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

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

Report prepared by

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In consultation with

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Prepared for

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Revised Report
8 November 2017

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[1] As of October 2017, the organization was renamed the Conservation Planning Specialist Group

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Introduction

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

Presentation of the extensive model input datasets is organized by population. Specification of wild population input data focuses strongly on the U.S. population south of Interstate 40, which is designated the Mexican Wolf Experimental Population Area (MWEPA). This area has been the subject of targeted research and monitoring since 1998 by biologists from the U. S. Fish and Wildlife Service and cooperating state and tribal wildlife agencies. The separate population currently inhabiting northern portions of Mexico's Sierra Madre Occidental, hereafter referred to as Sierra Madre Occidental – North or simply SMOCC-N, was established much more recently in 2011; consequently, we have comparatively little detailed knowledge of its demographic dynamics. A second habitat patch in the southern Sierra Madre Occidental, hereafter referred to as SMOCC-S, is currently unoccupied. Any model of wolf population dynamics in this area must assume demographic rates based on those that define both MWEPA and SMOCC-N populations. Input data for the captive population, hereafter referred to as the SSP (Species Survival Plan) population, are derived from analysis of the Mexican Wolf International Studbook (as of 31 December 2015) compiled annually by P. Siminski. Where appropriate, captive population input data have been checked with the recently completed demographic analysis of this population (Mechak et al. 2016) through the assistance of Kathy Traylor-Holzer (CBSG).

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

The *Vortex* package is a flexible simulation of the effects of a number of different natural and human-mediated forces – some, by definition, acting unpredictably from year to year – on the health and integrity of wildlife populations. *Vortex* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or random variables that follow specified distributions. The package simulates a population by recreating the essential series of events that describe the typical life cycles of sexually reproducing organisms. *Vortex* is used around the world by government agencies and independent researchers as a tool to create scientifically robust conservation strategies for endangered species. While no software application can be guaranteed to be completely error-free, the wide use of *Vortex* means that it is tested to a much greater extent than similar types of models that are created for specific projects. Simulations using this tool have been shown to produce predicted population abundance trajectories that are consistent with monitored wildlife populations (Brook et al. 2000a) and that are concordant with other similar software platforms (Brook et al. 2000b). *Vortex* is distributed freely and can be obtained online at www.vortex10.org/vortex10.aspx.

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

Guidance for PVA Model Development

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

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

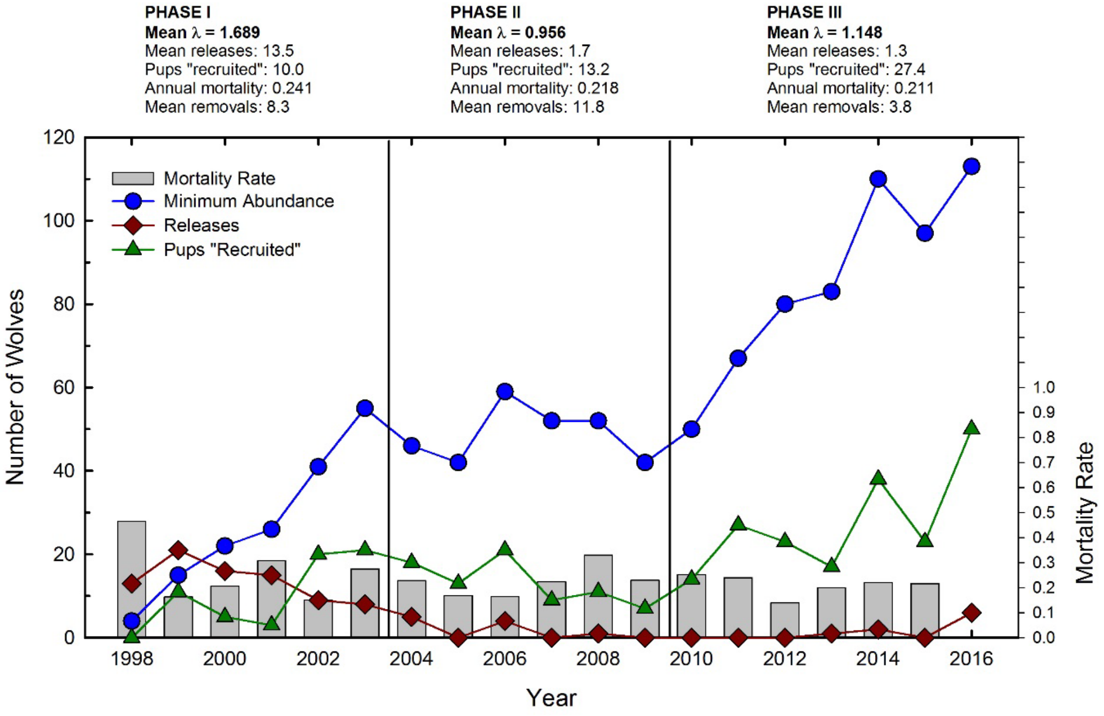

Figure 1. Population statistics for the MWEPA Mexican wolf population, 1998-2016. Data include minimum abundance, annual adult mortality rate, number of animals released from the SSP ex situ population, and the number of pups "recruited" (defined here as surviving to 31 December of their year of birth).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

Input Data for PVA Simulations: Wild Populations

Initial Population Specification

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

Reproductive Parameters

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

Age of first reproduction: Both females and males are capable of producing pups when they are two years of age.

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

Percentage of adult females "breeding" in a given year: For our specific model structure, this standard *Vortex* input parameter is more accurately defined as the percentage of adult females that pair with an adult male in a given year. This parameter is calculated through the complex function FPOOL derived by R. Fredrickson in the earlier 2013 PVA modeling effort. FPOOL determines which adult females pair within any one year, as a function of whether they were paired last year, the availability of breeding-age males in the population, and adult female age. We have retained this function for our current model.

The long-term annual mean expected proportion of paired adult females was set at 0.78. In other words, we expect approximately 78% of the wild adult females in a given year to be paired with an adult male. This value was informed by two sets of data analyzed by J. Oakleaf, USFWS: (1) direct observations of collared animals age 2+ that were paired, and (2) estimates of the number of females (1+ years old) in the entire population at time t-1 compared to the number of observed pairs at time t. Each of these two methods have inherent biases that serve to either underestimate or overestimate this parameter; consequently, the group decided to use the mean parameter value obtained by these two methods as model input. See Appendix A for more information on the process used to derive this parameter value.

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

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

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

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

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

Litters per year: A pack of wolves will produce one litter of pups per year.

Maximum number of pups per litter: For our modeling purposes, we are defining pup production at the mean time of first observation at or near the den. We recognize, therefore, that this does not account for *in utero* mortality or the unobserved death of pups before they are first seen after emergence from the den. With this as our definition, the largest litter documented from the MWEPA population prior to 2014 (the time period used to derive model input data) was 7 pups (note that a litter of 8 pups was documented in 2015 and 2017). Note that the specification of litter size for each successfully breeding female in a given year is determined by a complex function involving a number of independent variables (see "Distribution of litters per year" below).

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

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

Litter size = e^x, with

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

where

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

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

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

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

Density-dependent reproduction: There is no convincing evidence in the literature that links the number of pups born or their survival to population density. Moreover, because of the mechanics of wolf management expected to take place on the landscape (see below), it is considered highly unlikely to see wolf densities approach a level where this effect would be observed. Consequently, we have not implemented a density-dependent mechanism for reproduction in our model.

Mortality Parameters

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

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

Subadult (1-2) mortality: 32.7 ± 6.5%.

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

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

“Catastrophic” Event

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

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

Carrying Capacity

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

Population Management Target

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

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

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

Dynamic Diversionary Feeding

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

This dynamic diversionary feeding process was incorporated into all our population simulations. We assumed that the feeding rate will begin to decline five (MWEPA) or ten (SMOCC-N, SMOCC-S) years into the simulation, and will decline linearly to the minimum value by 20 (MWEPA) or 25 (SMOCC-N, SMOCC-S) years at a rate that is determined by the extent of growth toward that population's management target (i.e., populations closer to their target abundance at the beginning of the phase-out period will have their feeding rate reduced more rapidly). Authorities assume that the long-term feeding rate will not drop to zero but will likely be maintained at approximately 15% to allow for management of livestock depredations. That said, the impact of eliminating diversionary feeding across both U.S. and Mexico wolf populations was explored in additional scenarios (see the PVA addendum for results and discussion).

Metapopulation Dynamics

Our PVA model features a metapopulation structure in which wolves may naturally disperse from one population to another according to defined probabilities. We assume that only younger (1 to 4 years old), unpaired individuals are capable of dispersal, with males and females displaying equal tendencies to disperse. Furthermore, we assume a form of "stepping stone" model, where both the northernmost MWEPA population and the southernmost SMOCC-S populations are linked by dispersal to the central

SMOCC-N population. In this linear spatial configuration, we assume that there is no functional connectivity between MWEPA and SMOCC-S (See Martínez-Meyer 2017 for more information on the geography of these populations).

Rates of dispersal among candidate individuals are based loosely on wolf behavioral dynamics, the distances between populations and the nature of the intervening terrain. We assume that the distance from MWEPA to SMOCC-N, along with the presence of an international border subject to intense scrutiny, will severely limit the extent of demographic connectivity. In contrast, while the intervening terrain between the two Sierra Madre Occidental populations is more rugged than that across the international border, the closer proximity between these two Mexico habitat units likely increases the probability of successful dispersal among them. Therefore, in the absence of specific dispersal data for Mexican wolves across this recovery landscape, we set the individual dispersal probability between MWEPA and SMOCC-N at 0.175% and between Mexican SMOCC populations at 0.875%. These rates are symmetric between pairs of populations and are within the range of plausible values suggested by wolf population biologists participating in the current PVA effort. In addition, we assume that wolves pay a high cost to attempt cross-country dispersal. We use the estimate of 37.5% dispersal survival from the previous PVA effort based on the published analysis of Carroll et al. (2014). In terms of absolute numbers and with a candidate population of 100 unpaired wolves age 1-4, the MWEPA – SMOCC-N rate corresponds to approximately one wolf dispersing to the recipient population every 12 – 16 years. Note that the dispersal survival estimate does not include the probability of successful reproduction among dispersing animals. The impact of demographic isolation between the MWEPA and SMOCC-N populations through the removal of dispersal opportunities across the U.S. – Mexico border was also explored (see the PVA Addendum for results and discussion).

Input Data for PVA Simulations: SSP Population

Initial Population Specification

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

Reproductive Parameters

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

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

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

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

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

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

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

where

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

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

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

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

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

Litter size = e^x, with

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

where

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

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

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

Mortality Parameters

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

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

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

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

Carrying Capacity

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

Simulating the SSP Masterplanning Process

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

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

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

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

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

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

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

First, we included the actual release of wolves from the SSP to SMOCC-N that took place in 2016. Given that our simulations were initialized as of 1 January 2016, we wanted to include these releases to Mexico in order to more accurately portray the early dynamics of this population following the substantial demographic and genetic augmentation received from the SSP. While a total of 18 wolves were released in two separate events during the second half of the year, it is estimated that only 12 of those animals survived to the next breeding season: nine pups (seven females, two males) and three subadults (all male). This release takes place in all simulations in model year 1 (calendar year 2016).

Second, the 2014 Mexican Wolf EIS states that releases from the SSP to MWEPA will be conducted according to the following generic schedule:

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

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

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

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

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

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

MWEPA to SMOCC-N of four pairs with pups every other year in model years 2-10; no translocations from MWEPA to SMOCC-S.

- "EIS22_22": EIS releases into MWEPA; releases of two pairs with pups into SMOCC-N every year for five years (in addition to 2016 releases); releases of two pairs with pups into SMOCC-S every year for five years; translocations from MWEPA to SMOCC-N (two pairs with pups every other year in model years 2-10); translocations from MWEPA to SMOCC-S (two pairs with pups every other year in model years 7-15).

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

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

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

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

The numbers in Table 2 actually refer to the number of wolves that are removed from the source population (either SSP or MWEPA) – not the final number of animals that survive after release. Detailed analysis of release data from MWEPA by J. Oakleaf indicate that a substantial fraction of those wolves released from the SSP die within the first year following release from captivity or after translocation from another wild population. The results of this analysis are presented in Table 3. Translocation data include those events that involve an intermediate stop in a captive facility as described in the previous paragraph. These survival rates (mean only) were incorporated directly into the *Vortex* supplementation module, thereby specifying an "effective" number of released or translocated individuals that are assumed to survive to the next breeding season. For example, if we were to release two pairs with pups from the SSP to MWEPA, we would harvest four adults from the SSP but would only successfully release (4)*(0.284) = 1.14 adults into the MWEPA population. Similarly, if we were to translocate two pairs with pups from the MWEPA population to Mexico, we would harvest four adults from the MWEPA but only successfully translocate (4)*(0.527) = 2.11 adults. Those individuals that do not "survive" would be permanently removed from the simulation. In using this mechanic, we assume that all mortality takes place relatively quickly after the transfer event – thereby preventing those animals from reproducing before they die. This is consistent with recent observations of wolf transfers into and among wild populations. For more information on how these post-transfer mortalities were derived, refer to Appendix D.

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

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

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

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

PVA Simulation Structure

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

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

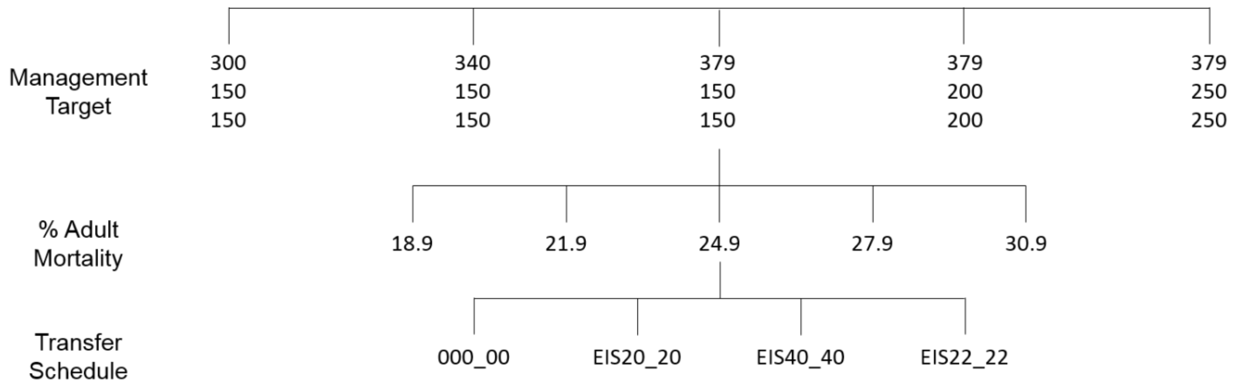

Figure 2. Diagrammatic sketch of Mexican wolf PVA scenario structure. The three values for population management target are listed as MWEPA (top), SMOCC-N (middle) and SMOCC-S (bottom). Adult mortality rates are listed as annual mean rates, and the transfer schedule nomenclature is defined in Table 2.

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

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

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

Results of Simulation Modeling

Confirmation of Selected Model Performance Elements

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

- Mean annual proportion of adult females paired: 0.77. This is consistent with expectations defined through the specification of the FPOOL pairing function. This value is also in accord with field observations of the number of packs observed in the MWEPA population.
- Mean annual proportion of paired females producing a litter: 0.72 (simulation beginning) to 0.64 (simulation end). These values are consistent with the values predicted from the relationship discussed in Appendix B (Figure B-2) across all adult ages and as inbreeding levels increase broadly from about 0.2 at the beginning of any given simulation to about 0.3 in the absence of significant genetic input from the SSP population.
- Mean annual proportion of adult females producing a litter: (0.77)*(0.68) = 0.52. This is consistent with the previous analysis of Carroll et al. (2014) where they assumed an annual overall breeding rate of 0.5.
- Mean litter size across reproducing females: 3.5 (early) to 2.95 (late). This is consistent with expectations defined through the specification of mean litter size in Appendix C (Figure C-1). Given that mean litter size among middle-aged females is predicted to be approximately five pups and the extent of diversionary feeding present at the start of the simulations is 0.7, we would expect approximately 3.5 pups per litter in the early years. Similarly, in the later stages of the simulation when the extent of diversionary feeding declines to about 0.15, a mean litter size of approximately three pups fits with the litter size predicted in the absence of diversionary feeding.

Based on this information, we believe our prospective models can be viewed as internally consistent and generating demographic dynamics that agree with baseline expectations of Mexican wolf reproductive characteristics.

Analysis of the Status Quo

Before evaluating the full set of prospective analyses making up this PVA, a preliminary scenario was designed where the population-specific management targets for MWEPA and SMOCC-N were set to a small increase above the 31 December 2015 abundances. This is meant to explore the viability of these two populations at approximately their current abundance. The management target for MWEPA was set at 135 wolves, while that for SMOCC-N was set at 40 wolves. Future adult mortality rates were set at either 18.9% (optimistic) or 24.9% (pessimistic). Neither population receives releases or translocations beyond the 2016 release to SMOCC-N from the SSP.

Under these conditions, the MWEPA population has a probability of persisting for the next 100 years of 0.97 (optimistic) to 0.46, while the analogous probabilities for SMOCC-N are just 0.04 to 0.0. Even if the MWEPA population persists for this period of time, the mean expected population size is likely to decline to between 40 and 100 animals, depending on the underlying adult mortality. Gene diversity for the

MWEPA population declines to less than 77% of the final value for the SSP. The accumulation of inbreeding and a reduction in the extent of diversionary feeding, with the resultant decrease in pup production, is the likely cause of this steady decline that begins about 20 years into the simulation.

Demographic Sensitivity Analysis

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

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

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

MWEPA population: Under the condition of no additional transfers, extinction risks for the simulated MWEPA populations remain below 10% as long as the mean adult mortality rate is below 24.9% (Figure 3). Above this rate, extinction probabilities increase more rapidly to above 0.8 when the management target is 300 wolves. At the lower mortality rates (< 25%), extinction risk is negligible and there is very little influence of management target on the extinction risk. While the risk of extinction is low at intermediate mortality rates, the long-term abundance typically reaches a maximum of 80 to 90% of the management target approximately 40 years into the simulation and then begins to decline thereafter. The decline is likely due to a combination of higher adult mortality in the face of reduced litter production as inbreeding increases and reduced litter size as the extent of diversionary feeding drops from 70% of reproducing females to 15% over the first 15 – 25 years of the simulation.

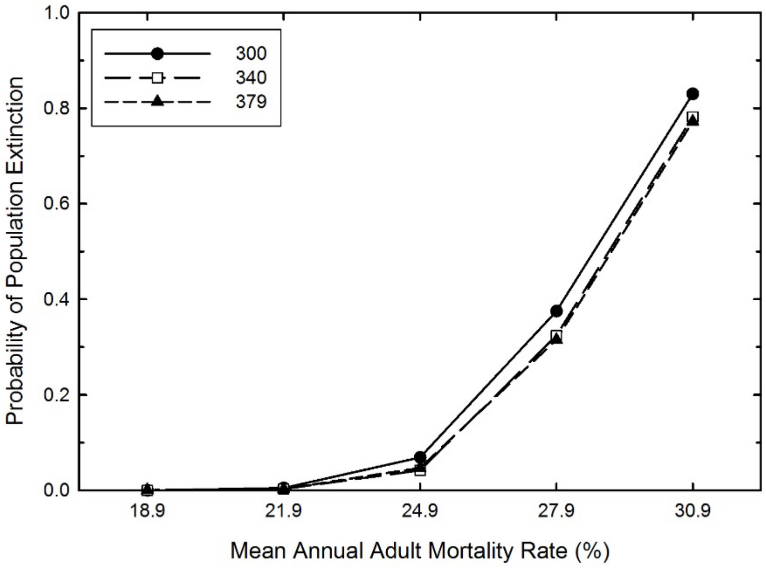

Figure 3. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “000_00”.

At low to intermediate adult mortality rates, simulated MWEPA populations retain approximately 88% to 93% of the initial gene diversity present in that population at the beginning of the simulation (Table 4). As expected, larger management targets result in larger GD retention, although the gains are modest. Despite reasonable GD retention relative to the initial starting conditions, the final GD value for MWEPA is just 83% to 88% that of the SSP population at the end of the simulation. This reduced relative retention reflects the greater capacity for genetic diversity maintenance in the SSP through more intensive breeding management, as well as the improved genetic starting conditions for the SSP relative to MWEPA.

Table 4. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the MWEPA population of Mexican wolves, under the range of tested annual adult mortality rates and population management targets and with the "000_00" wolf transfer scheme. The first value in each cell gives the final gene diversity value for that simulation at year 100. The first value in parentheses gives the proportional GD retention at year 100 relative to the starting value for MWEPA for all simulations (GD = 0.741), while the second value in parentheses gives the proportional GD retention at year 100 relative to the ending value for the SSP population (GD = 0.785). GD values for the target of 379 represent the average across the three SMOCC-N management targets. The last row of the table gives the GD and extent of retention for the SSP population as a reference.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.677 (0.914; 0.862)	0.668 (0.901; 0.851)	0.648 (0.874; 0.825)	0.614 (0.829; 0.782)	0.565 (0.762; 0.720)
340	0.683 (0.922; 0.870)	0.675 (0.911; 0.860)	0.657 (0.887; 0.837)	0.621 (0.838; 0.791)	0.582 (0.785; 0.741)
379	0.688 (0.928; 0.876)	0.681 (0.919; 0.868)	0.665 (0.897; 0.847)	0.633 (0.854; 0.806)	0.588 (0.793; 0.749)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

SMOCC-N population: The SMOCC-N population demonstrates a low risk of extinction at the lowest adult mortality rate, but the risk begins to increase at higher mortality rates (Figure 4). The rate of increase in extinction probability is greater when the management target is set to its lowest level (150 wolves), rising to approximately 0.4 at the intermediate mortality rate of 24.9%. This is a result of the higher rates of inbreeding and associated genetic impacts acting on this smaller population, as well as the negative impacts of occasional stochastic events reducing survival and/or reproduction from one year to the next. Note that the extinction probability is not markedly impacted by the size of the MWEPA management target. This is because the level of demographic connectivity between these two populations is very small, meaning that the SMOCC-N population is effectively isolated under the conditions described in this set of scenarios. Separate analysis of PVA model output not reported in detail here indicates that the level of dispersal featured in the model results in an annual rate of immigration from MWEPA into SMOCC-N of just 0.05 – 0.1 wolves.

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

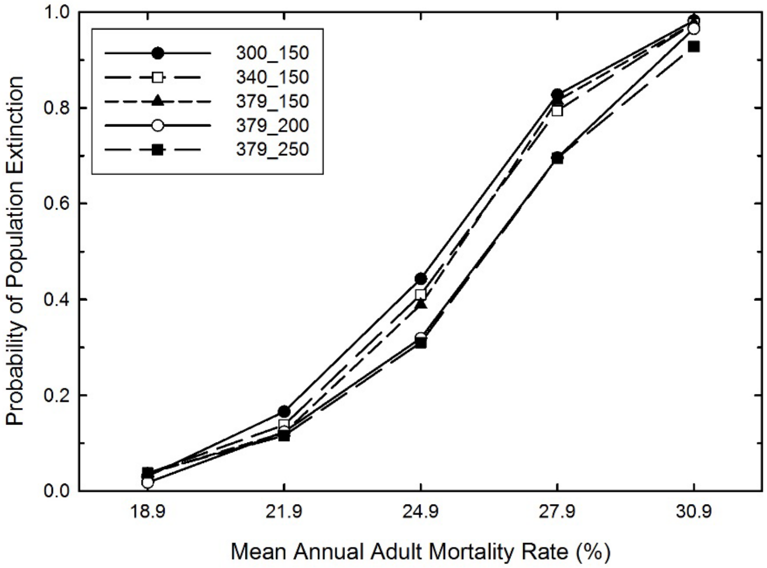

Figure 4. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "000_00". The first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

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.648 (0.938; 0.826)	0.631 (0.913; 0.804)	0.603 (0.873; 0.768)	0.558 (0.808; 0.711)	0.484 (0.700; 0.617)
340_150	0.650 (0.941; 0.828)	0.634 (0.918; 0.808)	0.602 (0.871; 0.767)	0.564 (0.816; 0.718)	0.534 (0.773; 0.680)
379_150	0.652 (0.944; 0.831)	0.633 (0.916; 0.806)	0.607 (0.878; 0.773)	0.570 (0.825; 0.726)	0.535 (0.774; 0.682)
379_200	0.671 (0.971; 0.855)	0.660 (0.955; 0.841)	0.630 (0.918; 0.803)	0.595 (0.861; 0.758)	0.563 (0.815; 0.717)
379_250	0.684 (0.990; 0.871)	0.669 (0.968; 0.852)	0.647 (0.936; 0.824)	0.623 (0.902; 0.794)	0.572 (0.828; 0.729)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

SMOCC-S population: The initially vacant SMOCC-S population unit can potentially be colonized with wolves via occasional successful dispersal of wolves from the SMOCC-N population to the north, although the conditions for establishment are very restricted. When the management target is just 150 wolves for both Sierra Madre populations, the probability of establishing a population in SMOCC-S is quite low at all mean adult mortality rates, and regardless of the MWEPA management target (Figure 5). This is expected since the MWEPA population is again effectively isolated from its counterparts in Mexico, so establishing a population in SMOCC-S is solely dependent on successful dispersal from SMOCC-N followed by successful reproduction once they have arrived. Interestingly, the probability of failing to establish a SMOCC-S population drops to just 0.4 when the SMOCC management targets are each expanded to 250 wolves and under the most optimistic adult mortality rate. Under the intermediate mortality rate, that probability of failure increases to more than 0.8. If a population were to become established there under conditions of low to intermediate adult mortality, the mean expected wolf abundance estimate ranges from 4 to 49 wolves for management targets of 150 to 250.

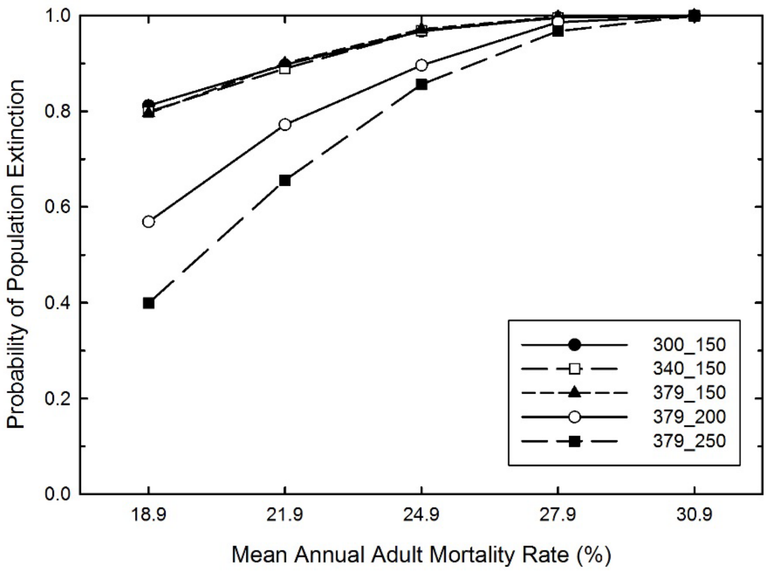

Figure 5. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “000_00”. The first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

The extent of gene diversity retained in the SMOCC-S population, as a proportion of that which is present in the SSP population, ranges from approximately 61% to 73% depending on the size of the SMOCC-S management target and the underlying mean adult mortality rate (Table 6). Actual GD values among extant populations are quite low, on the order of just 0.48 to 0.58. This is due to the small size of any wolf population that may persist in the SMOCC-S population unit for any extended period of time, with the resulting rapid loss of genetic variants through random genetic drift and inbreeding.

Table 6. Mean gene diversity (GD, or expected heterozygosity) at the end of the 100-year simulations for the SMOCC-S population of Mexican wolves, under the range of tested annual adult mortality rates and with the "000_00" wolf transfer scheme. The first value in each cell gives the final gene diversity value for that simulation at year 100. The value in parentheses gives the proportional GD retention in SMOCC-S at year 100 relative to the ending value for the SSP population (GD = 0.785). Empty cells represent scenarios where extinction probability is 1.0. The last row of the table gives the GD and extent of retention for the SSP population as a reference.

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.511 (0.651)	0.503 (0.641)	0.482 (0.614)	0.481 (0.613)	
340_150	0.516 (0.657)	0.510 (0.650)	0.487 (0.620)	0.474 (0.604)	
379_150	0.521 (0.664)	0.498 (0.634)	0.499 (0.636)	0.497 (0.633)	
379_200	0.548 (0.698)	0.526 (0.670)	0.505 (0.643)	0.488 (0.626)	0.493 (0.628)
379_250	0.574 (0.731)	0.546 (0.696)	0.531 (0.676)	0.518 (0.660)	0.477 (0.608)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

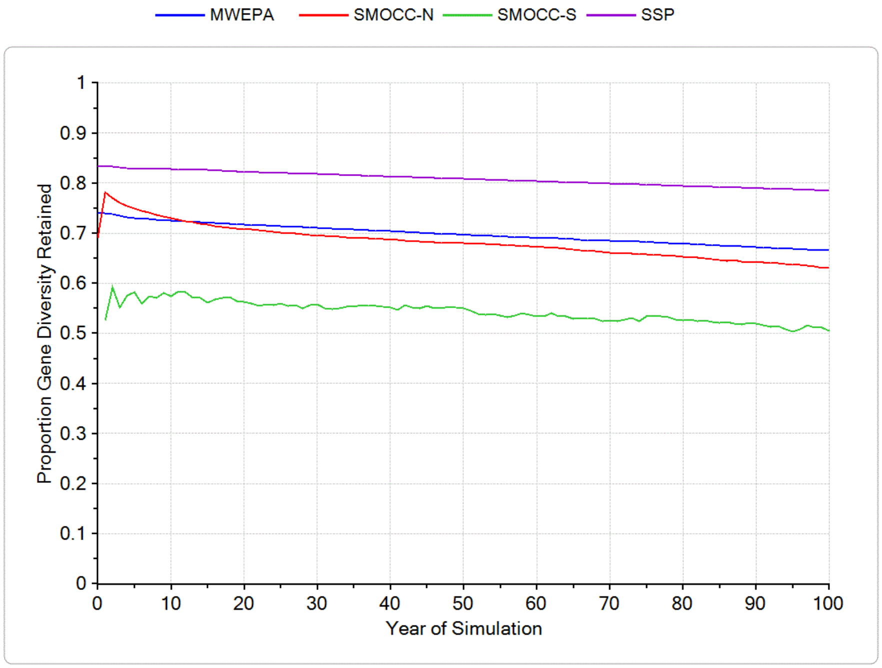

Figure 6. Average gene diversity over time for Mexican wolf populations subject to 24.9% mean annual adult mortality and under the “000_00” transfer scheme. Management targets are set at 379 for MWEPA and 200 for SMOCC-N and SMOCC-S.

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

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

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

EIS20_20 – MWEPA population: Under the EIS_20_20 strategy, the extinction risk for MWEPA remains low over the low and intermediate adult mortality rates, and again increases rapidly at higher mortality rates (Figure 7). Comparison with the “000_00” strategy featuring no releases or translocation reveals that the risk of extinction in MWEPA increases slightly with the inclusion of translocations out of MWEPA to SMOCC-N. For example, at the intermediate mortality rate of 24.9%, the risk of extinction (averaged across management targets) increases from 0.053 to 0.061. This is indeed a rather minor increase, but it highlights the additional demographic burden that a source population may incur when animals are moved out for translocation. It is important to recognize that the input of wolves to MWEPA through the release strategy does not balance the removal of wolves for translocation to SMOCC-N. The “EIS20_20” means that ten pairs with pups will be removed from MWEPA over five years, and is slated to receive seven pairs with pups from the SSP over about 16 years. However, the high rate of post-release mortality included in the models means that just less than two pairs (7*0.284) are expected to survive to the next breeding cycle. This rather large net loss of wolves over the early years of the simulation is likely the cause of any increased extinction risk. In particular iterations, stochastic processes in early years may lead to significant reductions in MWEPA population size that are exacerbated by removals for translocation. This could begin a cycle of continued demographic and genetic instability that, infrequently, could lead to the extinction of that population.

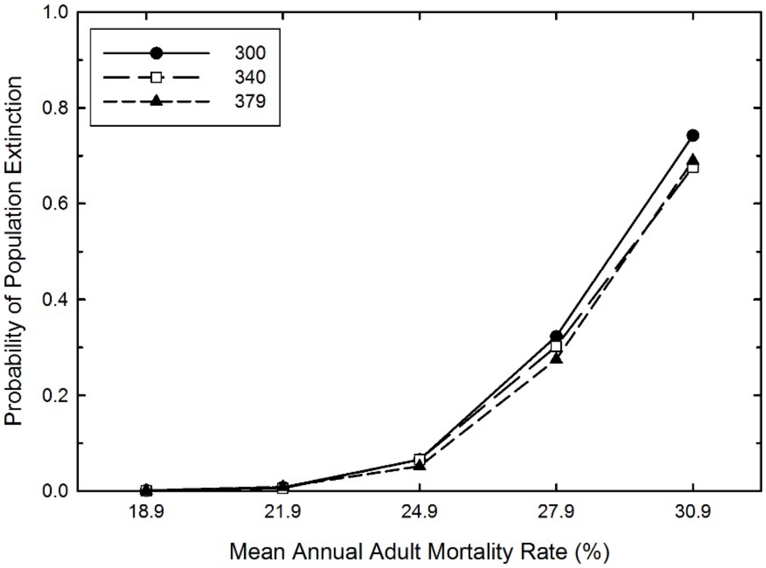

Figure 7. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS20_20”.

Among extant populations, the mean population abundance reaches a maximum at approximately 80% of the management target (240 to 310 at management targets of 300 to 379) at the intermediate adult mortality rate (24.9%), but then begins to decline slowly as pup production declines, likely due to inbreeding and reduced diversionary feeding. Lower mortality rates lead to more stable populations at 85% to 95% of the management target.

Gene diversity in the MWEPA population increases slightly in this set of scenarios compared to the “000_00” transfer strategy as some new genetic variation is added through the EIS releases strategy. Retention of GD in MWEPA is 90% to 95% of the initial value for that population over the low to intermediate mortality rates tested, and across the three proposed management targets (Table 7). However, the population retains only about 85% to 89% of the gene diversity present in the SSP. Higher mortality rates result in only 81% to 89% retention relative to MWEPA original values, and 77% to 84% GD retention relative to the SSP.

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.691 (0.933; 0.880)	0.685 (0.924; 0.873)	0.670 (0.904; 0.853)	0.645 (0.870; 0.822)	0.603 (0.814; 0.768)
340	0.697 (0.941; 0.888)	0.690 (0.931; 0.879)	0.678 (0.914; 0.864)	0.652 (0.880; 0.831)	0.610 (0.823; 0.777)
379	0.702 (0.947; 0.894)	0.697 (0.941; 0.888)	0.684 (0.923; 0.871)	0.659 (0.889; 0.839)	0.623 (0.841; 0.794)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

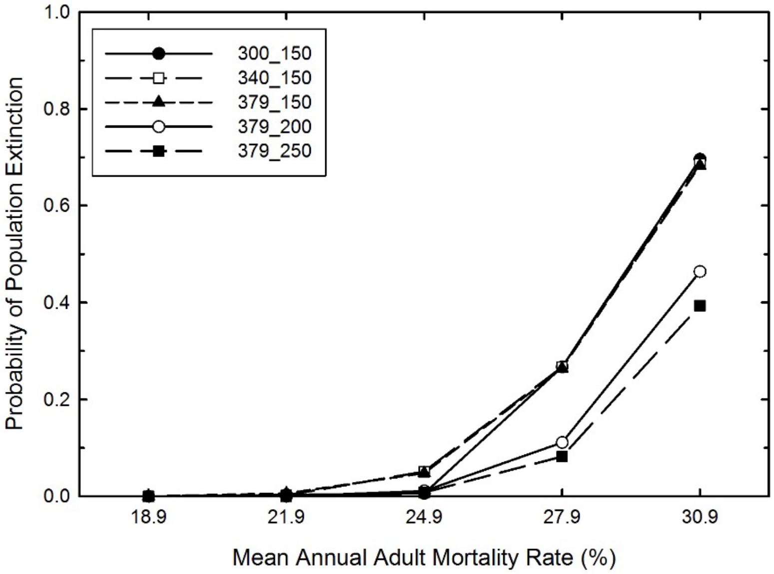

Figure 8. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS20_20". The first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

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

The "EIS20_20" transfer schedule also leads to significant increases in gene diversity in the SMOCC-N population (Table 8). Once again, the impact of the 2016 releases to SMOCC-N is dramatic; the final GD value is 95% to 106% relative to the initial value before the releases at low to intermediate mortality rates. The retention relative to the SSP under these same mortality rates is 84% to 93%. When the SMOCC-N management target increases to 200-250, GD retention approaches and exceeds 90% relative to the SSP.

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.689 (0.997; 0.878)	0.679 (0.983; 0.865)	0.658 (0.952; 0.838)	0.622 (0.900; 0.792)	0.582 (0.842; 0.741)
340_150	0.690 (0.999; 0.879)	0.680 (0.984; 0.866)	0.662 (0.958; 0.843)	0.624 (0.903; 0.795)	0.576 (0.836; 0.734)
379_150	0.691 (1.000; 0.880)	0.682 (0.987; 0.869)	0.663 (0.959; 0.845)	0.627 (0.907; 0.799)	0.577 (0.835; 0.735)
379_200	0.716 (1.036; 0.912)	0.710 (1.027; 0.904)	0.696 (1.007; 0.887)	0.666 (0.964; 0.848)	0.619 (0.896; 0.789)
379_250	0.732 (1.059; 0.932)	0.726 (1.051; 0.925)	0.715 (1.035; 0.911)	0.693 (1.003; 0.883)	0.653 (0.945; 0.832)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS20_20 – SMOCC-S population: The increased demographic stability of the SMOCC-N population under the "EIS20_20" release strategy leads to an increased opportunity for population establishment in SMOCC-S, even when transfers to this habitat area are not explicitly included as simulated in this set of scenarios. When the management target is 200 or 250, the probability of failing to establish a population in SMOCC-S ranges from 17% to 75% at low to intermediate adult mortality rates (Figure 9). The probability of establishing a population remains low at a management target of 150. If a population were to become established in SMOCC-S, the abundance at year 100 would range from about 12 to 22 wolves at intermediate mortality rates and at a management target of 200 or 250.

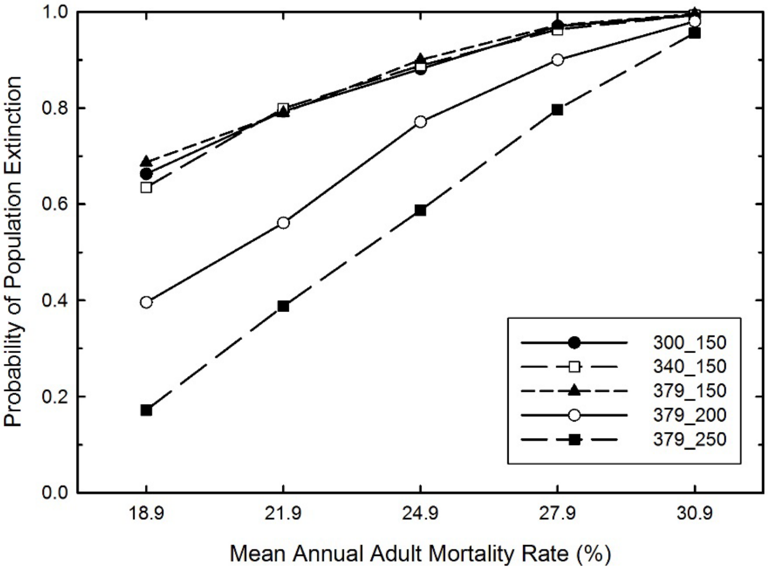

Figure 9. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS20_20". The first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

Despite some tenuous level of demographic stability that may be observed in an established SMOCC-S population under the conditions or our simulations, the extent of gene diversity retention in the population remains low (Table 9). Under the smallest management target of 150 wolves and at low to intermediate adult mortality rates, the extent of GD retained relative to the final value for the SSP ranges from 67% to 72%. Increasing the management target to 200 or 250 increases final GD retention in SMOCC-S to 70% to 80% of the final SSP value.

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.557 (0.710)	0.528 (0.673)	0.523 (0.666)	0.490 (0.624)	0.479 (0.610)
340_150	0.558 (0.711)	0.538 (0.685)	0.521 (0.664)	0.499 (0.636)	0.508 (0.647)
379_150	0.567 (0.722)	0.533 (0.679)	0.517 (0.659)	0.504 (0.642)	0.488 (0.622)
379_200	0.595 (0.758)	0.573 (0.730)	0.550 (0.701)	0.523 (0.666)	0.520 (0.662)
379_250	0.629 (0.801)	0.604 (0.769)	0.577 (0.735)	0.556 (0.708)	0.549 (0.699)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

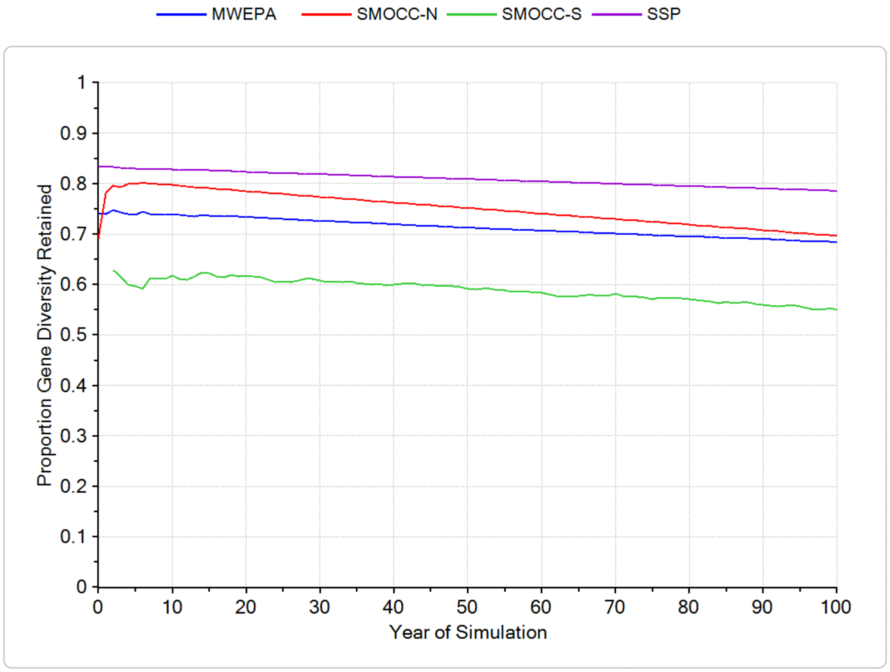

Figure 10. Average gene diversity over time for Mexican wolf populations subject to 24.9% mean annual adult mortality and under the "EIS20_20" transfer scheme. Management targets are set at 379 for MWEPA and 200 for SMOCC-N and SMOCC-S.

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

EIS40_40 – MWEPA population: Despite the infusion of SSP wolves into the population through the EIS release strategy, the removal of 20 pairs of wolves with pups in the first ten years of the simulation leads to a further reduction in viability of the MWEPA population (Figure 11). Extinction risk is low (<0.10) only at the lowest adult mortality level (18.9%) and increases to about 0.30 at the intermediate mortality rate of 24.9%. As before, the risk of MWEPA population extinction is not impacted by the size of the management target, suggesting that the removals for translocation in the early years of the simulation can set in motion a process of demographic and genetic destabilization that can lead to extinction in later years.

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

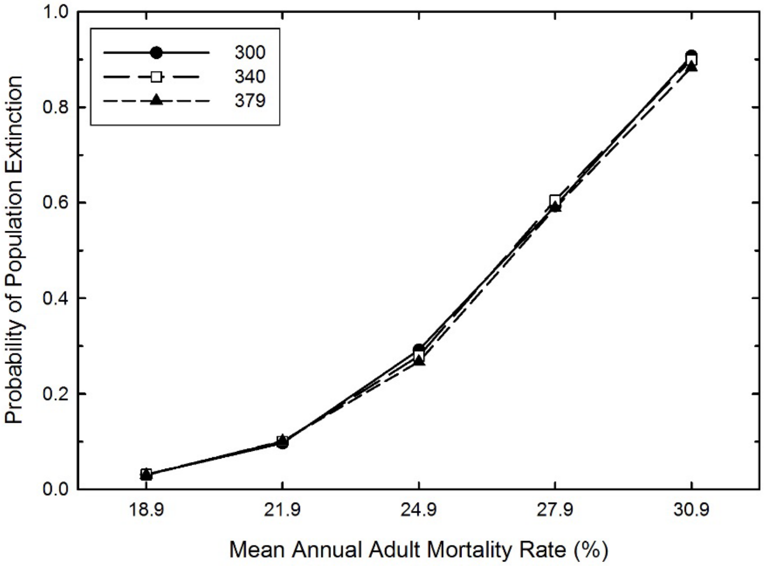

Figure 11. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS40_40”.

Gene diversity in the MWEPA population does not improve relative to the less intense release strategy previously described. Retention of GD in MWEPA is 89% to 94% of the initial value for that population over the low to intermediate mortality rates tested, and across the three proposed management targets (Table 10). However, the population retains only about 84% to 89% of the gene diversity present in the SSP. Higher mortality rates result in only 81% to 88% retention relative to MWEPA original values, and 77% to 83% GD retention relative to the SSP.

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.687 (0.927; 0.875)	0.677 (0.914; 0.862)	0.662 (0.893; 0.843)	0.637 (0.860; 0.811)	0.603 (0.814; 0.768)
340	0.694 (0.937; 0.884)	0.685 (0.924; 0.873)	0.668 (0.901; 0.851)	0.642 (0.866; 0.818)	0.609 (0.822; 0.776)
379	0.698 (0.942; 0.889)	0.690 (0.931; 0.879)	0.675 (0.911; 0.860)	0.648 (0.875; 0.825)	0.618 (0.834; 0.787)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

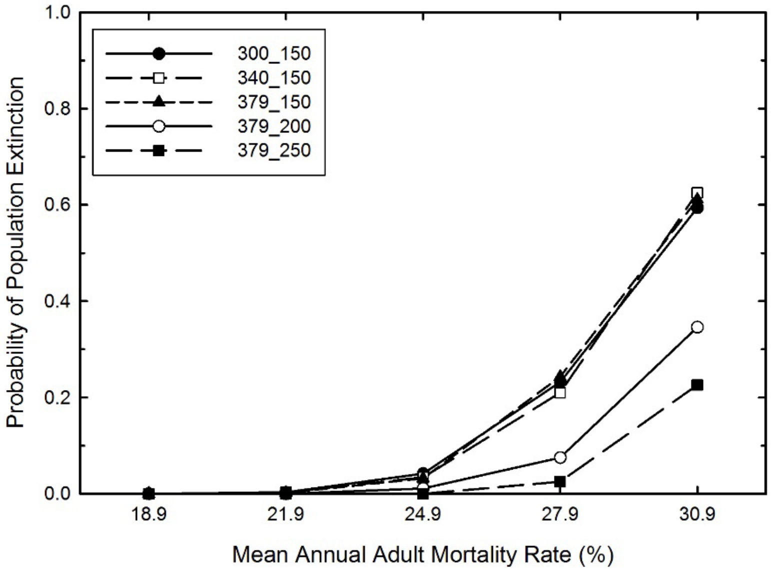

Figure 12. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS40_40". The first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

At low to intermediate adult mortality rates, final gene diversity retention ranges from 96% to 107% relative to the initial value for SMOCC-N, and from 85% to 94% relative to the final SSP value (Table 11). When the management target is at least 200 wolves, final GD relative to the final SSP value is very near or above 90% for all low and intermediate adult mortality levels. The maximum GD retention relative to the final SSP value that is observed under the smallest SMOCC-N management target (150) is 89%, at the lowest adult mortality rate tested (18.9%).

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.687 (0.994; 0.875)	0.684 (0.990; 0.871)	0.664 (0.961; 0.846)	0.629 (0.910; 0.801)	0.587 (0.849; 0.748)
340_150	0.695 (1.006; 0.885)	0.686 (0.993; 0.874)	0.664 (0.961; 0.846)	0.631 (0.913; 0.804)	0.583 (0.844; 0.743)
379_150	0.696 (1.007; 0.887)	0.687 (0.994; 0.875)	0.666 (0.964; 0.848)	0.633 (0.916; 0.806)	0.586 (0.848; 0.746)
379_200	0.724 (1.048; 0.922)	0.717 (1.038; 0.913)	0.705 (1.020; 0.898)	0.681 (0.986; 0.868)	0.640 (0.926; 0.815)
379_250	0.740 (1.071; 0.943)	0.735 (1.064; 0.936)	0.726 (1.051; 0.925)	0.706 (1.022; 0.899)	0.671 (0.971; 0.855)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS40_40 – SMOCC-S population: The extinction/establishment dynamics for the SMOCC-S population are for the most part unchanged from the results of the "EIS20_20" models, with the exception of slightly reduced extinction risks at the larger population management targets of 200 and 250 (Figure 13). With a population management target of 250, low adult mortality rates (18.9% - 21.9%) result in extinction risk (failure to establish a population) of 0.181 to 0.336. At the intermediate adult mortality rate of 24.9%, this risk increases to 0.545 – 0.734 at a management target of 250 to 200, respectively. If a population becomes established here, the population abundance at the end of the simulation ranges from 65 wolves at a management target of 31 to 128 wolves at intermediate to low adult mortality rates, respectively and at a management target of 250.

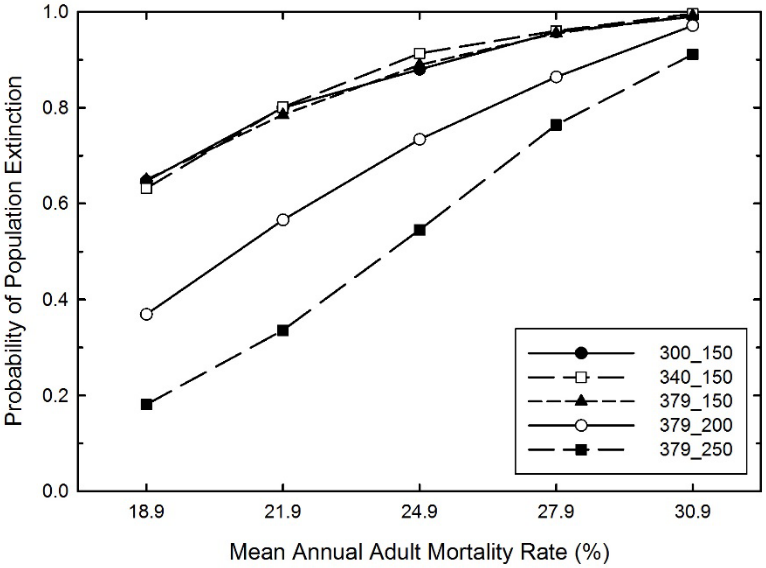

Figure 13. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS40_40". The first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

Increasing the extent of transfers to the SMOCC-N population in the "EIS40_40" strategy brings only modest improvements to gene diversity retention in the SMOCC-S population (Table 12). Under the smallest management target of 150 wolves and at low to intermediate adult mortality rates, the extent of GD retained relative to the final value for the SSP ranges from 67% to 73%. Increasing the management target to 200 or 250 increases final GD retention in SMOCC-S to 72% to 82% of the final SSP value.

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.568 (0.724)	0.548 (0.698)	0.527 (0.671)	0.507 (0.646)	0.477 (0.608)
340_150	0.568 (0.724)	0.549 (0.699)	0.523 (0.666)	0.508 (0.647)	0.459 (0.585)
379_150	0.571 (0.727)	0.547 (0.697)	0.524 (0.668)	0.513 (0.654)	0.493 (0.628)
379_200	0.608 (0.775)	0.590 (0.752)	0.564 (0.718)	0.542 (0.690)	0.514 (0.655)
379_250	0.641 (0.817)	0.620 (0.790)	0.594 (0.757)	0.563 (0.717)	0.544 (0.693)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

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

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

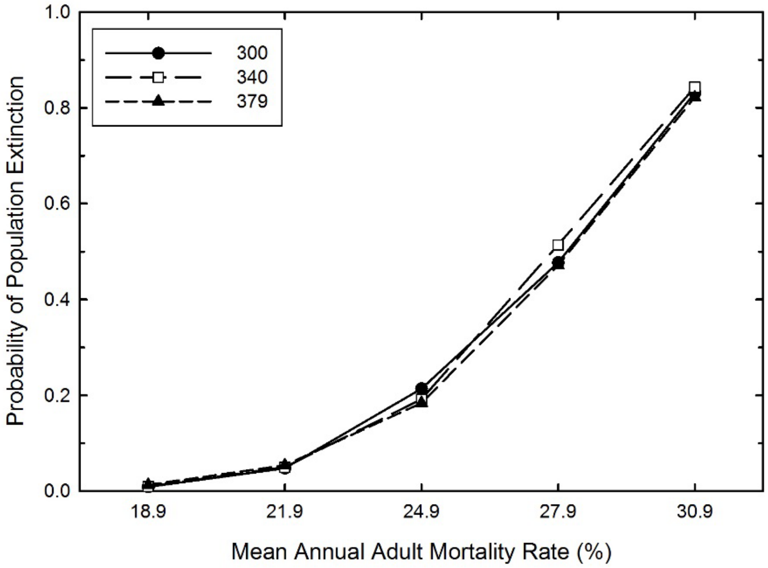

Figure 14. Extinction probabilities (proportion of simulations that become extinct) for the MWEPA population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS22_22”.

Gene diversity retention in the MWEPA population closely follows that for the “EIS40_40” transfer strategy. Retention of GD in MWEPA is 90% to 95% of the initial value for that population over the low to intermediate mortality rates tested, and across the three proposed management targets (Table 13). However, the population retains only about 85% to 89% of the gene diversity present in the SSP. Higher mortality rates result in only 81% to 89% retention relative to MWEPA original values, and 77% to 84% GD retention relative to the SSP.

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300	0.689 (0.930; 0.878)	0.681 (0.919; 0.868)	0.665 (0.897; 0.847)	0.643 (0.868; 0.819)	0.602 (0.812; 0.767)
340	0.695 (0.938; 0.885)	0.689 (0.930; 0.878)	0.673 (0.908; 0.857)	0.652 (0.880; 0.831)	0.624 (0.842; 0.795)
379	0.701 (0.946; 0.893)	0.694 (0.937; 0.884)	0.683 (0.922; 0.870)	0.657 (0.887; 0.837)	0.621 (0.838; 0.791)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

EIS22_22 – SMOCC-N population: When the SMOCC-S population is targeted for releases and translocations, the SMOCC-N population appears to show a slightly lower risk of population extinction compared to the "EIS40_40" strategy described earlier (Figure 15). For example, with a SMOCC-N management target of 200 and with the largest MWEPA management target of 379, the risk of extinction to the SMOCC-N population under the "EIS22_22" population declines to 0.005 compared to 0.011 in the "EIS40_40" strategy. While this specific difference may result from stochastic variation across the set of iterations that make up this analysis, this qualitative difference is consistent across the majority of scenarios that were tested across these two transfer strategies. The slight improvement in demographic stability of the SMOCC-N population may result from occasional dispersal events of wolves from SMOCC-S into SMOCC-N throughout the duration of the simulation, acting to bolster SMOCC-N populations through time. Extant populations reach a long-term abundance of approximately 140 to 220 wolves with a population management target of 150 to 250, respectively. Under the 250 management target, the populations is able to maintain at that level but smaller management targets tend to lead to slow rates of decline in abundance to 160 or 100 wolves for management targets of 200 and 150, respectively. As discussed previously, factors playing a role in reducing reproductive output in these populations over time can lead to gradual erosion of demographic and genetic viability.

Retention of gene diversity in the SMOCC-N population under the "EIS22_22" transfer strategy follows the results of the "EIS40_40" analyses, with perhaps a slightly higher level of GD retention in these scenarios in the presence of occasional connectivity with SMOCC-S as it becomes established. At low to intermediate adult mortality rates, final gene diversity retention ranges from 99% to 108% relative to the initial value for SMOCC-N, and from 87% to 95% relative to the final SSP value (Table 14). When the management target is at least 200 wolves, final GD relative to the final SSP value is at or above 90% for all low and intermediate adult mortality levels. The maximum GD retention relative to the final SSP value that is observed under the smallest SMOCC-N management target (150) is 90%, at the lowest adult mortality rate tested (18.9%).

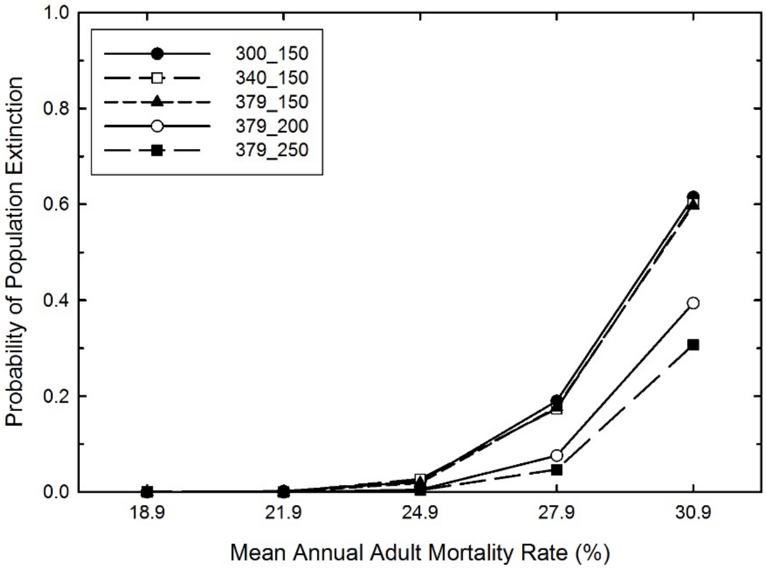

Figure 15. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-N population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme "EIS22_22". The first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

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.706 (1.022; 0.899)	0.699 (1.012; 0.890)	0.681 (0.986; 0.868)	0.648 (0.938; 0.825)	0.596 (0.863; 0.759)
340_150	0.707 (1.023; 0.901)	0.700 (1.013; 0.892)	0.681 (0.986; 0.868)	0.646 (0.935; 0.823)	0.597 (0.864; 0.761)
379_150	0.707 (1.023; 0.901)	0.700 (1.013; 0.892)	0.683 (0.988; 0.870)	0.645 (0.933; 0.822)	0.594 (0.860; 0.761)
379_200	0.729 (1.055; 0.929)	0.725 (1.049; 0.924)	0.713 (1.032; 0.908)	0.687 (0.994; 0.875)	0.639 (0.925; 0.814)
379_250	0.743 (1.075; 0.946)	0.739 (1.069; 0.941)	0.730 (1.056; 0.930)	0.708 (1.025; 0.902)	0.666 (0.964; 0.848)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

Extending transfers to the SMOCC-S population in the “EIS22_22” strategy brings significant improvements to gene diversity retention (Table 15). While the extent of GD retained relative to the final value for the SSP ranged from 67% to 82% across the three population management targets under conditions of low to intermediate adult mortality rates in the absence of direct releases and translocations (Table 12), GD retention under the “EIS22_22” strategy in the SMOCC-S population increases across that same set of scenarios to a range of 85% to 93% (Table 15). Even under the highest rates of annual adult mortality tested here, GD retention relative to the final SSP value remained above 82% when the population management target was set at 250.

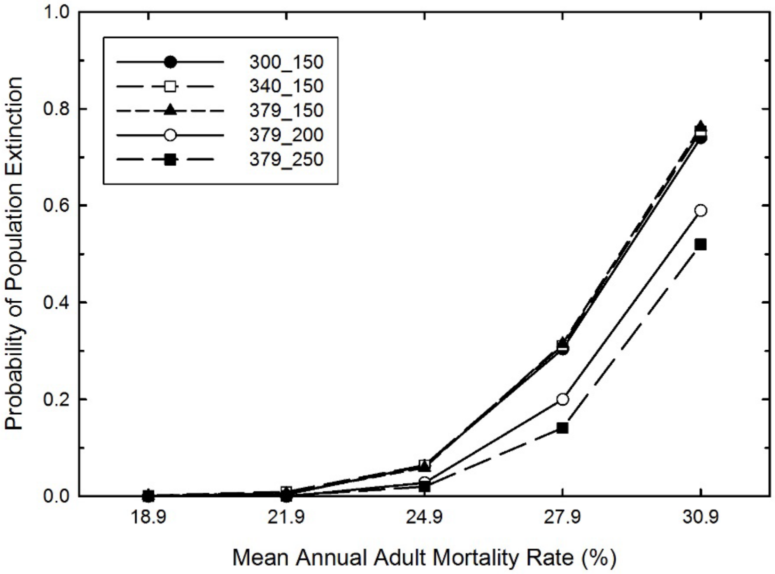

Figure 16. Extinction probabilities (proportion of simulations that become extinct) for the SMOCC-S population of Mexican wolves at the end of 100-year projections as a function of mean annual adult mortality rate and for different population management targets under transfer scheme “EIS22_22”. The first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

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

Management Target	Annual Adult Mortality Rate (%)				
	18.9	21.9	24.9	27.9	30.9
300_150	0.691 (0.880)	0.684 (0.871)	0.666 (0.848)	0.630 (0.803)	0.589 (0.750)
340_150	0.691 (0.880)	0.684 (0.871)	0.664 (0.846)	0.630 (0.803)	0.592 (0.754)
379_150	0.692 (0.882)	0.682 (0.869)	0.663 (0.845)	0.629 (0.801)	0.587 (0.748)
379_200	0.715 (0.911)	0.709 (0.903)	0.694 (0.884)	0.665 (0.847)	0.620 (0.790)
379_250	0.729 (0.929)	0.723 (0.921)	0.711 (0.906)	0.682 (0.869)	0.641 (0.817)
SSP	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)	0.785 (0.942)

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

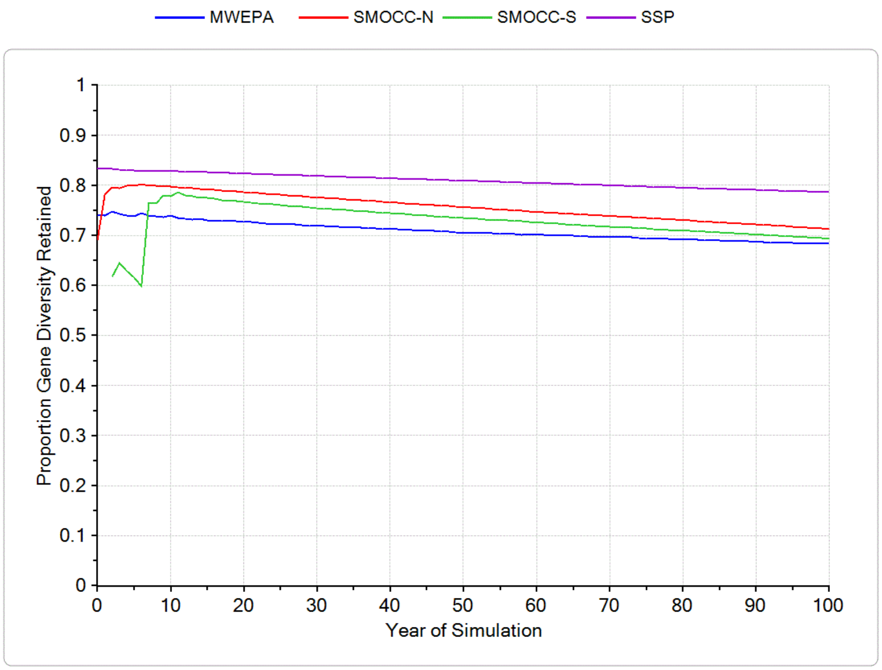

Figure 17. Average gene diversity over time for Mexican wolf populations subject to 24.9% mean annual adult mortality and under the "EIS22_22" transfer scheme. Management targets are set at 379 for MWEPA and 200 for SMOCC-N and SMOCC-S.

Scenario Set 4: Additional Transfer Strategy Scenarios

Based on the models discussed above, the MWEPA population was shown to experience a relatively low (0.052) risk of extinction over the 100-year simulation timeframe, and to retain 87.1% gene diversity relative to the intensively managed SSP population in captivity, under an intermediate level of mean annual adult mortality (24.9%), with the "EIS20_20" wolf transfer management scheme, and with a long-term population management target of 379 wolves. Under alternative transfer schemes that placed a higher demographic burden on the MWEPA population in the form of additional removals of wolves for translocation to Mexico, model results indicated that extinction risks would increase and gene diversity retention would decline. The mean MWEPA population trajectory under the "EIS20_20" transfer scheme and a population management target of 379 wolves revealed that the mean long-term abundance would reach a maximum of approximately 300 wolves, but it would require about 45 years to reach this abundance. These results stimulated further interest in identifying the management conditions – defined in terms of transfers of wolves among populations – that would lead to more robust levels of viability in the

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

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

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

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

MWEPA outcomes (Table16, Figure 18): In the original "EIS20_20" transfer scheme, and with a mean annual adult mortality rate of 24.9%, the risk of the MWEPA population declining to extinction within the 100-year simulation timeframe was 0.052 and the extent of gene diversity retention in that population relative to that retained in the SSP was 0.871. If the population were to remain extant, it would increase in abundance at an average rate of approximately 5% per year for the first 20 years of the simulation and would ultimately reach a maximum abundance of 300 wolves after 45 years before showing a slow rate of decline through accumulation of inbreeding and loss of pup productivity.

When the EIS release schedule from the SSP to the MWEPA population is doubled (transfer scheme "[EISx2]20_20"), the risk of extinction declines to 0.019 and the length of time required to reach a population abundance of 300 wolves (chosen here arbitrarily for comparative purposes) is reduced in half to just 25 years. The mean population abundance reaches a maximum of about 320 wolves with a slower rate of subsequent population decline, and the extent of gene diversity retained relative to that in the SSP also increases to just under 90%. When the number of wolves pulled from MWEPA for translocation to SMOCC-N is reduced and replaced by a larger number of wolves pulled from the SSP for initial releases to Mexico (transfer schemes "[EISx2]30_10" and "[EISx2]40_00"), the MWEPA population grows at a more rapid rate, achieves a larger long-term equilibrium abundance, and retains a larger proportion of gene diversity relative to that retained in the SSP.

SMOCC-N outcomes (Table 16, Figure 19): The output metrics for SMOCC-N across these new transfer scheme scenarios show very little deviation from the "EIS20_20" scenario used here for reference. Risk of population extinction through the 100-year simulation ranges from 0.01 to 0.014, and the population grows to its maximum abundance of about 175 wolves in 15 to 16 years. Furthermore, the population retains approximately 89% gene diversity relative to the SSP population at the end of the simulation. The SMOCC-N population displays a more pronounced rate of decline from the maximum abundance of 175 at year 15 to approximately 155 – 160 wolves by the end of the simulation, as a result of reduced litter production through slow accumulation of inbreeding depression and reduced incidence of diversionary feeding.

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

	Transfer Scheme			
	EIS20_20	[EISx2]20_20	[EISx2]30_10	[EISx2]40_00
MWEPA				
Prob(Ext)	0.057	0.019	0.012	0.003
Years to N=300	45	26	18	14
N_{Max}	300	323	333	333
N_{100}	280	311	313	312
$GD(SSP)_{100}$	0.870	0.897	0.901	0.899
SMOCC-N				
Prob(Ext)	0.011	0.010	0.011	0.014
Years to N=175	15	15	15	16
N_{Max}	180	179	178	178
N_{100}	153	154	158	153
$GD(SSP)_{100}$	0.887	0.889	0.892	0.889

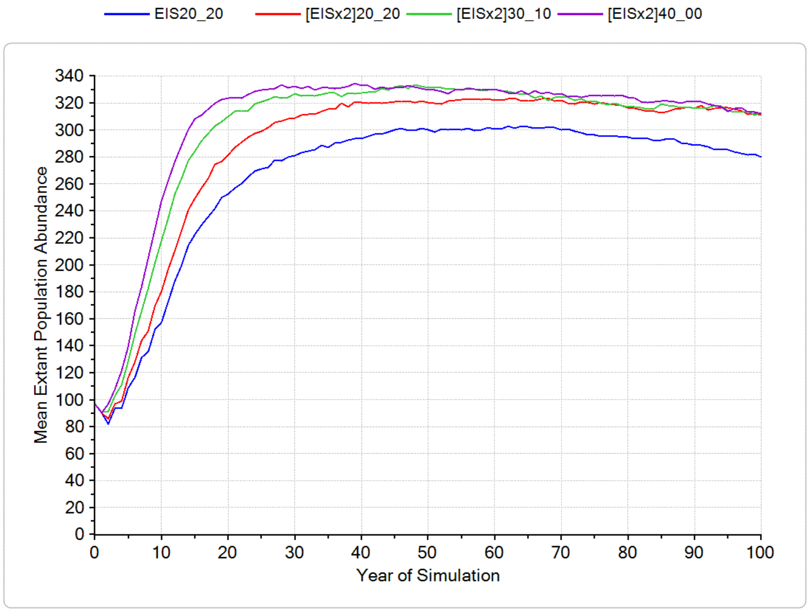

Figure 18. Mean MWEPA population abundance among extant iterations across alternative transfer scheme scenarios. See accompanying text for transfer scheme definitions and underlying scenario characteristics.

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

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

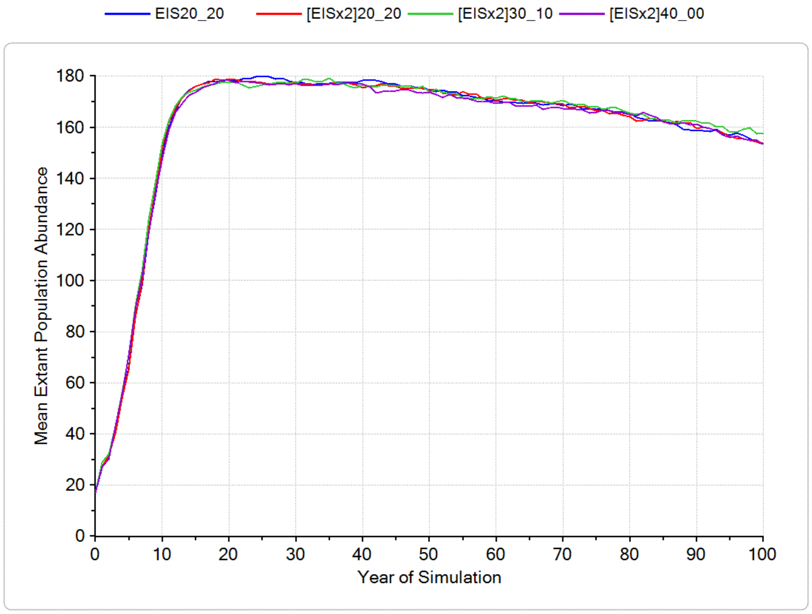

Figure 19. Mean SMOCC-N population abundance among extant iterations across alternative transfer scheme scenarios. See accompanying text for transfer scheme definitions and underlying scenario characteristics.

Conclusions and Discussion

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

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

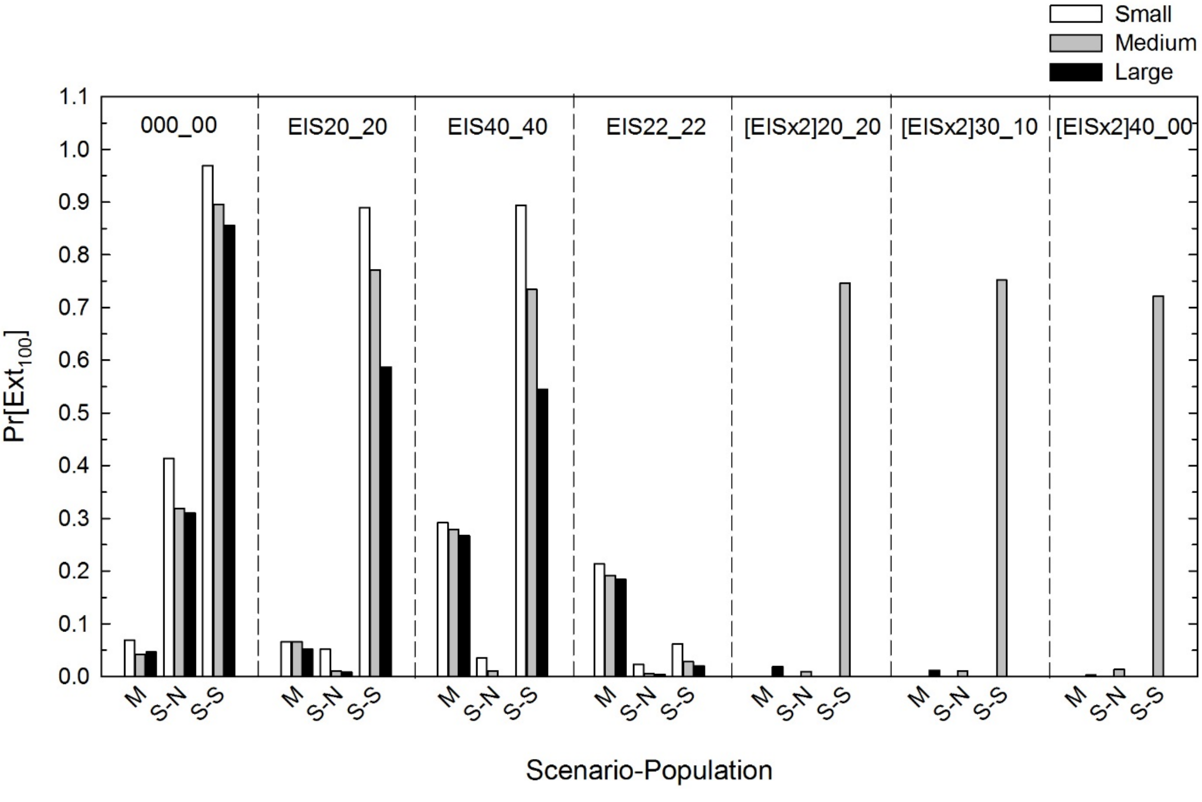

Figure 20. Extinction risk at 100 years for wild populations of Mexican wolves among selected PVA scenarios across each of the tested transfer schemes and featuring 24.9% mean annual adult mortality. Population designations: M, MWEPA; S-N, SMOCC-N; S-S, SMOCC-S. Population-specific management targets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

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

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

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

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

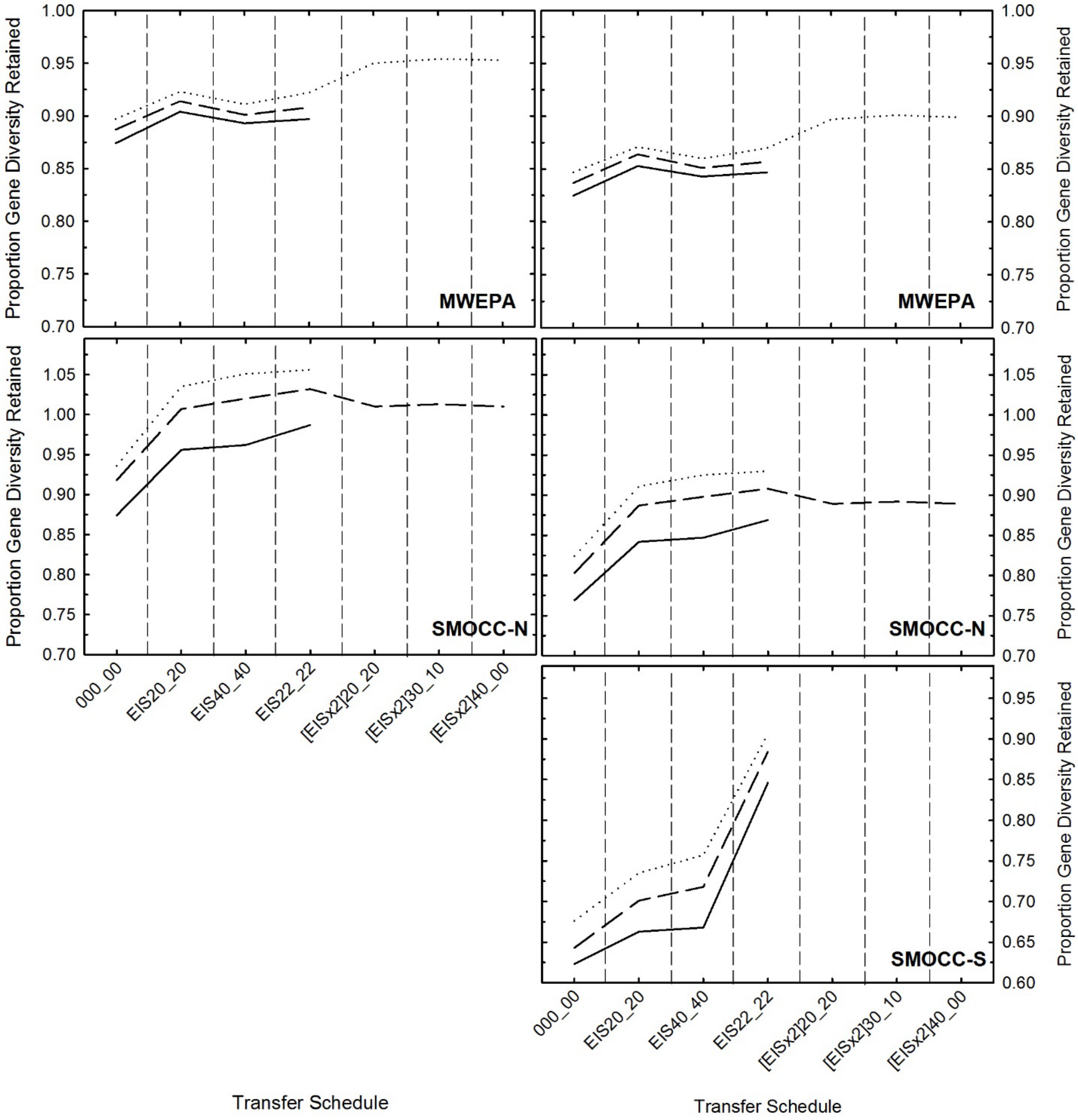

Figure 21. Proportional gene diversity (GD) retention for wild populations of Mexican wolves among selected PVA scenarios across each of the transfer schemes addressed in this analysis, and featuring 24.9% mean annual adult mortality. Lines within each plot refer to alternative population management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

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

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

This PVA includes a harvest function that is triggered at a designated population management target. However, long-term management of the MWEPA population to remove wolves from the landscape when the population is at or near the management target will likely involve responses to livestock depredation and/or unacceptable impact to native ungulate herds. Thus, simulation of this management activity may not be as flexible or as nuanced as what may be undertaken in reality, as decisions may be made in the presence of a broader range of information than what is being considered here. Nevertheless, it may be instructive to briefly explore the extent of removals required to maintain a population at a designated management target. Assuming a mean annual adult mortality rate of 24.9% in MWEPA, and under the "EIS20_20" transfer scheme, our model suggests that an average of no more than approximately 15 to 17 wolves would need to be removed in a given year to keep the wolf population at the management targets below 200 and 379 in Mexico and the U.S., respectively. If releases to MWEPA from the SSP population are doubled as per the "[EISx2]20_20" transfer scheme, the maximum number of wolves removed from that population increase to 21 individuals while the number from SMOCC-N remains unchanged. As time progresses through the simulation and longer-term population growth rates are expected to decline through processes discussed earlier, the rate of removal declines.

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

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

The information summarized in Figures 20 and 21 comes from model scenarios that feature the best estimates for the full range of demographic parameters discussed in the Input Data sections. As discussed in this report, this PVA does not include a comprehensive sensitivity analysis, instead referring to the detailed analysis of Carroll et al. (2014) for information that helps shape the range of scenarios evaluated here. The range of adult mortality rates and population management targets that define the bulk of scenarios discussed in this report is a direct reflection of the insight gained from the earlier sensitivity analysis work.

During the construction of this PVA model, extensive exploration of the available field demographic and genetic data led to crafting a series of functional relationships between demographic rates and a host of biological factors such as individual age, inbreeding coefficient, previous breeding history, etc. Indeed, the complexity of this data analysis effort resulted in a long list of measurement uncertainties across a range of model input variables, with each element of uncertainty contributing to either an improvement or a decline in our final prediction of population demographic performance. While recognizing this reality, it is also unknown whether a comprehensive examination of the impact of this range of uncertainty on population viability, using methods like those promoted by Bakker et al. (2009), would significantly alter the strategic decisions proposed by the relevant management authorities to promote Mexican wolf recovery in the wild. As discussed in the vast literature on ecological risk assessment (e.g., NRC 2013), the depth of analytical effort applied to such assessments should be appropriate to the broad decision context. Uncertainty in our understanding of the complex biology of Mexican wolf population management should be accepted, and the evidence-based management guidelines and targets emerging from this PVA should be viewed as guideposts that must be frequently reviewed and adjusted as new data are made available from continued population monitoring, and predictive models using updated input from revised analyses are made available to decision-makers. Through this iterative process of model construction, implementation and refinement, wildlife managers can improve their ability to define the conditions required to recover endangered species in their care.

Acknowledgements

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

A sincere expression of thanks to the set of peer reviewers who provided valuable comments throughout a draft of this document. Thanks also go to Matthew Clement (AZ Game and Fish), Mason Cline (NM Game and Fish), Maggie Dwire (USFWS), Rich Fredrickson, John Oakleaf (USFWS), John Sahrmann (St. Louis Zoo), and Kathy Traylor-Holzer (CBSG) for their valuable assistance in data analysis to generate model input.

Special thanks to Bob Lacy (Chicago Zoological Society) and Kathy Traylor-Holzer for their reviews and many helpful comments and suggestions throughout the model development process.

Addendum to the Mexican Wolf PVA Report

Introduction

After a period of extensive peer and public review of the original PVA report (dated 13 June 2017) as a component of the draft Mexican Wolf Recovery Plan, a small set of additional simulation models were constructed and evaluated in order to explore selected elements of the simulation model structure and resultant dynamics. These models are meant only to provide supplementary information to the U.S. Fish and Wildlife Service that they may use to review and potentially revise specific elements of the Recovery Plan.

The additional scenarios discussed in this Addendum are designed to explore two specific simulation model elements:

1. Impact of demographic isolation between the MWEPA and SMOCC-N wolf populations through the removal of dispersal opportunities across the U.S. – Mexico border; and
2. Impact of eliminating diversionary feeding across both U.S. and Mexico wolf populations.

Impacts of Demographic Isolation across the International Border

All model scenarios discussed in the original PVA report included a low level of natural connectivity between the northernmost MWEPA population in the southwestern United States and the Sierra Madre Occidental – North population (SMOCC-N) in northern Chihuahua, Mexico. Specifically, members of the Mexican Wolf PVA Development Team assumed that a non-breeding (unpaired) wolf between one and four years of age had a 0.175% annual probability of dispersing between the MWEPA and SMOCC-N populations (i.e., the dispersal probability is symmetric). Moreover, there is an assumed cost to dispersal in the form of a 37.5% survival rate of wolves that arrive in a recipient population after dispersing from a source population. (See the subsection titled "Metapopulation Dynamics" in the "Input Data for PVA Simulations: Wild Populations" section of this report.) These parameters yield an expected average successful dispersal rate on the order of approximately one individual dispersing from the MWEPA population to the SMOCC-N population every 12 – 16 years.

Estimating these dispersal parameters is, of course, fraught with uncertainty as we have had only very little time to observe natural dispersal between these two newly-established populations. It is therefore instructive to assess the sensitivity of our model structure to different dispersal parameter values. Even more importantly, there is concerned about the potential for physical barriers along the U.S. – Mexico border to be constructed in the near future, which may reduce or more likely eliminate the prospects for natural connectivity. These concerns make it important to use the PVA tool to test the impact of removing this transboundary dispersal capability, thereby evaluating the degree to which the current level of metapopulation structure improves the viability of the smaller Mexico populations and the metapopulation as a whole.

To conduct this evaluation, a separate scenario was constructed in which the dispersal probability between MWEPA and SMOCC-N populations was reduced from 0.175% to 0.0%. The connectivity between SMOCC-N and SMOCC-S population units was maintained, thereby simulating the maintenance of dispersal among Sierra Madre habitat units despite the elimination of trans-border dispersal.

Other pertinent scenario characteristics include:

- Mean annual adult mortality rate: 24.9%
- MWEPA population management target: 379
- SMOCC-N, SMOCC-S population management target: 200
- [EISx2]20_20 transfer scheme

All other model input values were set to those defining the baseline model scenario.

The results from this analysis are summarized in Table 17. Under the baseline condition of trans-border connectivity, SMOCC-N receives an immigrant wolf from either the MWEPA or SMOCC-S populations (if wolves are resident there) approximately once in 12 years (annual rate = 0.087), while MWEPA receives a wolf approximately once in 22 years (annual rate = 0.045). A wolf from the SMOCC-N population successfully disperses to the SMOCC-S population approximately every three years (annual rate = 0.370 – 0.379), regardless of the presence or absence of trans-border dispersal opportunity. When the trans-border connectivity is removed from the simulation, the number of immigrants successful dispersing into the SMOCC-N population declines by more than 95% (annual rate = 0.004) compared to the baseline connected scenario. In this situation, SMOCC-N is connected only to the very small (if extant) SMOCC-S population, which is itself derived from the SMOCC-N population in the absence of direct supplementation of wolves into the southern population from either the MWEPA or SSP populations. These dispersal results are derived directly from the *Vortex* model output, and are in agreement with the values expected from knowledge of the mean population abundances, general population age structure, and dispersal characteristics used as model input.

Table 17. Results from metapopulation connectivity scenarios using the "[EISx2]20_20" transfer scheme, 24.9% mean annual adult mortality, and 379/200 management targets for MWEPA/SMOCC populations. Immigrants$_{20+}$, mean annual number of individuals successfully dispersing into the selected population after simulation year 20; Emigrants$_{20+}$, mean annual number of individuals dispersing out of the selected population after simulation year 20. N_{100}, mean extant population abundance at year 100. GD_{100}, mean gene diversity at year 100, with values in parentheses giving the proportion of GD retained relative to that population's starting value (first number) and to the final value for the SSP population (second number). Single value in parentheses for the SMOCC-S population shows GD retained relative to the final value for the SSP population.

	MWEPA		SMOCC-N		SMOCC-S	
	Connected	Isolated	Connected	Isolated	Connected	Isolated
Immigrants$_{20+}$	0.045	0.0	0.087	0.004	0.370	0.379
Emigrants$_{20+}$	0.219	0.0	0.723	0.603	0.039	0.032
Pr(Ext)	0.019	0.018	0.010	0.013	0.746	0.757
N_{100}	311	308	154	154	15	12
GD_{100}	0.704 (0.950; 0.897)	0.700 (0.945; 0.892)	0.698 (1.010; 0.889)	0.689 (0.997; 0.877)	0.554 (0.706)	0.548 (0.698)

Removing dispersal opportunity between the MWEPA and SMOCC-N populations did not appreciably affect the risk of population extinction across the three wild populations. Similarly, removing trans-border dispersal did not alter the abundance trajectory of either population across the full time course of the simulation, with essentially identical final abundance values. This is not surprising given the relatively low level of observed demographic exchange between populations.

Final gene diversity in the MWEPA population dropped by 0.6% (0.704 to 0.700) when connectivity to SMOCC-N was removed from the simulation. The proportion of GD retained relative to the SSP also dropped by the same amount when dispersal was eliminated. The extent of reduction in final gene diversity in the SMOCC-N population was twice that in MWEPA, with a 1.3% decrease in final GD (0.698 to 0.689) and the same proportional decline in GD relative to the final SSP value.

This exploratory analysis of metapopulation stability indicates that, given the expert judgment used to generate metapopulation dispersal input data for the PVA model assessed here, the demographic impact to long-term Mexican wolf population viability of prohibiting successful dispersal across the U.S. – Mexico border is negligible. The underlying growth potential of these populations, defined by the reproductive and survival rates used as model input, is sufficient to offset the loss of occasional introgression of individual wolves across the international border. The genetic impact of lost metapopulation connectivity across the international border is more substantial, with a more rapid loss of gene diversity in both MWEPA and SMOCC-N populations when dispersal opportunity is eliminated. This effect is more pronounced in the SMOCC-N population, where the long-term abundance is comparatively smaller and where the expected immigration rate is higher given the larger MWEPA source population to the north.

The importance of dispersal connectivity for maintaining overall metapopulation genetic integrity has long been appreciated by the conservation biology community, and was a major focus of the previous Mexican wolf PVA effort (Carroll et al. 2014). While the absolute reductions in MWEPA and SMOCC-N population gene diversity resulting from loss of connectivity may appear small, it is clear that any level of accelerated loss of genetic diversity in populations that become demographically isolated can compromise those populations' progress toward long-term recovery. As a result, it may become necessary to offset the negative impacts of loss of metapopulation function through other management activities, such as increased translocation or release efforts.

Our assessment of the realism of these impacts is, of course, dependent on the initial conditions used in the PVA scenarios. In particular, the dispersal mechanic used in our models is a key factor that ultimately determines the intensity of the effect imposed by prohibiting successful dispersal of wolves across the international border. A robust method for estimating true dispersal rates between the MWEPA and SMOCC-N populations is necessary to evaluate the long-term impacts of losing this important capability.

An Exploratory Analysis of Dynamic Diversionary Feeding

The original set of PVA scenarios explored in this analysis included a diversionary feeding element that attempted to simulate the activity currently practiced by the U.S. Fish and Wildlife Service as a tactic to reduce the incidence of cattle depredation in the MWEPA. The model element featured a gradual reduction in the extent of diversionary feeding (defined in terms of the proportion of breeding females receiving this benefit) from the current rate of approximately 70% to 15% within the next 20 years. This element was then used to modify the mean size of litters produced by adult females as a function of their probability of being a part of the diversionary feeding program. (See the subsections titled "Calculation of mean litter size" and "Dynamic Diversionary Feeding" in the "Input Data for PVA Simulations: Wild Populations" section of this report.) The 15% long-term feeding rate represents a low level of activity that managers anticipate will be necessary to address chronic depredation issues. However, reviewers of this PVA report noted that this long-term effort may constitute a level of conservation reliance for this species that is not compatible with the spirit of recovery as defined by the U.S. Endangered Species Act. This concern leads to obvious questions around the extent to which Mexican wolf populations – at least as constructed within this PVA framework – can be considered viable in the complete absence of diversionary feeding and under the conditions identified in the original analysis as being supportive of demographic and genetic viability.

To begin exploring these questions, an additional set of PVA scenarios was constructed that used the same base scenario used for the metapopulation connectivity models discussed in the previous section:

- Mean annual adult mortality rate: 24.9%
- MWEPA population management target: 379
- SMOCC-N, SMOCC-S population management target: 200
- [EISx2]20_20 transfer scheme

All other model input values were set to those defining the baseline model scenario.

The main modification to these scenarios targeted the dynamic diversionary feeding element of the model. In this additional set of models, the diversionary feeding rate was reduced to 0% ("Feed0" scenarios) instead of 15% ("Feed15" scenarios) after the appropriate amount of time. This would lead to a larger reduction in the proportion of larger litters produced by the adult female population as a whole.

With all other model input parameters unchanged from their baseline values, the elimination of diversionary feeding as a management tool in model years 15 – 20 leads to lower overall population growth in both MWEPA and SMOCC-N populations, and a lower long-term population abundance (Figure 22). The annual growth rate for both populations under the "Feed0" scenario begins to decline approximately 10 to 15 years into the simulation, and the final abundance values ultimately decline by a little more than 20% relative to the baseline "Feed15" scenarios by model year 100. The risk of extinction in the MWEPA population increases under the "Feed0" scenario from 0.019 to 0.073, and in the SMOCC-N population from 0.010 to 0.058. Final gene diversity in the MWEPA population also declines from 0.704 to 0.695, and in the SMOCC-N population from 0.698 to 0.683.

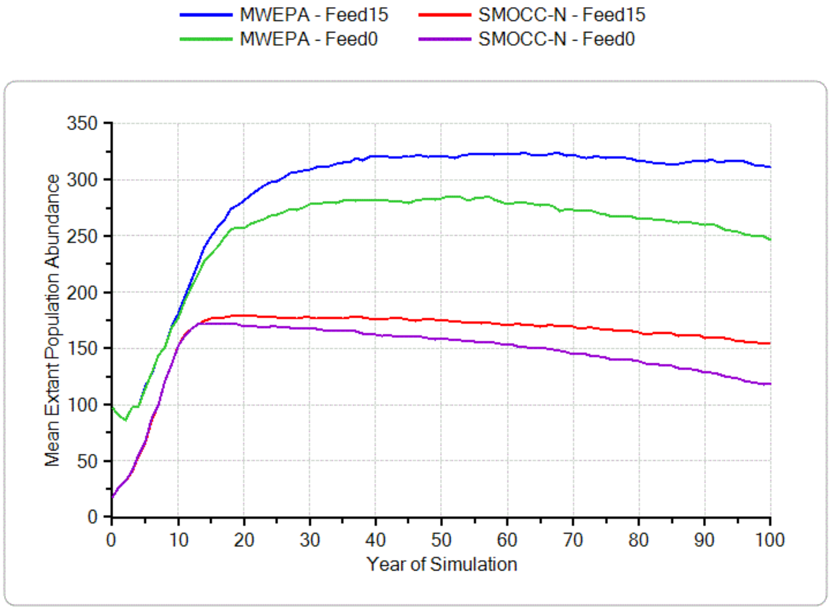

Figure 22. Mean abundance among extant iterations for MWEPA and SMOCC-N populations across alternative dynamic diversionary feeding scenarios. See accompanying text for underlying scenario characteristics.

It is evident that, under the conditions simulated in this analysis, the elimination of diversionary feeding further reduces the demographic and genetic viability of both the MWEPA and SMOCC-N populations. This conclusion is, to reiterate, dictated by the underlying conditions of the scenarios under consideration – most importantly, the mean annual adult mortality rate and the long-term population management target. It may be possible to reverse the decline in population viability if more active management were to achieve more favorable demographic conditions for wolves on the ground. As an example of exploratory analyses designed to explore the conditions under which our simulated Mexican wolf populations may demonstrate an acceptable level of viability in the absence of diversionary feeding, additional scenarios were constructed that featured modifications to mean annual adult mortality and to the population-specific long-term management targets. The resultant MWEPA and SMOCC-N population abundance trajectories for selected scenarios in this exploratory analysis are displayed in Figure 23.

For the MWEPA population, long-term demographic stability was achieved when the mean annual adult mortality rate was reduced from 24.9% to 20.9% while maintaining the population management target at 379 individuals. In this case, population demographic stability is defined as a population abundance that does not decline appreciably from an apparent equilibrium value over time. Under the higher annual adult mortality rate, the mean population growth rate from simulation year 30 (when the population approaches the management target) to 100 is estimated to be $\lambda = 0.9982$. When the annual adult mortality rate is reduced to 20.9%, the growth rate over this same period is estimated to be $\lambda = 0.9997$. This growth rate in the presence of an imposed ceiling on abundance can be taken to indicate an acceptable level of demographic stability over the observed course of the simulation. In addition, retention of gene diversity is increased under more favorable mortality conditions in the MWEPA population. With the baseline adult mortality rate of 24.9%, final gene diversity retained at model year 100 is 0.695 which is just 88.5% of that retained within the SSP over that same time period. When the adult mortality rate is reduced to 20.9%, final gene diversity retained increases to 0.714 which is 91.0% of that retained within the SSP.

In evaluating the SMOCC-N population, the analysis indicates that improving viability requires both reducing mean annual adult mortality and increasing the population management target. Under the higher annual adult mortality rate (24.9%) and the smaller management target of 200, the mean population growth rate from simulation year 15 (when the population reaches the maximum abundance) to year 100 is estimated to be $\lambda = 0.9957$. When the annual adult mortality rate is reduced to 20.9% and the management target is increased to 300, the growth rate under the same conditions (year 25 – 100) is estimated to be $\lambda = 0.9998$. It should be noted here that if adult mortality is reduced without increasing the management target, the growth rate over that same time period becomes $\lambda = 0.9990$ with the population abundance declining from 185 to 170 wolves in that timeframe. In addition, retention of gene diversity is increased under more favorable mortality and management target conditions in the SMOCC-N population. With the smaller management target and the baseline adult mortality rate of 24.9%, final gene diversity retained at model year 100 is 0.683 which is just 87.0% of that retained within the SSP over that same time period. When the management target is increased to 300 and the adult mortality rate is reduced to 20.9%, final gene diversity retained increases to 0.735 which is 94.0% of that retained within the SSP.

Taken together, these simulations indicate that the demographic costs of a more substantial proposed reduction in future rates of diversionary feeding, or even its total elimination, could potentially be mitigated by reducing adult mortality and, perhaps in the case of Mexico's northernmost Sierra Madre population, increasing the population management target. In reality some amount of diversionary feeding will probably continue to be used as a management tool in specific situations, so a complete elimination of this tactic is considered unlikely. Continued monitoring of population dynamics will be required when diversionary feeding is reduced or potentially eliminated in order to assess the impact of pup production and mortality rates on population growth. In light of this information, enhanced management actions directed at reducing human-caused mortality may be necessary to overcome the consequences of reducing diversionary feeding as a long-term management tool.

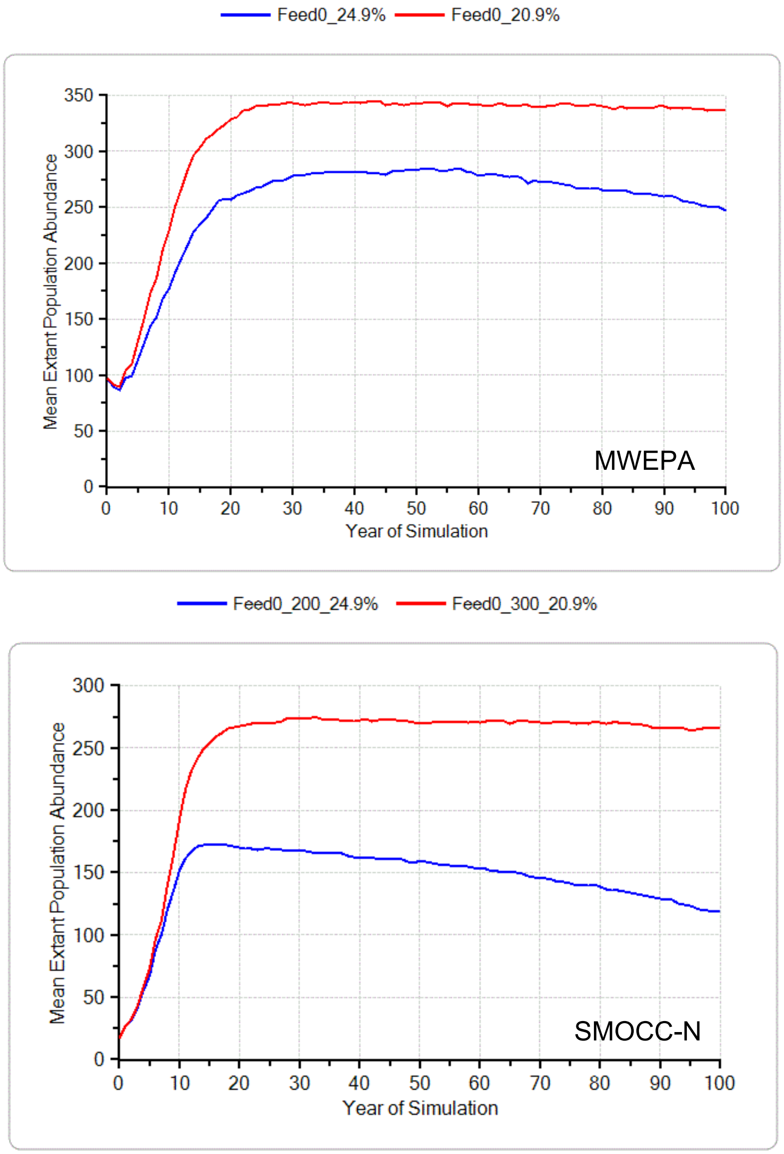

Figure 23. Mean abundance among extant iterations for MWEPA (top panel) and SMOCC-N (bottom panel) populations across alternative scenarios featuring the gradual elimination of diversionary feeding. Percentages in the figure legends refer to the mean annual adult mortality rate used in the scenarios, with additional numerical values in the legend for SMOCC-N referring to population management targets. See accompanying text for underlying scenario characteristics.

The choice of 300 as an increased population management target for SMOCC-N in these simulations reflects the desire among management authorities in Mexico to avoid constraining population abundance to a management target that is less than the assumed ecological carrying capacity for this habitat area (K = 300) estimated by Martínez-Meyer et al. (2017). Instead, the wolf population is allowed here to grow until natural ecological factors act to regulate long-term abundance.

The impacts of the diversionary feeding activity are multi-faceted and complex. This PVA uses the best available information to assess these impacts (see Appendix C), but it is recognized that additional consequences of diversionary feeding on other aspects of population demography, such as individual wolf removal rates, may not be fully understood and, as a result, may not be incorporated into the model with the intended accuracy. Future population management activities will require careful implementation and associated monitoring to reduce the risk of unintended outcomes and improve the likelihood of continued population growth and genetic stability.

References

Adams, L.G., R.O. Stephenson, B.W. Dale, R.T. Ahgook, and D.J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs* **170**:1-25.

Almberg, E.S., P.C. Cross, and D.W. Smith. 2010. Persistence of canine distemper virus in the Greater Yellowstone ecosystem's carnivore community. *Ecological Applications* **20**: 2058–2074.

Bakker, V.J., D.F. Doak, G.W. Roemer, D.K. Garcelon, T.J. Coonan, S.A. Morrison, C. Lynch, K. Ralls, and R. Shaw. 2009. Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. *Ecological Monographs* **79**:77-108.

Beissinger, S. and D. McCullough (Eds.). 2002. *Population Viability Analysis*. Chicago, IL, USA: University of Chicago Press.

Brook, B.W., J.J. O'Grady, A.P. Chapman, M.A. Burgman, H.R. Akçakaya, and R. Frankham. 2000a. Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**:385-387.

Brook, B.W., M.A. Burgman, and R. Frankham, 2000b. Differences and congruencies between PVA packages: The importance of sex ratio for predictions of extinction risk. *Conservation Ecology* 4(1): 6. [online] URL: http://www.consecol.org/vol4/iss1/art6/

Carroll, C., R. Fredrickson, and R.C. Lacy. 2014. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. *Conservation Biology* **28**:76-86.

Doak, D.F., G.K. Himes Boor, V.J. Bakker, W.F. Morris, A. Louthan, S.A. Morrison, A. Stanley, and L.B. Crowder. 2015. Recommendations for improving recovery criteria under the US Endangered Species Act. *Bioscience* **65**:189-199.

Ellner, S.P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision in population viability analysis. *Conservation Biology* 16:258–261.

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

Fuller, T.K., L.D. Mech, and J.F. Cochrane. 2003. Wolf population dynamics. Pages 161-191 in: Mech, L.D., and L. Boitani (Eds.). *Wolves: Behavior, Ecology and Conservation*. Chicago, IL, USA: University of Chicago Press.

Hamlin, K. L., J. A. Cunningham, and K. Alt. 2009. Monitoring and assessment of wolf-ungulate interactions and population trends within the Greater Yellowstone Area, southwestern Montana, and Montana statewide, final report. Montana Fish, Wildlife & Parks, Helena, MT.

Hebblewhite, M. 2013. Consequences of ratio-dependent predation by wolves for elk population dynamics. *Population Ecology*: Published online. DOI 10.1007/s10144-013-0384-3.

Hedrick, P.W., P.S. Miller, E. Geffen, and R. Wayne. 1997. Genetic evaluation of the three captive Mexican wolf lineages. *Zoo Biology* **16**:47-69.

Lacy, R.C. and J.P. Pollak. 2017. *Vortex: A Stochastic Simulation of the Extinction Process*. Version 10.2.8. Brookfield, IL, USA: Chicago Zoological Society.

Lacy, R.C., P.S. Miller, and K. Traylor-Holzer. 2014. *Vortex 10 User's Manual*. Apple Valley MN: IUCN SSC Conservation Breeding Specialist Group and Chicago Zoological Society.

Lotts, K.C., T.A. Waite, and J.A. Vucetich. 2004. Reliability of absolute and relative predictions of population persistence based on time series. *Conservation Biology* 18:1–9.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310.

Martínez-Meyer, E., A. González-Bernal, J.A. Velasco, T.L. Swetnams, Z.Y. González, and J. Servín. 2017. Mexican wolf habitat suitability analysis in historical range in the Southwestern U.S. and Mexico. Report to the U.S. Fish and Wildlife Service.

Mechak, L., P. Siminski, J. Kiseda, and K. Bauman. 2016. Mexican Gray Wolf (*Canis lupus baileyi*) AZA Animal Program Population Viability Analysis Report. The Association of Zoos and Aquariums.

NRC (National Research Council). 2009. *Science and Decisions: Advancing Risk Assessment*. Washington, DC: The National Academies Press.

Reed, J.M., L.S. Mills, J.B. Dunning Jr., E.S. Menges, K.S. McKelvey, R. Frye, S.R. Beissinger, M.-C. Anstett, and P.S. Miller. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16:7–19.

Smith, D. W., E.E. Bangs, J.O. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D.H. Pletscher, C.C. Niemeyer, T.J. Meier, D.R. Stahler, J. Holyan, V. Asher, and S.L. Murray. 2010. Survival of colonizing wolves in the northern Rocky Mountains of the United States 1982–2004. *Journal of Wildlife Management* **74:**620–634.

U.S. Fish and Wildlife Service. 2014. Proposed Revision to the Regulations for the Nonessential Experimental Population of the Mexican Wolf (*Canis lupus baileyi*). Final Environmental Impact Statement.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *Journal of Animal Ecology* 80:1236-1245.

Appendix A.

Estimation of the Mean Pairing Rate among Wild Mexican Wolves[3]

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

Date: 19 October, 2016 and 25 January, 2017

Methods

Method 1: Direct observation

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

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

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

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

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

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

Method 2: Indirect estimation

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

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

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

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

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

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

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

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

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

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

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

Appendix B.

Analysis of Independent Variables and their Impacts on the Probability of Live Birth and Detection in Wild Mexican Wolves in Arizona and New Mexico[4]

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

Date: 16 September, 2016

Methods

Population Monitoring and Pup Counts

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

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

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

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

Statistical Methodology

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

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

Results and Discussion

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

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

References

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

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

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

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

Table B-1. (cont.)

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

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

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

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

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

Parameter Estimates

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

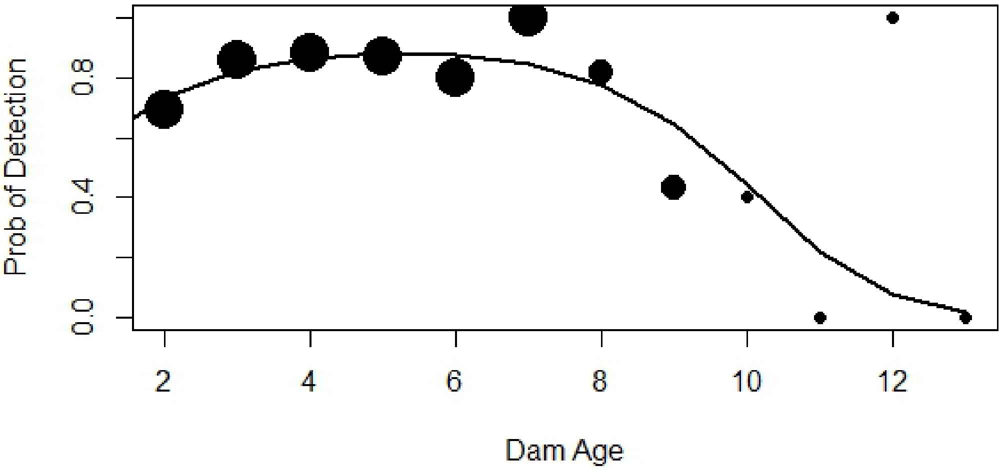

Figure B-1. Model results and data comparing probability of documenting live pups versus dam + dam age squared (the best linear representation of the relationship). Circles are scaled with larger circles representing a larger sample size at a particular age.

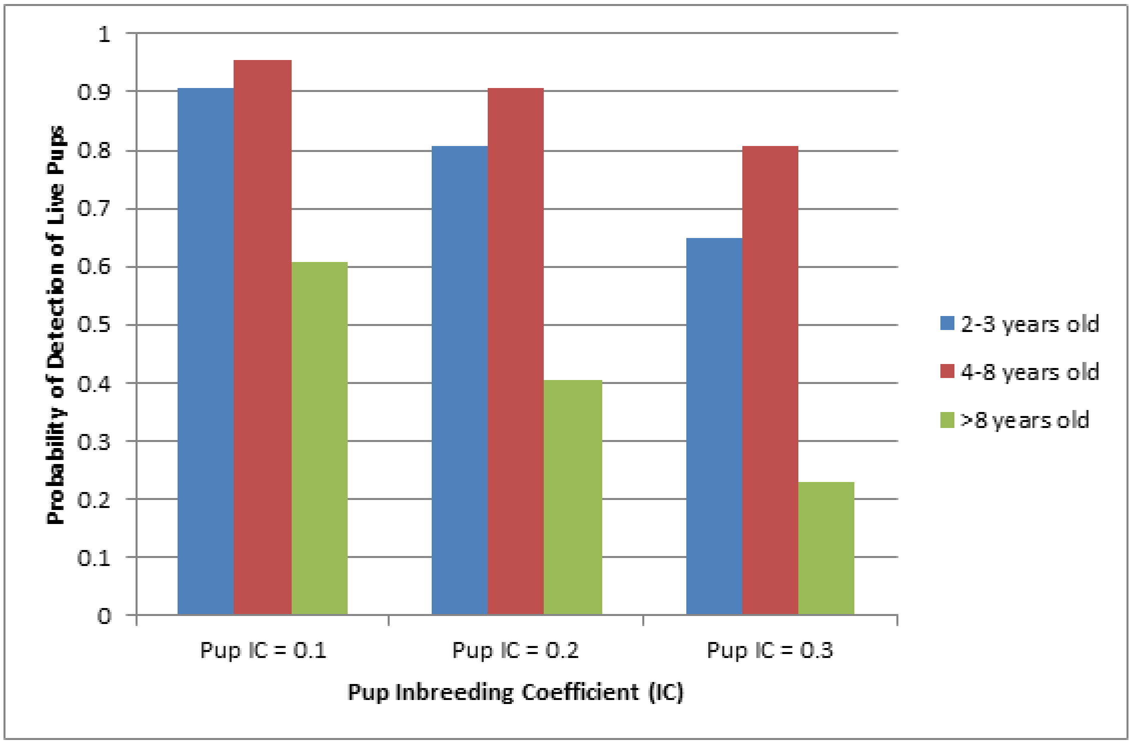

Figure B-2. A comparison of the probability of detection of live pups across the age of the reproducing dam in the pair and various pup inbreeding coefficients, using the regression results from Table B-5.

Appendix C.

Analysis of Inbreeding Effects on Maximum Pup Count in Wild Mexican Wolves[5]

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

Date: 9 September, 2016

Introduction

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

Methods

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

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

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

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

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

Results

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

References

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

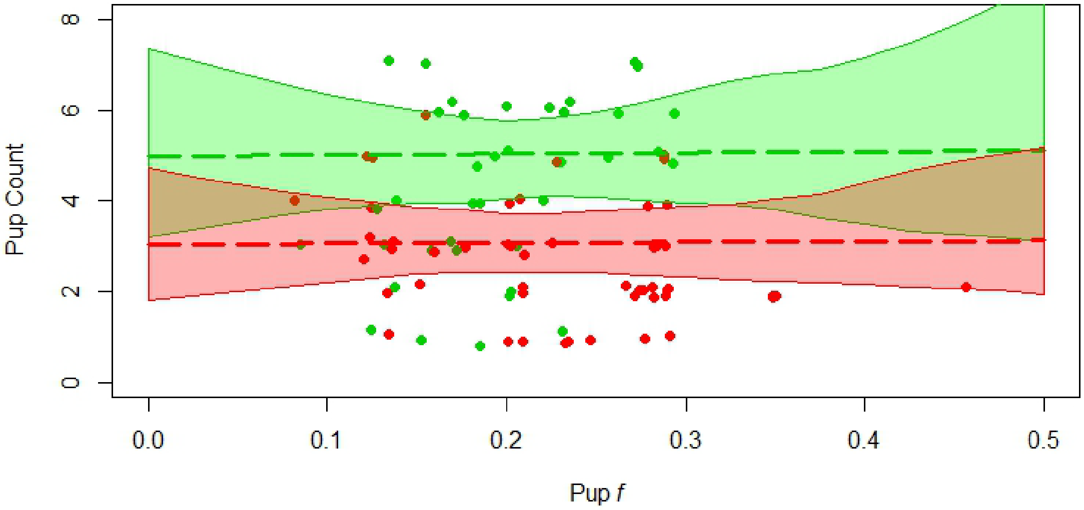
Fredrickson R.J., P. Siminski, M. Woolf, and P.W. Hedrick. 2007 Genetic rescue and inbreeding depression in Mexican wolves. *Proceedings of the Royal Society B* **274**:2365-2371.

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

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

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

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



Appendix D.

Survival and Related Mexican Wolf Data for Population Model Parameterization[6]

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

Date: 5 March, 2017

Input Data: Average number of pups born

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

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

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

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

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

Baseline analytical approach

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

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

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

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

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

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

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

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

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

References

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

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

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

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

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

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

Addendum

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

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

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

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

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

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

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

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

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

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

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

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

Table D-7. Summary of information used for survival analyses of Mexican wolves within one year of translocation from captivity or the wild during 1998 – 2015. Data was modified to reduce the number of livestock related removals by 50% during 2003-2008. This resulted in 4 fewer adult livestock related removals and 1 fewer pup related removal (see Table D-5).

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

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

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