically expressed as the population size necessary to increase probability of persistence (reduces probability of extinction) to acceptable levels (expressed as <x% probability of extinction over x years). A population viability analysis (PVA) model may be used to evaluate alternative criteria in terms of their implications for population persistence. Even if expressed in terms of results from PVA models, such criteria can be seen as implicitly threat-based. The Service has concluded that “PVA should not be viewed as a replacement for criteria based on threats, but as a supplement to them. The criteria describe the conditions under which it is anticipated the PVA would indicate long-term viability” (Interim Recovery Guidance 5.1:18).

Scientific peer reviewers of previous wolf conservation plans (e.g., Washington state; WDFW 2010) have characterized the role of PVA as “an analytical tool that can be used proactively to evaluate how various management options affect the likely persistence of a species and understand what aspects of a population are critical to its growth...PVA cannot be used to make precise estimates of wolf sustainability...but PVA definitely can and should be used to evaluate the relative likelihood that recovery targets will produce self-sustaining wolf populations” (Fuller et al. 2010). Based on these and other published recommendations, we concluded that a rigorous PVA was essential for developing recovery criteria for the Mexican wolf.

Lambda, a measure of population growth rate, is the amount that the population must be multiplied by to give the population size in the next year. A population with lambda of 1 is stable. Long-term studies of the wolf metapopulation in the Northern Rocky Mountains suggest that both central Idaho and Yellowstone populations have shown lambdas significantly
exceeding 1 (Smith et al. 2010). In contrast, at least until 2009, demographic rates from the Blue Range population suggest a lambda below 1, characteristic of a population that would decline in the absence of supplementation (Oakleaf et al. in prep.).

Deterministic lambda can be estimated using simple models. If deterministic factors are favorable (lambda exceeds 1), a population has the potential for a stable or increasing trend, and more complex PVA models become useful in evaluating additional stochastic threats that may further limit growth of small populations. If deterministic lambda exceeds 1, a population may show high probability of persistence if a) lambda sufficiently exceeds 1 in normal years that it can recover from stochastic factors such as disease outbreaks; and b) population size and metapopulation connectivity are sufficient to mitigate threats related to low levels of genetic diversity.

To illustrate the context of the PVA, we present a conceptual diagram of the influence of demographic and genetic factors on viability (Figure 1). For a population to fall within the ‘zone of viability’ both demographic and genetic threats must be mitigated. Currently, Northern Rocky Mountains (NRM) wolf populations fall largely within that zone. The small and semi-isolated Swedish wolf population is an example of a population with favorable levels of deterministic demographic threats (low mortality and abundant prey), but which is threatened by genetic factors. The Blue Range Mexican wolf population has historically fallen outside the zone of viability due to both low genetic diversity and deterministic threats to demographic viability. Recovery actions must be designed to move the population towards viability on both threat axes. Progress on a single axis (e.g., reducing mortality rates) is not in itself sufficient to achieve long-term viability.

C. DEVELOPING CRITERIA FOR METAPOPULATION CONNECTIVITY

Guiding Principle: Ensure sufficient connectivity among populations.

The ESA requires that recovery plans define objective and measurable recovery criteria that comprehensively address the threats that led to listing of the taxa as threatened or endangered. The three fundamental processes of a population are reproduction, mortality, and dispersal. To be considered self-sustaining, a recovered population should be able to perform these fundamental processes without the direct assistance of humans. For example, one could not consider a population to be recovered if it required the regular addition of individuals from a captive population to offset either low recruitment or survival in the wild. For the same reason, a population would not be considered recovered if it did not exhibit critical levels of natural dispersal.
Wolves are able to travel and disperse more widely than most terrestrial mammals. Natal dispersal averages 100 km (Boyd and Pletscher 1999). Numerous long-distance dispersal events (greater than 800 km) have been recorded (Boyd and Pletscher 1999). Two recent long-distance dispersal events from the NRM metapopulation demonstrate the potential for restoring natural population connectivity in the western U.S. In 2010, a female wolf from Yellowstone (341F) dispersed over 1,000 km to Colorado. In 2011, a male wolf from eastern Oregon (OR7) dispersed over 900 km to California.

Unexploited wolf populations typically show a considerable degree of genetic and demographic connectivity (Wayne and Hedrick 2011). Wolves were historically present throughout their range in the contiguous 48 states as a largely continuous population with some degree of genetic isolation-by-distance (i.e. increasing genetic difference with increasing geographical distance) and additional heterogeneity reflecting specific ecological factors (Carmichael et al. 2007, Musiani et al. 2007, Muñoz-Fuentes et al. 2009). However, due to loss of suitable habitat, human intolerance, and other factors, wolf distribution in most areas of the contiguous 48 states (i.e. outside of Alaska), even after delisting, is likely to consist of subpopulations which are relatively small when compared to historic population sizes (which have been estimated at 380,000; Leonard et al. 2005). As has been discussed in relevant wolf recovery plans and conservation documents for the NRM region (e.g., FWS 1994), connectivity among these subpopulations is necessary to alleviate genetic and demographic threats posed by small population size. Considering the natural genetic population structure of gray wolves and their distributional range in the recent past, it follows that recovery must be secured by ensuring connectivity at the metapopulation level. Population connectivity is thus a necessary component of criteria for recovery and delisting of the Mexican wolf.

For subpopulations to benefit from the genetic diversity of the larger metapopulation, they must be linked via ‘genetically-effective’ dispersal, which can be specified as the number of effective migrants (those migrants that survive to produce offspring in the recipient population) per generation. The ratio between genetically effective migrants and the total (census) number of migrants may be similar to the Ne/N ratio, but it is also possible that the two ratios differ. Therefore direct assessment of genetically effective migrants (vonHoldt et al. 2010) is preferable to indirect methods based on total number of migrants. To facilitate development of objective and measurable connectivity criteria, we developed methods for using the Vortex model to evaluate alternate recovery criteria expressed in terms of the number of genetically effective migrants.

Because of the wolf’s dispersal ability, achieving adequate connectivity via natural dispersal (rather than artificial translocation) is relatively feasible in wolf metapopulations. VonHoldt et al. (2010) documented a minimum estimate of 5.4 effective migrants per generation (over the metapopulation as a whole) in the NRM, and concluded that sufficient gene flow from natural dispersal was occurring to counteract the loss of future genetic variation within populations.
because of drift. The vonHoldt et al. (2010) study covered approximately 2.4 wolf generations from 1995 through 2004 when the NRM region contained between 101 and 846 wolves. The study documented 1 genetically effective natural dispersal from Central Idaho into the Greater Yellowstone population for an average effective migration rate of 0.42 migrants per generation, lower than that into either of the two other NRM wolf populations (0.83 migrants each per generation for Central Idaho and Northwest Montana). However, the migration rates documented in vonHoldt et al. (2010) represent minimum estimates recorded over a period in which the metapopulation size grew by 800%.

Achieving natural population connectivity for Mexican wolves does not require expensive habitat restoration measures, but rather management to sustain survival of dispersers. Mitigation of threat factors (e.g., overexploitation) to a level sufficient to allow natural dispersal between populations will also help achieve additional recovery goals. Recovery of metapopulations that are large enough to ensure long-term genetic potential may also help achieve goals for recovery of ecologically effective populations, consistent with the Endangered Species Act’s mandate to restore self-sustaining wild populations of species and the ecosystems on which such species depend (ESA, Section 2(b) Purposes).

Connectivity may be important both within and beyond the Mexican wolf metapopulation. For example, genetic data indicate that historically, the southern Rocky Mountains were part of a zone of intergradation between Mexican wolves and more northern wolf subspecies (Leonard et al. 2005). If wolves from the NRM, disperse southward (as occurred with wolf 341F in 2010, see below) and breed with free-ranging Mexican wolves, resultant gene flow has the potential to restore genetic variation that has been lost from Mexican wolves (genetic restoration, Hedrick 2005), and increase the fitness of Mexican wolves (genetic rescue, Tallmon et al. 2004). However, it is important to evaluate the potential effects of such gene flow from northern populations (e.g., genetic swamping) on the unique characteristics of the Mexican wolf genome (see Section III.B.9 below).

Recovery criteria focused on natural connectivity rather than artificial translocation are consistent with the intent of the ESA, which requires recovery of self-sustaining wild populations where feasible. The Services’ (FWS and National Marine Fisheries Service (NMFS)) joint Section 7 Handbook (p. 4-36) defines the term “recovery” as “the process by which species’ ecosystems are restored and/or threats to the species are removed so self-sustaining and self-regulating populations of listed species can be supported as persistent members of native biotic communities.” The Services have an extensive history of emphasizing recovery of self-sustaining wild populations (i.e., those that do not require measures such as controlled propagation or artificial translocation for their persistence) in recovery plans. For example, the Florida panther (Puma concolor coryi) recovery plan states “Restoring endangered or threatened animals or plants to the point where they are again secure, self-sustaining members of their ecosystems is a primary goal of the Service's endangered species program” (60 FR 478). Similarly, the Peregrine
Falcon (*Falco peregrinus*) recovery plan states “Recovery is the process by which the decline of an endangered or threatened species is arrested or reversed and threats to its survival are neutralized so that long-term survival in nature can be ensured. The goal of this process is the maintenance of secure, self-sustaining wild populations of species with the minimum investment of resources” (63 FR 45446). In delineating critical habitat for Canada lynx (*Lynx canadensis*), the Service emphasized that “retaining connectivity with larger lynx populations in Canada is important to ensuring long-term persistence of lynx populations in the United States” (74 FR 8641).

III. STAGES IN MODELING APPROACH

A. OVERVIEW

Several modeling tools are available to inform development of recovery criteria based on best available science. It is important to acknowledge the strengths and weaknesses of each type of model and to consider information from multiple models in an appropriate decision-support context. We employed state-of-the-art modeling tools in a multi-stage analysis for evaluating alternative recovery criteria. Collectively, these modeling tools allow comparison of estimated population viability (probability of population recovery) and distribution among alternative recovery scenarios under a variety of potential conditions. The evaluation approach the modeling team developed consists of three main stages:

Stage 1 - Population Simulation Model

This stage is relevant to the following Guiding Principles:
1. Ensure sufficient abundance and trend indices to support population viability;
2. Ensure sufficient redundancy in populations;
5. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, demographic stochasticity, and other factors; and

Because of the magnitude of genetic threats to the Mexican wolf, we selected a population simulation model (Vortex; Lacy et al. 2010) with the capability to explore how genetic threat factors vary with population size and metapopulation structure. This informs development of criteria for the size, number and connectivity of subpopulations. Details of Stage 1 analysis are described in Appendix 2.

Stage 2 - Habitat-based Model

This stage is relevant to the following Guiding Principles:
1. Ensure sufficient abundance and trend indices to support population viability;
4. Ensure distribution of populations across representative habitats; and
5. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, and other factors.

The Vortex model lacks sophisticated treatment of spatial dynamics or habitat. Once Stage 1 of criteria development is completed, a second stage of the process determined where on the landscape such criteria could be achieved given distribution of suitable habitat. Information sources for this second stage included results from a spatially-explicit population model (PATCH; Carroll et al. 2006). The PATCH model lacks consideration of genetic issues, so if used in isolation would underestimate extinction risk for taxa with genetic threats such as the Mexican wolf.

Stage 3 - Connectivity Model

This stage is relevant to Guiding Principle 3. Ensure sufficient connectivity among populations.

The Vortex analysis suggested that population connectivity was especially important for persistence in Mexican wolves due the current population being derived from only seven founders. We therefore examined what rate of natural dispersal between primary core populations was sufficient for population persistence and could be achieved given the distribution of suitable habitat. We did this by relating observed connectivity rates in other regions to relative habitat connectivity between primary core populations in those regions, and extrapolating to evaluate rates expected given habitat connectivity between potential primary core populations of Mexican wolves.

B. DETAILS OF HABITAT-BASED MODEL

1. OVERVIEW

We developed information on habitat suitability as the second stage of a two stage modeling process. The first stage was development of criteria for subpopulation and metapopulation size and connectivity as described above. This analysis was informed by a simulation model, Vortex, which does not require information on spatial distribution of habitat (see Appendix 2 for more information). The second stage was to determine where a metapopulation of the size and connectivity suggested as necessary for viability by the Vortex analysis could be recovered given the distribution of suitable habitat. This stage of analysis is designed to address the question: what potential recovery areas are large and secure enough that they might be expected to achieve numeric recovery criteria sufficient to alleviate genetic and other threats? We have prepared a comprehensive summary of best available information concerning the distribution and suitability
of habitat for Mexican wolves in the United States and Mexico (Section I.H.). We reference Section I.H. where appropriate in this appendix rather than repeat this material. It is appropriate to provide a general assessment of habitat suitability in the recovery plan, in order to provide general guidance on geographic locations that would be best suited for achieving recovery criteria. However, a detailed assessment of habitat data for individual areas would be more appropriately presented as part of an Environmental Impact Statement associated with future actions to implement recovery in those areas.

Conservation planners assess the distribution of wildlife habitat (including potentially suitable but currently unoccupied areas) with the aid of computer models of varying complexity. Broadly speaking, large carnivores such as the wolf can persist in areas where there is sufficient food and where persecution by humans is low (Fuller et al. 2003, see also Section I.H.). A simple model of recovery potential could therefore highlight large roadless areas with sufficient productivity or extensive forest habitat. More complex spatially explicit population models (SEPMs) might also begin with data on road density and productivity, but would then integrate additional information on species characteristics such as demographic rates and dispersal behavior. For example, social carnivores, such as the wolf, often require larger territories than solitary species of similar size, and may thus be more vulnerable to landscape fragmentation (Carroll et al. 2003a). Unlike the simpler model, an SEPM can provide insights on the effects of population size and connectivity on viability and can help identify the locations of population sources and the degree of threat to those areas from landscape change (Carroll et al. 2003b). An effective recovery strategy requires establishing well-distributed source populations in core areas of highly suitable habitat and then allowing natural dispersal to re-establish a regional metapopulation. To merit attention as a potential reintroduction site, a ‘core area of suitable habitat’ would need to be both be relatively secure habitat and be well situated to facilitate growth of the regional wolf metapopulation.

Spatially explicit population models (SEPM) are a class of simulation models that are both individual-based and retain spatially-explicit information on habitat distribution (DeAngelis and Gross 1992). These models track the fates of many individuals through time as they move across a grid of cells, age, reproduce and die. The behavior of large numbers of individuals collectively determine the aggregate characteristics that form the model output. SEPM span a range of complexity, depending on the degree of biological realism and number of demographic parameters they incorporate. Model output may include the mean population size, mean time to extinction, or the percentage of suitable habitat occupied. Because these models can incorporate habitat-specific demographic parameters, the development of SEPM has allowed data gathered from intensive demographic studies to be combined with GIS maps of landscape composition and pattern in dynamic models (Murphy and Noon 1992). If SEPM results are considered in the proper context, they have the potential to offer insights on both spatial and non-spatial factors that might influence the success of recovery efforts.
2. THE PATCH MODEL AND ANALYSES OF HABITAT IN THE UNITED STATES

PATCH, the SEPM used in the previously-published study described below (Carroll et al. 2006), links the survival and fecundity of individuals or groups of animals to GIS data on mortality risk and habitat productivity at the scale of an individual or pack territory (Schumaker et al. 2004). Territories are allocated by intersecting the GIS data with an array of hexagonal cells. The different habitat types in the GIS maps are assigned weights based on the relative levels of fecundity and survival expected in those habitat types. Base survival and reproductive rates, derived from published field studies, are then supplied to the model as a population projection matrix. The model scales these base matrix values using the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output. Each individual in the population is tracked through a yearly cycle of survival, fecundity, and dispersal events. Environmental stochasticity is incorporated by drawing each year’s base population matrix from a randomized set of matrices whose elements were drawn from a beta (survival) or normal (fecundity) distribution. Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a parameter for site fidelity, but floaters must always search for available breeding sites. Movement decisions use a directed random walk that combines varying proportions of randomness, correlation, and attraction to higher-quality habitat (Schumaker et al. 2004). The PATCH model lacks consideration of genetic issues, so if used in isolation would underestimate extinction risk for taxa with genetic threats such as the Mexican wolf. Hexsim, the successor to PATCH, was recently used in recovery planning for the Northern Spotted Owl (Dunk et al. 2012).

We summarize below the results from a previously-published study (Carroll et al. 2006) that were used as one source of information for evaluating areas in the United States in this second stage of the modeling process. More recent studies (Araiza et al. 2012) were used to evaluate potential recovery areas in Mexico. Carroll et al. (2006) identified four potential reintroduction sites in the United States, based on the results of initial SEPM simulations. These sites were labeled Carson (northern New Mexico), Grand Canyon (northern Arizona), Mogollon Rim (central Arizona), and San Juan Mountains (southwestern Colorado). A fifth site in the Blue Range Wolf Recovery Area (BRWRA; Arizona and New Mexico) was also included to provide comparability with current recovery program results. Each of these sites was evaluated in detail by simulating the effects of releasing wolves at that site alone. Each reintroduction site comprised five adjacent potential wolf territories, totaling 2500 km². The model approximated the standard reintroduction protocol (Bangs and Fritts 1996) by introducing five breeding-age females in the first year and setting survival for the first 5 years at close to 100% under the assumption that new animals would be released to replace mortality among the initial releases.

In addition to the current reintroduced population in the Blue Range, the Grand Canyon reintroduction site showed a high probability of success (low extinction rates) and rapid geographic expansion. Several other reintroduction sites showed higher, but still relatively low,
extinction rates. The probability that a reintroduction at a single site will fail (extinction probability) under scenario A ranges from near zero (0 of 1000 simulations) for the Blue Range and Grand Canyon sites to near 10% for the Mogollon Rim and San Juan Mountains sites. Under scenario C (which projected future landscape change trends), the extinction probability for the Mogollon and San Juan Mountains sites increases to 16–20%. The probability of extinction for the Blue Range, Grand Canyon, and Carson sites also increased slightly but remained low (< 3%). Occupancy of the larger (10,000-km²) restoration zone surrounding each 2500-km² reintroduction site gives a sense of the extent of suitable habitat that might be important in the early stages of population establishment. The Blue Range restoration zone has the highest occupancy, at 72.5%, followed closely by the Carson and Grand Canyon zones. The Grand Canyon zone is more resilient to landscape change than the Blue Range or Carson; thus, it shows the highest wolf population density among US restoration zones under scenario C. A scenario that incorporated cattle density as an additional mortality risk factor resulted in a similar ranking of restoration zones, except that the San Juan Mountains zone appeared less vulnerable, and thus only the Mogollon zone showed high relative extinction risk.

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

3. ANALYSES OF HABITAT IN MEXICO

We primarily used results from more recent studies (Araiza et al. 2006, Araiza et al. 2012) to evaluate potential recovery areas in Mexico, consistent with our goal to use the best currently available data. However, it is relevant to briefly review here Carroll et al. (2005)’s comparison
of four potential recovery areas in Mexico. The areas analyzed correspond to four areas
described in Araiza et al. (2006, 2012; see Table 1): Sierra San Luis/Ajos-Bavispe
(Chihuahua/Sonora near U.S. border), Tutuaca/Sierra Tarahumara (westcentral Chihuahua),
Chihuahua/Durango, and Maderas del Carmen/Serranias de Burro (northern Coahuila). Carroll et
al. (2005) concluded from the SEPM analysis that the Durango site contained the most
productive wolf habitat, but the Tutuaca and Carmen sites appeared to have lower risk from
conflict with livestock production. Under current landscape conditions, the PATCH model
projected that northern Mexico as a whole might support 82% as many wolves as could be
supported in the southwestern US (2600 versus 3166).

Although the analysis of Carroll et al. (2005) served as a useful initial comparison between
potential recovery areas in Mexico, the authors cautioned against using results to compare habitat
between the US and Mexico or to make absolute estimates of wolf carrying capacity in Mexico.
Because of these concerns, results from analysis of the Mexican sites were not included in the
subsequent peer-reviewed paper (Carroll et al. 2006). Accuracy of Carroll et al. (2005)’s analysis
of sites in Mexico was reduced by two factors. Firstly, Carroll et al. (2005) concluded that the
sparseness of the available digital data on human impacts (roads and altered habitat types) in
Mexico affected their estimates of potential wolf habitat in Mexico “to an extent that
significantly limits comparability between Mexican and US reintroduction sites.” Secondly,
Carroll et al. (2005)’s analysis of prey productivity was based on surrogate data (vegetation
types, greenness). These surrogate data are likely to show lower correlation with actual prey
density in Mexico than in the United States because 1) estimates of prey abundance in Mexico
with which to test surrogate data are more limited in Mexico, and 2) what prey data are available
indicate that prey populations are further below ecological carrying capacity than in the
reasons, the results of Carroll et al. (2005) for wolf recovery areas in Mexico have largely been
superseded by more recent studies.

In 2006, a workshop convened researchers involved with several of the studies described above,
in order to derive a consensus opinion of which areas held potential for wolf reintroduction in
Mexico (Araiza et al. 2006). Six areas were identified as having the greatest potential to support
populations of Mexican wolves. This conclusion was based on several sources of expert
judgement and qualitative analysis. For example, Martínez Gutiérrez (2007) first identified
patches with suitable vegetation, and then identified areas with low levels of roads and
settlements within those patches. The area between the Tutuaca/Sierra Tarahumara and
Chihuahua/Durango area could be identified as unsuitable in this analysis based on high levels of
roads and settlements. In other cases, both the regional-scale GIS analysis and expert knowledge
were used by Araiza et al. (2006). Subsequently, Araiza et al (2012) performed more detailed
modeling of risk as described below which confirmed that areas of lowest risk are somewhat
fragmented even within the 6 recovery areas.
In a subsequent analysis, Araiza et al. (2012) performed a quantitative analysis of habitat suitability and human-associated mortality risk to validate and extend the expert-based conclusions. Historical locations of wolves were compared with historical vegetation types using a utilization-availability analysis. Contemporary vegetation types were ranked in six quality classes based on a combination of the results obtained in the selection analysis and the current status of transformation. Point data on the locations of population centers was buffered to a zone of influence based on their population size. Roads were also buffered based on reported zones of avoidance (Kaartinen et al. 2005). Three alternate scenarios were developed for human-associated risk (low, intermediate, and high risk) that made alternate assumptions as to the extent of the zone around roads and human settlements in which wolves would experience increased mortality. Information on vegetation suitability and distance to settlements and roads maps were combined to identify large patches of the high quality habitat in which further fieldwork to evaluate prey availability was conducted. The largest clusters of suitable patches were found in Sonora-Chihuahua (area 1) and Chihuahua-Durango (area 3) (15,705 and 8,344 km2 in area, respectively, under the intermediate risk assumptions) (see Section I.H.).

Araiza et al. (2006) estimated potential size of wolf populations in the six core areas of suitable habitat in Mexico. Subsequent fieldwork to evaluate prey availability (Lara-Diaz 2011, J. Servín unpublished data) further refined these estimates (see Table 1). Based on these sources, the two areas in the northern Sierra Madre Occidental are predicted to support larger wolf populations (80 wolves each) than are the two areas in the southern Sierra Madre Occidental (60 and 24 wolves). However, the relative potential for successful reintroductions within each of these areas may also depend on public attitudes and details of land use that are not quantifiable using available data (Servín et al. 2007).

4. CONCLUSIONS FROM HABITAT ANALYSES

Several conclusions emerged from our review of the results of Carroll et al. (2006), Araiza et al. (2012) and other relevant data on e.g., prey abundance (section I.H.):

1) Under current habitat conditions, three major core areas of suitable habitat exist in the area encompassing Arizona, New Mexico, southern Colorado and southern Utah. The three core areas of suitable habitat are a) the Blue Range Wolf Recovery Area and adjacent public lands, b) the Grand Canyon and adjacent public lands, and c) two linked areas of public lands and private lands with conservation management in northern New Mexico and southern Colorado (labeled Carson and San Juans in Carroll et al. (2006)) (see section I.H.). These areas are projected to become more distinct and separated as landscape change factors such as exurbanization continue (Carroll et al. 2006). Each of the three areas (but not western Texas) holds a secure core area of
public lands subject to conservation mandates (National Park, wilderness) where wolves are predicted to experience the lowest human-induced mortality.

2) The US/Mexico border area is likely to serve as sink habitat for wolves under current conditions (Carroll et al. 2006). However, the area’s key role in facilitating dispersal between US and Mexican wolf populations suggests that it be given significant attention in recovery planning, through recovery actions which increase the likelihood of these sites being naturally recolonized by dispersers from the Blue Range or Mexican populations.

3) Potential recovery areas in Mexico contain areas of suitable habitat that are smaller and have lower prey abundance than those in the U.S. In particular, the contrast in prey density between the US and Mexico core areas results in a contrast in estimates of the number of wolves that could be potentially supported in each of the core areas. They are thus unlikely to support the primary core populations necessarily for metapopulation persistence but may play a role in increasing connectivity and distribution of populations across representative habitats. Secure habitat (areas with low human-associated mortality risk) are appears smaller and more fragmented within potential recovery areas in Mexico. Smaller secondary core populations (e.g., in Mexico or Texas) may be important for enhancing connectivity, as well as meeting representation goals.

5. POTENTIAL SHIFTS IN SUITABLE HABITAT UNDER CLIMATE CHANGE

Previous studies (Carroll et al. 2006) have projected effects of development trends on suitable habitat but have not evaluated potential effects of climate change. To evaluate this potential threat, we used data on projected shifts in biome boundaries in the southwestern US in the period 2000-2062 (50 years from date of recovery plan). The MC1 model (Daly et al. 2000, Bachelet et al. 2001) is a DGVM (dynamic global vegetation model). Such models add complexity in terms of the interaction of vegetation components (competition, etc.) but have low thematic resolution (biomes are broad categories)(Figure 6). Spatial resolution is also limited by the resolution of the climate model inputs. The figures contrast projections from three GCMs (general circulation models) developed by three different research groups (CSIRO, Hadley, and MIROC). Results from two contrasting IPCC emissions ‘storylines’ are also contrasted (Figure 5). The A1 storyline and scenario family describes a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. The A1 scenario family develops into three groups that describe alternative directions of technological change in the energy system. The three A1 groups are distinguished by their technological emphasis: fossil intensive (A1FI), non-fossil energy sources (A1T), or a balance across all sources (A1B). The A2 storyline and scenario family describes a very heterogeneous world. Emissions under the two storylines are similar at first, but eventually the A2 scenario projects higher emissions.
The MC1 biome projections suggest that there is substantial variation between the projections of the different models. There are greater contrasts between GCMs than between the A2 (Figure 7) and A1B (Figure 8) storylines. However, there is agreement between model projections in many areas. The greatest change in vegetation and above-ground carbon may occur to the south of the Blue Range and along the southern edge of the Mogollon Rim. A northward expansion of both temperate and subtropical grassland is shown. The steep elevational gradient of the Mogollon Rim prevents a large northward shift in biome boundaries in that area. Southern Arizona remains primarily desert with some expansion of subtropical grassland, especially to the south of the Blue Range. The Blue Range and potential recovery areas in northern Arizona and New Mexico are currently primarily temperate grassland or conifer forest, with some subalpine areas in the San Juan Range. These areas remain primarily temperate grassland or conifer, with the exception that in the more extreme projections of the MIROC GCM, the subalpine areas in the San Juans are replaced by temperate conifer habitat. Given the limitations of the biome classification, it appears from these projections that potential wolf habitat in central and northern Arizona and New Mexico will remain relatively stable under climate change for the next 50 years. This suggests that core habitat areas identified based on current habitat condition (e.g., in Carroll et al. 2006) will remain suitable under future projected climates. We have described here the mapped information on climate change impacts we considered in stage 2 of the modeling process. We considered additional non-mapped information on potential climate change impacts as part of the threats assessment (Section I.).

C. DETAILS OF CONNECTIVITY MODEL

1. OVERVIEW

The most commonly proposed rule of thumb for connectivity is the “one genetically effective migrant per generation” rule (Frankel & Soule 1981; Allendorf 1983). This rule states that one migrant per generation into a subpopulation is sufficient to minimize the loss of polymorphism (the occurrence of multiple alleles at one locus) and genetic heterozygosity within subpopulations. Because this generalized rule depends on simplifying assumptions (e.g. ideal populations whose effective population size equals census size), other researchers have suggested a more ambitious rule of up to 10 effective migrants per generation (Mills & Allendorf 1996; Vucetich & Waite 2000).

One (or 10) migrants per generation is applicable across a range of population sizes because genetic effects of population size and connectivity are interrelated. Because genetic drift is stronger in a small population, a greater proportion of heterozygosity is lost per generation and divergence of allele frequencies is faster. However, when a small population receives a single migrant, that migrant comprises a larger proportion of the population and has a larger impact in
restoring genetic variation. This was illustrated in the wild with the recent genomic sweep of the Isle Royale wolf population by a single immigrant from the mainland (Adams et al. 2011).

A connectivity criterion of one effective migrant per generation (“migrant”) was supported by evidence from the Vortex analysis that a higher connectivity rate was especially beneficial for population persistence in Mexican wolves due the subspecies derived from inbred and interrelated founders. Additionally, data from the Northern Rocky Mountains (NRM) suggested that such a rate had been achieved there between 2 of 3 primary core populations (vonHoldt et al. 2010). The 1 migrant rate was also endorsed as a recovery criterion in the NRM wolf delisting documents (FWS 2011).

2. METHODS

We projected connectivity rates between primary core populations in the Mexican wolf metapopulation by relating observed connectivity rates in an extant wolf metapopulation (the NRM) to relative habitat connectivity (in both the NRM and the southwestern US). Habitat data inputs were derived from the habitat model used in Carroll et al. (2006). Observed connectivity rates in NRM were derived from vonHoldt et al. (2010) with the adjustment suggested by Hebblewhite et al. (2010) to account for the fact that vonHoldt et al. (2010) analyzed data from a subsample of the NRM wolf population.

Connectivity between wolf populations was based on two metrics: least-cost distance and resistance distance. Least-cost distance is the basis of the corridor delineation methods available in most GIS software. These methods analyze raster data representing cost of movement as distance, and use computationally efficient algorithms to identify the route between two predetermined endpoints that has the shortest total distance (least total cost). Least-cost distance was calculated using the Linkage Mapper software (McRae 2011).

In contrast to least-cost distance, which focuses on a single optimal path, resistance distance considers movement across multiple paths. Resistance is calculated using algorithms from electrical circuit theory. These methods treat landscapes as conductive surfaces, i.e. networks of nodes connected by resistors. Current flow models integrate the contributions of all possible pathways across a landscape or network. As in electrical circuits, the addition of new pathways increases connectivity by distributing flows across more routes (McRae et al. 2008). Resistance distance was calculated using the Circuitscape software (McRae et al. 2008).

3. RESULTS

Linkages between primary core populations were ranked similarly under both metrics (least-cost distance and resistance distance). The “shortest” (best) linkages were between central Idaho and
both northwestern Montana and Yellowstone (figure 9 and 10). Effective migration rates of 1.67 and 0.83 EMPG, respectively have been estimated for these linkages (accounting the adjustment suggested by Hebblewhite et al. (2010) of doubling rates documented in vonHoldt et al. (2010)). Projected connectivity between the Blue Range and Grand Canyon primary core populations was somewhat less than that of the two “best” linkages described above. Projected connectivity between the Blue Range and southern Colorado/northern New Mexico primary core populations was somewhat less than that of between the Blue Range and Grand Canyon. The Grand Canyon and southern Colorado/northern New Mexico primary core populations were projected to be poorly connected, with distances similar to that between Yellowstone and northwestern Montana, a linkage where no effective migrants have been documented (vonHoldt et al. 2010).

Based on these results, rates equivalent to or somewhat below 0.83 EMPG might be expected between 2 of three primary core populations in the southwestern U.S., but few direct migrants would be expected between the Grand Canyon and southern Colorado/northern New Mexico. Given these projections, a connectivity criterion of 0.5 EMPG for the Mexican wolf in the southwestern US (specifically between the Blue Range and both Grand Canyon and Carson) would be analogous to a 1 EMPG criterion for the NRM (specifically between central Idaho and both NW Montana and Yellowstone). Limited dispersal expected between Grand Canyon and Carson would be analogous to the low or no dispersal between Yellowstone and northwestern Montana. Thus the three largest populations would be connected as an archipelago rather than a network. Although not ideal, this arrangement has the benefit of providing increased demographic and genetic support to the centrally located Blue Range population.

Araiza et al. (2006) considered all of the six potential recovery areas in Mexico described above as adequately connected with at least one other potential core area of suitable habitat. However, the authors noted that areas in the southern Sierra Madre Occidental (e.g., Chihuahua/Durango and Valparaiso/Mezquital) were likely to be better connected to the wolf metapopulation than were areas to the east in Coahuila and Nuevo Leon. Servín et al. (2007) proposed that the six Mexican core areas of suitable habitat in Mexico might form two disjunct metapopulations. The larger metapopulation would include the four areas in the Sierra Madre Occidental, with interchange of dispersers along the Sierra Madre Occidental from Sonora to Zacatecas. The two areas in eastern Mexico (Coahuila and Nuevo Leon) could potentially exchange dispersers with any Mexican wolf populations in Texas. The four areas in the Sierra Madre Occidental might be largely connected with each other and to a lesser degree, through the Sierra San Luis Complex, to the Blue Range primary core population. However, realized dispersal rates (expressed as EMPG) are influenced by both habitat connectivity and the size of the source population. The projected smaller size of secondary core populations would lower realized connectivity rates between those populations. This would not affect dispersal rates from primary core populations (e.g., Blue Range) to adjacent secondary core populations (e.g., Sky Islands-Sonora).
IV. CONCLUSION

A. NORMATIVE ELEMENTS OF RECOVERY CRITERIA DEVELOPMENT

Because a population’s extinction risk is never zero, establishing risk thresholds in listing and recovery actions involves a normative dimension (i.e., specifying what level of endangerment is acceptable) and a scientific dimension (i.e., determining whether a species meets that level of endangerment) (Vucetich et al. 2006). Although the U.S. Congress mandated that agencies consider “solely” the best science in making listing decisions (16 U.S.C. §1533 (3b)(1A)(a1)), lawmakers addressed the normative nature of such decisions only qualitatively when they emphasized in the ESA the high degree of protection they intended to afford to biodiversity.

While the ESA’s legislative history indicates that Congress intended the Act to afford a high level of security to listed species, the statute established no numeric risk thresholds which would provide an explicit judgment as to the minimal likelihood of persistence and minimal geographic distribution that would separate species considered secure or recovered from those considered threatened or endangered. While the ESA does not explicitly define quantitative thresholds for acceptable risk, this does not mean that administrative agencies may apply such risk thresholds inconsistently. To be effective, conservation strategies must be based on the rates of species’ population dynamics, that is, the time from endangerment to recovery. Clear and consistent implementation of statutes helps to maintain the continuity in conservation policy necessary to realize the essentially ethical goals of the ESA.

Although threat assessment criteria prioritize which species are most at risk of extinction, they typically do not offer justification for why one level of risk is acceptable and another is not (IUCN 2001). Wilhere (2012) noted that recovery plans seldom contain explicit statements of acceptable extinction risk, but among those that did the recovery criteria span two orders of magnitude of risk. Gilpin (1987), one of the few authors to consider the normative aspects of this issue, argued for considering risks of extinction for 200-year time frames simply because he believes humanity’s immediate challenge is to eke through the next two centuries while losing as few species as possible. Shaffer (1981) adopted a 99% persistence probability for 1000 years as a viability criterion for grizzly bears. Soule (1987) and Shaffer (1992) expressed concern that targeting a minimum population level is inadequate for sound conservation (because by design they provide minimal capacity for populations to withstand unforeseen circumstances) and larger populations are necessary to ensure long-term persistence.

The statutory language is consistent with this concern to the extent that is does not require the agencies to define recovery for a given species as the absolute minimum population size and geographic distribution that equates to a specified persistence level. For species that are experiencing severe declines, the recovery goal is often to reverse the decline and restore the population to a previous status rather than some minimum size. Recovery goals may also address
the minimum population size necessary for a species to be ecologically functional. For example, recovery plans may set a lower acceptable level of risk for species that play disproportionately large roles in their ecosystems (Estes et al. 2011), in order to increase the probability of conserving “ecosystems on which species depend,” one of the ESA’s express purposes (16 U.S.C. §1531 (a)(5)(b)).

While data for many species are too limited for quantitative PVA-based risk estimates, such estimates are possible for relatively well-studied taxa such as the gray wolf. However, scientists have generally rejected use of a single point estimate of minimum viable population size in recovery planning. They argue that PVA results should be used instead to provide information on the general relation between risk and factors such as abundance, genetic diversity, and distribution (Shaffer et al. 2002). Most estimates of minimum viable population size are probably too low because they underestimate long-term uncertainty in stochastic events. Recovery goals may appropriately include a margin of safety to ensure that unanticipated future events do not cause species to fall below the threshold that would again make listing warranted.

One benefit of considering geographic distribution or population redundancy as a recovery criterion (see section II above) is that situations in which a species is well distributed geographically in multiple populations will generally correspond with the conditions necessary for genetic viability. However, evaluating the appropriate levels of geographic distribution for listing and recovery similarly involves normative and biological determinations.

Consistent with best practice in recovery planning, we used point estimates of population viability (from the Vortex model) as one source of information in a decision-support context. We considered 100 years as an appropriate timeframe for evaluating effects of population size on genetic health, but deemphasized the significance of arbitrary thresholds (95%, 99%). We use such thresholds as only one of several factors for evaluating alternate recovery options, and focus primarily on patterns of how persistence changes with population size across a range of thresholds and alternative parameter sets. For example, in the Vortex simulations, populations of >=250 individuals had low extinction rates (<1% over 100 years) and maintained substantial numbers of wolves, especially when multiple connected populations were connected via dispersal. In contrast, smaller populations of 150 individuals had relatively high extinction risk (4-17% over 100 years). However, several aspects of model parameters and structure were potentially overly optimistic, and these multiple factors could act synergistically to reduce population viability. Consistent with Congress’ intent to institutionalize caution in order to avoid uncertainty about a species’ future status, we identified criteria that provide a margin of safety because they resulted in conditions under which the species is unlikely to become threatened or endangered again in the foreseeable future: 1) a low predicted potential for extinction (<1% over 100 years), and 2) a greater than 50% probability that populations would meet specified size criteria (200, 250, or 350) over the long term. Due to the role wolves play in their ecosystems...
such precautionary criteria also increase the probability of conserving ecosystems and ecosystem function (16 U.S.C. §1531 (a)(5)(b)).

B. ADDRESSING UNCERTAINTY

The appropriate role of PVA models in recovery planning is not to predict outcomes, but rather to provide one of several sources of information that support decisions on appropriate recovery criteria. Therefore sensitivity analyses using a range of parameters are often more informative than would be a single estimate based on the best estimate of parameter values. Results from PVA models are subject to two general sources of uncertainty. Model parameters such as mortality and fecundity rates are based on best available field data but are uncertain both in their accuracy for the studied population and their generality to the range of populations which the PVA is attempting to evaluate (i.e., subpopulations in several different potential recovery areas). More importantly, model structure introduces uncertainty into the results. For example, density dependent variation in reproductive rates affects the level of threat from ‘catastrophes’ (e.g., diseases). If reproductive rate increases at low population sizes, populations recover more quickly from population decline associated with episodic threats. Thus alternate assumptions concerning density dependence can significantly alter PVA estimates of metrics such as extinction risk.

Despite these sources of uncertainty, PVA models can provide qualitative insights on the relative level of threat to different populations, and relative strength of the different threat factors (demographic, disease, genetic) at different population sizes. To derive guidance from the PVA despite model uncertainty, we used an ‘ensemble modeling’ approach. We developed multiple alternate plausible model structures and evaluated these across a range of plausible parameters. We evaluated the sensitivity of results to a range of demographic and genetic parameters and based decisions where possible on metrics that were relatively robust to variation in input parameters. Decisions concerning recovery criteria were informed based on the ‘strength of evidence’ across multiple models, combined with an approach based on the precautionary principle that sought to minimize both Type I and Type II error. “By identifying the sources and magnitude of our uncertainties, we can build better criteria and more accurately target those aspects of our criteria that may bear refining in the future” (Interim Recovery Guidance 5.1:18).

Although more demographic data exists for the wolf than for most species, the plausible range of demographic parameters nonetheless causes simulations to span a range of outcomes from deterministic decline (lambda < 1) to deterministic increase (lambda >> 1) for all alternative recovery criteria. Increasing the magnitude of catastrophes and genetic effects accentuated contrasts between alternate recovery criteria, whereas increasing or decreasing demographic rates (deterministic lambda) reduced the contrasts between alternate recovery criteria. The stochastic and genetic factors that cause contrasts in persistence between populations of different
sizes are significant for demographic parameter sets in the middle of the range of plausible values, but generally not for demographic parameter sets at the extremes of this range.

Although it is often recommended that PVAs focus on ranking scenarios rather seeking a ‘magic’ MVP number, this is of limited utility given the idealized nature of the scenarios we evaluated. It is intuitive that 3 subpopulations of 250 will persist longer than 2 subpopulations of 250. It is more informative to focus on the question: over the range of demographic rates at which stochastic and genetic factors are important, what thresholds caused by population size and connectivity are evident? This allows the PVA to complement analyses of other recovery criteria such as representation goals.

Additional uncertainty is inherent in the analysis due to several factors. Firstly, the reproductive system as modeled does not represent the complexities of breeding in social animals such as wolves. Incorporating realistic wolf social dynamics would reduce the Ne/N ratio of the population because reproductive contribution would be more unequal between individuals. Secondly, potential effects of inbreeding on survival were not modeled. Although this effect was not evident in past studies of Mexican wolves (Fredrickson et al. 2007), findings from other species suggest that this may be due to lack of sufficient data. Thirdly, survival rates were based on optimistic assumptions concerning the ability to mitigate current threat factors. Fourthly, we considered disease and other catastrophes at acting at a relatively low magnitude and predominantly affecting fecundity rather than survival. Finally, we did not quantitatively evaluate metapopulation size necessary for maintaining long-term adaptive potential (mutation-drift balance). Conversely, other assumptions such as concerning density dependence would increase the pessimism of the Vortex results. We addressed this issue through sensitivity analysis where feasible (e.g., impact of increased inbreeding effects). In some cases, the best available models were inadequate to assess these factors (e.g., mutation-drift balance, wolf social structure). As stated above, given uncertainty, and to be consistent with Congress’ intent to institutionalize caution in order to avoid uncertainty about a species’ future status, we identified criteria that provide a margin of safety because they predicted a low potential for extinction (<1% over 100 years).

C. SUMMARY

The Service employed a 3 stage process to evaluate potential recovery criteria for the Mexican wolf. Stage 1 consisted of comparison of population performance across a range of scenarios with alternative metapopulation size and structure. Based on the results of these comparisons, we evaluated in Stage 2 which areas within the recovery region held suitable habitat sufficient to recover populations of the necessary size. In Stage 3, we evaluated what rates of dispersal could be expected between the areas identified in Stage 2. The process was then iterated to evaluate persistence of a metapopulation with the projected dispersal rates. The composite set of recovery
criteria represents an effort to maximize efficiency and realism by focusing on well-connected high quality habitat while maintaining the best possible population performance. The composite set of recovery criteria represents an assessment, based on best available scientific data, of what conditions are necessary to recover Mexican wolf populations to the point at which they are unlikely to become threatened or endangered again in the foreseeable future.
Figure 1. Conceptual diagram of analysis context of Mexican wolf PVA.
Figure 5. Contrasts in projected emissions between IPCC storylines.

Figure 6. Current (2000) biomes as predicted by the MC1 model. Potential wolf recovery areas as derived from Carroll et al. (2006) are outlined.
Figure 7. Projected biomes for 2062 under A2 scenario: a) CSIRO, b) Hadley, and c) MIROC GCM.
Figure 8. Projected biomes for 2062 under A1B scenario: a) CSIRO, b) Hadley, and c) MIROC GCM.
Figure 9. Map of potential linkages and relative connectivity rate (as inverse of least cost distance), between existing or potential wolf population core areas in the western US. Link colors range from green (better connected, or lower least cost distance) to red (worse connected).
Figure 10. Potential connectivity (inverse of distance), expressed as inverse least cost and resistance distance, between existing or potential wolf population core areas in the western US. Values in red are estimates of effective migration rates per generation in the NRM based on Vonholdt et al. 2010 (multiplied by 2 to account for incomplete sampling).
ASSESSING POTENTIAL RECOVERY SCENARIOS AND IDENTIFYING FACTORS AFFECTING SUCCESS

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A. CONSERVATION OF GENETIC DIVERSITY AND ADAPTIVE POTENTIAL AND ASSESSING POTENTIAL RECOVERY SCENARIOS

1. OVERVIEW: USING GENETICS TO INFORM VIABILITY CRITERIA

The increase in knowledge of conservation genetics over the last decade has made development of genetic criteria an increasingly important component of recovery planning (Allendorf and Luikart 2006, Frankham et al. 2010). Genetic criteria are especially relevant for taxa such as the Mexican wolf that are currently genetically depauperate (Hedrick et al. 2007). Genetic criteria are important because the genetic composition of a population affects both short-term demographic trends and viability (via inbreeding depression or accumulation of genetic load; Hedrick and Fredrickson 2010) and the long-term potential of the population to adapt to changing conditions. Genetic robustness may be defined as the genetic capacity to survive and respond to environmental changes within populations, among populations, and across the range (Redford et al. 2011).

The ESA’s primary goal is recovery of wild populations that are self-sustaining over the long term. This requires that recovered populations experience minimal loss of genetic health. Because much of our knowledge of the importance of genetics in recovery stems from relatively recent research, some have argued that genetic criteria are ‘theoretical’ and thus of limited relevance to real-world wolf conservation (Fritts et al. 1995). On the contrary, evidence for the relevance of genetics to wolf population persistence arises from multiple lines of evidence including theory, captive wolf populations, and wild wolf populations. For example, the Isle Royale wolf population was long used as an example of a small and isolated population without apparent genetic issues. New research demonstrates that this population shows effects of inbreeding and also documents a recent example of genetic rescue via dispersal from the larger mainland population (Raikonen et al 2009, Adams et al 2011).
Due to recent advances in genetic research, genetic recovery criteria are increasingly ‘objective and measurable’ in wild populations as required under the ESA. Genetic health can be measured via population-level metrics such as heterozygosity and allelic diversity (Frankham et al. 2010). Additionally, new methods allow assessment of individual-level metrics such as the number of genetically-effective migrants between subpopulations. For example, vonHoldt et al. (2010) assessed the level of genetically-effective dispersal in the Northern Rocky Mountains (NRM) wolf metapopulation and concluded that the metapopulation currently met connectivity criteria that would be sufficient to limit loss of heterozygosity to <1% per generation.

The relatively recent nature of much conservation genetics research in wild populations has resulted in a scarcity of in-depth analyses of the effects of genetics on persistence. This has led to two divergent viewpoints. On the one hand, some authors have concluded that, because detailed genetic data are often unavailable, general ‘rules of thumb’ may be used to determine recovery criteria (e.g., MVP (minimum viable population) numbers) across a range of taxa (Traill et al. 2010). Other authors have contested these generalizations. For example, Flather et al. (2011) reanalyzed the data used by Traill et al. (2007, 2010) and concluded that there is little evidence for a pattern across taxa supporting generalized MVP thresholds. The broader and more defensible conclusion from Traill et al. (2007, 2010)’s meta-analyses is that a comprehensive consideration of genetic threat factors can greatly increase estimates of the MVP required for long-term viability. Although genetic rules of thumb may be insufficient in isolation for devising recovery criteria, they are helpful in contextualizing results from more detailed species-specific PVAs such as we conducted.

2. USING EFFECTIVE POPULATION SIZE ($N_e$) TO INFORM CRITERIA

Effective population size, or $N_e$, is a useful and appropriate metric to inform recovery and recovery criteria for a variety of reasons, including: 1) it integrates ecological as well as purely “genetic” considerations, and 2) it gives insight to the current and future genetic functioning of populations. Typically, the metrics produced by PVAs that seem most directly relevant to recovery criteria, such as probability of extinction, are highly sensitive to uncertainty in model parameters and structure. Effective population size ($N_e$) provides a metric that is relevant to recovery and potentially more robust to model uncertainty. The effective population size of a set of individuals denotes the number of individuals in an “ideal” population that would give rise to the same rates of inbreeding accumulation or random genetic drift that is observed in the set of individuals in question. An ‘ideal’ population is defined as a random mating population in which all parents have an equal probability of being the parents of any individual progeny (Hedrick 2005).

Effective population size is an appropriate metric to inform recovery criteria because it can be directly linked to genetic effects on viability. For example, heterozygosity is expected to be lost
from a population at a rate of $1/2 \, N_e$ per generation. Therefore a population with an $N_e$ of 50 is expected to lose 1% of existing heterozygosity per generation.

Effective population size is a more robust metric than alternate genetic metrics such as inbreeding coefficient ($F$). Whereas effective population size provides information on the current functioning of the population (e.g. the relative strengths of genetic drift and natural selection, the rate at which heterozygosity is expected to be lost), mean inbreeding coefficient simply provides a snapshot in time of the estimated levels of identity by descent (homozygosity resulting from inbreeding accumulation). Subpopulations with rapid inbreeding accumulation will also tend to be those that go extinct earlier, leaving the remaining populations with relatively low inbreeding.

Effective population size integrates considerations of subpopulation census size and connectivity in a non-arbitrary manner. A small subpopulation will require greater connectivity to achieve the same $N_e$ as a larger subpopulation with low connectivity.

Molecular markers may be used to estimate the effective population size through a variety of statistical methods (Aspi et al. 2006). A review of genetically effective population sizes among wildlife populations (Frankham 1995) found that comprehensive estimates of effective population size were on average 10% of census population sizes, whereas a more recent review found an average ratio of 14% (Palstra & Ruzzante 2008). The estimated $N_e/N$ ratios in gray wolves range from ca. 0.2 – 0.42 (Aspi et al. 2006; Peterson et al. 1998; vonHoldt et al. 2008). Two recent studies on wolves found that effective sizes were 28% and 42% of census population sizes (Aspi et al. 2006; vonHoldt et al. 2008), but the ratio for the Mexican wolf population is expected to be lower than that of the wolf populations in these studies because of its high mean kinship suggesting that on average wolves in the Blue Range population are about as related to one another as full siblings born to unrelated parents (Siminski and Spevak 2013). The high relatedness results in part from the high number of wolf removals from 2005 through 2007 combined with few releases of minimally related wolves over the last nine years. In addition, these removals resulted in unequal contributions from wolves in breeding positions that are still evident in the population. Finally the the long history of small litter sizes and low recruitment of wolves to alpha status in the Blue Range would also be expected to reduce the ratio of effective to census population sizes. In contrast, the Greater Yellowstone area population studied by Von Holdt et al. (2008) was founded by 31 presumably outbred and unrelated wolves drawn from two large wolf populations in Canada. This population quickly grew to much larger size minimizing the loss of genetic variation and accumulation of inbreeding. And the Finnish wolf population (Aspi et al. 2006) had relatively high gene flow, around 3 migrants per generation, from the larger and genetically differentiated Karelian wolf population to the east in Russia for at least part of the sampling period (Aspi et al. 2009).

3. ESTIMATING AN EFFECTIVE POPULATION SIZE THAT MINIMIZES SHORT-TERM GENETIC EFFECTS AND MAINTAINS LONG-TERM ADAPTIVE POTENTIAL
The 50/500 rule is perhaps the mostly widely-accepted ‘rule of thumb’ for consideration of effective population size in conservation planning (Frankham 1980). The ‘50’ component specifies that populations important for conservation should have a minimum effective population size of at least 50 to minimize inbreeding accumulation in the short-term until populations can be grown to much larger size. This would correspond to a maximum rate of inbreeding accumulation of 1% per generation, which is approximately half the maximum rate tolerated by domestic animal breeders (Franklin 1980). Allendorf & Ryman (2002) proposed a stricter criteria in which the recommended effective population size should allow retention of 95% of heterozygosity over a 100 year period, which in wolves would be equivalent to loss of <0.2% of heterozygosity per generation, or an $N_e$ of ~250. While the 1% per generation rule underlying the $N_e = 50$ rule was approximate, it was based on a literature review over a wide variety of taxa of the inbreeding coefficient (and associated effective population size) that led to substantial inbreeding depression over the short term. This criterion is a well-established generalization that can be tested against species-specific modeling as we do here.

In their review of MVP rules of thumb, Flather et al. (2011) critique use of the 50/500 rule, stating that "the 50/500 values of $N_e$ are simply viability goals for maintaining genetically diverse populations; they provide little direct connection with extinction risk." However, although we agree with Flather et al. (2011) that the specific threshold embodied in the 50 rule may be somewhat arbitrary, the genetic processes they represent are directly connected with extinction risk and should be assessed in any comprehensive PVA.

In order to maintain its ability to adapt to new environments (such as caused by climate change or novel diseases), a population should be of sufficient size to maintain a balance between loss of alleles via genetic drift and new alleles produced by mutation. The ‘500’ portion of the 50 / 500 rule specifies that retention of allelic diversity through a long-term balance between mutation and genetic drift requires that a population or metapopulation maintain an $N_e \geq 500$, which in wolves might require a census population of >2500. More recent studies suggest that an $N_e$ of 500 may be inadequate. Estimates of “evolutionary” MVP, the minimum population size required for species to adapt to changing environments through evolution, have ranged from effective population sizes of 500-1000 (Franklin et al. 1980; Franklin & Frankham 1998) to 5,000 (Lynch & Lande 1998).

Population sizes of these magnitudes would secure long-term sustainability of the population, addressing both genetic and demographic requirements (Frankham et al. 2002). Recovery of wolf populations of thousands of individuals, that obtain effective population sizes that secure a potential for future evolution, is challenging to achieve at the scale of any one region but may be feasible at broader scales (Carroll et al. 2006). Recovery goals should consider 1) securing sufficiently high population sizes within the present fragments (subpopulations) within the
historical range and adjacent areas and 2) securing sufficient connectivity among the subpopulations through natural migration.

4. GENETIC THREATS AND STRATEGIES FOR THEIR AMELIORATION IN THE MEXICAN WOLF

Addressing genetic threats are especially relevant to ensuring recovery of the Mexican wolf due to their few founders, strong inbreeding and inbreeding depression, and continuing history of small population sizes (Hedrick and Fredrickson 2010). Mexican wolves were rescued from extinction by the establishment of three captive lineages founded by a total of seven wolves (Hedrick et al. 1997). These lineages were managed separately until the mid-1990’s by which time all three lineages had become strongly inbred. Inbreeding coefficients ($f$) for McBride, Aragon, and Ghost Ranch lineage pups born in the mid-1990’s averaged about 0.23, 0.33, and 0.64, respectively. Heterozygosity was also low. Observed heterozygosity at 20 microsatellite loci averaged 0.457, 0.128, and 0.255 for McBride, Aragon, and Ghost Ranch lineage wolves, respectively. Although the McBride lineage was fixed for a single allele at two loci, the Aragon and Ghost Ranch lineages were fixed at 11 loci (Hedrick et al. 1997). Overall, heterozygosity was about half of that observed for other subspecies of northern gray wolves. At that time the “captive population” consisted of three tiny, separate, and highly inbred populations that were each experiencing severe genetic bottlenecks.

Out of concern for the low number of founders and rapid inbreeding accumulation the decision was made to merge the three lineages. Pairings between McBride lineage wolves and Aragon lineage wolves and between McBride and Ghost Ranch lineage wolves began in 1995 with the first F1 pups born in 1997. Although both parents of each F1 wolf were strongly inbred, the F1 wolves themselves were expected to be free of inbreeding and free of any deleterious effects on fitness due to inbreeding, called inbreeding depression. Ultimately 47 F1 wolves were produced from 1997 to 2002. Upon reaching maturity, the F1 wolves were paired among themselves, backcrossed with pure McBride wolves, and paired with the descendants of F1 wolves called “cross-lineage” wolves.

Although the F1 wolves had high reproductive fitness relative to wolves from the three founding lineages, there was evidence of strong inbreeding depression among cross-lineage wolves in captivity affecting dams, sires, and pups (Asa et al. 2007; Fredrickson et al. 2007). There was also evidence of strong inbreeding depression in the reintroduced Blue Range population.

Despite the merging of the three founding lineages, and a rapid increase in size, the captive population of Mexican wolves is still small with limited potential to support recovery. As of September 2013, it consisted of 248 wolves, of which 36 were reproductively compromised, leaving 212 wolves as the managed population (Siminski & Spevak 2013). The age structure of the population, however, is heavily skewed with wolves eight years old and above comprising
about 51% of the population. This senescent age structure has resulted from the high reproductive output of the F1 wolves and their descendants in captivity along with the combination of few releases of captive-born wolves to the reintroduced Blue Range population (BRP), and removals of wolves from the Blue Range population to captivity. It is estimated that more than half of the alleles from the seven founders have been lost from the population. The genetically effective population size ($N_e$) is estimated to be 21 and the ratio of effective to census size ($N_e / N$) is estimated to be 0.098 (Siminski & Spevak 2013). Thus the captive population is expected to lose about 2.4% of its heterozygosity each generation.

Data from about 6,000 SNPs suggest that while heterozygosity was restored in the F1 wolves, heterozygosity among cross-lineage wolves has declined to levels similar to that of mid-1990’s McBride lineage wolves (R. Fitak, unpublished data).

Unfortunately the reintroduced Blue Range population is currently a poor representation of the genetic variation remaining in the captive population. Founder representation is more strongly skewed than in the captive population. Mean inbreeding levels are 61% greater in the BRP (0.1924 versus 0.1197), and only about two thirds of the alleles present in the captive population are estimated to be in the Blue Range population (Siminski & Spevak 2013). In addition, the estimated mean relatedness (mean kinship) of wolves in the Blue Range is about 50% greater than that in the captive population, with wolves on average about as related to one another as full siblings born to unrelated parents (Siminski & Spevak 2013). Without substantial management action to improve the genetic composition of the BRP, inbreeding will accumulate and heterozygosity and alleles will be lost much faster than in the captive population. A program of selective removals and initial releases over several years could greatly improve the genetic composition of the Blue Range as well as increase its demographic vigor.

Recovering Mexican wolves will entail reintroducing genetically diverse wild populations and growing them quickly to large sizes. Rapid growth of reintroduced populations is needed to minimize heterozygosity loss and inbreeding accumulation while the populations are small. This has not been done, however, in the Blue Range. Given the sizes of habitat patches potentially available for reintroductions, these restored populations would still lose heterozygosity at a rapid rate if they were isolated. Ensuring substantial levels of connectivity between the reestablished populations, however, could greatly slow heterozygosity loss and inbreeding accumulation within each population. In the long-term, failure to establish genetically diverse and connected wild populations would compromise the Mexican wolf’s demographic vigor as well as its ability to adapt to future environmental challenges.

B. DETAILS OF VORTEX POPULATION SIMULATION MODEL
1. OVERVIEW OF VORTEX MODEL

Vortex is a simulation model of the effects of deterministic forces as well as stochastic demographic, environmental and genetic events on wildlife populations. It is an attempt to model the many factors composing the “extinction vortex” (Soule & Mills 1998) that can threaten the persistence of small populations (hence, its name). VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, dispersal between populations, harvest, supplementation, and then truncation of populations (if necessary) to the carrying capacity, and finally incrementing age by one year. The simulation of the population is iterated many times to generate the distribution of fates that the population might experience. VORTEX is an individual-based model. That is, it creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. VORTEX keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur.

We parameterized Vortex based on best available information from the Mexican wolf population (Fredrickson et al. 2007) and, where appropriate, other wolf populations. Vortex output allows tracking of both demographic criteria (population size, time to extinction) and genetic criteria (heterozygosity, allelic diversity, inbreeding coefficient). We evaluated both of these classes of output metrics under a range of scenarios with varying a) subpopulation size [N=100-350]; b) number of subpopulations [3-4], and c) dispersal rate between subpopulations [0-2 “effective” migrants per generation]. We compared results from populations founded by outbred and unrelated individuals with results based on populations founded by individuals with pedigree data based on the current captive and wild Mexican wolf populations.

In order to assess the effects of stochastic and genetic factors within a PVA, it is common to analyze parameter sets that contain ‘boosted’ demographic rates when data from existing populations suggest current demographic rates are inadequate for population persistence, under the assumption that deterministic factors that affect these rates will need to be addressed as a first priority, in order for criteria mitigating stochastic and genetic factors to be relevant (Caughley 1994). We first evaluated deterministic population growth rates (lambda) across a range of sets of demographic rates derived from field data (Oakleaf unpublished data). Because mortality rates based on these data resulted in population growth rates < 1, we then selected a baseline set of mortality rates based on data from the Greater Yellowstone Area that allowed population persistence (lambda > 1). This allowed us to evaluate additional threats from stochastic and genetic factors. We then added parameterization of catastrophes (disease). We evaluated
population persistence and genetic metrics for the ensemble of scenarios across a range of population size and connectivity.

2. MORTALITY RATES

We first evaluated deterministic lambda (intrinsic population growth rate) for the Blue Range population of Mexican wolves based on mortality rates from Oakleaf (unpublished data) and found that lambda was substantially below 1. Consequently we used mortality rates based on those observed in the Greater Yellowstone area (GYA) which were intermediate to those estimated for the northwestern Montana and central Idaho wolf populations (Smith et al. 2010). For pups, we used an annual mortality rate of 24.4% with a standard deviation of 5.072. For yearlings and adults Smith et al. (2010) estimated an annual mortality rate of 22.9% in the GYA. To explore how different levels of yearling / adult mortality may affect Mexican wolf populations we used three mortality values in our simulations, 22, 23.5, and 25%. We estimated process variance for adult / yearling mortality from the GYA data used in Smith et al. (2010) by subtracting the variance due to annual demographic stochasticity from the total variation associated with annual adult / yearling mortality. From this we calculated a coefficient of variation of 0.2127 for adult / yearling mortality. We then used this value to set standard deviations for the three yearling / adult mortality rates used in our simulations.

3. DOWNLISTING CRITERION RELATED TO MORTALITY RATES

Wolf populations are generally limited in distribution to areas where the risk of being killed by humans is not excessive (Fuller et al. 2003). High rates of human-caused mortality are documented as a specific threat factor for Mexican wolves (see Section I.i.). We developed a downlisting criterion that addresses this threat factor. The criterion is expressed as in terms of the estimated rate of human-caused losses during an 8 year period. This criterion is relevant to downlisting (and not delisting) because wolf populations of a size that merit downlisting (150 individuals per population) will exist far enough below carrying capacity that the primary limiting factor on population growth will be human-associated mortality. At the time of delisting, populations will be closer to carrying capacity and may also be limited by other environmental factors. We derived an appropriate downlisting criterion from a separate analysis as described below (Vucetich et al. in review). However, a population that meets this criterion will also show total mortality rates similar to those assumed in the Vortex baseline scenarios. Thus our conclusions as to appropriate criteria for population size and connectivity will be more relevant for a metapopulation that meets the downlisting criterion for human-associated mortality.

Annual survival rate ($S$) is the proportion of animals in a population that survive from one year to the next. Evidence clearly indicates that $S$ has an important influence on the population
dynamics of wolves (e.g., Fuller et al. 2003; Peterson et al. 1998). That is, as $S$ decreases there is a strong tendency for lambda, the population growth rate, to decrease. Population growth rate is the fundamental determinant of a population’s numerical dynamics. Because recruitment rate (the process that balances mortality rate) in the Mexican wolf population is affected by inbreeding depression, the population may be more sensitive to fluctuations in $S$ than most other wolf populations. Significant human-caused mortality ($m_{hc}$)(poaching, vehicle collisions, lethal management removal actions, etc.) occurs in most wolf populations. Four recently published papers present analyses that quantify the relationship between $m_{hc}$ and $S$ for wolf populations (Adams et al. 2008; Creel and Rotella 2010; Murray et al. 2010, Sparkman et al. 2011). Collectively these papers indicate that $S$ and $r$ tend to decrease as $m_{hc}$ increases.

Previous analyses of $m_{hc}$ and $r$ were based on data that would also allow one to calculate the probability that $r$ would fall below any specified level, given $m_{hc}$. For this reason, we developed this downlisting criterion by first reasoning that the rate of human-caused losses should be low enough to correspond with a reasonably high chance that the population’s growth rate would be sufficiently positive to allow reasonably fast growth as the population begins to recover from its status of endangered to threatened. The need for a reasonably fast growth rate is further justified by the irreparable damage that inbreeding may cause if the population grows too slowly during these early stages of recovery. Based on this reasoning, we calculated the value of $m_{hc}$ that corresponds to a relatively low risk (25%) of $r$ falling below 2.5%/yr. We refer to this threshold value as $X$.

The downlisting criteria are expressed as: the estimate for the expected value for the average rate of human-caused losses during an 8-year period should be less than $X$. Mexican wolves have also been experiencing high rates of management removals from the wild. These removals are functionally equivalent to a mortality event from the perspective of the free-ranging population. For this reason, the downlisting criterion that we develop will pertain to the rate of human-caused losses, where losses include human-caused mortalities (poaching, vehicle collisions, etc.) and management removals.

We calculated $X$ by analyzing data collected from wolf populations across North America where $m_{hc}$ and $r$ had been monitored. One set of such data was compiled by Creel and Rotella (2010). Those data included: 1) 18 populations from across North America (originally compiled by Fuller et al. (2003), where each population had been observed for one or several years; and 2) 29 estimates from wolf populations living in the Northern Rocky Mountains. We used this data set along with others to make our calculations. Based on the analysis of Vucetich et al. (in review), we propose that to be considered for downlisting, the best estimate for the expected value for the average rate of human-caused losses during an 8-year period should be less than 17%.
4. REPRODUCTIVE PARAMETERS

The following parameters related to reproduction were set to values that are standard for previous Vortex analyses of wolf populations:
1) Mating system: Long Term Monogamous
2) Age of first reproduction for females/males = 2 years
3) Maximum age of reproduction = this was set to 11 years, but functionally wolves older than 9 years old could not reproduce (see Density Dependence below)
4) Maximum number litters per year = 1
5) Maximum number progeny per litter = 11
6) Probability of female in breeding pool having no litter: 0
7) Sex Ratio = 50/50
8) % Males in Breeding Pool = 100

Fecundity for wolf populations in the Vortex simulations is a function of litter size and the proportion of adult females breeding. The function for litter size was based on Fredrickson et al. (2007) as described below. Previous Mexican wolf PVAs have set the proportion of adult females breeding at 50% (Seal 1990) to 60% (IUCN 1996). vonHoldt et al. (2010) used an estimate of 35% for the Yellowstone population, while a PVA for the Algonquin (Ontario) wolf population used a value of 57% derived from the mean from estimates ranging from 50-64% (Ewins et al. 2000). We set the proportion of adult females breeding at 50%, with an SD of 12.5% for our simulations but the sensitivity analysis of Carroll et al. 2013 also conducted simulations incorporating a density dependent function for this parameter (see below).

5. DENSITY DEPENDENCE, CARRYING CAPACITY, AND HARVEST

Two forms of density dependence were incorporated into the simulations. The first was density dependence on survival of adults greater than 6 years old. In well-studied populations of northern gray wolves, relatively few adults live past eight years old (e.g. Smith et al. 2010). And very few females produce pups after eight years. But in the BRP, a relatively large proportion of wolves have been documented to survive to up to 11 years while retaining alpha status, even though only one female wolf is known to have produced pups after nine years old. It is thought that the longevity of wolves in the BRP is a function of the small population size and low density of the population, and that as the population gets larger the proportion of very old wolves will drop.

Consequently we have incorporated a function into the simulations that causes mortality to increase with age past six years, and the rate of mortality increases is greater at high wolf densities (Figure 1). At very low wolf densities, wolves may live up to 11 years, but at high wolf densities no wolves live past nine years old. For example, mortality rates for nine year old
wolves increased from 31.5% to 93.5% as wolf numbers increased from 10% of K to 75% of K, when the baseline mortality rate was 22%.

In the simulations below we set the % of adult females breeding at a constant value of 50 with a standard deviation of 12.5. In the sensitivity analysis of Carroll et al. 2013, however, we investigated the effects density dependence on the % of adult females breeding. We developed a density dependent function (Figure 2) based on data from Yellowstone National Park (Smith and Stahler unpublished) from years in which both the numbers of females breeding was known and total wolf numbers could be estimated. With this function, about 59% of adult females were expected to breed each year when populations were at very low densities. At maximal densities (N = K), however, only 30% of adult females were expected to breed in a given year. The standard deviation of the % adult females breeding with density dependence was set to 25% of the mean value for each year.

Targeted sizes for individual populations in simulations ranged from 100 to 300 individuals. We assumed that “recovered” wolf populations would likely exist at numbers below ecological carrying capacity due to human caused mortality. Consequently, in the simulations we set carrying capacities of individual populations to 133% of the targeted size. Vortex uses carrying capacity (K) to impose a ceiling model of density-dependence on wolf numbers, i.e. if wolf numbers are above K at the end of a timestep, Vortex randomly kills additional wolves until the population size is equal to K. To maintain wolf numbers below K, we used the “Harvest” function in Vortex. We parameterized the function to “harvest” wolves each year that the population size exceeded the target population size, beginning in year 25. By this time, population size had reached or exceeded K in most iterations. When harvest occurred, 12.5% of the wolves above the target population size were taken, from each of four sex / age classes: male pups, female pups, male yearling and adult, and female yearlings and adults. We set the standard deviation in carrying capacity due to environmental variation (drought, etc.) to 10%.

Previous Mexican wolf PVAs (Seal 1990, IUCN 1996) did not incorporate density dependence in reproduction. We propose that limiting density dependence to survival is the most parsimonious strategy because 1) data is scarce on the response of reproductive parameters to density, and 2) once Mexican wolf subpopulations reached moderate densities, dispersal to adjacent areas with lower survival rates would be expected, and thus ‘saturated’ conditions would rarely occur given the fragmented distribution of wolf habitat in the southwestern U.S.

6. DISEASE AND OTHER “CATASTROPHIC” EVENTS

We parameterized episodic threats based on data from the Yellowstone wolf population which showed distemper outbreaks occurring on average of every 5 years, and affecting primarily fecundity rather than survival (Fecundity: 20% of baseline, Survival (all age classes): 95% of
Because we did not model additional episodic threats such as other diseases or drought, this can be seen as an optimistic parameterization of catastrophes. All catastrophes were ‘local’ rather than ‘global’, i.e., were not simultaneous across populations. Carroll et al. (2013), however, considered frequencies of catastrophes from four to six years as part of their sensitivity analysis.

7. GENETIC EFFECTS

Previous Vortex wolf PVAs have either ignored genetic effects (Ewins et al. 2000), or used a fraction of the default number of lethal equivalents in Vortex (3.14), which is a median value obtained in a study of captive populations of 40 mammalian species (Ralls et al. 1988). This likely represents an underestimate of inbreeding effects in wild populations (e.g. Keller and Waller 2002). The Mexican wolf PVAs of Seal (1990) and IUCN (1996) set this value at 1.7 and 3.14 LE, respectively.

Fredrickson et al. (2007), however, found evidence of strong negative effects of inbreeding on reproduction in both the captive and wild populations of Mexican wolves. Among captive wolves with ancestry from at least two of the founding lineages, they found that inbreeding accumulation in the both sires and dams rapidly reduced the probability of a pair producing at least one live pup. Of those pairings that produced at least one live pup, inbreeding in the dam and in the pups were found to have strong negative effects on litter size. In the BRP they also found that inbreeding accumulation in the pups reduced observed litter sizes, but a lack of data prevented them from meaningfully examining the effects of parental inbreeding on litter sizes. These results are consistent with those of Asa et al. (2007) who found that inbreeding reduced semen quality in Mexican wolves.

Strong inbreeding effects have also been observed in other wolf populations. In the Scandinavian wolf population, inbreeding accumulation has been found to reduce both litter sizes and the probability of a wolf attaining a breeding position (Liberg et al. 2005; Bensch et al. 2007). Inbreeding has also been tied to high incidences of severe skeletal defects among Scandinavian and Isle Royal wolves (Raikonen et al. 2006; 2009). And the recent genomic sweep of the Isle Royale wolf population by a single immigrant from the mainland illustrates the low relative fitness of the highly inbred Isle Royale wolves (Adams et al. 2011). More generally, inbreeding depression has been shown to be common in wild populations where inbreeding is occurring, resulting in reduced individual fitness and producing population level effects among a wide range of plants, invertebrates and vertebrates (e.g. Keller & Waller 2002).

In the simulations we incorporated inbreeding effects on litter size using the best model from the Blue Range data in Fredrickson et al. (2007). Although this is a significant advance in realism
relative to previous Mexican wolf PVAs, our treatment of inbreeding likely underestimates of the overall effects of inbreeding depression among wild Mexican wolves.

8. FOUNDING POPULATIONS
For the simulations we assumed that releases to found new populations of Mexican wolves would begin in 2018 and be completed by spring of 2022. Thus the simulations are assumed to begin in the spring of 2022.

To “update” the Blue Range population to 2022, we first constructed a Blue Range pedigree based on the results of the January 2013 wolf count. During this count 75 wolves and 14 packs were detected, but one wolf was permanently removed leaving 74 wolves. Based on the results of the count we assumed there would be one unknown pair among the uncollared wolves detected, and that one radio collared yearling female disperser that was traveling with another wolf would form a new pair. We also assumed that the Hawks Nest alpha male (whose collar does not work) would pair with an undetected wolf. In the spring of 2013 the USFWS had two pairs together in captivity with intentions of releasing both in 2013. We assumed that both would be released before pups were produced. In total, we assumed there would 79 wolves and 17 pairs in the BRP at the start of 2013. Two of the pairs, however, had alphas that are post-reproductive (10+ years old) and would not produce pups in the simulations, leaving 15 reproductive pairs in the BRP in spring 2013.

To “update” the BRP from spring 2013 to spring 2022 we ran a simulation with only the BRP for nine years, with an adult mortality rate of 22.75%. The median population size for the BRP at year 9 was 121 wolves, based on 1000 iterations. We next ran single iteration simulations until we got an ending population size close to 121. From this simulation we used simulation output from Vortex to extract the pedigree over the previous nine years. The simulation we chose had N=122 wolves at year 9. The information extracted from the simulation included not just the pedigree, but the sexes and ages of the wolves alive at the end of the simulation (2022). So in the simulations presented below the BRP was started with 122 wolves and 21 pairs.

We next created new wolves and wolf pairs to found new wild populations during the period 2018 – 2022. Because few of the existing captive wolves will be suitable for release during this period, we first created a new generation of captive wolves which could be used in releases. In total, a pool of about 800 wolves was generated from which founding wolves could be selected. We used the program PMx (Ballou et al. 2011) to select wolves from the pool to create two populations of ten pairs and two populations of nine pairs. Individuals chosen for each population were to be minimally related and collectively provide a good representation of the existing genetic variation in the existing captive and wild populations. We then used PMx to pair the wolves in each population. The result was four new populations of 20, 20, 18, and 18 wolves that each had better representation for the existing genetic variation than the current captive population.
The wolves selected by this process, however, would result in some individual wolves producing offspring for the released populations with up to five different mates. This is unrealistic for the captive population. So we then revised the parental pairings so that the individual wolves producing the release wolves would have no more than two mates over time.

Once the 38 founding pairs were determined, a timetable was developed for when each pair would be released. For the Grand Canyon and Southern Rockies populations, we assumed that two new pairs would be released each year from 2018 to 2022 for a total of 10 pairs released into each population. These alphas potentially produced offspring each year after release. They also experienced mortality so that by 2022 only about half of the founding pair members were still alive. We then paired single alphas and 2–4 year old offspring among themselves such that at the start of 2022 each population had a total of 50 wolves and 10 pairs. Sex was randomly assigned for descendants of the founding pairs. We used the same process for the Mexican populations, but used only 7 of the 9 pairs noted above, resulting in starting populations of 35 wolves with seven pairs in 2022. Throughout the process of developing the new populations, no artificial insemination was used. All wolves were produced by natural pairings. Table 1 presents the numbers of wolves and packs used to found simulated wolf populations. Departures from these numbers are noted in the results below.

9. CONNECTIVITY BETWEEN POPULATIONS

Carroll et al. (2006) identified three major core areas of suitable habitat in the area encompassing Arizona, New Mexico, southern Colorado and southern Utah which may be most suitable for restoring large populations \((N \geq 250)\) of Mexican wolves. The three core areas of suitable habitat are a) the Blue Range Wolf Recovery Area and adjacent public lands, b) the Grand Canyon and adjacent public lands, and c) two linked areas of public lands and private lands with conservation management in northern New Mexico and southern Colorado (labeled Carson and San Juans in Carroll et al. (2006))(see section I.H.).

In addition two areas in the western Sierra Madre of Mexico have been identified that may each be able to support around 100 wolves (Araiza et al. 2007; C. Lopez personal communication). The northern area (Sonora) spans the Sonora / Chihuahua border from New Mexico south about 240 km. The southern area (Durango) is primarily in southwestern Durango extending south into Zacatecas.

Based on habitat modeling for the southwestern USA, we assumed that the Grand Canyon and southern Rockies populations would both be linked by dispersal to the Blue Range, but there would be no natural dispersal between the Grand Canyon and southern Rockies. Similarly, we also assumed that the Sonora population would be linked by dispersal to both the Blue Range and Durango populations, but that there would be no natural dispersal between Durango and the
Blue Range. For these networks of populations we simulated three levels of connectivity between populations in our simulations: no dispersal between populations, dispersal sufficient to provide an average of 1 genetically effective mpg (1 mpg) to each population, and dispersal sufficient to provide 2 genetically effective mpg to the centrally located Blue Range and 1 genetically effective mpg to each of the other populations (2/1/1 mpg). Simulations were parameterized such that the burden of providing immigrants into the Blue Range was equitably split among neighboring populations based on population size. Dispersal between populations was modeled as a constant proportion of young wolves (1 – 4 years old) moving to a neighboring population each timestep.

We defined an effective migrant as a wolf that immigrated into a non-natal population, paired and produced at least one pup in its new population. We quantified the number of effective migrants into each population by tallying the numbers of effective migrants reported by Vortex in each iteration from years 31 -100 and dividing the total by the number of wolf generations. We used a generation time of 4.2 years. Numbers of effective migrants reported are averages over all iterations for each population. Iterations of a given population were omitted from the calculation of effective migrants if a donor population became extinct during the iteration. In the simulations, we attempted to ensure that populations received at least the minimum number of effective migrants. We also attempted to limit the numbers of effective migrants into each population to no more than 10% above the desired average. We chose the years 31 – 100 for quantifying effective migrants, because migration rates were typically highest early in the simulations e.g. years 20-35, and declined over time. By omitting a portion of the highest migration years we ensured that our parameterization of dispersal rates provided for migration even when populations were below targeted sizes.

10. CONTEXT: COMPARISON WITH PREVIOUS VORTEX-BASED MEXICAN WOLF PVAS

The Vortex software used in the PVA simulates the life cycle of individuals in a population and the interacting effects of the population’s demographic and genetic composition. Although Vortex does not evaluate habitat distribution and other spatial issues, its detailed evaluation of genetic issues complements results from habitat models. Although Vortex has been used in previous Mexican wolf recovery planning efforts (Seal 1990, IUCN 1996), we now have better genetic and demographic data and a more developed software (Vortex version 10) that allow more complex analyses than were previously possible. Neither of the previous Mexican wolf PVAs rigorously addressed genetic issues. The 1990 PVA simulations suggested that a population of 100 or more animals would have less than 5% probability of extinction over the 100 year time period (Seal 1990). However, because larger populations were required in order to retain a large proportion of the starting heterozygosity, the authors speculated that “in order to biologically recover the Mexican wolf, a meta-population of at least 1000 wolves will need to be free-ranging in the wild.”
The 1996 PVA (IUCN 1996) predicted that the risk of extinction over a 100-year time frame for a population reintroduced into the White Sands Recovery Area was considerable. In contrast, the authors concluded that a population inhabiting the Blue Range Recovery Area would have a reduced risk of extinction due to its larger size. The authors found considerable sensitivity of the Blue Range population to catastrophic events (drought, disease). They also cautioned that “the genetic picture Vortex paints is an optimistic one, since the program assumes that each new individual supplemented to the existing population is completely unrelated to all individuals in that population. Because of the very-restricted number of founders making up the captive Mexican wolf population, captive individuals will have some degree of relatedness to each other as well as to those individuals recently reintroduced into the wild.” The current PVA is the first to quantitatively assess the speculations concerning genetic MVPs in the 1990 and 1996 PVAs. Our analysis using pedigree data confirmed earlier concerns regarding increased extinction risk to populations derived from inbred founders.

In addition to the enhanced genetic capabilities of the current version of Vortex, we have substantially increased the amount and types of information that can be output from each simulation. For example, for each population it is now possible to quantify the numbers of census and effective migrants received, the rate of inbreeding accumulation, and changes in heterozygosity, and census population sizes in each timestep of each iteration in a simulation.

Finally, we have extensively tailored the simulation to incorporate several important aspects of wolf natural history including: 1) allowing wolves to survive past their reproductive years, when the population is at low density, 2) incorporating density dependent survival senescence for older wolves, 3) incorporating realistic dispersal between populations by limiting the pool of potential dispersers to young, non-breeding wolves and assigning increased mortality to those that move between populations, 4) preventing full sibling and parent-offspring pairings, 5) inclusion of a density dependent function for the % adult females breeding based on empirical data (used in sensitivity analysis of Carroll et al. 2013), and 6) incorporating a mechanism to allow wolf populations to be maintained at densities substantially below carrying capacity.

Finally, we have also incorporated perhaps the most defining feature of the wolf social system – the monopolization of breeding opportunities by a subset of adult wolves. In natural wolf populations, breeding is typically limited to a single adult male and female in each pack, and these individuals restrict breeding by others for the duration of their tenure as breeders. From a population genetic perspective this has the effect of excluding some wolves from contributing their genes to future generations and reducing the contribution by other wolves. This aspect of the wolf social system reduces the genetically effective population size ($N_e$) of natural wolf populations. All of these enhancements make the demographic and population genetic functioning of the simulated populations more realistic.
C. RESULTS OF VORTEX SIMULATIONS

We used Vortex in a two-step process to identify scenarios that may provide a suitable basis for recovery criteria. We first considered seven scenarios that varied widely in the numbers and sizes of populations included. Based on the results from the first step, we identified three scenarios to examine in greater detail.

1. FOUR SCENARIOS

Because previous Vortex modeling indicated that multiple large populations of Mexican wolves will be needed for recovery and habitat availability indicated these large populations will need to be in the USA, we further investigated three potential recovery scenarios. Scenario 1 required three populations each with at least 250 wolves for a total of at least 750 wolves (3x250). The second recovery scenario was an adaptation of scenario 1 that would allow greater management flexibility. It required three populations of at least 200 wolves for a minimum of 750 total wolves; the “extra” 150 wolves could be distributed among any of the three populations. The most extreme outcome of this scenario would be two populations of 200 and one population of 350. This would also potentially be the most detrimental configuration. To better understand the potential viability costs and benefits of this proposed management flexibility we simulated two different metapopulations with two populations of 200 wolves along with a single population of 350 wolves. The first assumed at least 350 wolves would be maintained in the Grand Canyon population and at least 200 wolves would be maintained in each of the other two populations (Grand Canyon 350). The second assumed that at least 350 wolves would be maintained in the Blue Range and that the Grand Canyon and Southern Rockies populations would each support at least 200 wolves (Blue Range 350). In the simulations below, the Grand Canyon and Blue Range populations were the strongest and weakest populations, respectively. It should be noted that because Vortex is not truly a spatially explicit simulation model the locations of the “Grand Canyon” and “Southern Rockies” populations are interchangeable, i.e. the population called Grand Canyon below could have instead been called the Southern Rockies. The third recovery scenario required three populations of at least 250 wolves as well as a fourth population of at least 100 wolves in Mexico (3x250 + Sonora). Requiring at least one population be established and maintained in Mexico would expand the geographic range of the recovered Mexican wolf population and address significant portion of range concerns. Finally we simulated a fourth scenario which was not considered a recovery scenario. This scenario would require at least 250 wolves in the Blue Range and two populations in Mexico each supporting at least 100 wolves (Blue Range+2MX100).

2. SCENARIO 1: 3X250
At the start of the simulations the three populations differed in their mean kinship levels. The Blue Range had a mean kinship of 0.2446, whereas the Grand Canyon and southern Rockies had lower mean kinships of 0.194, and 0.1954, respectively (Table 2). Mean kinship is a measure of the average relatedness of each individual to all individuals in the population including itself. A mean kinship of 0.25 would mean that on average individuals in the population were as related to each other as are full siblings from unrelated parents. In the absence of immigration from other populations, the initial mean kinship of a population will affect how quickly heterozygosity is lost and inbreeding accumulates. The simulated BRP started with a mean kinship slightly less than the actual Blue Range (0.2472) despite being “advanced” by nine years. The low mean kinship of the simulated Blue Range relative to the actual Blue Range is in large part a result of the inclusion of two new pairs that were planned for release in 2013. One of these pairs was released but one member died and the other was brought back into captivity. The other pair was not released. Mean kinships for the Grand Canyon and southern Rockies at the start of the simulations were 26 and 25% lower, respectively, than that for the Blue Range, but substantially higher than that for the captive population (0.1665; Table 3).

When there was no dispersal between populations, the Blue Range initially increased rapidly in size from 122 wolves at the start of the simulations. By year 24 the mean size of extant iterations had peaked at 244 wolves when there was 22% adult mortality (Figure 3A). Wolf numbers declined steeply starting at year 25 due to the initiation of harvests, and continued to decline to the end of the of the simulation. By year 100 the mean size of extant iterations had declined to 134 wolves – only eight more than the Blue Range started with at year zero. In contrast, the Grand Canyon began the simulation with 50 wolves and increased rapidly to a mean of 241 wolves at year 24 (Figure 3B). Initiation of harvest at year 25 resulted in a small decline in mean population size, followed by a slow decline in numbers to a mean of 193 wolves among extant populations. The southern Rockies population performed similarly to the Grand Canyon ending the simulation with a mean size of 189 wolves. Despite starting the simulation with nearly 2.5 times as many wolves as the Grand Canyon (and southern Rockies) the Blue Range ended the simulation with 44% fewer wolves. The differences in mean sizes of the three populations was a result of the differences in initial mean kinships of the populations and provided an illustration of the effects that the composition of the starting populations may have on their viability.

With 1 mpg and 22% adult mortality the Blue Range peaked at 213 wolves before declining to a mean of 156 wolves at year 100 (Figure 3A). But for the first 68 years of the simulation the mean population size of the Blue Range with 1 mpg was smaller than that with no dispersal between populations. This illustrated the demographic cost of the 1 mpg dispersal regime to the centrally located Blue Range. Whereas the Blue Range sent out about 2 migrants per generation (1 mpg each to the Grand Canyon and southern Rockies), the other populations each sent about 0.5 migrants per generation to the Blue Range. The demographic cost of this dispersal regime was in large part a result of the high mortality rate (62.5%) assumed for wolves dispersing between populations. In addition some wolves which successfully moved to non-natal populations died
before producing a pup and were not considered as genetically effective migrants. With 25% adult mortality, the demographic cost of the 1 mpg dispersal regime to the Blue Range became extreme (Figure 3C). Mean wolf numbers peaked at 129 wolves in year 6 before declining to a mean of 49 wolves at year 100. For the entire 100 year period the Blue Range had fewer wolves than with no dispersal between populations. It should be noted that the Blue Range received a mean of 1.28 mpg (Table 3), notably above the 1 - 1.1 mpg range targeted. Without these “extra” migrants the Blue Range would have supported even fewer wolves over time. The mean number of migrants received by the Blue Range was increased to ensure that the Grand Canyon and southern Rockies each received at least 1 mpg. Based on many trial simulations it appeared that the parameter space in which the Blue Range could send at least 1 mpg to each of the two peripheral populations while receiving 1 – 1.1 mpg may have been very limited.

With 2/1/1 mpg, there was still a demographic cost to the Blue Range in the early years of the simulations. When there was 22% adult mortality, mean population size for the Blue Range with 2/1/1 mpg lagged that with no dispersal for the first 27 years of the simulation (Figure 3A). But for the remaining 73 years, the Blue Range was larger than that with no dispersal between populations. At year 100, the Blue Range averaged 216 wolves with 2/1/1 mpg, and exceeded that with no dispersal between populations by 82 wolves on average. With 25% adult mortality, the demographic cost of 2/1/1 mpg extended through the first 48 years (Figure 3C). But by year 100, the Blue Range averaged 117 wolves, exceeding that with no dispersal between populations by an average of 58 wolves.

In contrast to the Blue Range, the Grand Canyon had the highest mean population sizes with 1 mpg (Figure 3B and D). But with 2/1/1 mpg, the peripheral Grand Canyon population bore a small demographic cost relative to 1 mpg as a result of having to send twice as many migrants to the Blue Range. The southern Rockies population performed similarly to the Grand Canyon. Although mean wolf numbers were relatively steady after harvests began for the Blue Range with 2/1/1 mpg and for the Grand Canyon with 1 mpg when there was 22% adult mortality (Figure 3A and B), the modest harvest “buffer” incorporated into the simulations was inadequate to allow wolves to be maintained above the numerical criteria for delisting. Incorporation of a numerical buffer above the 250 wolf goal would have allowed populations to remain “recovered” even while being harvested.

The adult / yearling mortality rates used in these simulations had a large effect on the numbers of wolves present and whether wolves were able to maintain their numbers over time. Mean peak wolf numbers and mean numbers of wolves at year 100 were highest with 22% adult mortality (Figure 3). With 23.5% and 25% adult mortality, mean peak wolf numbers for the Blue Range were 15% and 35% lower, respectively, than with 22% adult mortality and 2/1/1 mpg. For the Grand Canyon mean peak wolf numbers with 23.5% and 25% adult mortality were 11% and 27% lower, respectively, with 2/1/1 mpg.
Mean number of wolves at year 100 among extant iterations in the Blue Range were 17% and 46% lower when there was 23.5% and 25% adult mortality, respectively, than with 22% adult mortality and 2/1/1 mpg. For the Grand Canyon, mean wolf numbers at year 100 with 23.5% and 25% adult mortality were 16% and 38% lower, respectively, with 2/1/1 mpg. By year 30, the mean numbers of wolves among extant iterations had stabilized following the initiation of harvests when there was 22% adult mortality and 2/1/1 mpg (Figure 3A and B). From year 30 to the end of the simulations, the mean numbers of wolves present in the Blue Range and Grand Canyon populations declined by 2% and 5% respectively. But with higher adult mortality the mean trend in wolf numbers from year 30 to year 100 became increasingly negative. With 23.5% adult mortality, the Blue Range and Grand Canyon populations declined by 5% and 12%, respectively. And with 25% adult mortality, both populations declined by 22% by year 100 (Figure 3C and D).

Whereas the mean size of the Blue Range initially increased and then sharply declined over the last 76 years of simulations when there was no dispersal between populations (Figure 3A and C), mean expected heterozygosity declined in a roughly linear fashion throughout the 100 year period of the simulations (Figure 4A and C). With 1 mpg, heterozygosity losses at year 100 were reduced by 60, 49, and 41% with 22, 23.5 and 25% mortality, respectively, relative to when there was no dispersal between populations, despite the substantial demographic costs of this dispersal regime to the Blue Range. When there was 2/1/1 mpg heterozygosity losses were reduced by 89, 85, and 68% with 22, 23.5, and 25% mortality, respectively, relative to when there was no dispersal between populations (Figure 4A and C).

The Grand Canyon population also grew rapidly in size up to year 24, but the subsequent declines in population size in the absence of dispersal between populations were not as extreme as that for the Blue Range (Figure 3). When there was no dispersal between populations mean expected heterozygosity declined rapidly for approximately the first 20 years but then slowed (Figure 4B and D). This suggested that the genetically effective size of the population increased as the population grew from 50 wolves at the start of the simulations to much larger sizes. But the proportion of initial mean expected heterozygosity lost by year 100 was similar to that of the Blue Range. With 2/1/1 mpg, heterozygosity losses at year 100 were reduced by 35, 35 and 27% with 22, 23.5, and 25% adult mortality, respectively, relative to when there was no dispersal between populations. Heterozygosity loss was similar for the 1 mpg and 2/1/1 mpg dispersal regimes even though census population sizes were somewhat larger with 1 mpg (Figure 3B and D). By year 100, mean expected heterozygosity among extant populations was 1-2% higher in the Blue Range than in the Grand Canyon for all three mortality rates considered. With 1 mpg, however, mean expected heterozygosity at year 100 was 2-4% lower for the Blue Range.

Each of the simulated populations had a significant heterozygosity excess at the start of the simulations, a characteristic of populations that have suffered a genetic bottleneck. A heterozygosity excess occurs when the observed heterozygosity for a population is greater than the heterozygosity expected based on Hardy-Weinberg genotypic proportions (expected
heterozygosity). A heterozygosity excess arises as rare or uncommon alleles are lost quickly from the population due to the strong genetic drift associated with small effective population sizes during a genetic bottleneck. In this case the loss of alleles is immediately reflected in the calculated expected heterozygosity even though actual genotypic frequencies within the population have not yet reverted to Hardy-Weinberg proportions.

Although all simulated populations had heterozygosity excesses at the start of the simulations, the Blue Range was unique in starting with a relatively low heterozygosity excess and having its excess increase over the 100 period of the simulation, in some cases. In contrast, the Grand Canyon and southern Rockies started the simulations with high heterozygosity excesses, but ended with reduced excesses in all cases. An increasing heterozygosity excess indicates the population is still losing alleles at a rapid rate as the bottleneck continues. A declining heterozygosity excess indicates that the population is moving towards a new genotypic equilibrium following a bottleneck.

When there was no dispersal between populations, the Blue Range heterozygosity excess increased over time for all adult mortality levels, but the heterozygosity excess for the Grand Canyon declined over time (Figure 5). Results for the southern Rockies were similar to that of the Grand Canyon (not shown). Increases in adult mortality rate resulted in increased heterozygosity excesses at year 100 for all populations. When there was 1 mpg and 22% adult mortality the Blue Range heterozygosity excess at years zero and 100 were identical. But with 23.5 or 25% mortality the Blue Range heterozygosity excess increased over time. For the Grand Canyon, the heterozygosity excesses remaining at year 100 with 1 mpg were reduced relative to that with no dispersal. When there was 2/1/1 mpg the Blue Range heterozygosity excess declined over the 100 years of the simulation with 22 and 23.5% adult mortality. But with 25% adult mortality the Blue Range heterozygosity excess increased over time. The excess, however, was < half that observed with 1 mpg. For the Grand Canyon, the heterozygosity excess at year 100 was nearly identical to that observed with 1 mpg, for all three mortality rates.

In addition to having lower census population sizes, greater heterozygosity losses, and more prolonged genetic bottlenecks, the Blue Range also had higher extinction rates than the Grand Canyon and southern Rockies populations. We defined the extinction rate as the percentage of iterations that became extinct at any time during the simulation, even if they were later recolonized by dispersers. When adult mortality was 22% and there was no dispersal between populations the Blue Range became extinct in 18% of iterations, but the Grand Canyon and southern Rockies became extinct in only 10 and 12% of iterations, respectively (Figure 6A). Although the Blue Range started the simulation with nearly 2.5 times as many wolves as the other populations (122 versus 50), it had an extinction rate 73 and 46% higher than the other two populations. When there was 1 mpg, extinction rates for all three populations were greatly reduced but the Blue Range still had the greatest rate. But with 2/1/1 mpg the Blue Range had the lowest extinction rate.
When adult mortality rates were increased to 23.5%, extinction rates roughly doubled for all populations with 1 mpg, except for the Blue Range which increased five-fold (Figure 6B). The Blue Range extinction rate with 1 mpg was about triple that of the Grand Canyon and southern Rockies. But with 2/1/1 mpg the Blue Range again had the lowest extinction rate. With 25% adult mortality extinction rates were high for all three populations, but they were highest for the Blue Range, except when there was 2/1/1 mpg (Figure 6C). With no dispersal between populations extinction rates were 63, 38, and 49% for the Blue Range, Grand Canyon and southern Rockies populations, respectively. With 1 mpg, extinction rates were 51, 21, and 24% for the Blue Range, Grand Canyon and southern Rockies populations, respectively. With 2/1/1 mpg, extinction rates were 20, 22, and 24%, respectively. Extinction rates for the Grand Canyon and southern Rockies were similar with either 1 mpg or 2/1/1 mpg. The extinction cost to these populations from the 2/1/1 mpg dispersal regime was very minimal, but the benefits to the Blue Range in the form of dramatically lower extinction rates were large.

Among the nine simulations described above, there was a strong, negative relationship between mean population size at year 100 for extant iterations and variability in population size, as quantified by the coefficient of variation (standard deviation / mean; Figure 7). This suggested that factors that act to decrease population size also increase the relative amount of variation around the mean. Conversely, factors (or management actions) that increase population size also act to reduce variability in population size. Increased variability in population size is known to increase extinction risk, decrease stochastic population growth rates, and is a component of the “extinction vortex” experienced by small populations. It is interesting to note that at least three disparate factors acted to affect mean population sizes in these nine simulations: degree of connectivity, adult / yearling survival rate, and the degree of relatedness within populations. But the tandem effects on the coefficient of variation were linear, for mean population sizes at least as low as 59 wolves. Similar negative, linear relationships were observed for other simulation sets described below, although the slopes varied (results not shown). The four smallest populations in Figure 7 are representations of the Blue Range with either zero or 1 mpg and either 23.5 or 25% adult mortality.

Finally, the 2/1/1 mpg dispersal regime also increased the percentage of iterations in which all three populations met the numerical delisting criterion. With 2/1/1 mpg, all three populations met the delisting criterion in 90, 69, and 32% of iterations with 22, 23.5, and 25% adult mortality, respectively (Table 4). This represented 11, 47, and 78% increases relative to 1 mpg. The percentage of iterations in which all three populations exceeded the numerical criterion for being endangered at some point during years 81-100 was also increased with 2/1/1 mpg, relative to 1 mpg (Table 5). But few iterations exceeded the criterion with either 2/1/1 or 1 mpg.

3. SCENARIO 2: GRAND CANYON 350 AND BLUE RANGE 350
In Scenario 1, 3x250, simulations without dispersal between populations indicated that the Grand Canyon was demographically the strongest population. Consequently in scenario 2 we first examined the effects on population viability if the numerical recovery goal for this population was set at 350 wolves and the Blue Range and southern Rockies had recovery goals of at least 200 wolves each. But because the Blue Range was the central population and demographically weaker than the other two populations, we also examined metapopulation viability when the numerical goal for the Blue Range was set at 350 wolves with the Grand Canyon and Southern Rockies required to support at least 200 wolves each. In simulations that included populations with numerical recovery goals that were < > 250 wolves, we assumed for the purposes of this analysis that the population would be considered “endangered” if its eight year running mean dropped below 60% of its numerical goal. Consequently populations with numerical goals of 350 and 200 were considered endangered when their eight year mean dropped below 210 and 120 wolves, respectively.

For this scenario, and for scenarios 3 and 4, we ran simulations with 22 and 23.5% adult / yearling mortality, but we did not run simulations with 25% adult / yearling mortality. As the adult mortality rate increased it became increasingly difficult to parameterize dispersal rates for each population that would achieve the desired connectivity rates. This difficulty arose because the parameter space for achieving the desired numbers of migrants per generation decreased as adult mortality increased, particularly with the 1 mpg dispersal regime. In some cases, it appeared that the parameter space did not exist in which the desired connectivity could be achieved. These cases are noted in the text.

a. Grand Canyon 350

The main themes apparent from the 3x250 scenario were present in the Grand Canyon 350 simulations. When there was 22% adult mortality and 2/1/1 mpg, the mean size of the Blue Range peaked at 192 wolves at year 23 (Figure 8A). Following the initiation of harvests at year 25 the mean size declined, but the Blue Range was able to maintain itself at or above 174 wolves from years 30 through 71. But ultimately the Blue Range declined by 5% to a mean of 166 wolves at year 100. With 1 mpg, the demographic costs of this dispersal regime relative to 2/1/1 mpg were apparent. The Blue Range reached a maximum mean population size of 173. Following the start of harvests mean population size declined linearly to a mean of 111 wolves at year 100. This was 33% lower than the size of the Blue Range at year 100 with 2/1/1 mpg.

As before, wolf numbers were slightly higher in the Grand Canyon and southern Rockies with 1 mpg than with 2/1/1 mpg (Figure 8C and E). With 22% adult mortality and 1 mpg, the mean size of extant populations in Grand Canyon reached 335 before harvest began. Following a dip due to the start of harvests, mean wolf numbers increased to 341 before declining to 317 wolves at year 100 (Figure 8C). In the southern Rockies mean wolf numbers reached 210 wolves before harvesting began when there was 22% adult mortality and 1 mpg (Figure 8E). But in contrast to the Grand Canyon, the southern Rockies population did not continue to increase in later years.
Instead mean population size declined to 164 wolves at year 100. This constituted a 14% drop in wolf numbers from year 30 (Figure 8E).

With 23.5% adult mortality, the Blue Range reached a mean population size of 162 wolves at year 20 when there was 2/1/1 mpg (Figure 8B). Mean wolf numbers declined slightly shortly before the start of harvests at year 25, suggesting that without harvests mean wolf numbers among extant populations in the Blue Range may not have reached 200. By year 100, the mean number of wolves among extant iterations in the Blue Range had dropped to 129 – 32% lower than that with 22% adult mortality. With 1 mpg and 23.5% adult mortality, the mean number of wolves in the Blue Range peaked in year 8 at 136. By year 100 the mean number of wolves had dropped to 47. This was 64% fewer wolves than with the 2/1/1 mpg dispersal regime.

In the Grand Canyon, mean wolf numbers among extant iterations dipped at the start of harvests, but then continued to increase when there was 23.5% adult mortality (Figure 8D). Mean wolf numbers peaked in year 50 at 309 with 1 mpg. By year 100 mean wolf numbers were slightly higher with the 2/1/1 mpg dispersal regime than with 1 mpg (268 vs. 266 wolves). Mean wolf numbers at year 100 with 23.5% adult mortality and 1 mpg were 17% lower than with 22% adult mortality.

In the southern Rockies, mean wolf numbers among extant populations peaked at 192 wolves in year 24 when there was 23.5% adult mortality and 1 mpg. By year 100, mean wolf numbers were greater with 2/1/1 mpg than with 1 mpg (128 vs. 124). With 23.5% adult mortality and 1 mpg wolf numbers were 24% lower than with 22% adult mortality at year 100.

All three populations had patterns of mean expected heterozygosity over time that were qualitatively similar to those with the 3x250 scenario, despite the differences in census population sizes (Figure 9). Mean expected heterozygosity at year 100 for the Grand Canyon was about 0.01 greater than in the 3x250 scenario for each of the four simulations. Heterozygosity at year 100 for the Blue Range and southern Rockies was lower than in the 3x250 scenario for all simulations. Across the four simulations, mean heterozygosity in the Blue Range averaged 0.008 less than in the 3x250 simulations; the greatest difference, 0.012, occurred when there was 1 mpg and 23.5% adult mortality. The southern Rockies averaged 0.012 less than in the 3x250 scenario, with the greatest difference, 0.015, again occurring when there was 1 mpg and 23.5% mortality.

Heterozygosity excesses increased over time for the Blue Range when there was 1 mpg, but excesses decreased or were about the same at years zero and 100 when there was 2/1/1 mpg (Figure 10A). Heterozygosity excesses for the Grand Canyon and southern Rockies populations dropped substantially by year 100 in all four simulations (Figure 10C). The excess was eliminated in the Grand Canyon when there was 1 mpg and 22% adult mortality. Relative to the 3x250 scenario, heterozygosity excesses were increased for the Blue Range and decreased for the Grand Canyon (Figures 5 and 10).
The Grand Canyon also had lower extinction rates than in similar simulations under the 3x250 scenario. Simulations with 22% adult mortality had approximately half the extinctions as in the 3x250 scenario, but extinction rates were already low in the 3x250 simulations (Figures 6A and 12A). With 23.5% mortality, the Grand Canyon had about 20% fewer extinctions than in the 3x250 scenario. Extinction rates for the Blue Range and southern Rockies were somewhat higher than in similar simulations of the 3x250 scenario, particularly for the Blue Range with 1 mpg and 23.5% mortality (34.3 vs. 20.2%).

Mean metapopulation sizes at year 100 were slightly larger than those under the 3x250 scenario when there was 1 mpg (Figure 12), but the sums of population extinctions were higher (Figure 13). This metric simply sums the number of iterations in which each population became extinct. The maximum number of extinctions possible was 3,000 for these simulations. With 2/1/1 mpg, however, mean metapopulation sizes were slightly smaller than in the 3x250 scenario, and the numbers of population extinctions were lower than with 3x250 (22% adult mortality) or slightly higher (23.5% adult mortality). The percentages of iterations in which all three populations met their numerical delisting goals (350, 200, 200 for the Grand Canyon, Blue Range, and southern Rockies, respectively) were slightly lower than under the 3x250 scenario when there was 1 mpg (Table 4). With 2/1/1 mpg, however, the percentages of iterations in which all three populations met numerical goals were nearly identical between this scenario and the 3x250 scenario. Finally, the percentages of iterations in which all three populations exceeded their numerical thresholds for being endangered during years 81-100 (>210, 120 and 120 for the Grand Canyon, Blue Range, and southern Rockies, respectively) were somewhat lower than under the 3x250 scenario (Table 5).

b. Blue Range 350

When there was 22% adult mortality and 2/1/1 mpg, mean population size among extant iterations for the Blue Range peaked at 325 wolves in year 24 (Figure 14A). After a dip following the start of harvesting, mean wolf numbers slowly increased through the remainder of the simulation ending with a mean of 319 wolves among extant iterations. With 1 mpg, mean wolf numbers decreased following the start of harvests and continued to slowly decrease through year 100. By year 100 mean population size among extant iterations for the Blue Range with 1 mpg was 262 wolves, 22% lower than that with 2/1/1 mpg (Figure 14A). The Grand Canyon and southern Rockies populations performed similarly to each other. Both had higher mean wolf numbers with 1 mpg (Figure 14C and E). With 1 mpg and 22% adult mortality, mean population sizes among extant iterations peaked at 204 and 197 wolves in year 24, for the Grand Canyon and southern Rockies, respectively. Both populations then declined in mean size through year 100. With 2/1/1 mpg, the mean sizes of extant iterations were 7 and 5% lower by year 100 for the Grand Canyon and southern Rockies, respectively.
Increasing the adult mortality rate to 23.5% had the greatest effect on the Blue Range. With 2/1/1 mpg, mean size of extant iterations peaked at 272 wolves at year 24, but then increased further to 276 before decreasing to a mean of 250 wolves by year 100. By year 100 the mean sizes of extant populations were 22 and 32% lower with 2/1/1 mpg and 1 mpg, respectively, than that with 22% adult mortality. For the Grand Canyon and southern Rockies, the increase in adult mortality exacerbated the demographic costs of the 2/1/1 mpg dispersal regime relative to the 1 mpg, as determined by the increased differences between mean wolf numbers for the two dispersal regimes (Figure 14D and F). This was not seen with the 3x250 scenario nor in the Grand Canyon 350 simulations (Figure 8E and F). By year 100 the mean sizes of extant populations for the Grand Canyon were 29 and 15% lower with 2/1/1 mpg and 1 mpg, respectively, than that with 22% adult mortality. For the Southern Rockies, the mean sizes of extant populations at year 100 were 30 and 17% lower with 2/1/1 mpg and 1 mpg, respectively, than that with 22% adult mortality.

Mean expected heterozygosity at year 100 for the Blue Range was greater than that in the 3x250 scenario for all four simulations (Figures 4 and 15). When there was 2/1/1 mpg, mean expected heterozygosity at year 100 for the Blue Range was also greater than that for the Grand Canyon and southern Rockies populations. But when there was 1 mpg, the Blue Range had the lowest expected heterozygosity at year 100. This pattern was also present among simulations in the 3x250 scenario. When there was 22% adult mortality and 2/1/1 mpg, the mean expected heterozygosity of the Blue Range initially declined at the start of the simulation, but then increased as a result of gene flow to a level before slowly declining to year 100.

For the Grand Canyon and southern Rockies populations mean expected heterozygosity at year 100 was lower than that in similar simulations for the 3x250 scenario as a result of their smaller census population sizes. Mean expected heterozygosity was greatest when there was 1 mpg (Figure 15C – F), as in the 3x250 scenario. For the southern Rockies, mean expected heterozygosity at year 100 was greater than that in similar simulations for the Grand Canyon 350 scenario in three of four cases. But the differences were not large.

Mean heterozygosity excesses at year 100 for the Blue Range were greatly reduced relative to that with the Grand Canyon 350 simulations (Figure 10A and B) and the 3x250 scenario (Figure 5). For the Grand Canyon, excesses were greater than in the Grand Canyon 350 simulations (Figure 10C and D) and the 3x250 scenarios (Figure 5). For the southern Rockies, mean excesses were lower than those with the Grand Canyon 350 simulations when there was 1 mpg, but slightly higher when there was 2/1/1 mpg (Figure 10E and F) even though the population size targets were the same in the two scenarios. Interestingly, at year 100 the excesses were smallest with 1 mpg for both the Grand Canyon and southern Rockies in the Blue Range 350 simulations, suggesting that the reduced population size and greater emigration demands required in the 2/1/1/ mpg simulations slowed the elimination of the initial heterozygosity excess.
With the Blue Range 350 simulations, extinction rates for the Blue Range were reduced relative to the Grand Canyon 350 simulations particularly when there was 1 mpg (Figure 11A and B). With 22% adult mortality, Blue Range extinction rates were reduced from 7% to 2%, and with 23.5% adult mortality extinction rates were reduced from 34% to 9%. Blue Range Extinction rates were also lower than with the 3x250 scenario when there was 1 mpg (Figures 6 and 11). With 2/1/1 mpg, Blue Range extinction rates were similarly low for both scenarios. For the Grand Canyon, extinction rates were similar to those with the Grand Canyon 350 simulations and 3x250 scenarios when there was 1 mpg, but higher when there was 2/1/1 mpg (Figures 8 and 11). For the southern Rockies, extinction rates were similar to those under the 3x250 scenario when there was 1 mpg and when there was 2/1/1 mpg and 22% adult mortality. But when there was 2/1/1 mpg and 23.5% mortality, extinction rates were 55 and 71% higher, respectively, than those under the 3x250 scenario.

Mean metapopulation sizes were slightly greater than either the Grand Canyon 350 simulations or the 3x250 scenarios and the summed population extinctions substantially lower when there was 1 mpg (Figures 12 and 13). When there was 2/1/1 mpg and 22% adult mortality, metapopulation sizes and summed extinctions were similar for the Blue Range350 and Grand Canyon 350 simulations, and 3x250 scenarios (Figures 12 and 13). With 2/1/1 mpg and 23.5% adult mortality, however, the Blue Range 350 scenario resulted in a slightly smaller mean metapopulation size and higher summed extinctions than the either Grand Canyon 350 simulation and the 3x250 scenario (Figures 12 and 13). But overall, mean metapopulation sizes were larger and summed extinctions fewer with 2/1/1 mpg than with 1 mpg.

The percentages of iterations in which all three populations met their numerical delisting goals (350, 200, and 200 for the Blue Range, Grand Canyon, and southern Rockies, respectively) were greater than either the 3x250 or Grand Canyon 350 scenarios when there was 1 mpg (Table 4). With 2/1/1 mpg, however, the percentages of iterations in which all three populations met numerical goals were slightly lower than the 3x250 scenario and the Grand Canyon 350 simulations. But like mean metapopulation size, delisting rates were higher with 2/1/1 mpg than with 1 mpg.

The percentages of iterations in which all three populations exceeded their numerical criteria for being endangered during years 81 -100 (>210, 120 and 120 for the Grand Canyon, Blue Range, and southern Rockies, respectively) were also somewhat higher than the 3x250 scenario and the Grand Canyon 350 simulations when there was 1 mpg (Table 5). But when there was 2/1/1 mpg, percentages were somewhat lower.

c. Costs and Benefits

Of these two extreme scenarios, the Blue Range 350 scenario appeared to provide greater overall benefits with fewer costs than the GC350 scenario, particularly when there was 1 mpg. The Blue Range 350 scenario had highest mean metapopulation sizes at year 100 and the fewest numbers
of population extinctions when there was 1 mpg. When there was 2/1/1 mpg and 22% adult mortality the three scenarios had nearly the same mean metapopulation sizes and summed extinctions (Figures 12 and 13). When there was 2/1/1 mpg and 23.5% adult mortality, the 3x250 scenario had the largest mean metapopulation size, but the other two scenarios were only slightly lower. The 3x250 scenario also had the lowest summed extinctions, but the GC350 simulation had nearly as few extinctions. The Blue Range350 simulation had the highest summed extinction rate with about 33% more extinctions. But the overall population extinction rate was still only 7.5%.

The Blue Range350 scenario had the highest % of iterations in which all three populations met the delisting criteria when there was 1 mpg (Table 4). When there was 2/1/1 mpg, the 3x250 scenario had the highest % and the Blue Range350 scenario had the lowest, but the differences were small. The same pattern was evident for the % of iterations in which all three populations exceeded the numerical criteria for being endangered (Table 5).

The Blue Range350 scenario had the lowest heterozygosity excesses and the highest expected heterozygosity at year 100 for the Blue Range. Similarly, the GC350 scenario had the lowest heterozygosity excesses and the highest expected heterozygosity at year 100 for the Grand Canyon. Heterozygosity was highest at year 100 for the southern Rockies under the 3x250 scenario. The 3x250 scenario had intermediate levels of heterozygosity at year 100 for the Blue Range and Grand Canyon.

Collectively, these results suggested that the level of management flexibility allowed under this scenario is unlikely to impede recovery or substantially reduce the viability of the recovered metapopulation.

4. SCENARIO 3: 3X250 + SONORA

This scenario was the same as Scenario 1 except that it added a fourth population which had a numerical goal of at least 100 wolves. In the simulations we assumed that the fourth population, “Sonora”, would be located in northern Mexico along the border of Sonora and Chihuahua. Therefore the only population with which it was likely to be connected by natural dispersal was the Blue Range. Because the Sonora population was much smaller than the other populations, we assumed it would likely not be able to provide 1 mpg to the Blue Range, but it likely would provide some migrants. For the 2/1/1 dispersal regime in this scenario, dispersal was parameterized such that the Blue Range would receive a total of about 2 mpg from the three peripheral populations. But the Blue Range would attempt to provide 1 mpg to each of the three peripheral populations. Thus the 2/1/1 dispersal regime in this scenario had the potential to be more stressful on the Blue Range than the previous scenarios. We founded the Sonora population with seven pairs, and the simulations started with a total of 35 wolves. Overall, the inclusion of
Sonora reduced the demographic performance of the Blue Range but slightly enriched it genetically. Sonora had little effect, however, on the Grand Canyon and southern Rockies populations, relative to the 3x250 scenario.

When there was 22% adult mortality and 2/1/1 mpg, the Blue Range reached a maximum mean population size among extant iterations of 224 wolves in year 24 (Figure 16A). Following the dip in wolf numbers caused by the initiation of harvests, the mean population size slowly increased before declining during the last few years of the simulation. At year 100 the Blue Range averaged 203 wolves among extant populations. When there was 1 mpg the Blue Range peaked in year 20 with a mean population size of 178. The early peak in mean wolf numbers suggested that the Blue Range had already started to decline before the start of harvests. By year 100 the Blue Range declined to a mean of 111 wolves which was 45% fewer wolves than that with the 2/1/1 mpg dispersal regime and less than the 122 wolves in the Blue Range at the start of the simulation (Figure 16A). Relative to similar simulations in the 3x250 scenario, the mean Blue Range size at year 100 when there was 2/1/1 mpg was only 6% lower than in the 3x250 scenario, but when there was 1 mpg mean population size was 29% lower than with the 3x250 scenario. With 23.5% adult mortality, mean population sizes for the Blue Range at year 100 were 145 and 56 wolves with 2/1/1 mpg and 1 mpg, respectively (Figure 16B). Relative to the 3x250 simulations, the Blue Range ended the simulations with 19 and 40% fewer wolves.

In contrast, mean population sizes among extant iterations over time for the Grand Canyon and southern Rockies were similar to that under the 3x250 scenario for 22 and 23.5% adult mortality and both dispersal regimes (Figure 16C and D). Mean population sizes among iterations extant at year 100 for the Grand Canyon and southern Rockies were 227 and 221, respectively, when there was 22% adult mortality and 1 mpg. When there was 23.5% adult mortality and 1 mpg, mean population sizes at year 100 were 185 and 181 for the Grand Canyon and southern Rockies, respectively.

Sonora grew rapidly at the start of the simulations to a mean population size among extant populations of 109 wolves at year 23 when there was 22% adult mortality and 1 mpg (Figure 16E). As with the other peripheral populations (Grand Canyon and southern Rockies), Sonora peaked at a smaller mean size of 105 wolves at year 23 when there was 2/1/1 mpg (Figure 16E). The flattening of the curves prior to the start of harvesting appeared to be caused by the truncation of an increasing number of iterations at the carrying capacity of 133 wolves. Following the start of harvesting, mean population sizes declined steadily to 71 and 75 at year 100 for simulations with 1 mpg and 2/1/1 mpg, respectively. When there was 23.5% adult mortality, Sonora peaked in year 23 with mean population sizes of 101 and 97 wolves when there was 1 mpg and 2/1/1 mpg, respectively (Figure 16F). By year 100, mean population sizes among extant iterations had declined to 51 and 58 wolves when there was 1 mpg and 2/1/1 mpg, respectively. Mean population sizes over time were little affected by the choice of dispersal regime with either 22 or 23.5% adult mortality. It is interesting to note, however, that for the first portion of the simulations, those with 1 mpg supported greater mean numbers of wolves,
consistent with the demographic cost to peripheral populations of the 2/1/1 mpg dispersal regime. But by the end of the simulations, the 2/1/1 mpg dispersal regime supported higher mean wolf numbers and reduced the extinction rate for the Sonora population (see below). As the Blue Range declined in size with 1 mpg, its ability to send migrants to the peripheral populations also declined, and fewer migrants were received by each of the peripheral populations. With 2/1/1 mpg, the Blue Range supported substantially higher wolf numbers in the latter half of the simulations. For the small Sonora population, the additional migrants it received from the Blue Range with 2/1/1 mpg outweighed the added costs of this dispersal regime. But for the relatively large and stable Grand Canyon and southern Rockies populations the demographic costs of the 2/1/1 mpg dispersal regime were not outweighed by the benefits of receiving more migrants in the later years of the simulations.

Despite smaller census population sizes than that under the 3x250 scenario, mean expected heterozygosity for the Blue Range at years 24 and 100 exceeded that with the 3x250 scenario when there was 2/1/1 mpg for both 22 and 23.5% adult mortality rates. In addition, the maximum mean heterozygosity for the Blue Range (0.7579 at years 48 and 49) exceeded that at simulation start (0.7555) when there was 2/1/1 mpg and 22% adult mortality (Figure 17). Although the difference was slight, this did not occur under the 3x250 scenario. These differences between the two scenarios appeared to be a result of the inclusion of immigrants from a third donor population, Sonora. Although the mean number of migrants per generation received by the Blue Range was only slightly greater than that under the 3x250 scenario (2.21 vs. 2.02; Table 3), the inclusion of migrants from a third differentiated population (Sonora) appeared to genetically enrich the Blue Range.

With 1 mpg, however, mean expected heterozygosity for the Blue Range was lower than that under the 3x250 scenario. By year 100, heterzygosity was 1.2 and 1.6% lower than similar simulations under the 3x250 scenario when adult mortality was 22 and 23.5%, respectively. This outcome, reduced heterozygosity, was not surprising given that the Blue Range received an average of 1.12 and 1.13 mpg with 22 and 23.5% adult mortality, respectively, but exported totals of 2.96 and 2.53 mpg on average to the three peripheral populations (Table 3). In contrast, under the 3x250 scenario the Blue Range received an average of 1.03 and 1.12 mpg, and exported a mean of 2.15 and 2.02 mpg with 22 and 23.5% adult mortality, respectively to the two peripheral populations (Table 3). Even though mean wolf numbers among extant populations were substantially lower than under the 3x250 scenario, mean expected heterozygosity was only slightly lower.

Although the three peripheral populations in the simulation with 1 mpg and 23.5% adult mortality were intended to each receive an average of 1 – 1.10 mpg, they received an average of about 0.84 (Table 3). This shortfall was a result of the combination of increased emigration demands on the Blue Range to meet connectivity goals and the demographic decline of the Blue Range. The increased demographic demands on the Blue Range for emigration, relative to that under the 3x250 scenario, appeared to accelerate the decline of the Blue Range. In the
simulations, it may not have been possible for the Blue Range to provide 1 mpg to each of three populations while receiving a total of 1 mpg, when adult mortality was < 23.5%. This dynamic was also seen in 3x250 scenario with 25% adult mortality and 1 mpg. In this case the Blue Range received an average of 1.28 mpg even though the target was 1-1.10 mpg. Several simulations with < 1.10 mpg into the Blue Range suggested that the Blue Range would only be able to provide 1 mpg to the two peripheral populations if it received substantially more than 1.10 mpg. This dynamic was also apparent for the BR + 2MX100 simulations with 1 mpg (see below). In these cases, the centrally located Sonora population was unable to provide 1 mpg to the two peripheral populations under the 1 mpg dispersal regime (Table 3).

For the Grand Canyon (Figure 17 C and D) and southern Rockies, the choice of dispersal regime had only a small effect on mean expected heterozygosity (Figure 17C and D). At year 100 mean expected heterozygosity for the Grand Canyon was about 0.735 with 22% adult mortality and 0.719 with 23.5% mortality for both dispersal regimes. For the southern Rockies mean expected heterozygosity at year 100 was about 0.730 and 0.715 with 22 and 23.5% adult mortality, respectively. Expected heterozygosities, however, were less than that with the 3x250 scenario, but the differences were slight. When there was 2/1/1 mpg and 23.5% adult mortality the mean expected heterozygosity for the Grand Canyon and southern Rockies were 1.8 and 1.6% lower, respectively, at year 100 than that under the 3x250 scenario. But in all other cases the differences were <1%.

For Sonora, the pattern of mean expected heterozygosity over time (Figure 17E and F) was similar to that observed for mean population size among extant iterations (Figures 16E and F). Heterozygosity was initially highest with 1 mpg, but by the end of the simulations heterozygosity was greatest with the 2/1/1 mpg dispersal regime for both 22 and 23.5% adult mortality. With 2/1/1 mpg, mean expected heterozygosity at year 100 was 3.1 and 4.7% greater than that with 1 mpg with 22 and 23.5% adult mortality, respectively. Mean expected heterozygosity dropped as low as 0.648 with 23.5% adult mortality and 1 mpg (Figure 17F).

Heterozygosity excess for the Blue Range increased over time when there was 1 mpg, but with 2/1/1 mpg it declined or was similar to that at the start of simulations (Figure 18A). The excesses at year 100, however, were greater than those for the Blue Range under the 3x250 scenario (Figure 5). Excesses for the Grand Canyon and southern Rockies declined over time in all cases and the excesses at year 100 were similar to those in the 3x250 scenario. For Sonora, the heterozygosity excess at year 0 was higher than the other three populations. Although the excesses declined over time with both dispersal regimes, the decline was greater with 2/1/1 mpg (Figure 18B).

Extinction rates were greatly reduced for the Blue Range and Sonora when there was 2/1/1 mpg versus 1 mpg (Figure 19). When there was 22% adult mortality the extinction rate for the Blue Range was reduced from 10% with 1 mpg to <1% with 2/1/1 mpg, and the extinction rate for Sonora was reduced from 9 to 4%. For simulations with 23.5% adult mortality, the extinction
rate for the Blue Range was reduced from 33% with 1 mpg to 5% with 2/1/1 mpg, and the extinction rate for Sonora was reduced from 32 to 18% with 2/1/1 mpg. For the Grand Canyon and southern Rockies, there was little difference in extinction rates due to dispersal regime. But extinction rates were 4-6 times greater with 23.5% adult mortality than with 22% mortality.

For the Grand Canyon and southern Rockies populations there was little difference in extinction rates between this and the 3x250 scenario. But for the Blue Range extinction rates were 150 and 60% higher than those under the 3x250 scenario when there was 1 mpg (Figures 6 and 19). When there was 2/1/1 mpg extinction rates were roughly similar between the two scenarios.

Mean metapopulation sizes at year 100 exceeded that for the 3x250 scenario in three of four simulations by 2 – 9% (Figure 20). The exception was when there was 1 mpg and 23.5% adult mortality. In this case mean metapopulation size under 3x250 was 3% larger. For the current simulations, mean metapopulation size was 19 and 22% smaller with 1 mpg than 2/1/1 mpg, with 22 and 23.5% adult mortality, respectively. But the summed population extinctions for the three large populations were higher somewhat higher than with 3x250, in three of four cases (Figure 21). The exception this time was Summed extinctions were lower than the 3x250 simulation when there was 2/1/1 mpg and 22% adult mortality, but the difference was small. Summed extinctions for the current simulations were 4.8 and 2.5 times higher with 1 mpg than 2/1/1 mpg, with 22 and 23.5% adult mortality, respectively.

Although the Sonora population met numerical delisting criteria in 88-97% of iterations, the proportion of iterations in which all three of the other populations met numerical criteria for delisting ranged from 33 to 90% (Table 6). This was 28 and 31% lower than in the 3x250 scenario when there was 1 mpg (Table 4). The similarity in delisting rates for the Blue Range and the three large populations suggested that the Blue Range was the primary determinant of when all three large populations simultaneously met delisting criteria (Tables 4 and 6). When there was 2/1/1 mpg, delisting rates for the three large populations were 90% for both this and the 3x250 scenarios when there was 22% adult mortality. But with 23.5% adult mortality the 3x250 scenario had a higher delisting rate (69 vs. 59%; Tables 4 and 6). Interestingly, Sonora had higher rates of delisting than the Blue Range except when there was 2/1/1 mpg and 22% mortality (Table 6).

Similarly, inclusion of the Sonora population reduced the percentage of iterations in which the three large populations exceeded the numerical criteria for being endangered in the years 81-100 relative to the 3x250 scenario (Tables 5 and 7). And Sonora exceeded numerical criteria for being endangered far more often than the Blue Range when there was 1 mpg, but not when there was 2/1/1 mpg (Table 7).

5. SCENARIO 4: BLUE RANGE + 2MX100
This scenario assumed three populations would be restored: the Blue Range in the US supporting at least 250 wolves and two small populations in Mexico each supporting at least 100 wolves. The two populations in Mexico were assumed to be located along the border of Sonora and Chihuahua states (Sonora) and in the southern portion of the western Sierra Madre (Durango). We assumed that these populations would be connected in a linear fashion by natural dispersal, with Sonora as the central population. This differed from the previous scenarios in that for this scenario the Blue Range was a peripheral rather than the central population, and it was the only large population. We based the Sonora and Durango starting populations on the pedigrees of the Grand Canyon and southern Rockies populations, respectively. But instead of founding each population with 10 pairs and starting the simulations with 50 wolves in each population, we chose seven pairs to found each population and started the simulations with 35 wolves in each of the two Mexican populations. Thus the Sonora population in this scenario was different from the Sonora population in Scenario 3. Overall, this scenario was characterized by low census population sizes, rapid heterozygosity loss, and high extinction and endangerment rates, particularly for the centrally located Sonora population.

Mean population size among extant iterations over time for the Blue Range was similar to that under the 3x250 scenario when there was no dispersal between populations (Figures 3 and 22). But unlike that under the 3x250 scenario, mean population size after the start of harvesting was greatest with 1 mpg. In addition, the mean number of wolves did not plateau after the start of harvesting, but instead declined from year 25 to 100. By year 100 wolf numbers averaged 171 and 118 for simulations with 22 and 23.5% adult mortality, respectively. It should be noted, however, that that under 1 mpg, the Blue Range received only about 0.77 mpg (Table 3). With 2/1/1 mpg, mean wolf numbers at year 100 were 7 and 9% lower than that with 1 mpg, when there was 22 and 23.5% adult mortality, respectively. This difference represented the demographic cost of the 2/1/1 mpg dispersal regime to the peripherally located Blue Range, relative to 1 mpg. Mean population sizes at year 100 with 1 mpg were 21 and 34% smaller than that under the 3x250 scenario with 2/1/1 mpg and 22 and 23.5% adult mortality, respectively. Relative to the peripheral populations under the 3x250 scenario (Grand Canyon and southern Rockies), the Blue Range averaged about 22 and 36% fewer wolves at year 100 when there was 1 mpg and adult mortality was 22 and 23.5%, respectively.

The centrally located Sonora population grew the fastest at the start of the simulations when there was no dispersal between populations and peaked at substantially higher mean population sizes than simulations with dispersal between populations (Figure 22C and D). But by year 100, simulations without dispersal between populations averaged only 26 and 17 wolves among extant iterations when there was 22 and 23.5% adult mortality, respectively. This was less than the 35 wolves at the start of simulations. Simulations with 2/1/1 mpg supported the greatest mean numbers of wolves at year 100. With 22% adult mortality the Sonora population averaged 49 wolves at year 100; with 23.5% adult mortality Sonora averaged 34 wolves at year 100.
Mean population sizes among extant iterations for Durango were similar with either 2/1/1 mpg or 1 mpg dispersal regimes (Figure 22E and F). But by year 100, simulations with 2/1/1 mpg supported means of 60 and 40 wolves, with 22 and 23.5% adult mortality, respectively, which was slightly higher than mean population sizes with 1 mpg. It should be noted, however, that Durango received only about 0.77 mpg under 1 1mpg (Table 3). If Durango had received the full 1 mpg, its mean population sizes would may have been larger than that with 2/1/1 mpg. The dispersal shortfall into Durango and the Blue Range resulted from the small and declining population size of Sonora. By year 100 Durango supported 22 and 18% more wolves than Sonora when there was 2/1/1 mpg with 22 and 23.5% adult mortality, respectively.

The Blue Range retained greater expected heterozygosity over time than either of the other two populations, even though it started with the lowest mean expected heterozygosity (0.755 versus 0.795 for Sonora and Durango). Mean expected heterozygosity in the Blue Range declined in a nearly linear fashion with or without dispersal between populations (Figure 23A and B). When there was no dispersal between populations, mean heterozygosity for the Blue Range dropped to 0.65 and 0.62 at year 100, with 22 and 23.5% adult mortality, respectively. When there was dispersal between populations, mean expected heterozygosity was similar for the two dispersal regimes even though mean census population sizes were larger with 1 mpg (Figure 22A and B). At year 100, expected heterozygosity averaged about 0.69 and 0.66 with 22 and 23.5% adult survival, respectively. Relative to that under the 3x250 scenario, the Blue Range averaged 3-10% lower heterozygosity at year 100 than that under the 3x250 scenario.

Mean expected heterozygosity for Sonora dropped to 0.545 and 0.524 at year 100 in the absence of dispersal between populations, with 22 and 23.5% adult mortality, respectively (Figure 23C and D). But with 2/1/1 mpg, mean heterozygosity at year 100 dropped to only 0.681 and 0.65 for 22 and 23.5% adult mortality, respectively. With 1 mpg, mean expected heterozygosity at year 100 was 5% lower than that with 2/1/1 mpg. Relative to the central population under the 3x250 scenario (Blue Range) with 2/1/1 mpg, mean heterozygosity at year 100 for Sonora was 8 and 11% lower with 22 and 23.5% adult mortality, respectively.

For Durango, mean expected heterozygosity was highest when there was 2/1/1 mpg (Figure 23E and F). At year 100, expected heterozygosity averaged 0.665 and 0.633 with 22 and 23.5% adult survival, respectively. With 1 mpg, mean heterozygosity at year 100 was 2.8% lower. As noted above, the Blue Range and Durango each received about 0.77 mpg under the 1 mpg dispersal regime (Table 3). This suggested that the demographic costs to Durango of the 2/1/1 mpg dispersal regime were more than offset by providing additional support to the struggling Sonora population. This additional support allowed Sonora to provide one mpg to each of the peripheral populations. Relative to the peripheral populations from the 3x250 scenario, mean heterozygosity at year 100 for Durango was about 9 and 13% lower for 22 and 23.5% adult mortality, respectively.
Mean heterozygosity excesses at year 100 for the Blue Range were somewhat different than with 3x250. With 1 mpg heterozygosity excesses were 11 and 24% lower than that in the 3x250 scenario, for 22 and 23.5% adult mortality, respectively (Figures 5 and 24A). With 22% adult mortality the excesses at year zero and 100 were equal under the 3x250 scenario, but in the current scenario the excess had declined by year 100. With 23.5% adult mortality, the excess in the current scenario increased over time, but to a lesser amount than that in the 3x250 scenario.

With 2/1/1 mpg, mean heterozygosity excesses for the Blue Range at year 100 were 97 and 132% larger than that in the 3x250 scenario when adult mortality was 22 and 23.5%, respectively. Although the excesses decreased in both scenarios relative to that at year zero, when there was 22% adult mortality, with 23.5% adult mortality the excess increased substantially from year zero to 100. Under the 3x250 scenario, the excess decreased over time under these circumstances. The change in the pattern of heterozygosity excesses in the Blue Range appeared to result from the different position of the Blue Range in the metapopulation. In the current scenario, the Blue Range was not the central population, but a peripheral population. Throughout the simulations considered here, the 2/1/1 mpg dispersal regime provided demographic and genetic benefits to the central population, but presented costs to peripheral populations, in most cases. The primary exception to this pattern was Durango in the current scenario. Durango benefited demographically and genetically from the 2/1/1 mpg dispersal regime because it and the central Sonora populations were so small, particularly late in the simulations.

Sonora (in this scenario) and Durango had the highest initial heterozygosity excesses (0.054 and 0.055 respectively) of all the populations considered among the four scenarios. When there was no dispersal between populations, heterozygosity excesses increased over time in all cases (Figure 24 B and C) suggesting a deepening genetic bottleneck. In all previous cases, heterozygosity excesses decreased over time among populations that had initial excesses > 0.04 (i.e. Grand Canyon, southern Rockies, and Sonora in scenario 3) when there was no dispersal between populations. With 1 mpg, excesses at year 100 were smaller than those when there was no dispersal between populations, but the excesses at year 100 were still > that at year zero in three out of four cases (Figure 24B and C). For Sonora the excess at year 100 with 1 mpg and 23.5% adult mortality was only marginally lower than that with no dispersal. With 2/1/1 mpg mean heterozygosity excesses were lower in Sonora and Durango than that at year zero when there was 22% adult mortality. But when there was 23.5% adult mortality, excesses still exceeded that at year zero. Consistent with previous scenarios, however, the centrally located Sonora population derived substantially greater benefit from the 2/1/1 mpg dispersal regime than the peripheral Durango population.

Extinction rates for the Blue Range were similar to that under the 3x250 scenario, when there was no dispersal between populations (Figures 6 and 25). But with either 1 mpg or 2/1/1 mpg, extinction rates were greater than with 3x250. With 1 mpg, extinction rates for the Blue Range were 95 and 26% higher than that under the 3x250 scenario with 22 and 23.5% adult mortality.
With 2/1/1 mpg, extinction rates were 14 times and 11 times higher than that under the 3x250 scenario with 22 and 23.5% adult mortality. Although Blue Range extinction rates were high relative to those under the 3x250 scenario, they were low relative to that for Sonora and Durango.

With no dispersal between populations, Sonora and Durango had similar extinction rates. With 22% adult mortality, extinction rates were 69 and 71% for Sonora and Durango, respectively. With 23.5% adult mortality, extinction rates were 87 and 86% for Sonora and Durango, respectively. With 1 mpg extinction rates were substantially lower, but still very high. For Sonora, 38 and 70% of iterations became extinct when there was 22 and 23.5% adult mortality, respectively. For Durango, 26 and 56% of iterations became extinct. With 2/1/1 mpg, Extinction rates for Sonora dropped to 14 and 48% for 22 and 23.5% adult mortality. Durango had 17 and 47% extinction rates.

Mean metapopulation sizes at year 100 were far lower than that for any of the other three scenarios. And the summed extinctions were far higher than with the other scenarios. When there was 1 mpg, mean metapopulation sizes at year 100 for extant iterations averaged 139 and 85 wolves with 22 and 23.5% adult mortality, respectively. The summed extinctions were 1,559 and 2,110 with 22 and 23.5% adult mortality, respectively. In other words, with 22% adult mortality there was a mean population extinction rate of 52%, and with 23.5% adult mortality the mean population extinction rate was 70%. When there was 2/1/1 mpg, mean metapopulation sizes at year 100 averaged 237 and 142 wolves for extant iterations, with 22 and 23.5% adult mortality, respectively, still substantially lower than the 450 wolf numerical goal. And the summed extinctions were 720 and 1,493, with 22 and 23.5% adult mortality, respectively. This translated into mean population extinction rates of 24 and 50% with 22 and 23.5% adult mortality, respectively.

The % of iterations in which all three populations reached numerical criteria for delisting was highest when there was 2/1/1 mpg (Table 8). But the Blue Range was most likely to meet delisting criteria with 1 mpg. In the simulations with 1 mpg the % of iterations meeting delisting criteria for the Blue Range was > that under the 3x250 scenario. With 2/1/1 mpg, however the Blue Range met delisting criteria less often than under the 3x250 scenario. These results were consistent with the Blue Range having the highest mean population sizes with 1 mpg (Figure 22) in the current scenario. In contrast, Sonora was most likely to meet delisting criteria with 2/1/1 mpg, consistent with this population having the greatest mean population sizes and lowest extinction rates with 2/1/1 mpg (Figures 22 and 24). The percentages of iterations in which Durango met delisting criteria were similar with either dispersal regimen and similar to the Blue Range. Overall, all three populations met delisting criteria in 58 and 30% of iterations when there was 1 mpg and 22 and 23.5% adult mortality, respectively. With 2/1/1 mpg, all three populations met delisting criteria in 72 and 39% of iterations when there was 22 and 23.5% adult mortality, respectively.
Numerical criteria for being endangered in the last 20 years of the simulations were exceeded by all three populations in < 8% iterations (Table 9). Of the three populations, Sonora was most likely to become endangered. Overall, patterns were similar to that with delisting except that Durango was slightly more likely to exceed endangered criteria with 2/1/1 mpg than with 1 mpg (Table 9).

D. DISCUSSION

1. FACTORS AFFECTING POPULATION VIABILITY AND RECOVERY

In the simulations, we highlighted the effects of adult / yearling mortality rates, connectivity between populations, and the composition of the founding populations based on mean kinship. We did this because each of these may have substantial effects on population viability and the prospect for recovery under the Endangered Species Act. But we also highlighted these because they can be affected by management.

The Blue Range had the highest initial mean kinship of all the populations considered in the simulations (0.2446 versus 0.1940 – 0.2064 for other simulated populations; Table 2). The effects of the Blue Range population’s high mean kinship were illustrated in simulations with no dispersal between populations. With the 3x250 scenario the Blue Range and the Grand Canyon both peaked at similar mean population sizes around year 24, but the Blue Range ended the simulations with 31-50% fewer wolves than the Grand Canyon and about 70% higher extinction rates, despite starting with nearly 2.5 times as many wolves. In addition, the Blue Range lost heterozygosity faster than the Grand Canyon and southern Rockies populations. And its heterozygosity excess increased over time suggesting ongoing genetic bottlenecks, whereas the excesses in the other two populations decreased over time. Similar simulations with each population founded by 20 outbred and unrelated wolves (mean kinship = 0.025) and no dispersal between populations averaged 52% larger populations and 60% larger metapopulation sizes at year 100 with 40% fewer extinctions, when there was 22% adult / yearling mortality. With 25% adult / yearling mortality, populations and metapopulations averaged 144 and 236% more wolves at year 100, with 66% fewer population extinctions (results not shown). These results suggested that recovery prospects for Mexican wolves would be enhanced by establishing genetically diverse populations that have low relatedness within each population. These results further suggested that growing the Blue Range larger without substantially improving its poor genetic composition will impede recovery of Mexican wolves and reduce the overall viability of the “recovered” metapopulation.

The adult mortality rate also had large effects on simulation outcomes. When there was no dispersal between populations in the 3x250 scenario, increasing the adult mortality rate from 22
to 23.5% reduced the mean number of wolves among extant iterations by 32% in the Blue Range at year 100. Further increasing the adult mortality rate to 25% reduced mean wolf numbers in the Blue Range at year 100 by 56% relative to 22% adult mortality. For the Grand Canyon, increasing the adult mortality rate from 22% to 23.5 and 25% reduced the mean numbers of wolves at year 100 by 19 and 40%, respectively. Similarly, in the southern Rockies, increasing the adult mortality rate from 22% to 23.5 and 25% reduced the mean numbers of wolves at year 100 by 22 and 42%, respectively. In addition, increasing the adult mortality rate from 22 to 23.5% doubled the extinction rate for all three populations. Increasing the adult mortality rate to 25% raised the extinction rate about 3.5 – 4 fold for the three populations relative to that with 22% adult mortality. The adult mortality rate also affected heterozygosity. Increasing the adult mortality rate from 22% to 23.5 and 25% increased the loss of mean expected heterozygosity by 19 and 39%, respectively in the Blue Range, and by 13 and 30%, respectively, in the Grand Canyon. Increasing the adult mortality rate from 22 to 25% also doubled the mean heterozygosity excesses at year 100 for the Blue Range and Grand Canyon (Figure 5). It should be noted that the range of mortality rates used in the simulations have been associated with vigorous wolf populations, e.g. Smith et al (2010), estimated a mean adult / yearling mortality rate of 22.9% for wolves in the Greater Yellowstone Area. It should also be noted that the consistent performance differences between the three populations were driven by differences in starting mean kinships.

The two dispersal regimes interacted with adult / yearling mortality rates in the Blue Range to affect the mean numbers of wolves among extant iterations and heterozygosity excesses. In the 3x250 scenario, when there was 1 mpg the mean numbers of wolves at year 100 increased 16 and 2% with 22 and 23.5% adult mortality, respectively, relative to that with no dispersal between populations. But with 25% adult mortality, the mean number of wolves present at year 100 was 17% less than that with no dispersal. This represented a linear decrease in wolf numbers as the adult mortality rate increased. The 2/1/1 mpg dispersal regime, however, greatly increased the mean numbers of wolves present at year 100, but in a non-linear manner. With 22, 23.5, and 25% adult mortality, mean wolf numbers were increased by 61, 98, and 100%, respectively, relative to that with no dispersal between populations.

The two dispersal regimes also had different effects on Blue Range heterozygosity excesses at year 100. With 1 mpg heterozygosity excesses were lower than that with no dispersal between populations when there was 22% adult mortality. But with 23.5 and 25% adult mortality heterozygosity excesses with 1 mpg were greater than that with no dispersal between populations. With 2/1/1 mpg, however, heterozygosity excesses were much lower than with either 1 mpg or no dispersal between populations for all three adult survival rates. But with 2/1/1 mpg heterozygosity excesses increased in a non-linear manner with adult mortality increased with the greatest increase occurring when adult mortality increased from 23.5 to 25% (Figure 5).

Overall, the 2/1/1 mpg dispersal regime outperformed 1 mpg in every viability and recovery metric considered in all four scenarios. The reasons were that 2/1/1 mpg better supported the
central population in each scenario. And the costs of this dispersal regime to the peripheral 
populations were small while the benefits to the central populations were large. And in a few 
cases even the peripheral populations benefitted over the long-term with 2/1/1 mpg. In contrast, 
with 1 mpg the central population bore a large demographic cost relative to 2/1/1 mpg, while the 
peripheral populations somewhat benefitted.

Under the 1 mpg dispersal regime, the central populations were required to export enough 
wolves to provide a total of about 2 mpg to the two peripheral populations, in scenarios 1, 2, and 
4. But each of the peripheral populations provided only about 0.5 mpg to the central population. 
This suggests the central population bore four times the demographic cost of the peripheral 
populations. But because the Blue Range was on average smaller than the Grand Canyon and 
southern Rockies (except in the Blue Range350 simulations), a greater percentage of its young 
wolves were required to disperse than that from the other populations to achieve a given 
effective number of migrants. And the relative burden on the central population increased as 
adult mortality rates increased. It should be noted that most dispersers did not become effective 
migrants. Most (62.5%) died before reaching their destinations, which also disproportionate 
ly increased the number of wolves leaving the central populations. Of the dispersing wolves that 
survived, only a fraction paired in the new population and produced at least one pup.

In scenario 3 (3x250 + Sonora), the central population was required to provide a total of about 
three mpg, while receiving a total of 1 mpg. In this case mean wolf numbers were substantially 
lower and extinction rates substantially higher for the central Blue Range than in similar 
simulations under 3x250. This was not a problem specific to the Blue Range. In scenario 4 the 
Blue Range was a peripheral population and Sonora was the central population. Sonora 
performed similarly to Durango when there was no dispersal between populations. But with 1 
mpg, Durango had substantially larger mean population sizes and lower extinction rates. With 
2/1/1 mpg the demographic differences between Sonora and Durango narrowed greatly.

Carroll et al. (2013) conducted a relative sensitivity analysis (Table 10; Cross & Beissinger 
2001) focused on the 3x250 scenario to examine the relative effects of nine parameters and two 
categorical variables (density dependent reproduction and initial composition of populations) on 
extinction risk and two levels of quasi-extinction corresponding to the proposed threatened and 
endangered statuses for scenario 1 (<250 wolves and <150 wolves, respectively). For this 
analysis, mean parameter values for eight of the continuous parameters were randomly drawn 
from a range within +20% of the mean values used in the simulations above. In addition, the 
target population sizes of the three populations were varied from 50 – 350 wolves, with each of 
the three populations having the same target sizes. One thousand parameter sets were generated 
and 100 iterations were run for each parameter set. They then used logistic regression to provide 
a quantitative ranking of the relative importance of the 11 covariates considered for each of the 
three outcomes considered (extinction and dropping below the two quasi-extinction thresholds).
They found that the mean adult mortality rate and the % of adult females in the breeding pool were the two covariates that had the greatest effects on all three population outcomes (Table 10). For the probability of extinction the “population size threshold” (target population size) and the strength of inbreeding depression were close runners-up. For the two levels of quasi-extinction, the strength of inbreeding depression was the third most important variable.

The number of effective migrants per generation was of secondary importance in determining extinction and quasi-extinction rates, based on the standardized regression coefficients. The analysis varied the numbers of mpg from zero to 2.4. But the dispersal regime, which provided at least two times as many migrants to the Blue Range as to each of the other populations, was not varied. This was similar to the 2/1/1 mpg dispersal regime considered here, but given that all three populations used the same dispersal rates the Blue Range probably received slightly more effective migrants than the two peripheral populations combined. Simulations with the 2/1/1 mpg dispersal regime had low extinction rates when adult mortality was moderate, e.g. 22% (Figure 6A), suggesting that sensitivity analysis iterations with connectivity rates > 1 mpg would have very low extinction rates except when adult mortality rates were high. But simulations with zero mpg had high extinction rates (Figure 6). Thus it appeared that most of the potential benefits of increasing connectivity to avoid extinction occurred in the lower portion of the connectivity range used in the sensitivity analysis. The relative insensitivity of simulation outcomes to the higher dispersal rates (>1 mpg) used in the sensitivity analysis would have reduced the relative importance ranking of connectivity.

“Variation between existing and new populations” (initial mean kinship of populations) was among the covariates with the least effects on extinction and quasi-extinction rates in the analysis (Table 9). The dispersal regime used in the sensitivity analysis, however, may have somewhat masked the effects of initial mean kinship on population outcomes. In the simulations described above, the performance of the centrally located Blue Range, which had the highest initial mean kinship, was enhanced with the 2/1/1 mpg dispersal regime. For example, the Blue Range had the lowest extinction rates (Figure 6) and highest mean expected heterozygosity at year 100 (Figure 4) of the three populations with 2/1/1 mpg, even though it started with the lowest heterozygosity and had the highest extinction rates when there was no dispersal between populations. In contrast, when the Blue Range was simulated as a peripheral population and the Grand Canyon was the central population the Blue Range had the highest extinction rates, lowest mean expected heterozygosity at year 100, and smaller mean population sizes at year 100 than when it was simulated as the central population (results not shown). As noted above, the dispersal regime used in the sensitivity analysis was similar to 2/1/1 mpg in that the central population received at least twice as many mpg as the peripheral populations. And thus it would be expected to have had similar positive effects on the Blue Range. If a dispersal regime similar to 1 mpg were included in the sensitivity analysis. Or if initial mean kinships of the peripheral populations were varied while the mean kinship of the central population remained constant, a truer picture of the relative importance of population mean kinships would be apparent. A
common management goal for small pedigreed populations managed for conservation is to minimize mean kinship. This is done to minimize the rate of inbreeding accumulation in populations. In populations with inbreeding depression, populations with low mean kinship will be less impacted by inbreeding depression and demographically more vigorous. If mean kinship of the Blue Range were to be reduced by genetic management, it would facilitate Mexican wolf recovery and support a stronger metapopulation. Conversely, if the Grand Canyon and southern Rockies populations were established with higher mean kinships than that assumed in the simulations, this would be expected to reduce their short and long-term performance and make recovery more difficult to attain and more tenuous to maintain. It should be noted that that it may be possible to establish new populations with lower mean kinships than those used in the simulations for peripheral populations, if new populations are reintroduced soon. If the Mexican wolf gamete bank is used in the creation of new populations it may be possible to reestablish populations with lower mean kinship than what currently exists in the captive population. It is encouraging, however, that the simulations suggested that relatively low rates of dispersal between populations has the potential to somewhat ameliorate the poor genetic composition of the Blue Range.

The population size threshold was the third or fourth most important covariate in determining whether a population became extinct or quasi-extinct (Table 10). That most populations in the simulations described above became extinct or quasi-extinct in a majority of iterations suggested that the minimal harvest buffer we incorporated would likely be inadequate to prevent populations from falling below the targeted population sizes once delisting targets are met. But the strong performance of the population size threshold suggested that adding numerical management buffers above the targeted population sizes would substantially reduce the probability of needing to relist Mexican wolves once they are delisted. In contrast, the sensitivity analysis suggested that reducing the efficiency by which wolves in excess of the target numbers are hunted would likely be ineffective in preventing the need for relisting.

Density dependent reproduction had the fifth largest effect on extinction rates in the sensitivity analysis (Table 10). Data from Yellowstone National Park suggested that the % of adult females that breed each year may be density dependent (Smith and Stahler unpublished data). The function used ranged from 30% of adult females breeding when the census population size (N) was equal to the carrying capacity (K) to a maximum of 60% when N / K approached zero (Figure 1). When the population size was 57% of K, the % adult females breeding dropped to 50%. Including density dependent reproduction decreased the probability of extinction. But it had relatively lesser effects on the probabilities of a population dropping below 150 and 250 wolves, ranking 8th and 12th, respectively (Table 10). This suggested that including density dependent reproduction in simulations reduced the probability of extinction but had relatively little effect on whether the population would drop below the quasi-extinction thresholds.

It should be noted that the sensitivity analysis by Carroll et al. (2013) may have under represented the effects of parameters that have wide variation (>20%) in mean rates or high
variability and in parameters with a high degree of uncertainty. Mortality rates for young of the year mammals are often high and highly variable. If the long-term Mexican wolf pup mortality rate turns out to be higher and / or more variable than considered in Carroll et al. (2013) its relative importance in determining extinction and quasi-extinction may also increase. In addition there is high uncertainty in the frequency and nature of catastrophes that may occur among reintroduced Mexican wolf populations. The catastrophe parameterization used by Carroll et al. (2013) and in the simulations described above was based on the observed occurrence of distemper in Yellowstone National Park. Available data suggested parvovirus outbreaks have occurred on a five-year periodicity within the Park. But it remains uncertain how often comparable catastrophes may occur among reintroduced Mexican wolf populations. If a wider range of parvovirus periodicity had been considered this parameter would likely have had a higher relative importance.

The results of the simulations presented here and in the sensitivity analysis by Carroll et al. (2013) suggest that our recovery criteria appropriately focus on major threats to Mexican wolf viability and recovery under the Endangered Species Act. Focusing management efforts on these metrics should facilitate recovery. And once Mexican wolves are delisted, continued monitoring of these metrics should inform management to prevent the need to relist Mexican wolves in the future.

2. REALISM

Although we incorporated a high degree of realism into the simulation model, there were two aspects of the simulations that were not realistic: the modeling of heterozygosity and some aspects of inbreeding depression.

In the founding pedigrees we assumed that each of the original seven Mexican wolf founders carried two unique alleles at each locus. This led to mean observed heterozygosities for neutral genetic variation ranging from 0.774 to 0.848 for the various populations at the start of the simulations. Empirical estimates of observed heterozygosity among Mexican wolves, however, have been much lower. Hedrick et al. (1996) used 20 microsatellite loci to estimate mean observed heterozygosity among McBride, Ghost Ranch, and Aragon lineage wolves. Based on these data, they estimated McBride lineage wolves had the highest observed heterozygosity at 0.457, while Ghost Ranch and Aragon wolves had mean heterozygosities of 0.128 and 0.255, respectively. They also found that the Ghost Ranch and Aragon wolves were fixed for single alleles at 11 of the 20 loci. Fitak (unpublished data) found similar results based on about 6,000 unlinked single nucleotide polymorphisms (SNPs) with genotypic frequencies consistent with Hardy Weinberg proportions. Recent McBride lineage wolves had a mean observed heterozygosity of 0.310, while Ghost Ranch and Aragon lineage wolves averaged 0.194 and
0.273, respectively. In addition F1 wolves created from pairings between McBride and Ghost Ranch wolves averaged 0.409, while wolves created by pairings between McBride and Aragon wolves averaged 0.460. As expected, heterozygosity for the F1 wolves was substantially higher than those of the founding lineages. Observed heterozygosity for a sample of 21 cross-lineage wolves born 2006 – 2008, were lower than that for the F1 wolves, averaging 0.360. Most of these cross-lineage wolves were born in the Blue Range. Thus, the heterozygosity values from the simulations were not approximations of what might be achieved in actual reintroduced populations of Mexican wolves. But they are still useful for illustrating relative differences between populations, scenarios, and simulation conditions, as well as exploring the interplay of demography, genetics and management options.

Our parameterization of inbreeding depression on litter sizes was based on the findings of Fredrickson et al. (2007). Although this constitutes the best available information, we did not include the potential for a portion of the genetic load to be purged over time. Inbreeding depression is thought to be primarily a result of the full expression of deleterious alleles that have become homozygous as a result of inbreeding (Charlesworth and Willis 2009). But theory suggests that purging in small populations is likely to be limited to lethal alleles (those that result in the death of individuals with two copies; Hedrick 1994, Wang et al. 2000, Whitlock et al. 2000). And while lethal alleles may be eliminated or reduced in frequency in small populations, many other mildly and moderately deleterious alleles may simultaneously become fixed (homozygous in all individuals) with little or no net reduction in the overall genetic load (Hedrick 1994; Wang et al. 2000; Whitlock et al. 2000). This mixed result may occur because natural selection is weak and genetic drift is strong in small populations (Hedrick 2005). As a consequence, natural selection may only operate effectively on alleles with large effects (positive or deleterious) in small populations. But given the Mexican wolf’s history of long-term small population size and close inbreeding, it is possible that lethal alleles carried by the seven Mexican wolf founders may have already been purged or reduced in frequency. If further purging were to occur among reintroduced Mexican wolf populations the strength of inbreeding depression may be reduced if it the fitness increases resulting from the elimination of lethal alleles was not offset by the increased frequency of moderately and mildly deleterious alleles. It is possible, however, that the strength of inbreeding depression estimated by Fredrickson et al. (2007) for wolves in the Blue Range may have been underestimated. In the captive population of Mexican wolves, they found that inbreeding levels in dams, sires, and pups affected the numbers of pups produced. But it was not possible to investigate potential inbreeding effects associated with dams and sires in the Blue Range due to the nature of the available data.

3. LIMITATIONS
Although our simulations explored a wide range of conditions, there were some we did not consider. These included the possibilities that dispersal between populations may be density dependent, and that populations may have different mean adult mortality rates or that mortality rates vary over time within populations. We also did not consider the effects of potential directional changes in carrying capacity over time. Finally we did not consider possible management options related to implementation of the recovery plan.

a. Dispersal

In our simulations, dispersal between populations was modeled by moving a mean percentage of young, unpaired wolves between populations each timestep from the start of the simulations. Thus even when populations were small, some dispersal between populations was occurring. If, however, dispersal among Mexican wolves may be driven by positive density dependence, i.e. the percentage of young wolves that emigrate from a population each year increases and decreases as the population increases and decreases in size, this could affect the simulation outcomes in a variety of ways. First, when all populations are small, e.g. at the start of simulations, there could be fewer effective migrants per generation than in the simulations described above (depending on parameterization). This may reduce the demographic costs of dispersal between populations, thereby reducing the rate of extinctions among small populations. If so, this could be particularly important for the centrally located Blue Range population with the 1 mpg dispersal regime. When all populations are large, the increased rate of effective migration may reduce the probability of decreasing to small size. If one population was small, while its neighbor(s) was large, the small population may be more likely to be demographically and/or genetically rescued by adjacent populations. But at the same time the large neighboring populations may be at increased risk of declining in size as a result of receiving few migrants.

Wolves, however, may be compelled to move between populations by considerations other than a crowded landscape. At least four Mexican wolves have made long-distance movements out of the Blue Range Wolf Recovery Area travelling straight line distances of 158 – 291 km before being recaptured, despite the small size of the Blue Range population (<59 wolves). When populations are small and wolf densities are low, finding a minimally related mate may be difficult, particularly in a population such as the Blue Range which has such high mean kinship. Consistent with this, Von Holdt et al. (2008) found that wolves in the recovering Yellowstone population used a variety of behavioral mechanisms to avoid inbreeding, and concluded that the population had levels of genetic variation similar to a population managed to retain variation and minimize inbreeding accumulation. This suggests that our assumption that some wolves will disperse (or at least attempt to) between populations even when source populations are small may be valid.

b. Adult mortality, carrying capacity, and recovery implementation
If mean adult mortality rates vary between populations, those with higher mortality may be slower to reach the delisting criteria and may be less able to maintain a given population size. Thus it may cause differences between populations in their long-term census sizes. Populations with higher mortality may also be more likely to become extinct. If mean adult mortality rates vary over time within a population, this could cause variation in population size between different periods. It would also be expected to reduce the retention of heterozygosity relative to a population with equivalent constant mean mortality rate.

Carrying capacity could change as a result of changes to prey populations. This could potentially be driven by management of prey populations and/or by changes in habitat. Climate change may have the potential to drive changes in both prey and habitat. Climate in the southwestern United States is projected to become warmer and drier with longer droughts. This is expected to result in increased disturbance by forest fires and forest insects. Over time this is expected to change the areal extent of forests and their nature in the Southwest (Adams et al. 2009; Cayan et al. 2010; Raffa et al. 2008; Seager & Vecchi 2010; Williams et al. 2010).

Finally, our simulations did not explore scenarios related to implementation of the recovery plan. For example we did not explore the potential consequences of substantially improving the genetic composition of the Blue Range, nor did we consider the use of artificial insemination or in vitro fertilization techniques in the founding of new Mexican wolf populations. Similarly, we did not explore the potential benefits of artificial migration, e.g. between the Grand Canyon and southern Rockies populations. We also did not attempt to determine the size of numerical management buffers that may be needed to avoid relisting of Mexican wolves once they have been delisted. Although it would be possible to investigate these topics and others via simulations, this was beyond the scope of our task.

4. SCENARIO REVIEWS

Scenario 1: 3x250

Under scenario 1, the Blue Range was able to support a roughly stable mean population size only when there was 22% adult mortality and 2/1/1 mpg (Figure 3). Under these circumstances, the Blue Range was also able to maintain stable levels of heterozygosity (Figure 4), low extinction rates (Figure 6), contain its heterozygosity excess (Figure 5) and meet the numerical delisting criterion in 90% of iterations (Table 3). Increasing the adult mortality or using the 1 mpg dispersal regime caused deterioration in all viability and recovery metrics considered.

In contrast, the choice of dispersal regime had relatively small effects on the Grand Canyon and southern Rockies populations. But both populations were strongly affected by increases in adult mortality rates. The greatest mean metapopulation sizes were, however, were supported by the
2/1/1 mpg (Figure 12). These simulations, as well as those from the other three scenarios, strongly support the adoption of the 2/1/1 dispersal regime as part of the recovery criteria, rather than the 1 mpg dispersal regime.

None of the three populations in these simulations were able to maintain mean population sizes over time greater than 250 wolves. The GC350 and Blue Range 350 simulations under scenario 2, however, suggest that all three populations could be maintained above 250 wolves if the numerical threshold for harvests was set higher than 250 wolves.

**Scenario 2: 3x200=750**

This scenario was intended to allow some management flexibility in achieving and maintaining a recovered Mexican wolf metapopulation. Under this recovery scenario unequal minimum census population sizes for the three populations would be allowed, which could lead to unequal genetically effective population sizes for the three populations. If taken to an extreme a metapopulation composed of populations with highly unequal effective population sizes could have reduced viability relative to one in which component populations were of more equal sizes. We simulated two extreme variations of this scenario. The first assumed that the peripheral Grand Canyon population would be managed to maintain at least 350 wolves, while the Blue Range and southern Rockies would each be managed to maintain at least 200 wolves. The Grand Canyon population had the lowest mean kinship and was demographically the strongest of the three populations. The second variation assumed that the central Blue Range population would be managed to support at least 350 wolves, while the other two populations would be managed to each support at least 200 wolves.

When there was 1 mpg, the Blue Range 350 variation performed better than the GC 350 variation and the 3x250 scenario. The Blue Range350 variation had the highest mean metapopulation sizes at year 100 (Figure 12) and the lowest number of population extinctions (Figure 13). It also had the highest % of iterations meeting delisting criteria and exceeding the endangerment criteria in the last 20 years of the simulations. Overall the GC350 variation performed the worst. Although it supported slightly higher mean metapopulation sizes at year 100 than the 3x250 scenario, it also had the most population extinctions, the lowest delisting rate, and the lowest % of iterations that exceeded endangerment criteria at the end of the simulations.

When there was 2/1/1 mpg, the 3x250 scenario and the Blue Range 350 and GC 350 variations performed similarly. The Blue Range 350 variation, however, had slightly lower mean metapopulation sizes at year 100, higher numbers of population extinctions, and slightly lower delisting and higher rates endangerment than the other two options.

These simulations suggested that this scenario allows a level of management flexibility that will likely not have a large negative effect on viability. In addition, other considerations suggested that allowing this level of management flexibility will likely not be detrimental to recovered Mexican wolf populations. First Mexican wolves will likely not be maintained at these extreme
numerical disparities and relative census sizes of recovered populations will likely change over time. Secondly, the recovered Mexican wolf population may be maintained at numbers substantially greater than 750 wolves, to minimize the probability of needing to relist Mexican wolves in the future. Maintaining a numerical buffer on each recovered population would reduce the functional differences between the scenarios. Finally the viability of the Blue Range may be increased by genetic management prior to delisting and/or the reintroduced Grand Canyon and southern Rockies populations may be founded by wolves with greater relatedness, reducing their long-term viability.

Long-term adult mortality rates and the choice of dispersal regime will likely have much larger effects on management outcomes than the management flexibility allowed under this scenario. These simulations, however, did not explore the potential effects of management flexibility when populations have substantially different adult mortality rates. The simulations also did not explore the effects of directional changes in relative wolf abundance over time among the three populations. If the smallest population increased in size to become the largest population, while the largest population became the smallest, this could cause an overall reduction in heterozygosity over time as individuals and genes from the formerly small population proliferate in the other two populations. This dynamic may, however, be minimized by land ownership patterns and prey abundances that suggest the southern Rockies may be most capable and the Grand Canyon region may be least capable of supporting large populations of Mexican wolves.

Collectively, these results suggested that Scenario 2 which allows management flexibility in the numerical targets for delisting is unlikely to be severely detrimental to the recovered Mexican wolf population relative to the 3x250 scenario.

**Scenario 3: 3x250 + Sonora**

This scenario would extend the geographic scope of the recovered Mexican wolf metapopulation into Mexico. It would also broaden the array of ecological communities inhabited by Mexican wolves. The inclusion of Sonora in the simulations, however, had mostly negative effects on the Blue Range and on overall metapopulation viability relative to the 3x250 scenario. The Grand Canyon and southern Rockies populations, however, largely performed similarly with or without Sonora.

The positive effects of including Sonora were limited. With Sonora, mean metapopulation sizes at year 100 were greater in three of four of the simulations (Figure 20). The sum of extinctions among the three large populations was lower (Figure 21) and mean expected heterozygosity for the Blue Range was higher when there was 2/1/1 mpg and 22% adult mortality. However, extinctions among the three large populations were higher and mean expected heterozygosity lower when there was 2/1/1 mpg and 23.5% adult mortality as well as when there was 1 mpg.

Additional negative effects on the Blue Range included 29 and 40% smaller mean population sizes at year 100 than that with the 3x250 scenario when there was 1 mpg, and 6 and 19%
smaller population sizes when there was 2/1/1 mpg, with 22 and 23.5% adult mortality, respectively. When there was 1 mpg, extinction rates for the Blue Range were 156 and 63% higher with Sonora than without, with 22 and 23.5% adult mortality, respectively. But with 2/1/1 mpg Blue Range extinction rates were only slightly higher with Sonora.

In addition, the % of iterations in which all three large populations exceeded numerical criteria for being endangered was lower with Sonora (Tables 5 and 7). And delisting rates for the three large populations were lower in three of four cases (the fourth simulation was tied; Tables 4 and 6).

The Sonora population outperformed the Blue Range when there was 1 mpg, driven by the demographic costs of this dispersal regime to the centrally located Blue Range. At year 100 the mean population size for the Blue Range was 34 and 22% of the target population size of 250 wolves, but Sonora was 71 and 51% of its target population size of 100 wolves, with 22 and 23.5% adult mortality, respectively. In addition, extinction rates for Sonora were somewhat lower than those for the Blue Range.

But with 2/1/1 mpg the Blue Range outperformed Sonora. Mean population sizes at year 100 for the Blue Range were 81 and 58% of the target population size of 250 wolves, while population sizes for Sonora were 75 and 58% of targeted numbers, with 22 and 23.5% adult mortality, respectively. Extinction rates for the Blue Range were also much lower than that for Sonora (Figure 19).

Although, the addition of Sonora increased mean metapopulation sizes relative to the 3x250 scenario, it appeared to reduce the viability of the metapopulation. Overall, Sonora and the Blue Range had smaller relative population sizes and were substantially more extinction prone than the Blue Range in the 3x250 scenario. In addition, there is substantial uncertainty whether the Sonora / Chihuahua area identified for potential reintroduction of Mexican wolves would be able to support 133 wolves in the foreseeable future, as assumed in the simulations.

Based on expert opinion, it was thought the Sonora and Durango reintroduction areas may each be able to support about 100 wolves (Araiza et al. 2007; C. Lopez Gonzalez personal communication). There is, however, little data available to inform estimates of ecological carrying capacity in these areas. Further, even if there is the biological potential to support at least 100 wolves in these areas, land ownership and land use patterns, and road densities may make the goal of 100 wolves difficult to achieve, as suggested by the recent unsuccessful reintroduction attempts into the Sonora area. Thus it is unclear whether either Sonora or Durango will be able to support 100 wolves in the foreseeable future. Consequently, the sum of available information suggests that recovery under scenario 3 may be more difficult to achieve and presents a higher risk of failure than scenarios 1 and 2.

Scenario 4: Blue Range +2MX100
This scenario was characterized by populations that declined steadily from the start of harvests to very low sizes by year 100 and by higher extinction rates and lower heterozygosity retention than the other three scenarios. As a result, this scenario had the lowest % of iterations exceeding the numerical delisting criteria and only 8% or fewer iterations exceeding the numerical criteria for being endangered in the last 20 years of the simulation.

With 1 mpg, mean sizes of extant metapopulations at year 100 were only 53 and 32% of the targeted 450 wolves, with 22 and 23.5% adult mortality, respectively. Mean metapopulation sizes at year 100 for the 3x250 scenario were 78 and 58% of the targeted population size of 750 wolves (Figure 20). Summed extinctions across the three populations were 720 and 1,493, with 22 and 23.5%, respectively (Figure 21). This was 10.3 and 4.5 times greater than the summed extinctions for the 3x250 scenario. Averaged over the three populations, the mean population extinction rate for this scenario was 49.8% with 23.5% adult mortality.

Although none of the three populations performed well, Sonora, the central population, performed the worst. The mean sizes of extant populations at year 100 were only 37 and 20 wolves, and extinction rates for Sonora were 38 and 70% with 22 and 23.5% adult mortality, respectively. Durango fared somewhat better. But mean sizes of extant populations at year 100 were only 56 and 38 wolves, and extinction rates for Durango were 26 and 56% with 22 and 23.5% adult mortality, respectively. The Blue Range performed the best. Mean sizes of extant populations at year 100 were 171 and 118 wolves with 22 and 23.5% adult mortality, respectively, slightly higher than that with the 3x250 scenario. But with extinction rates of 8 and 24% with 22 and 23.5% adult mortality, respectively, more iterations became extinct than with the 3x250 scenario.

With 2/1/1 mpg, mean metapopulation sizes at year 100 were 56 and 34% of the targeted size of 450 wolves. This was substantially lower than that under the 3x250 scenario which supported 86 and 71% of the targeted 750 wolves at year 100. The summed population extinctions, 385 and 1,238 with 22 and 23.5% adult mortality, respectively, were 9 and 8.4 times greater than that with the 3x250 scenario. The centrally located Sonora population supported averages of 49 and 34 wolves at year 100 among extant iterations and had extinction rates of 15 and 48% with 22 and 23.5% adult mortality, respectively. Durango supported mean population sizes among extant populations of 60 and 40 wolves at year 100, and had 17 and 47% extinction rates, with 22 and 23.5% adult mortality, respectively. The Blue Range supported 159 and 108 wolves on average at year 100, along with extinction rates of 7 and 29%, with 22 and 23.5% adult mortality, respectively.

These results suggested that this alternative would be the least likely to result in delisting of Mexican wolves and the most likely to result in the need to relist Mexican wolves under the Endangered Species Act - if they were ever delisted. Coupled with the high uncertainty, noted above, of whether the Sonora and Durango regions will each be capable of supporting 100
wolves in the foreseeable future, makes this alternative unacceptable as recovery criteria for Mexican wolves.

E. LITERATURE CITED


Table 1. Numbers of wolves, packs and pairs used to found populations and the range of target population sizes.

<table>
<thead>
<tr>
<th>Population</th>
<th>Target population sizes</th>
<th>Number of wolves at founding</th>
<th>Pairs at founding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Range</td>
<td>200 – 350</td>
<td>122</td>
<td>21</td>
</tr>
<tr>
<td>Grand Canyon</td>
<td>200 - 350</td>
<td>50</td>
<td>10</td>
</tr>
<tr>
<td>Southern Rockies</td>
<td>200 - 350</td>
<td>50</td>
<td>10</td>
</tr>
<tr>
<td>Sonora</td>
<td>100</td>
<td>35</td>
<td>7</td>
</tr>
<tr>
<td>Durango</td>
<td>100</td>
<td>35</td>
<td>7</td>
</tr>
</tbody>
</table>
Table 2. Mean kinship for founding populations, the reintroduced Blue Range population, and the captive population as of fall 2013.

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean kinship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Range (simulated)</td>
<td>0.2446</td>
</tr>
<tr>
<td>Blue Range (actual)$^a$</td>
<td>0.2472</td>
</tr>
<tr>
<td>Grand Canyon</td>
<td>0.194</td>
</tr>
<tr>
<td>Southern Rockies</td>
<td>0.1954</td>
</tr>
<tr>
<td>Sonora (Scenario 3)</td>
<td>0.2064</td>
</tr>
<tr>
<td>Sonora (Scenario 4)</td>
<td>0.2053</td>
</tr>
<tr>
<td>Durango</td>
<td>0.2049</td>
</tr>
<tr>
<td>SSP population$^a$</td>
<td>0.1665</td>
</tr>
</tbody>
</table>

$^a$Siminski and Spevak (2013).
Table 3. Mean numbers of effective migrants per generation into each population from years 30 to 100.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Dispersal regime</th>
<th>Mortality rate (%)</th>
<th>Blue Range</th>
<th>Grand Canyon</th>
<th>S. Rockies</th>
<th>Sonora</th>
<th>Durango</th>
</tr>
</thead>
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<tr>
<td>3x250</td>
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<td>22</td>
<td>1.10</td>
<td>1.01</td>
<td>1.06</td>
<td>1.00</td>
<td>na</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23.5</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>na</td>
</tr>
<tr>
<td></td>
<td>2/1/1 mpg</td>
<td>22</td>
<td>2.07</td>
<td>1.02</td>
<td>1.01</td>
<td>1.02</td>
<td>na</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23.5</td>
<td>2.07</td>
<td>1.02</td>
<td>1.01</td>
<td>1.02</td>
<td>na</td>
</tr>
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<td>GC350</td>
<td>1 mpg</td>
<td>22</td>
<td>1.10</td>
<td>1.01</td>
<td>1.06</td>
<td>1.00</td>
<td>na</td>
</tr>
<tr>
<td>BR&amp;SR200</td>
<td>1 mpg</td>
<td>22</td>
<td>1.07</td>
<td>1.02</td>
<td>1.03</td>
<td>1.00</td>
<td>na</td>
</tr>
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</tr>
<tr>
<td></td>
<td>2/1/1 mpg</td>
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<td>2.07</td>
<td>1.02</td>
<td>1.01</td>
<td>1.02</td>
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</tr>
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<td>1.01</td>
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</tr>
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<td>1.00</td>
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<td>1.00</td>
<td>0.99</td>
</tr>
<tr>
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<td>22</td>
<td>1.11</td>
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<td>0.86</td>
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<td>1.01</td>
<td>1.02</td>
<td>1.04</td>
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<td>2/1/1 mpg</td>
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<td>2.24</td>
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<td>1.03</td>
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<td>2.24</td>
<td>1.02</td>
<td>1.03</td>
<td>1.04</td>
<td>1.04</td>
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<tr>
<td>3x250 + Sonora</td>
<td>1 mpg</td>
<td>22</td>
<td>1.12</td>
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<td>0.97</td>
<td>na</td>
</tr>
<tr>
<td>5 pairs</td>
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<td>23.5</td>
<td>1.13</td>
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<td>1.03</td>
</tr>
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<td>1.01</td>
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<tr>
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<td>na</td>
<td>1.13</td>
<td>0.77</td>
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<tr>
<td>7 pairs</td>
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<td>23.5</td>
<td>0.76</td>
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<td>na</td>
<td>1.17</td>
<td>0.78</td>
</tr>
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<td>2/1/1 mpg</td>
<td>22</td>
<td>0.99</td>
<td>na</td>
<td>na</td>
<td>2.39</td>
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</tr>
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<td></td>
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<td>1.03</td>
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<td>na</td>
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<td>0.77</td>
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<td>0.78</td>
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<tr>
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<td>2/1/1 mpg</td>
<td>22</td>
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<td>na</td>
<td>na</td>
<td>na</td>
<td>2.26</td>
<td>0.98</td>
</tr>
</tbody>
</table>
Table 4. Percentage of iterations in which all three populations met numerical delisting criteria (the mean size of each population averaged over eight years was $\geq 250$ wolves for $3 \times 250$ simulations; $>350$ and $\geq 200$ wolves for the Grand Canyon 350 and Blue range 350 simulations).

<table>
<thead>
<tr>
<th>Adult / yearling mortality rate (%)</th>
<th>3 x 250</th>
<th>Grand Canyon 350</th>
<th>Blue Range 350</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mpg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>81</td>
<td>79</td>
<td>86</td>
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<td>42</td>
<td>58</td>
</tr>
<tr>
<td>25</td>
<td>18</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>2/1/1 mpg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
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<td>90</td>
<td>89</td>
</tr>
<tr>
<td>23.5</td>
<td>69</td>
<td>68</td>
<td>62</td>
</tr>
<tr>
<td>25</td>
<td>32</td>
<td>na</td>
<td>na</td>
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</tbody>
</table>
Table 5. Percentage of iterations in which all three populations exceeded the numerical criteria for being endangered during the last 20 years of the simulations (the mean size of each population averaged over eight years was $\geq 150$ wolves for 3x250 simulations; $\geq 210$ and $\geq 120$ wolves for the Grand Canyon 350 and Blue range 350 simulations).

<table>
<thead>
<tr>
<th>Adult / yearling mortality rate (%)</th>
<th>3 x 250</th>
<th>Grand Canyon 350</th>
<th>Blue Range 350</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mpg</td>
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<td>3</td>
<td>15</td>
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<tr>
<td>25</td>
<td>1</td>
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</tr>
<tr>
<td>2/1/1 mpg</td>
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<tr>
<td>22</td>
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<td>19</td>
<td>15</td>
</tr>
<tr>
<td>25</td>
<td>4</td>
<td>na</td>
<td>na</td>
</tr>
</tbody>
</table>
Table 6. Percentage of iterations in which all four populations, just the three large populations, the BR and Sonora met numerical delisting criteria for the 3x250+Sonora scenario (the mean population size averaged over eight years was ≥ 250 wolves for the BR, GC, and SR populations, and ≥ 100 for Sonora).

<table>
<thead>
<tr>
<th>Adult / yearling mortality rate (%)</th>
<th>All 4 populations</th>
<th>BR+GC+SR</th>
<th>BR</th>
<th>Sonora</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>64</td>
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<td>97</td>
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</tr>
<tr>
<td>22</td>
<td>86</td>
<td>90</td>
<td>96</td>
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<td>89</td>
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</tbody>
</table>
Table 7. Percentage of 3x250+Sonora iterations in which all four populations, the three large populations, the BR, and Sonora exceeded numerical criteria for being endangered during the last 20 years of the simulations for the option (the mean size of each population averaged over eight years was ≥ 150 wolves for the BR, GC, and SR populations, and > 60 for Sonora).

<table>
<thead>
<tr>
<th>Adult / yearling mortality rate (%)</th>
<th>All 4 populations</th>
<th>BR+GC+SR</th>
<th>BRP</th>
<th>Sonora</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>12</td>
<td>17</td>
<td>21</td>
<td>52</td>
</tr>
<tr>
<td>23.5</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>24</td>
</tr>
<tr>
<td>2/1/1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>26</td>
<td>41</td>
<td>68</td>
<td>57</td>
</tr>
<tr>
<td>23.5</td>
<td>7</td>
<td>14</td>
<td>32</td>
<td>35</td>
</tr>
</tbody>
</table>
Table 8. Percentage of iterations in which all three populations, the BR, Sonora, and Durango populations met numerical delisting criteria for the BRP+2MX100 scenario (the mean population size averaged over eight years was ≥ 250 wolves for the BR and ≥ 100 for Sonora and Durango).

<table>
<thead>
<tr>
<th>Adult / yearling mortality rate (%)</th>
<th>All 3 populations</th>
<th>BR</th>
<th>Sonora</th>
<th>Durango</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>58</td>
<td>92</td>
<td>64</td>
<td>90</td>
</tr>
<tr>
<td>23.5</td>
<td>30</td>
<td>79</td>
<td>40</td>
<td>77</td>
</tr>
<tr>
<td>2/1/1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>72</td>
<td>90</td>
<td>80</td>
<td>91</td>
</tr>
<tr>
<td>23.5</td>
<td>39</td>
<td>71</td>
<td>54</td>
<td>73</td>
</tr>
</tbody>
</table>
Table 9. Percentage of iterations in which all three populations, the BR, Sonora, and Durango populations exceeded numerical criteria for being endangered during the years 81-100 under the BRP+2MX100 scenario (the mean population size averaged over eight years was ≥ 150 wolves for the BR and ≥ 60 wolves for Sonora and Durango).

<table>
<thead>
<tr>
<th>Adult / yearling mortality rate (%)</th>
<th>All 3 populations</th>
<th>BR</th>
<th>Sonora</th>
<th>Durango</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>5</td>
<td>49</td>
<td>12</td>
<td>32</td>
</tr>
<tr>
<td>23.5</td>
<td>&lt;1</td>
<td>25</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>2/1/1 mpg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>8</td>
<td>44</td>
<td>24</td>
<td>38</td>
</tr>
<tr>
<td>23.5</td>
<td>1</td>
<td>19</td>
<td>8</td>
<td>13</td>
</tr>
</tbody>
</table>
Table 10. Results of sensitivity analysis of Vortex population model assessed using standardized coefficients from logistic regression of parameter sets against probability of extinction and quasi extinction (reproduced from Carroll et al. 2013).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Maximum</th>
<th>z value for extinction</th>
<th>Quasi-ex-150</th>
<th>Quasi-ex-250</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult mortality</td>
<td>18.32</td>
<td>27.48</td>
<td>167.46</td>
<td>162.48</td>
<td>111.15</td>
</tr>
<tr>
<td>Percentage of females in breeding pool</td>
<td>40</td>
<td>60</td>
<td>-160.67</td>
<td>-156.80</td>
<td>-104.49</td>
</tr>
<tr>
<td>Population size threshold</td>
<td>50</td>
<td>350</td>
<td>-158.63</td>
<td>-136.53</td>
<td>-72.03</td>
</tr>
<tr>
<td>Strength of inbreeding depression</td>
<td>6.586</td>
<td>9.789</td>
<td>152.81</td>
<td>141.54</td>
<td>92.90</td>
</tr>
<tr>
<td>Density dependent reproduction</td>
<td>categorical</td>
<td></td>
<td>-92.42</td>
<td>-54.95</td>
<td>-8.35</td>
</tr>
<tr>
<td>Effective migrants per generation</td>
<td>0.0</td>
<td>2.4</td>
<td>-88.13</td>
<td>-56.17</td>
<td>-35.49</td>
</tr>
<tr>
<td>Average number of years between disease events</td>
<td>4</td>
<td>6</td>
<td>76.54</td>
<td>81.23</td>
<td>41.31</td>
</tr>
<tr>
<td>Pup mortality</td>
<td>19.52</td>
<td>29.28</td>
<td>75.37</td>
<td>60.22</td>
<td>43.56</td>
</tr>
<tr>
<td>Variation between existing and new populations</td>
<td>categorical</td>
<td></td>
<td>-34.12</td>
<td>-32.62</td>
<td>-24.79</td>
</tr>
<tr>
<td>Carrying capacity buffer</td>
<td>1.07</td>
<td>1.60</td>
<td>-5.44</td>
<td>-51.50</td>
<td>-52.47</td>
</tr>
<tr>
<td>Harvest efficiency</td>
<td>6.4</td>
<td>9.6</td>
<td>-3.86</td>
<td>-2.44</td>
<td>-12.65</td>
</tr>
</tbody>
</table>

Footnotes
a Quasi-extinction occurs when the 8-year running mean population size falls below 150 or 250. All regressions are based on 1000 scenarios derived from randomized parameter sets, with 100 replicate runs per scenario. Standardized regression coefficients (z-values), created by dividing a regression coefficient by its standard error, are unitless values whose magnitude indicates the relative importance of a parameter in the model.
b From Smith et al. (2010) for Greater Yellowstone Area wolf population.
c Slope parameter in equation of Fredrickson et al. (2007) relating litter size to inbreeding coefficient.
d Variation in population performance arising from contrasts between populations in initial pedigree.
e Ratio of ecological carrying capacity to the population size threshold parameter.
f Reciprocal of proportion of the population above the population-size threshold that is removed annually.
Figure 1. Mean mortality rates with density dependent senescence when the baseline mortality rate was 22% for a range of census population sizes relative to the carrying capacity ($N/K$).
Figure 2. Mean % of adult females breeding when there was density dependent reproduction for census population sizes relative to carrying capacity (N/K) ranging from 0 to 1.
Figure 3. Mean census population size among extant iterations over time under the 3x250 scenario for the BR and Grand Canyon populations: A) BR with 22% mortality; B) Grand Canyon with 22% mortality; C) BR with 25% mortality; and D) Grand Canyon with 25% mortality.
Figure 4. Mean expected heterozygosity over time for the 3x250 scenario of the Blue Range and Grand Canyon populations with 22% yearling / adult mortality (A, B) and 25% mortality (C, D).
Figure 5. Heterozygosity excesses at years zero and 100 for the Blue Range and Grand Canyon populations under the 3x250 scenario.
Figure 6. Population extinction rates for the 3x250 scenario with three different adult / yearling mortality rates and three dispersal regimes: 
A) 22% annual mortality;  
B) 23.5% annual mortality; and  
C) 25% annual mortality.
Figure 7. Relationship of mean size of extant populations at year 100 and its coefficient of variation from the 3x250 scenario with three levels of adult/ yearling mortality (22, 23.5, and 25%) and three levels of population connectivity. Each symbol represents a single population from a simulation.
Figure 8. Mean census population sizes among extant iterations over time for the Grand Canyon 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.
Figure 9. Mean expected heterozygosity over time for the Grand Canyon 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.
Figure 10. Mean heterozygosity excesses for the Grand Canyon 350 simulations (A, C and E) and BRP 350 simulations (B, D, and F) simulations: A, B) Blue Range; C, D) Grand Canyon; E, F) southern Rockies.
Figure 11. Subpopulation extinction rates for Grand Canyon 350 simulations (A,C) and BRP 350 simulations (B,D) with two adult/yearling mortality rates and two dispersal regimes: A) 22% adult mortality Grand Canyon 350; B) 22% adult mortality BRP 350; C) 23.5% adult mortality Grand Canyon 350; and D) 23.5% mortality BRP350.
Figure 12. Mean metapopulation size at year 100 for the 3x250, the Grand Canyon 350, and BRP 350 simulations.
Figure 13. Total number of population extinctions for the 3x250, the Grand Canyon 350, and BRP 350 simulations.
Figure 14. Mean census population sizes among extant iterations over time for BRP 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.
Figure 15. Mean expected heterozygosity over time for BRP 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.
Figure 16. Mean census population sizes among extant iterations over time for the 3x250 + Sonora scenario: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) Sonora with 22% adult mortality; and F) Sonora with 23.5% adult mortality.
Figure 17. Mean expected heterozygosity over time for the 3x250 + Sonora scenario: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) Sonora with 22% adult mortality; and F) Sonora with 23.5% adult mortality.
Figure 18. Mean heterozygosity excesses for the 3x250 + Sonora scenario: A) BRP; and B) Sonora.
Figure 19. Subpopulation extinction rates for 3x250+Sonora scenario: A) 22% annual mortality; and B) 23.5% annual mortality.
Figure 20. Mean metapopulation sizes at year 100 for the BRP+2MX100, 3x250+Sonora, and the 3x250 scenarios.
Figure 21. Total number of population extinctions for the BRP+2MX100, 3x250+Sonora, and the 3x250 scenarios.
Figure 22. Mean census population sizes over time among extant iterations for the BRP + 2MX100 scenario: A) BRP with 22% adult mortality; B) BRP with 23.5% adult mortality; C) Sonora with 22% adult mortality; D) Sonora with 23.5% adult mortality; E) Durango with 22% adult mortality; and F) Durango with 23.5% adult mortality.
Figure 23. Mean expected heterozygosity over time for the BRP + 2MX100 scenario: A) BRP with 22% adult mortality; B) BRP with 23.5% adult mortality; C) Sonora with 22% adult mortality; D) Sonora with 23.5% adult mortality; E) Durango with 22% adult mortality; and F) Durango with 23.5% adult mortality.
Figure 24. Mean heterozygosity excesses for the BRP + 2MX100 scenario: A) BRP; B) Sonora; C) Durango.
Figure 25. Subpopulation extinction rates for the BRP + 2MX100 scenario: A) 22% adult mortality; and B) 23.5% adult mortality.