The following is a preliminary planning document (Population Viability Analysis for the Jaguar (*Panthera onca*) in the Northwestern Range – April 11, 2013, version) generated by contractors for and in collaboration with the Jaguar Recovery Team (JRT). This preliminary document is being released for public viewing in anticipation of requests under the Freedom of Information Act.

It should be noted that this **preliminary** document may still undergo revision and incorporation of additional population and habitat modeling runs, and as such was not intended for release until the Draft Jaguar Recovery Plan (DJRP) was completed. The JRT is concerned that the release of this preliminary document prematurely could result in misinterpretation of the results out of context, and cause distraction from the primary duty of the JRT, which was to produce the DJRP.

The JRT is made up of experts and stakeholders from a wide array of backgrounds and knowledge. The strongest Recovery Plan is one that can bring all this diversity and knowledge together into one agreed-upon set of information, analyses, and recommendations. Thus, the JRT felt that deliberations should not be constrained by concerns of release of partially-formed analyses and incomplete reports. The intent was to release supporting documents, when completed, in context with the DJRP. Understanding the intention of the JRT, the release of the documents at this time should be viewed in light of the fact that some of the material released is **preliminary** in nature.

To reiterate, the contents of the attached document produced by contractors for and in collaboration with the JRT (with the exception of the Recovery Outline, which is a final standalone document) is still considered part of the evolution of the DJRP — and thus is still considered preliminary by the JRT. Final supporting documents will be included as appendices in the DJRP.

Population Viability Analysis for the Jaguar (*Panthera onca*) in the Northwestern Range

Report prepared by

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In consultation with

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Under Solicitation

F12PX00876

11 April, 2013

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Executive Summary

Since January 2011, the U.S. Fish and Wildlife Service (USFWS) has been engaged in a process of developing a population viability analysis (PVA) to evaluate the stability and long-term viability of jaguar populations in the northwestern portion of the species' global range. This analysis will help inform the recovery planning effort underway with USFWS biologists, state wildlife management authorities, and other relevant stakeholders that make up the bi-national Recovery Team across the United States – Mexico border. This report describes the most recent phase of this analysis, centered on a meeting of the Recovery Team in July – August 2012, with a particular emphasis on two important questions informing jaguar management in the northwestern part of the species' range:

- How stable are core jaguar populations in Jalisco and Sonora, and how important are they in determining overall metapopulation stability of jaguar subpopulations in the northwestern portion of the species' range?
- Given a specific level of overall metapopulation growth potential, is there sufficient connectivity among patches of jaguar habitat in the northwestern portion of the species' range to facilitate the expansion of jaguars into the borderlands area (i.e., northern Sonora and southwestern U.S.) of the Northwestern Recovery Unit (NRU)?

Earlier meetings of the Recovery Team's Technical Subgroup were instrumental in defining the basic demographic parameters used in the PVA. The analyses were conducted using the software package *Vortex*, a widely-used demographic simulation tool for demographic modeling of threatened wildlife populations. More recent modeling efforts have been focused on deriving more accurate estimates of habitat connectivity among subpopulations making up the Northwestern Recovery Unit, defined from south to north as the Jalisco Core Area; Sinaloa Secondary Area; Sonora Core Area; and the Mexico and U.S. portions of the Borderlands Secondary Area (BSA). Additionally, recent analyses have concentrated on using improved habitat suitability information and model structures to derive estimates of jaguar carrying capacity for each of these subpopulations. This habitat modeling was conducted separately by staff of the Wildlife Conservation Society's Living Landscapes Program. Their two most recent model scenarios differed primarily in the assumption regarding the suitability of what some experts would consider to be intervening habitat separating more appropriate jaguar habitat patches. Using results from the two most recent carrying capacity analyses, *Vortex* models were constructed that systematically varied in two important attributes: (1) the underlying subpopulation growth potential, defined by the specific age-specific rates of reproduction and mortality used for each scenario; and (2) the extent of connectivity among subpopulations, defined as the rate of dispersal among those subpopulation units.

Results from our analyses suggest that the larger and more central components of the Northwestern Recovery Unit – namely, the Jalisco and Sonora Core Areas – are sufficiently large with regards to both current abundance and habitat carrying capacity to serve as effective source populations for the NRU metapopulation. The Sinaloa Secondary Area, which is thought to support a smaller population that may suffer the ill effects of inbreeding depression, demonstrates less vigorous growth potential, especially when dispersal amongst nearest neighbors is rare. Poaching of jaguars can significantly increase mortality in these Core Areas, which could in turn reduce the number of dispersing individuals received by smaller population units like those in the Borderlands Secondary Area. Dedicated efforts by the jaguar research and management community in estimating the magnitude of poaching-based mortality are an important component of ongoing metapopulation management within the NRU.

Establishing a demographically functional jaguar population in the Borderlands Secondary Area requires northward dispersal of individuals from the Core Areas into habitat of sufficient quality and abundance to promote breeding of resident individuals. The Mexico portion of the BSA, being closer to the Sonora Core Area, has a relatively high probability of housing a resident jaguar population if that Core Area is able to maintain its own demographic stability and if the local habitat distribution facilitates northward dispersal. However, this “established” population will likely comprise no more than 8 – 10 adult females and be highly susceptible to frequent local extinction if dispersal is infrequent. Depending on the assumption used for habitat availability and associated jaguar carrying capacity in the area, this long-term adult female abundance could be reduced by 50% to just a few individuals. Situated even further to the north, the U.S. portion of the BSA has a much lower probability of population establishment through dispersal from the small population that may occupy the Mexico portion of the BSA. Because of the small amount of habitat available in the U.S., a resident population would likely include just 2 – 4 adult females and be even more susceptible to local extinction through unpredictable forces acting on rates of individual reproduction and mortality. It is evident from this analysis that conditions are not currently favorable for establishing a long-term viable population of jaguars in the northernmost portion of the Northwestern Recovery Unit, most likely due to low abundance of jaguars in the Mexico portion of the BSA, relatively low levels of dispersal across the United States - Mexico border, and habitat-mediated limitations to long-term robust population growth in the United States portion of the NRU. If there is a specific desire to facilitate such a process of establishment, directed attention to improving any or all of these limiting factors is an essential step to achieving the long-term goal.

Based on a large-scale view of the analyses reported here, it is likely that existing jaguar populations within the Northwestern Recovery Unit as a whole are currently and can remain viable in the future, given the absence of deleterious impacts of significant threats to individual survival. Populations within the northern reaches of the NRU may be able to expand and become important contributors to metapopulation viability if suitable habitat remains available in sufficient quantity to support a breeding population of adults over time.

Population Viability Analysis for the Jaguar (*Panthera onca*) in the Northwestern Range

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Introduction

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

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

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

The *VORTEX* system for conducting population viability analysis is a flexible and accessible tool that can be adapted to a wide variety of species types and life histories as the situation warrants. The program has been used around the world in both teaching and research applications and is a trusted method for assisting in the definition of practical wildlife management methodologies. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Lacy (2000) and Miller and Lacy (2005).

Review of Existing PVA Work to Date

The population viability simulation project began in January 2011 with a meeting of experts in jaguar biology and habitat ecology, largely comprising the Technical Subgroup of the Jaguar Recovery Team. This meeting was designed to develop an initial consensus dataset for use in the first round of demographic models, and to begin to explore issues around subpopulation viability and the factors influencing persistence of existing core populations and establishment of new populations. This preliminary analysis suggested that jaguar populations in the southern extent of the Northwestern Recovery Unit – namely, those in Jalisco, Sinaloa and southern/central Sonora – are of sufficient size to remain demographically viable as long as some level of dispersal acts to reduce the potentially deleterious effects that inbreeding depression may bring to a small and relatively isolated population. Moreover, this viability is critically dependent on at least minimal opportunities for population growth of key subpopulations in the absence of dispersal so that these areas can act as demographic source populations of dispersing individuals. The strength with which a source population can supply individuals for neighboring regions is critically dependent on its intrinsic capability for growth, itself a function of the threats imposed on it by local human activity. Establishment of a jaguar population along the Borderlands Secondary Area is critically dependent on (i) a demographically robust core source population in Sonora, facilitating the dispersal of individuals both north and south; (ii) the ability of the habitat in northern Sonora to sustain jaguars in the long-term and to provide key dispersal corridors to the international border; and (iii) a permeable border between northern Sonora and the region of Arizona and New Mexico south of the I-10 highway corridor.

Based on these early results and associated discussions among the PVA model development team, a number of key information gaps were identified that focused on the group’s understanding of jaguar abundance, demography, and habitat use in this part of the species’ range. Specific recommendations were developed in an attempt to fill in these gaps and therefore improve the accuracy and utility of future risk assessment efforts.

As new information on jaguar habitat use and suitability emerged from spatial analysis of available data, the Jaguar Recovery Team requested a revised demographic analysis and risk assessment. This report describes the structure of these new analyses, their results, and associated implications.

Primary Questions for PVA Modeling

In light of these new requested analyses, the Jaguar Recovery Team’s Technical Subgroup identified two primary questions for which construction and implementation of updated PVA models could be useful in addressing:

- How stable are core jaguar populations in Sinaloa and Sonora, and how important are they in determining overall metapopulation stability of jaguar subpopulations in the northwestern portion of the species’ range?
- Given a specific level of overall metapopulation growth potential, is there sufficient connectivity among patches of jaguar habitat in the northwestern portion of the species’ range to facilitate the expansion of jaguars into the Borderlands Secondary Area (BSA) (i.e., northern Sonora, southwestern U.S.) of the Northwestern Recovery Unit (Figure 1)?

Baseline Input Parameters for Population Viability Simulation Models

Timestep for all simulations: Since jaguar reproductive ecology is easily described on an annual basis, we have chosen the timestep for our simulations as one year.

Metapopulation structure: For all analyses presented here, we identify a total of five subpopulations that collectively comprise the Northwestern Recovery Unit. Arrayed from south to north, these include the Jalisco Core Area (JCA), the Sinaloa Secondary Area (SSA), the Sonora Core Area (SCA), and the U.S. and Mexico portions of the Borderlands Secondary Area (BSA). These regions are shown in Figure 1.

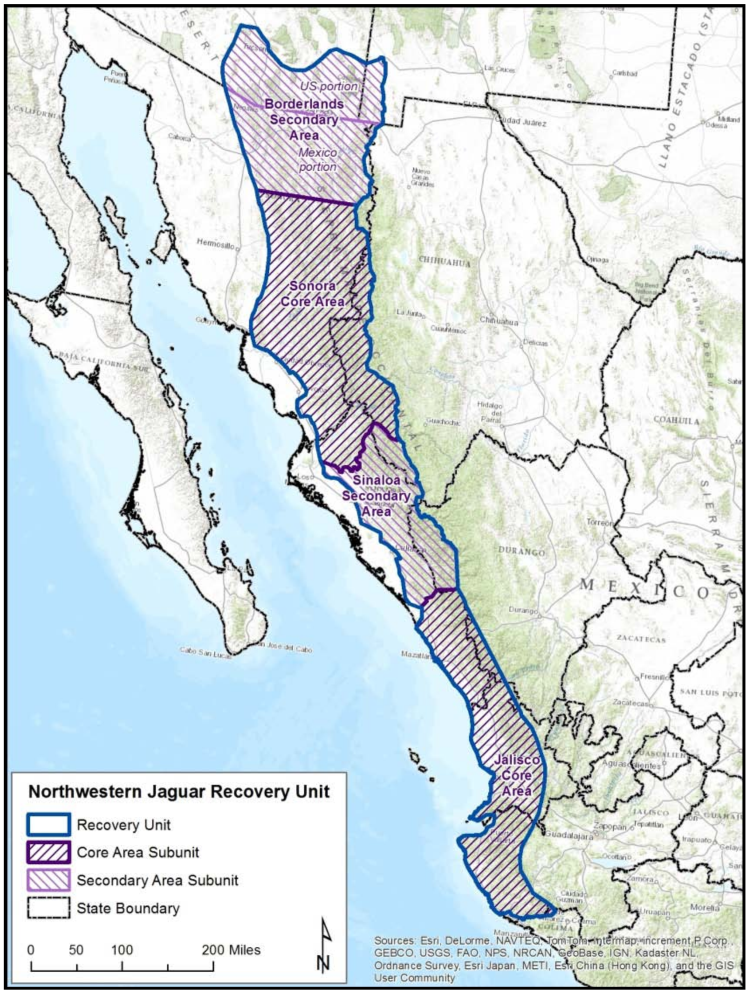


Figure 1. Map of the Jaguar Northwestern Recovery Unit and subpopulation designations used in this PVA.

The characteristics of dispersal, defined in *VORTEX* as the probability that an individual will move from subpopulation X to subpopulation Y in a given year, are a key factor in driving metapopulation dynamics. Based on expert input from the Technical Subgroup, we made the general assumption that dispersal in jaguars is strongly male-biased, with 90% of dispersing animals each year identified as males, on average, in our models. While both males and females are equally capable of dispersing based on physical characteristics, this bias results from a behavioral difference among genders in dispersal tendency (Quigley and Crawshaw 2002). Furthermore, through expert judgment among Technical Subgroup members, we assign dispersal capability only to those individuals that are two to three years old, i.e., those individuals leaving their natal ranges and seeking to establish new territories. We also assume for these models that dispersal is not density dependent, and there is no cost (defined as increased risk of mortality) to dispersal. We recognize that these assumptions may not be valid, but in the absence of specific data on these processes in this species we elected to reduce overall model complexity by not including processes where quantification is highly speculative.

Within Mexico, no physical barriers appear to be operating to limit jaguar dispersal. In contrast, the border region separating Mexico and the southwestern United States – for our purposes, Arizona and New Mexico – acts as a potentially significant obstacle to jaguar movement along segments of its length. The border fence is made up of two distinct types of structures:

- Pedestrian fencing, placed in areas that receive heavy pedestrian traffic and are closely monitored by United States Border Patrol personnel. This fence tends to be a substantial vertical structure, often times a few meters tall, and can act as a major barrier to jaguar movement.
- Vehicle fencing, placed in areas that are more difficult to monitor and which receive less pedestrian traffic. Vehicle fence can often prohibit passage by cars and trucks, but can potentially be porous to animal movement in the absence of disturbance through human presence.

In areas that cannot be monitored and where vehicle traffic is impossible, such as mountainous and especially rugged terrain, there is no fence along the border. These fence-free areas can actually act as a type of funnel to increase local density of people attempting to cross the border; the same phenomenon could act to increase local jaguar population densities along the border. While this may increase human – jaguar interactions, with the possibility of reduced jaguar dispersal across the border, the Technical Subgroup made the assumption that this would not be a significant deterrent to movement as animals could simply cross the border at a time or location that offers less human contact.

We also assume that a small fraction of dispersing individuals is capable of moving longer distances from the SCA to the U.S. portion of the BSA. Taken together, this information allows us to assign a relative rate of dispersal to neighboring subpopulations comprising the metapopulation, assuming that dispersal among neighboring subpopulations in Mexico is given a “reference” annual rate of 1.0 (note that this reflects total rates of dispersal, with the male bias implicit across all rates):

Jalisco Core Area → Sinaloa Secondary Area:	1.0
Sinaloa Secondary Area → Sonora Core Area:	1.0
Sonora Core Area → Borderlands Secondary Area (MX):	1.0
Borderlands Secondary Area (MX) → Borderlands Secondary Area (U.S.):	0.8
Sonora Core Area → Borderlands Secondary Area (U.S.):	0.1

With this as a basic dispersal structure, we developed sets of scenarios where the “reference” dispersal rate was set at 0.25%, 0.5%, 0.75%, and 1.0%.

Under this assumption, an assigned dispersal rate within Mexico of 1.0% leads to a rate across the Borderlands Secondary Area of 0.8% and a rate from the Sonora Core Area to BSA-U.S. of 0.1%. We assume that dispersal is symmetrical, i.e., southward dispersal rates are equal to those describing northward movement.

Finally, unless otherwise specified, we assume based on expert judgment of Technical Subgroup members that demographic rates are equivalent across subpopulations.

Breeding system: Jaguars are known to display a polygynous breeding system (e.g., Cavalcanti and Gese 2009), where a single male may mate with multiple females during a given year. This is simulated in *VORTEX* by allowing adult males to be sampled multiple times as mates for available females.

Age of first offspring: *VORTEX* considers the age of first reproduction as the age at which the first litter of kittens is born, not simply the onset of sexual maturity. We assume that both females and males can breed at three years of age. Males at four years become full grown and defend territory and can be reproductive. However, it's beneficial for males to become reproductive as soon as possible to help establish a territory. Males could be capable of reproduction at two years of age, but three years may be a better estimate than four if they follow the pattern of other large cats. On the other hand, it could take a year for a male to settle into a new territory. This is not a particularly sensitive parameter, as the presence of just a few males will ensure a successful level of breeding among the full complement of females. We do not know of any three-year-old female that has bred in the Northwestern Recovery Unit; despite the absence of such an observation, we maintain that three years is the best estimate for this parameter based on observations in other large cats (Brown and López-González 2001).

Maximum Age of Reproduction: In its simplest form, *VORTEX* assumes that animals can reproduce (at the normal rate) throughout their adult life. The oldest known female in the wild with kittens was observed in Sonora and was estimated at thirteen years of age, based on dentition data (Brown and López-González 2001). While this is set as the maximum age of reproduction, age-specific mortality rates may be set so that the probability of actually reaching this age is quite small.

% Adult Female Breeding: This describes the average proportion of females that reproduce in a year. Mountain lions produce a litter every other year, and this is also thought to be true for jaguars (Cavalcanti and Gese 2009). This translates into an annual probability of breeding of 50% for each adult female.

Litters per year: We assume that an adult female will produce only one litter per breeding cycle, i.e., one litter every other year.

Maximum progeny per litter: We assume that four kittens can be born in a litter. This estimate is derived from data on captive animals observed, and we assume this potential can be realized in the wild.

Offspring sex ratio: Without data to the contrary, we assume that across the entire population, newborn individuals do not deviate from a 50:50 sex ratio.

Density dependent reproduction: *VORTEX* can model density dependence with an equation that specifies the proportion of adult females that reproduce as a function of the total population size. In addition to including a more typical reduction in breeding in high-density populations, the user can also model an Allee effect: a decrease in the proportion of females that breed at low population density due, for example, to difficulty in finding mates that are widely dispersed across the landscape.

The equation that *VORTEX* uses to model density dependence is:

$$P(N) = \left(P(0) - \left[\left(P(0) - P(K)\right)\left(\frac{N}{K}\right)^B\right]\right)\frac{N}{N+A}$$

in which $P(N)$ is the percent of females that breed when the population size is N, $P(K)$ is the percent that breed when the population is at carrying capacity K, and $P(0)$ is the percent breeding when the population is close to zero (in the absence of any Allee effect). The exponent B can be any positive number and determines the shape of the curve relating the percent breeding to population size, as the population becomes large. If $B = 1$, the percent breeding changes linearly with population size. If $B = 2$, $P(N)$ is a quadratic function of N. The parameter A defines the magnitude of the Allee effect.

We assume that there is a reduced frequency of successful breeding as jaguar populations approach maximum long-term equilibrium density (i.e., carrying capacity). If 50% of adult females successfully produce a litter at optimal densities, we assume here that only 35% of adult females are successful when the population is at carrying capacity. This value was derived from expert judgment among Technical Subgroup members in the absence of specific field data on this parameter. This reduction in breeding occurs only at rather high densities; this is reflected in a steepness parameter, *B*, in the density dependence equation equal to 16. Finally, Allee effects are assumed to be absent for this species. Taken together, these data result in a density dependence function of the form shown in Figure 2.

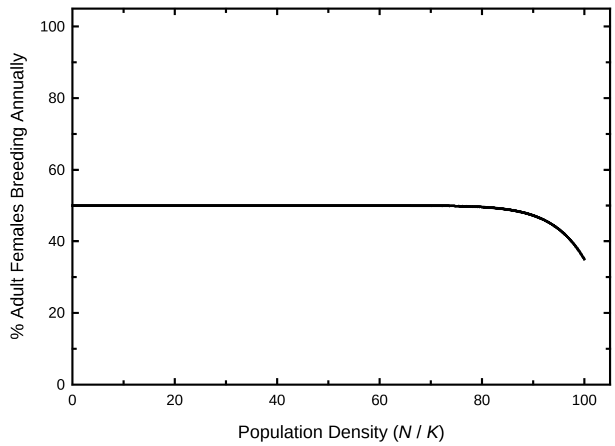


Figure 2. Functional form of density dependence in reproductive rate among adult jaguar in simulation models used in this analysis. Rate defined as the percentage of adult females breeding in a given year, with reduced rate at higher population density and the absence of an Allee effect impacting reproduction at low density.

<u>Environmental Variation (EV) in % Breeding</u>: Annual environmental variation in female reproductive success is modeled in *VORTEX* by specifying a standard deviation (SD) for the proportion of adult females that successfully produce offspring in a given year. In the absence of specific data on this parameter, we assume based on expert judgment among Technical Subgroup members that the variation is equal to 10%, thereby producing a full distribution of female breeding rates of 30% - 70% (mean ± 2SD). This is thought to be reasonable for variability in reproductive success for this species.

<u>Distribution of Litter Size</u>: Table 1 below gives the probability of a given breeding female producing a litter of the specified size. These values are based on expert judgment among Technical Subgroup members in the absence of specific field data for the species in the northern portion of its range.

Table 1. Estimated distribution of litter sizes among successfully reproducing adult female jaguars used in simulation models.

Number of offspring	Probability (%)
1	45
2	45
3	5
4	5

The one exception to this specification is the Mexico portion of the Borderlands Secondary Area, where the very low population abundance observed recently by López-González and others suggests some demographic factor limiting population growth. Specific data to explain this observation are lacking; expert judgment among Technical Subgroup members was used to suggest that reduced litter size is a primary factor. Therefore, we assume that in the Mexico portion of the Borderlands Secondary Area 85% of adult females produce just one kitten per year and 15% produce two kittens.

Mate monopolization: In many species, some adult males may be socially restricted from breeding despite being physiologically capable. This can be modeled in *VORTEX* by specifying a portion of the total pool of adult males that may be considered "available" for breeding each year. We assume here that each 3-year-old male has an opportunity to breed, even wandering males without territories. Therefore, we assume that 100% of the adult males have an opportunity to breed in a given year.
Mortality Rates: *VORTEX* defines mortality as the annual rate of age-specific death from year x to $x + 1$; in the language of life-table analysis, this is equivalent to $q(x)$. We assume that our model, intended to reflect the current Sonora Core Area population, will include the effects of human poaching in the age-specific mortality rates.

Very little quantitative data exist on population size trends for each of the subpopulations analyzed here. The best information comes from Sonora, where there is evidence to suggest that the population in the region studied by Carlos López-González is probably undergoing a slight decline in abundance over the period of observation in the past decade or, at best, maintaining a stable abundance (neither growing nor declining). Therefore, we have back-calculated an age-specific mortality schedule that, when including the reproductive parameters discussed above, will lead to a trajectory in population abundance within *VORTEX* that recreates the observed trajectory over the period of the simulation. This schedule is given in Table 2.

Table 2. Estimated annual mortality rates (with standard deviations representing environmental variation in parentheses) among age-sex classes of jaguars as used in simulation models.

	Mortality Rate (%) (SD)	
Age (years)	Female	Male
0 – 1	25.0 (6.0)	25.0 (6.0)
1 – 2	20.0 (4.0)	20.0 (7.0)
2 – 3	25.0 (5.0)	35.0 (9.0)
3 – 5	10.0 (3.0)	25.0 (5.0)
5 – 7	15.5 (3.0)	25.0 (5.0)
7 – 10	21.0 (3.0)	25.0 (5.0)
10+	26.5 (3.0)	25.0 (30)

Other models (described in more detail below) assume different levels of subpopulation growth, which we define here in terms of different levels of age-specific mortality. In other words, mortality schedules are adjusted to generate alternative scenarios with specific anticipated long-term annual population growth rates of 0.000, 0.005, 0.010, 0.015, and 0.020.

Inbreeding Depression: *VORTEX* includes the ability to model the detrimental effects of inbreeding, most directly through reduced survival of offspring through their first year. The metric used to describe the magnitude of inbreeding effects involves the concept of lethal equivalents, defined by Morton et al. (1956) as the average number of lethal genetic variants (alleles) per individual in the population of interest, if all deleterious effects of inbreeding were due entirely to recessive lethal genes. For example, a population in which the severity of inbreeding depression is estimated as one lethal equivalent may have one recessive lethal allele per individual, or it may have two recessive alleles, each of which confer a 50% decrease in survival. While specific data on inbreeding depression in either captive or wild jaguar populations were not available for this analysis, the preponderance of evidence for the deleterious impacts of inbreeding in mammal populations suggests that it can be a real factor in small populations. We therefore elected to include this process in our models, with a genetic load of 3.14 lethal equivalents, and with approximately 50% of this load expressed as lethal genes. These values are in accordance with the median value of inbreeding depression severity calculated for captive mammal populations assessed by Ralls et al. (1988).

Catastrophes: Catastrophes are singular environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival. Natural catastrophes can be tornadoes, floods, droughts, disease, or similar events. These events are modeled in *VORTEX* by assigning an annual probability of occurrence and a pair of severity factors describing their impact on mortality (across all age-sex classes) and the proportion of females successfully breeding in a given year. These factors range from 0.0 (maximum or absolute effect) to 1.0 (no effect), and in its most basic implementation in *VORTEX*, are imposed during the single year of the catastrophe, after which time the demographic rates rebound to their baseline values.

As of this stage in the long-term development of this PVA effort, we have not included any type of catastrophic event in our model. Specifically, long-term drought could be a significant factor that reduces jaguar prey population abundance and, by extension, jaguar demographic stability. Long-term changes in climate may also impact jaguar populations, perhaps by increasing prey population densities and thereby having a beneficial effect on jaguar demography. Of course, a modified climate may also introduce negative impacts such as increased risk of disease introduction and transmission, reducing jaguar demographic viability. Future research on better estimating frequency and severity of proposed catastrophic events could bring valuable improvements to existing jaguar PVA efforts.

Initial Population Size: Relatively little data exist on current abundance of jaguars in the region studied here. Based on survey estimates derived from recent efforts by Mexican government agencies, and recent research conducted in Sonora by López-González and in Jalisco by Nuñez, we derived estimates of current population abundance for each of the regions under consideration. These are shown in Table 3 below. Note that the Mexico portion of the Borderlands Secondary Area is initially composed of males as current research efforts have been unsuccessful in observing any females in the area. The abundance estimate for this population is derived from observations of the number of jaguars observed in the area over the past 15 years.

Carrying capacity: How close is a given subpopulation to its maximum, long-term equilibrium abundance – is there an opportunity for the population to grow to a larger size? If poaching is a factor in our mortality schedule, we assume the population would increase if poaching pressure were relaxed. Estimates of carrying capacity for each subpopulation were estimated using a habitat modeling approach (see Sanderson and Fisher 2012 for a more complete description). Data layers including vegetation, terrain roughness, distance to water, and exclusion of urban, rural and agricultural areas were used to produce a simple habitat model. Because of the cross-boundary nature of the exercise, only data inputs that were uniformly mapped across the entire NRU were used. The layers were combined following a modification of the Hatten et al. (2005) method developed in concert with the Recovery Team. These continuous habitat variables were binned into discrete categories and then the distribution of events across the categories were examined to determine which categories of variables were significant to jaguars. Layers were then combined according to the equation:

Jaguar Potential Habitat Score =
[Tree cover (1-50% north / 1-100% south)] + [intermediate, moderate, and high ruggedness] (0-2)
*
[Within 10km of water] (0-1)
*
[Elevation <= 2000 m] (0-1)

$$*$$
$$\text{[Potential habitat type weight] (0.08-4.57)}$$

The Hatten et al. (2005) method was modified to include a weight according to potential habitat type, to represent the Technical Subgroup's sense of the suitability of different habitat types in terms of prey and cover. This weight represents the wider range of habitat types that occur over the Northwestern Recovery Unit. This analysis produced a habitat suitability map for the full NRU.

Finally, the jaguar suitability map was rescaled to represent carrying capacity for jaguars by placing seven known adult jaguar density estimates from existing study areas, calculating the average suitability in those study areas, and then creating a regression between the habitat suitability scores and the density estimates. From this, estimates of potential adult jaguar carrying capacities (*K*) for each of the NRU sub-units were calculated, corresponding to the metapopulation model structure presented earlier. It is important to note that *VORTEX* requires carrying capacity values to be expressed in terms of the total population size immediately before breeding takes place, i.e., all individuals one year of age and older. Therefore, these estimates of *K* based on adults were converted to a total carrying capacity for all individuals at least one year of age for use in the *VORTEX* model. Analyses of the stable age distribution in baseline models (not shown here) indicated that adults typically comprise approximately 60% of a simulated jaguar population. Final *K* estimates were then scaled upwards by dividing the estimates derived from the habitat model by 0.60.

Habitat model Versions 12 (31 July, 2012) and 13 (2 August, 2012) differ in that the regression equation for Version 12 did not force the y-intercept through zero, while the intercept for Version 13 was forced through zero. This was at the request of Jaguar Recovery Team members attending the July / August 2012 Recovery Team meeting, based on their assessment of the lowest-quality habitat requiring a jaguar density designation of 0.0 animals/km^2.

Table 3. Estimated values of initial abundance N_0 and carrying capacity K for each simulated subpopulation evaluated in this analysis. Carrying capacity values are expressed in terms of both adult abundance and overall population abundance, under alternative assumptions of habitat models developed in parallel with this PVA effort (see Sanderson and Fisher 2012 for more information on model assumptions).

		K_{Adults}		K_{Total}	
Subpopulation	N_0	Model 12	Model 13	Model 12	Model 13
Jalisco Core Area	350[a]	1342	1318	2237	2197
Sinaloa Secondary Area	100[a]	949	929	1582	1548
Sonora Core Area	300[b]	1181	1124	1968	1873
Borderlands Secondary Area – MX	12*[b]	66	37	110	62
Borderlands Secondary Area – U.S.	0	31	5	52	8

* Males only
[a] Nuñez, pers. comm..
[b] López – González, pers. comm..

<u>Iterations and Years of Projection</u>: All population projections (scenarios) were simulated 1000 times, with each projection extending to 100 years. All simulations were conducted using *VORTEX* version 9.99b (May 2010) (Lacy et al. 2005; Miller and Lacy 2005).

Results from Simulation Models

In review, the metapopulation scenarios presented below focus on varying two sets of input parameters:

- Baseline male and female mortality rates to create approximate stochastic growth rates for each subpopulation within the NRU of r_s = 0.000, 0.005, 0.010, 0.015, or 0.020. These modifications represent underlying assumptions regarding the intrinsic demographic robustness of a given subpopulation as defined by the opportunity for growth of that subpopulation over time.
- Rates of dispersal among subpopulations (while maintaining the relative rates across the metapopulation). Reference annual dispersal rates – those among subpopulations within Mexico – are set at 0.25%, 0.5, 0.75%, or 1.0%. Dispersal rates across the international border and from the Sonora Core Area to the U.S. portion of the Borderland Secondary Area are then adjusted accordingly based on the information described in the previous subsection on model input parameters.

All scenarios discussed below use the habitat carrying capacities calculated from WCS habitat model Versions 12 and 13.

<u>NRU metapopulation stability</u>

Under all scenarios of underlying stochastic growth and subpopulation dispersal rates, the Jalisco and Sonora Core Areas and the Sinaloa Secondary Area maintained expected levels of demographic stability and were under no significant risk of subpopulation extinction over the 100-year timeframe of the simulations (e.g., Figure 3). The Sinaloa Secondary Area has a slightly lower rate of growth despite its connection to both Core Areas, a likely consequence of greater impact of demographic variability and low

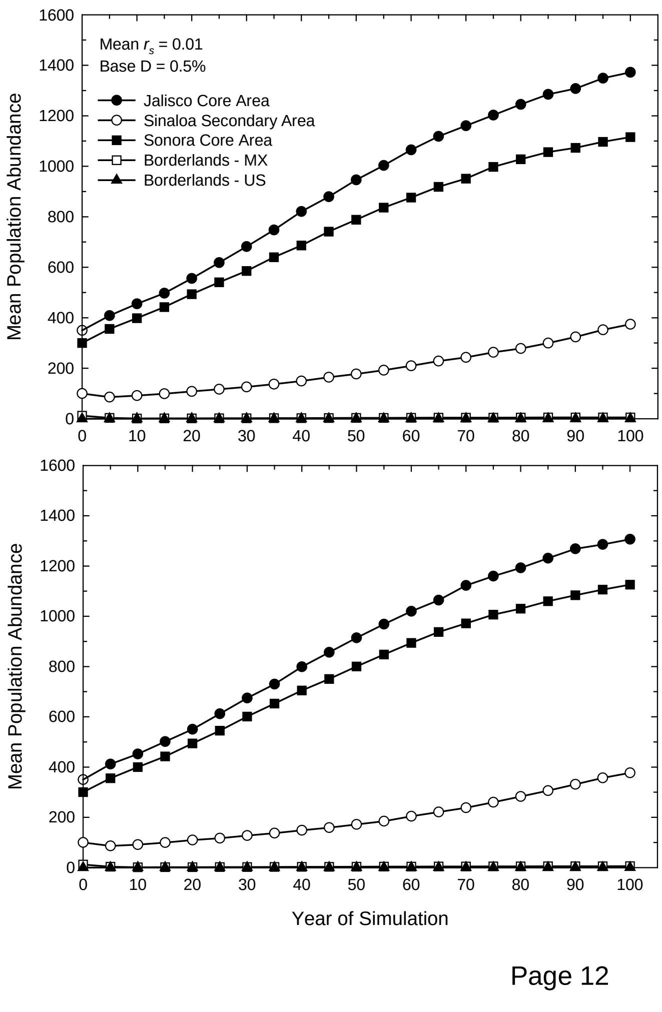


Figure 3. Mean abundance trajectories for simulated jaguar subpopulations within the Northwestern Recovery Unit, assuming a long-term stochastic population growth rate (r_s) of 0.010 and a base annual dispersal rate among subpopulations of 0.5%. Habitat carrying capacities calculated using habitat model 12 (top panel) and model 13 (bottom panel). See accompanying text for additional information on model structure and input data.

levels of inbreeding depression. Both the Mexico and U.S. portions of the Borderlands Secondary Area, starting the simulation as either composed of only males or unoccupied, show very small abundance values through low levels of dispersal from the southern units.

Both Core Areas show very similar abundance trajectories if habitat carrying capacities are calculated as per habitat model 13. This is due to the fact that, with the exception of the Borderlands Secondary Areas astride the international border, the habitat carrying capacity values farther south in Mexico are nearly identical.

The results displayed in Figure 3 represent scenarios featuring intermediate levels of both dispersal among subpopulations and underlying stochastic population growth rates. If population growth is not as robust, and if these populations become more demographically isolated, individual subpopulations may become more unstable in the longer term. For example, if all subpopulations are assumed to be isolated so that no dispersal is included in our models, and if the underlying growth rate is assumed to be just 0.0 per year – representing a population that, on average, is expected to neither grow nor decline over the time period of the simulation – and if we assume habitat carrying capacity estimates as per habitat model 12, the Sinaloa Secondary Area shows a 29% risk of declining to extinction within 100 years (Figure 4). [Note that results would be functionally identical if habitat model 13 was used as our estimate of K for the Sinaloa Secondary Area and surrounding populations are very similar in the two models.] This risk is significant in part because of the small initial size of the SSA population and the detrimental demographic impacts of inbreeding depression in the absence of introgression of unrelated animals over time. Even low levels of connectivity to the neighboring Core Areas greatly reduce this risk, demonstrating the importance of maintaining habitat connectivity among subpopulation units whenever possible.

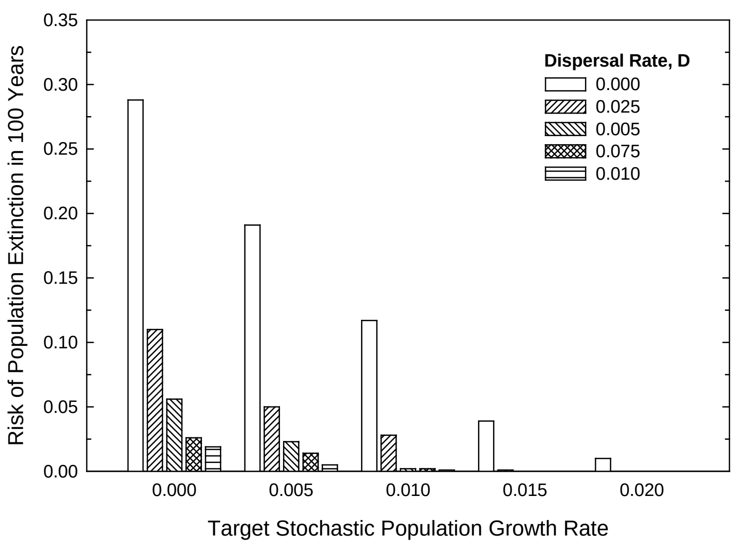


Figure 4. Extinction risk among simulated jaguar populations inhabiting the Sinaloa Secondary Area of the Northwestern Recovery Unit, as a function of underlying stochastic growth rate of the population. Individual bars depict mean annual rates of dispersal expected among subpopulations within the Unit. Habitat carrying capacities calculated as per habitat model 12. See accompanying text for information on model structure and input data.

Our results suggest that these larger Jalisco and Sonora Core Area populations are sufficiently large in both current abundance and habitat carrying capacity to serve as effective source populations for the metapopulation that defines the NRU. It is important to recognize, however, that some elements of overall metapopulation stability could be negatively impacted with a reduction in the long-term growth potential of either of these core units. The Core Areas, as with many similar populations throughout Mexico as well as those across the species' range, are threatened with increased mortality through hunting by ranchers and other types of people whose personal or professional security is thought to be compromised by the nearby presence of jaguars. It may therefore be instructive to investigate the demographic impact of additional mortality on the demographic stability of core jaguar populations in Jalisco and Sonora. To conduct this analysis, a new set of scenarios was created where the baseline mortality values for individuals of age 2+ were increased by 10% or 20% of their original value to simulate additional removal of individuals through hunting. This mortality is considered to be above and beyond the level that is assumed to already be included in our baseline mortality rates entered into our models. For example, if the baseline mortality for a 2-year-old male is assumed to be 30%, a 10% hunting scenario would raise that mortality rate to (30%)(1.1) = 33%. Given an initial abundance in the Jalisco Core Area of 350 individuals, and a knowledge of the population's stable age distribution calculated within *Vortex* as a function of the underlying fecundity and survival schedules used as model input, a 10% hunting rate applied to all individuals age 2+ roughly equates to approximately 27 animals removed in that year – approximately 7.7% of the total population in a pre-breeding population census (i.e., all individuals age one year and up). By extension, a 20% hunting rate would remove, on average, about 50-55 animals from that same starting population. Males and females of the appropriate age were assumed to be equally susceptible to this additional hunting mortality. We tested scenarios in which we assumed that the additional hunting pressure would be restricted to the Jalisco or Sonora Core Areas, or would occur at equivalent levels in both populations units (Table 4).

Table 4. Long-term stochastic growth rates (r_s) for the Jalisco and Sonora Core Areas, and for the overall metapopulation defined here as the Northwestern Recovery Unit, in the presence of increased mortality rates through increased hunting intensity by local human populations. Underlying annual stochastic growth rate is expected to be 0.02, and the base metapopulation annual dispersal rate among population units is 1.0%. In each cell, the first value is from models using habitat carrying capacities estimated from habitat model 12, while the second value uses carrying capacities estimated from habitat model 13. See accompanying text for additional information on model structure and input data.

		Additional Annual Hunting Rate		
Hunting Scenario	**Subpopulation**	**0%**	**10%**	**20%**
Jalisco Core Area	Jalisco	0.024 / 0.024	0.016 / 0.016	0.005 / 0.005
	Sonora	0.024 / 0.024	0.024 / 0.024	0.024 / 0.024
	Metapop	0.026 / 0.025	0.022 / 0.023	0.020 / 0.020
Sonora Core Area	Jalisco	0.024 / 0.024	0.024 / 0.024	0.024 / 0.024
	Sonora	0.024 / 0.024	0.016 / 0.016	0.004 / 0.005
	Metapop	0.026 / 0.024	0.023 / 0.023	0.021 / 0.021
Jalisco and Sonora	Jalisco	0.024 / 0.024	0.016 / 0.016	0.006 / 0.005
	Sonora	0.024 / 0.024	0.016 / 0.016	0.005 / 0.005
	Metapop	0.026 / 0.024	0.019 / 0.019	0.013 / 0.013

As expected, additional hunting pressure imposed on these Core Areas resulted in a marked decrease in that population unit's long-term growth rate (Table 4). A 10% hunting rate results in a 33% reduction in mean stochastic growth rate from 0.024 in the absence of additional hunting to 0.016 when hunting mortality is added. The growth rate declines by an additional 50-75% when the total added hunting mortality is increased to 20%. Overall, however, metapopulation growth is not as strongly affected, even in this particular example where we are starting with the highest underlying growth rate among populations (r_s = 0.02) and with the highest metapopulation dispersal rate (1.0%). As expected, given the small differences in carrying capacity between the two habitat models assessed here, the impacts of additional hunting mortality are virtually identical when either habitat model 12 or model 13 is used in the simulations.

A more detailed analysis, however, shows greater instability in selected components of the metapopulation in these hunting threat scenarios. Specifically, the Mexico portion of the Borderlands Secondary Area – initiated with just twelve males and which is the link to the U.S. portion of the BSA – can be significantly affected by reduced demographic stability of the Core Areas, particularly the Sonora Core Area (Figure 5).

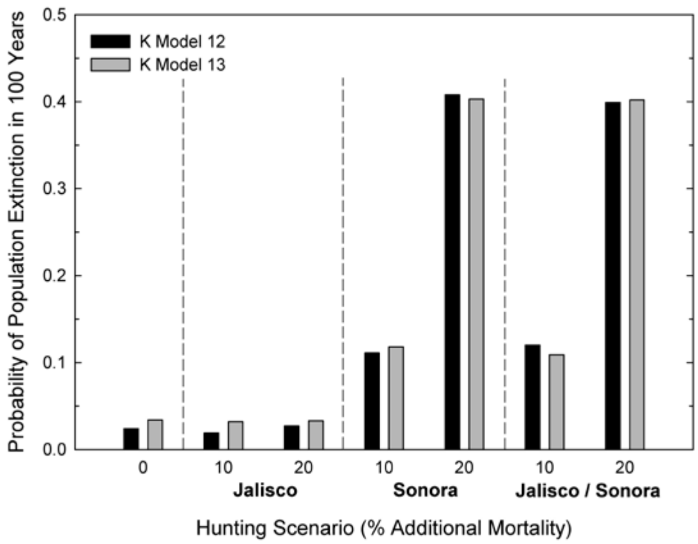


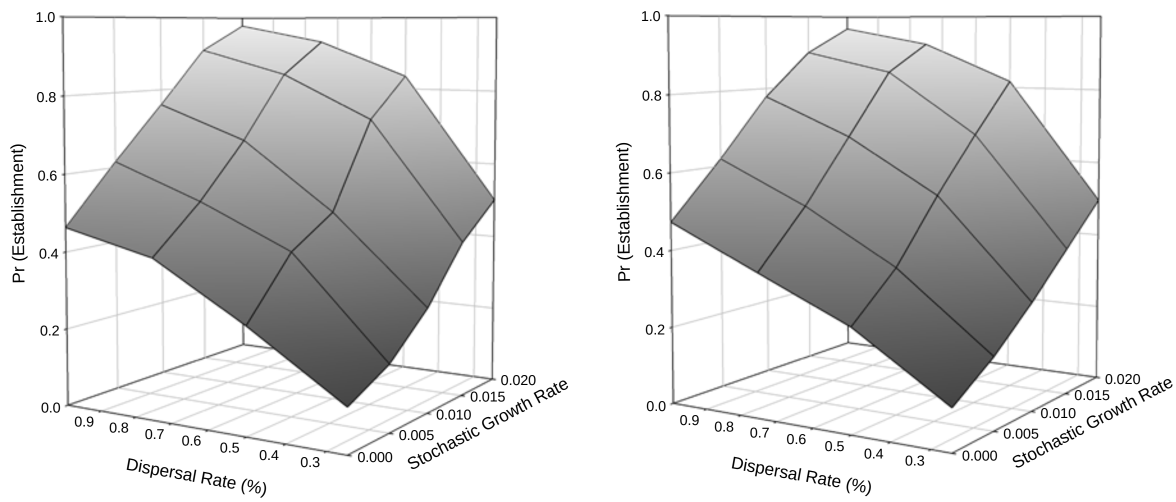
Figure 5. Probability of extinction in the Mexico portion of the Borderlands Secondary Area of the Northwestern Recovery Unit, assuming a long-term stochastic population growth rate (r_s) of 0.020 and a base annual dispersal rate among subpopulations of 1.0%. Additional mortality, assumed to arise from increased human hunting pressure, is imposed on baseline mortality rates within the Jalisco Core Area, the Sonoran Core Area, or both units simultaneously. See accompanying text for additional information on model structure and input data.

Additional hunting pressure imposed on the Jalisco Core Area has little if any impact on persistence of the Mexico portion of the BSA. This is not surprising, given that the Mexico portion of the BSA is near the northern extent of the NRU, is linked closely to the comparatively large Sonora Core Area, and is separated from the Jalisco Core Area by a large distance. In contrast, additional hunting pressure imposed on the Sonora Core Area leads to a dramatic increase in the likelihood of extinction in the Mexico portion of the BSA – nearly a 10-fold increase when 20% additional hunting pressure is imposed on the core population unit. Again, this is expected as the Sonora Core Area is the sole source of animals dispersing northwards to the Mexico portion of the BSA. A sharp reduction in the abundance of animals within this unit is likely to significantly reduce the opportunity for animals to move north and establish a viable population in northern Sonora (Mexico portion of the BSA). This analysis suggests the importance of maintaining a robust population source in Sonora if the goal is to improve the prospects for northward expansion of jaguars to the U.S. – Mexico border and into Arizona and New Mexico.

<u>Population establishment in the northern portions of the Northwestern Recovery Unit</u>

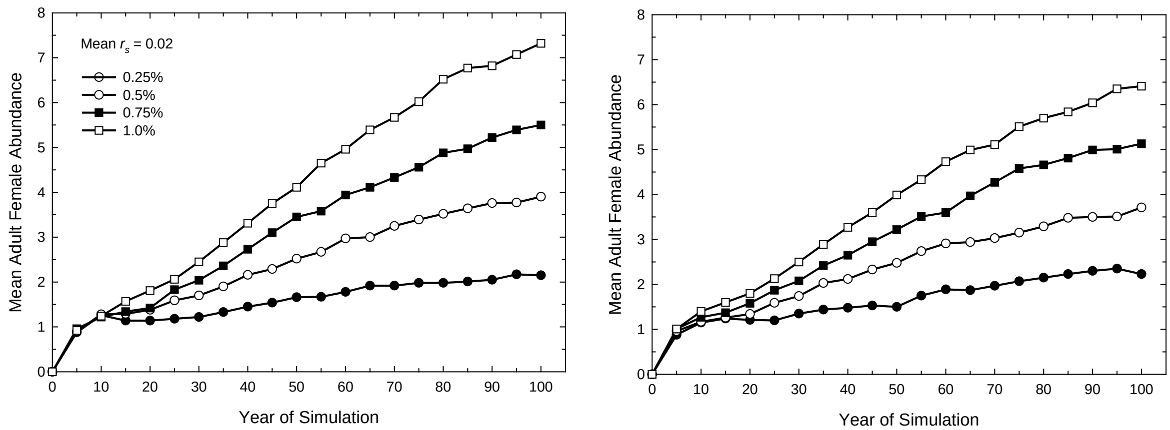
The likelihood of establishing a viable population of jaguars in the northern reaches of the Northwestern Recovery Unit is critically dependent on both the extent of robust population growth in the core regions to the south, and on the degree of connectivity between the population units. This is clearly evident in Figure 6, which shows dependence of establishment in the Mexico portion of the BSA. Under minimum estimates of demographic strength and connectivity, the probability of establishing a population within the Mexico portion of the BSA is just 10% in the 100-year timeframe of the simulation (the lowest corner of the surface). This probability increases to about 50% if either demographic strength or dispersal are held constant at their minimum value and the other variable is allowed to increase to its maximum. At the most optimistic estimate of both parameters, the probability of establishment approaches 96 – 97%. These results suggest that both demographic strength within populations and connectivity between populations contribute significantly to northern Sonora (Mexico portion of the BSA) population establishment. Also note that the risk profile for population establishment in the Mexico portion of the BSA is not functionally dependent on the carrying capacity within the habitat, as in both habitat models the value of *K* remains considerably higher than the total population size occupying the unit's habitat (see below). It is important to remember that the forces that are apparently limiting the growth of jaguars in this unit at present are largely unknown; we may therefore take the results shown in Figure 6 to be optimistic since the analyses do not specifically factor in these limiting forces. Nevertheless, we can use these analyses to gain understanding of the ways in which demographic strength within population units and connectivity between units interact to influence establishment.

Figure 6. Three-dimensional surface plots displaying the probability of establishing a population of jaguar in the Mexico portion of the Borderlands Secondary Area of the Northwestern Recovery Unit, as a function of underlying demographic characteristic defined by stochastic population growth rate in each population unit and base metapopulation dispersal rate. Habitat carrying capacities calculated by habitat model 12 are used in the left panel, and those from habitat model 13 are used in the right panel. Darker shades on the probability surface indicate lower probabilities of population establishment, while lighter shades indicate higher probabilities. See accompanying text for additional information on model structure and input data.



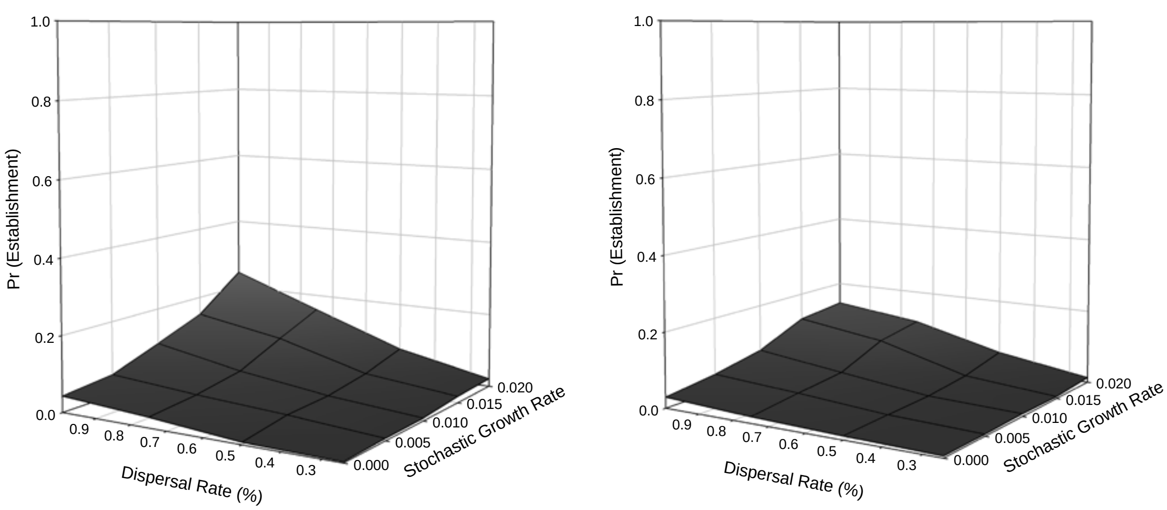
While the probability of establishing a population in the Mexico portion of the Borderlands Secondary Area may be quite high under optimal circumstances, this analysis says nothing about the size of that population if it is established. The trajectories shown in Figure 7 indicate that, even under the highest estimates of within-population demographic strength and between-population demographic connectivity, extant populations within this unit are comprised of only a small handful of adult females. This result suggests that there is likely a relatively high turnover rate among individuals that may not be diagnostic of a population that is viable in the long term.

Figure 7. Mean adult female abundance in the Mexico portion of the Borderlands Secondary Area under an assumed long-term stochastic population growth rate r_s of 0.02 and under different mean rates of dispersal to and from the Sonora Core Area. Habitat carrying capacities calculated by habitat model 12 are used in the left panel, and those from habitat model 13 are used in the right panel. The trajectories are means for only those iterations where the Mexico portion of the Borderlands Secondary Area population was extant at a given point in time. See accompanying text for additional information on model structure and input data.



The situation is magnified when we consider the northernmost portion of the Northwestern Recovery Unit – the U.S. portion of the Borderlands Secondary Area. Since this region is significantly smaller than the Mexico portion of the BSA, and is linked to the NRU only through that same already sparsely populated unit, we might expect that the prospects for establishing a population in the United States may be quite low (Figure 8).

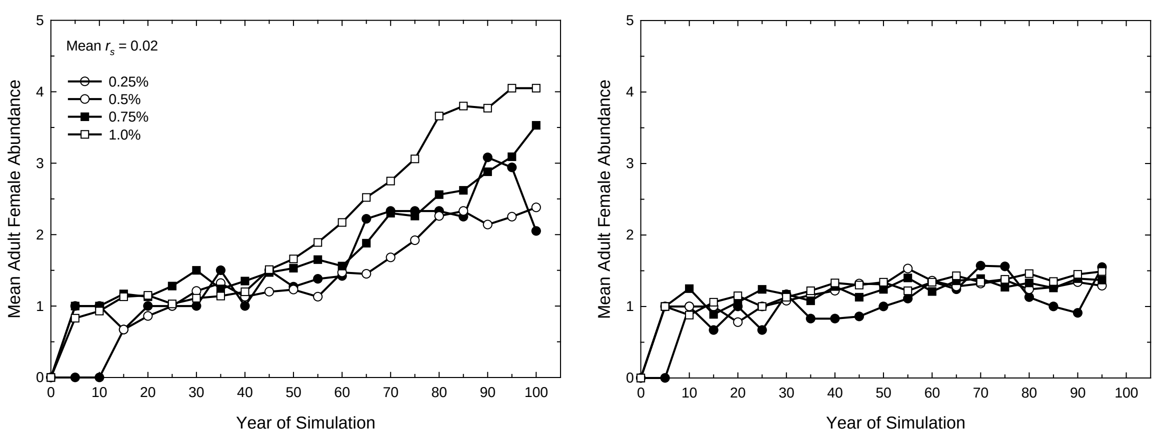
Figure 8. Three-dimensional plots displaying the probability of establishing a population of jaguars in the U.S. portion of the Borderlands Secondary Area of the Northwestern Recovery Unit, as a function of underlying demographic characteristic defined by stochastic population growth rate in each population unit and base metapopulation dispersal rate. Habitat carrying capacities calculated by habitat model 12 are used in the left panel, and those from habitat model 13 are used in the right panel. Darker shades on the probability surface indicate lower probabilities of population establishment, while lighter shades indicate higher probabilities. See accompanying text for additional information on model structure and input data.



The results in Figure 8 confirm our expectations. The likelihood of establishing a population in this northernmost unit is typically very small, even under more optimistic combinations of within-population demographic strength and between-population connectivity. The most optimistic combination of these parameters leads to a likelihood of jaguar population establishment of between 14% and 24%, depending on the assumptions around carrying capacity in this and other population units as discussed above. Moreover, an "established" population within this unit is typically composed of just 2-4 adult females under the larger carrying capacity estimates derived from habitat model 12, and just 1-2 females under the assumptions of habitat model 13 (Figure 9). In fact, the results under habitat model 13 suggest that the adult female population abundance observed in the simulations represents the maximum attainable under the proposed habitat restrictions in this portion of the BSA as defined in this set of scenarios.

It is evident from this analysis that conditions are not currently favorable for establishing a long-term viable population of jaguars in the northernmost portion of the Northwestern Recovery Unit, most likely due to low abundance of jaguars in the Mexico portion of the BSA, relatively low levels of dispersal across the United States - Mexico border, and habitat-mediated limitations to long-term robust population growth in the United States portion of the NRU. If there is a specific desire to facilitate such a process of establishment, directed attention to improving any or all of these limiting factors is an essential step to achieving the long-term goal.

Figure 9. Mean adult female abundance in the U.S. portion of the Borderlands Secondary Area under an assumed long-term stochastic population growth rate r_s of 0.02 and under different mean rates of dispersal to and from the Sonora Core Area and Mexico portion of the BSA. Habitat carrying capacities calculated by habitat model 12 are used in the left panel, and those from habitat model 13 are used in the right panel. The trajectories are means for only those iterations where the U.S. portion of the Borderlands Secondary Area population was extant at a given point in time. See accompanying text for additional information on model structure and input data.



Conclusions

Our models suggest that jaguar populations in the southern extent of the Northwestern Recovery Unit – namely, those in the Jalisco and Sonora Core Areas – are of sufficient size to remain demographically viable as long as they demonstrate some capacity for dispersal among units in order to reduce the potentially deleterious effects that inbreeding depression may bring to small and relatively isolated populations. This viability is critically dependent on the presence of at least minimal levels of growth of key subpopulations so that these areas can act as demographic source populations of dispersing individuals. The strength with which a source population can supply individuals for neighboring regions is critically dependent on its intrinsic capability for growth, itself a function of the threats imposed on it by local human activity. Additional mortality in these core areas, most likely through the process of hunting of jaguars by local human populations, may reduce the probability of expanding jaguar populations into the northernmost reaches of the Northwestern Recovery Unit, especially when this hunting mortality is focused on the critical Sonora Core Area that feeds the Mexico and U.S. portions of the Borderlands Secondary Area. Establishment of a jaguar population in the Mexico and U.S. portions of the BSA is critically dependent on (i) a demographically robust core source population in Sonora, facilitating the dispersal of individuals both north and south; (ii) the ability of the habitat in northern Sonora (Mexico portion of the BSA) to sustain jaguars in the long-term and to provide key dispersal corridors to the international border; and (iii) a permeable border between the Mexico and U.S. portions of the Borderlands Secondary Area.

The issue of long-term viability of populations in the Borderlands Secondary Area appears to be tightly linked to our estimates of suitable habitat availability in this region. Therefore, the choice of habitat model and the associated estimate of subpopulation-specific jaguar carrying capacity may be an important consideration in future jaguar metapopulation planning. Specifically, the most recent version 13 of the WCS habitat model leads to low estimates of available habitat and jaguar carrying capacity in the Borderlands Secondary Area, especially in the U.S. portion. While model version 12 also features relatively low estimates of these parameters, leading to optimistic demographic projections of less than a dozen adult female jaguars occupying the entire Borderlands area over the long term, the more restrictive model 13 yields a projection that is smaller still. Even with these small but meaningful differences between models, the choice of which habitat model to adopt as the baseline standard should be accompanied by a clear justification in support of that choice.

Based on a large-scale view of the analyses reported here, it is likely that existing jaguar populations within the Northwestern Recovery Unit as a whole are currently and can remain viable in the future, given the absence of deleterious impacts of significant threats to individual survival. Populations within the northern reaches of the NRU may be able to expand and become important contributors to metapopulation viability if suitable habitat remains available in sufficient quantity to support a breeding population of adults over time.

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