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

Report prepared by

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In consultation with

Technical Subgroup
U.S. Fish and Wildlife Service Jaguar Recovery Team

Prepared for

U.S. Fish and Wildlife Service
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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.

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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

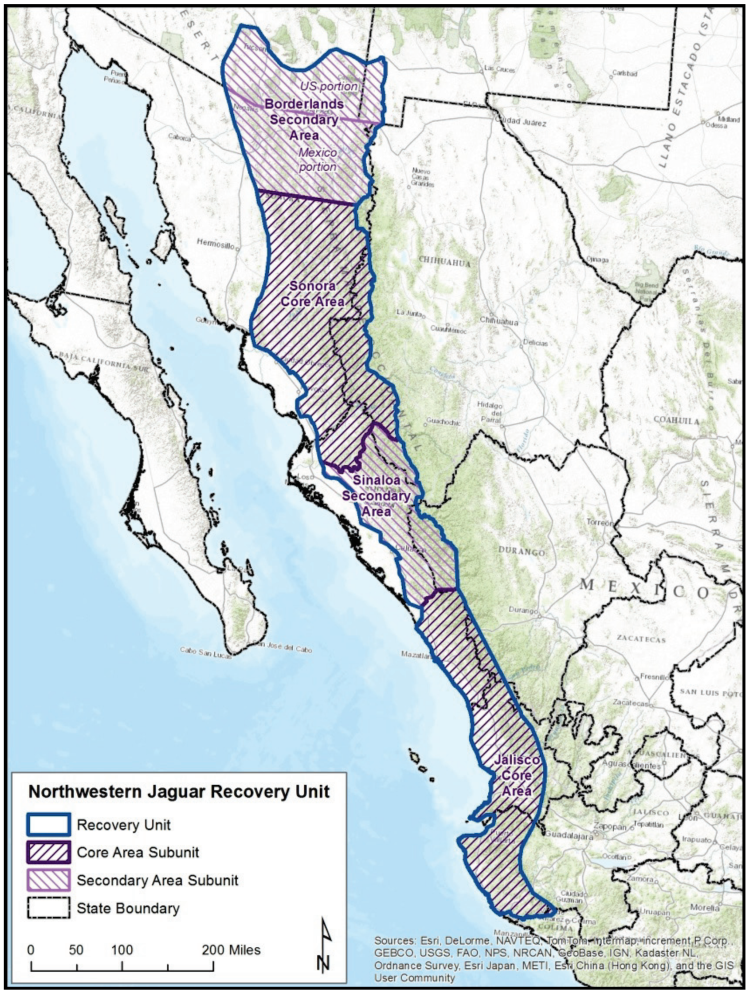
In light of these new requested analyses, the Jaguar Recovery Team's Technical Subgroup identified two primary questions for which construction and implementation of updated PVA models could be useful in addressing:

- 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.



Sources: Esri, DeLorme, NAVTEQ, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), and the GIS User Community

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.

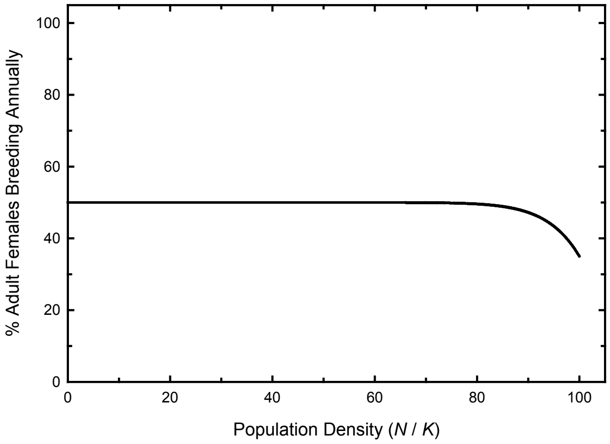


Figure 2. Functional form of density dependence in reproductive rate among adult jaguar in simulation models used in this analysis. Rate defined as the percentage of adult females breeding in a given year, with reduced rate at higher population density and the absence of an Allee effect impacting reproduction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

Environmental Variation (EV) in % Breeding: 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.

Distribution of Litter Size: 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)

$$*$$

[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..

Iterations and Years of Projection: 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 the jaguar habitat model versions 12 and 13.

NRU metapopulation stability

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

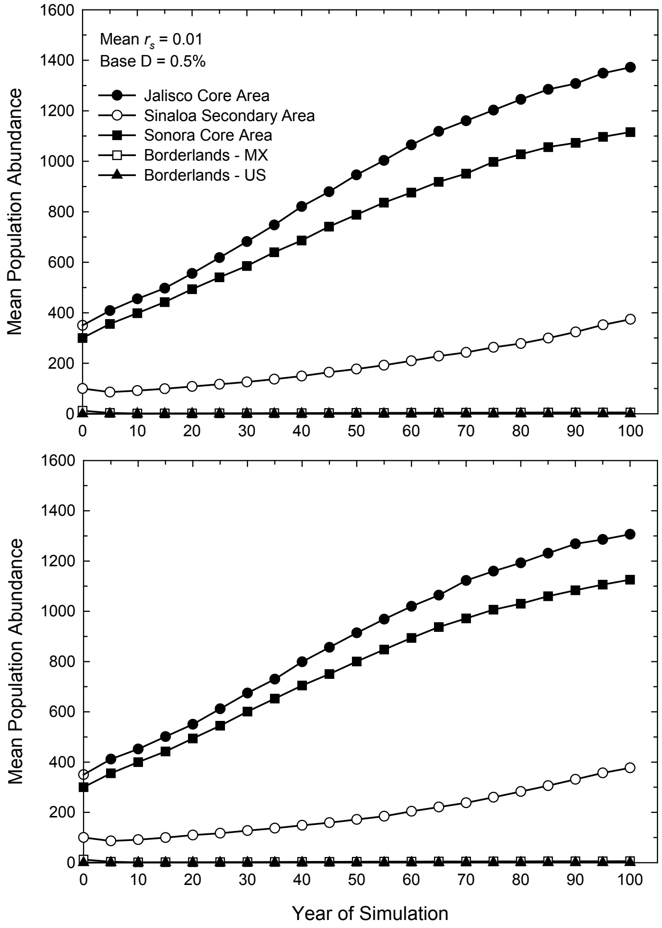


Figure 3. Mean abundance trajectories for simulated jaguar subpopulations within the Northwestern Recovery Unit, assuming a long-term stochastic population growth rate (r_S) of 0.010 and a base annual dispersal rate among subpopulations of 0.5%. Habitat carrying capacities calculated using habitat model 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.

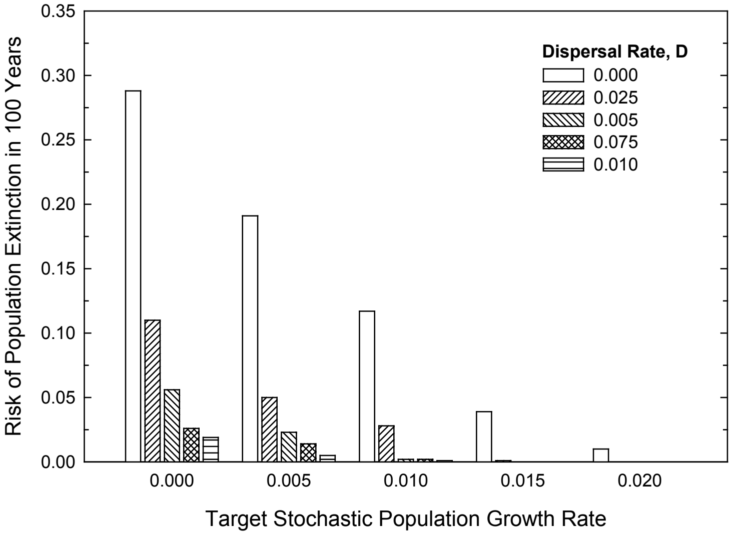


Figure 4. Extinction risk among simulated jaguar populations inhabiting the Sinaloa Secondary Area of the Northwestern Recovery Unit, as a function of underlying stochastic growth rate of the population. Individual bars depict mean annual rates of dispersal expected among subpopulations within the Unit. 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).

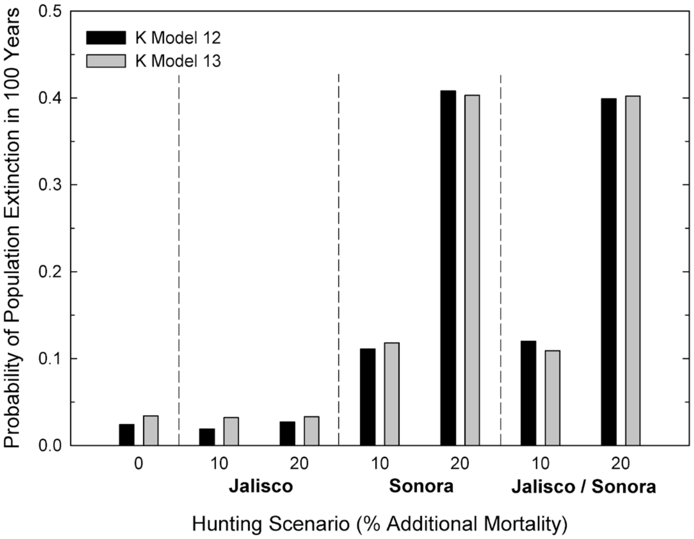


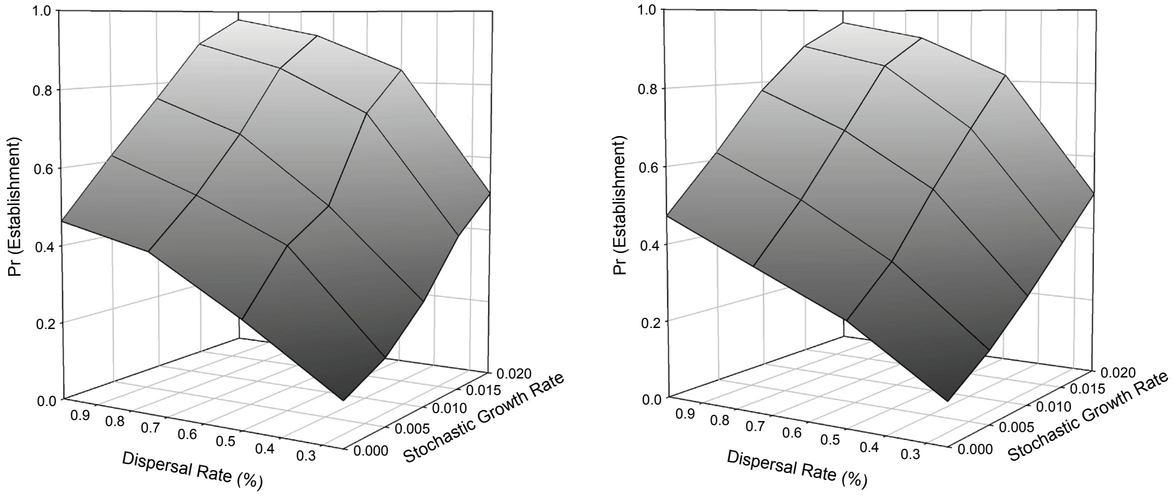
Figure 5. Probability of extinction in the Mexico portion of the Borderlands Secondary Area of the Northwestern Recovery Unit, assuming a long-term stochastic population growth rate (r_s) of 0.020 and a base annual dispersal rate among subpopulations of 1.0%. Additional mortality, assumed to arise from 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.

Population establishment in the northern portions of the Northwestern Recovery Unit

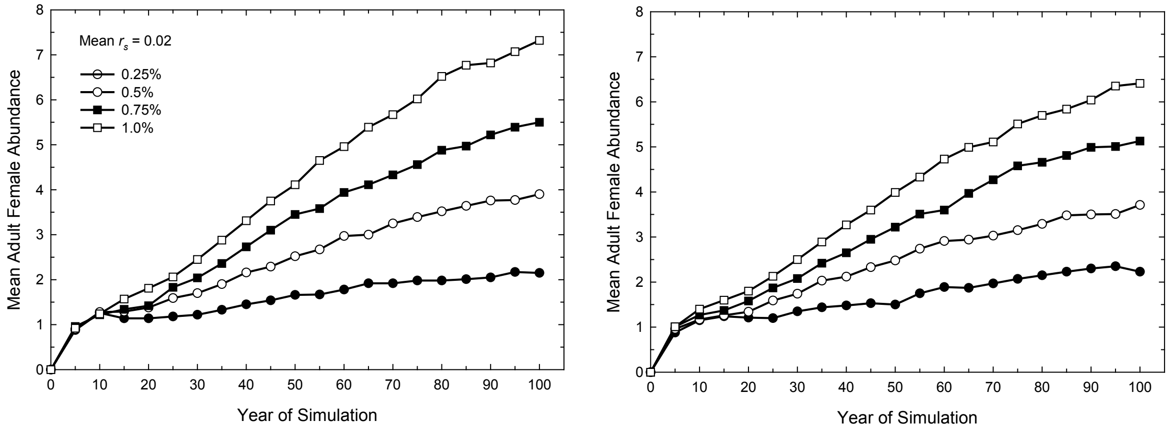
The likelihood of establishing a viable population of jaguars in the northern reaches of the Northwestern Recovery Unit is critically dependent on both the extent of robust population growth in the core regions to the south, and on the degree of connectivity between the population units. This is clearly 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.



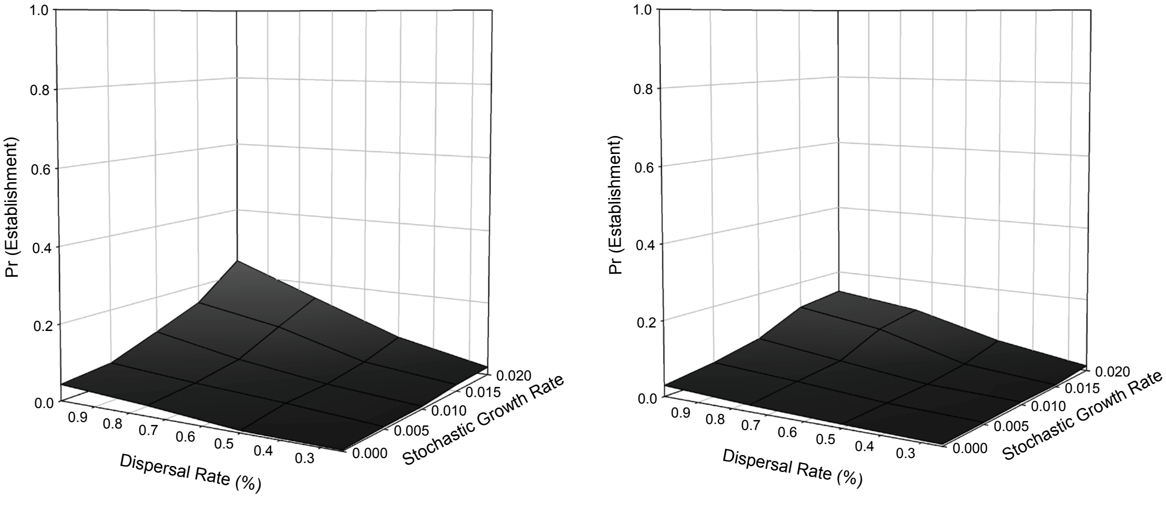
While the probability of establishing a population in the Mexico portion of the Borderlands Secondary Area may be quite high under optimal circumstances, this analysis says nothing about the size of that population if it is established. The trajectories shown in Figure 7 indicate that, even under the 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).

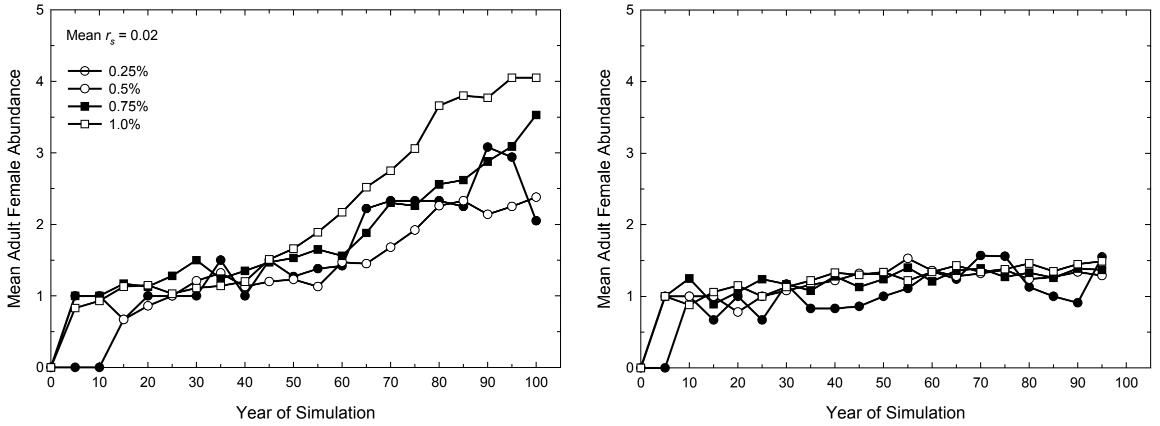
Figure 8. Three-dimensional plots displaying the probability of establishing a population of jaguars in the U.S. portion of the Borderlands Secondary Area of the Northwestern Recovery Unit, as a function of underlying demographic characteristic defined by stochastic population growth rate in each population 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 jaguar 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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Addendum:
Population Viability Analysis for the Jaguar (*Panthera onca*) in the Northwestern Range

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Under Solicitation

F12PX00876

11 August, 2014

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

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Introduction

This document describes the structure, implementation, and interpretation of a new set of demographic simulations of jaguar population viability in the northwestern portion of the species' range in northern Mexico. The new models were produced at the request of the United States Fish and Wildlife Service Jaguar Recovery Team in an effort to expand the original set of PVA simulations conducted and described by Miller (2013). Attention in these initial models was focused on the demographic viability of the metapopulation defined as the Northwestern Jaguar Recovery Unit, stretching northward from Jalisco at its southern boundary up to southeastern Arizona / southwestern New Mexico in the United States (Figure 1). Two components within this metapopulation contain relatively large jaguar populations, and serve as "core areas" for maintaining overall metapopulation stability. The Jalisco Core Area extends from the southern boundary of Jalisco to northern Nayarit and far western Durango. Farther north, the Sonora Core Area begins in northern Sinaloa and extends to north-central Sonora, including some habitat in far western Chihuahua. These two core areas serve as source populations, from which jaguars can disperse into neighboring "secondary areas" to, at least in theory, stabilize the demographic dynamics of the larger metapopulation and increase long-term viability.

Results of analyses described in Miller (2013) suggest that the two core areas within the Northwestern Jaguar Recovery Unit are sufficiently large – both in terms of current abundance and estimated long-term habitat carrying capacity – to serve as effective source populations within the larger metapopulation. However, the analyses also demonstrated that changes in mortality of either cubs or adults could significantly reduce the growth potential of these core areas. This could, in turn, reduce the dispersal rate of individuals from these core areas to the neighboring secondary areas, thereby potentially comprising long-term viability of the metapopulation.

The Sinaloa Secondary Area (Figure 1) might serve as a vital connection between the two core areas to maintain long-term demographic stability. In order to better understand this dynamic, a key element of the overall analysis is to explore the conditions under which the two jaguar populations currently occupying the core areas can survive on their own – in other words, assuming demographic isolation from neighboring subpopulations. Specifically, the analyses described in the addendum to Miller (2013) attempt to address the following questions:

- What are the critical levels of age-specific mortality that influence extinction risk in isolated core populations?
- Can we obtain rough estimates of the minimum viable population size of each core area?
- What are the potential consequences to population viability if our current estimates of habitat-specific carrying capacity are in error?

- What is the risk of core population extinction under a realistic “worst case scenario”, e.g., when core populations are demographically isolated, cub production is low, and adult mortality is high?

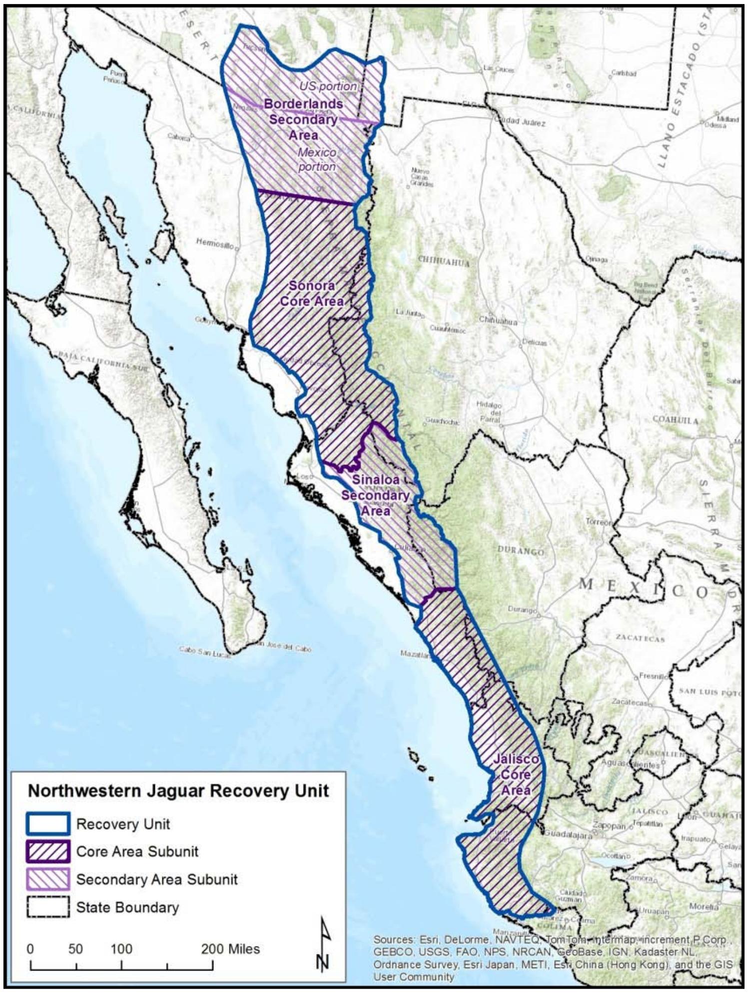

Figure 1. Map of the Jaguar Northwestern Recovery Unit and core area designations used in this addendum to the earlier PVA of Miller (2013).

As with earlier phases of this project, we have employed methods of population viability analysis (PVA) to address the questions listed above. 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. *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 in the context of long-term population stability.

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).

Revised Input Parameters for Population Viability Simulation Models

All of the models presented here use the baseline demographic input parameters described in detail in Miller (2013). Specific revisions to these parameters were made in order to create new models that address the questions outlined above. These revisions are discussed below.

Initial population size

As defined in the original PVA effort, the population of jaguar in the Jalisco core area was set at 350 individuals, including approximately 206 adults (134 females, 72 males). This was used as an initial population size in our baseline model. To investigate the impact of reduced abundance on long-term population viability, a set of models was constructed where the initial population size was reduced proportionally at the start of the simulation, from 90% of the baseline value (N_0 = 315) to 10% (N_0 = 35). The proportional distribution of individuals across all age classes was adjusted accordingly.

Because of the close similarity in both initial population size and carrying capacity (K; see below) between the Jalisco and the Sonora core areas, and because of the identical demographic rates used for each core area, the Sonora population is not explicitly modeled in this analysis. All models therefore use the initial population abundance and carrying capacity of the Jalisco core area, with the appropriate adjustments to N_0 and K according to the needs of the given scenarios. These similarities allow us to confidently apply the general results of the Jalisco models to the Sonora core area.

Carrying capacity

As described in detail by Miller (2013), habitat modeling conducted by staff of the Wildlife Conservation Society (WCS) was used to estimate the extent of available jaguar habitat within a given metapopulation unit and, by extension, the maximum number of individuals that habitat could support in the long-term. The most recent WCS habitat model, labeled Model 13 (2 August 2012), was used as the basis for estimating carrying capacity in the Jalisco core area at 2197 individuals, corresponding to 1318 adults based on the observation that a jaguar population reaching long-term abundance equilibrium (often referred to as a stable age distribution) typically is composed of 60% adults.

To investigate the impact of incorrectly estimating carrying capacity – specifically, underestimating the value of the parameter – a set of models was constructed where the carrying capacity was reduced proportionally at the start of the simulation, from 90% of the baseline value (total K = 1977) to 30% (total K = 659). Each of these models featured an initial population size of 350 animals, and all mortality values were at their baseline values (see below). As with scenarios investigating the impact of varying the initial population size, the Sonora core area was not explicitly studied for sensitivity to carrying capacity estimation as the value for K in the Sonora core area (1873 animals) is very close to that estimate for the Jalisco core area (2197 animals).

Age-specific mortality

The baseline survival rates used by Miller (2013), transformed from the corresponding mortality rates used by *VORTEX*, are given in Table 1. Models featured in this Addendum feature systematic changes to both adult and juvenile (cub, Age 0-1) mortality rates that may simulate lower survivorship through poaching, nuisance animal killing, and other activities arising in most instances from increased frequency of contact with local human populations. The modifications to first-year (cub) survival here represent effective changes in adult female reproductive output, or natality.

Table 1. Estimated annual survival rates (with standard deviations representing environmental variation in parentheses) among age-sex classes of jaguars as used in the original simulation models described by Miller (2013).

	Mortality Rate (%) (SD)	
Age (years)	Female	Male
0 – 1	75.0 (6.0)	75.0 (6.0)
1 – 2	80.0 (4.0)	80.0 (7.0)
2 – 3	75.0 (5.0)	65.0 (9.0)
3 – 5	90.0 (3.0)	75.0 (5.0)
5 – 7	84.5 (3.0)	75.0 (5.0)
7 – 10	79.0 (3.0)	75.0 (5.0)
10+	73.5 (3.0)	75.0 (30)

To begin our discussion of simulated changes in mortality rates, we focus our attention on adult females. Elasticity analysis (defined as proportional sensitivity: Caswell 2001) using a simple matrix demographic model (detailed results not presented here, but available by request from the author) indicates that adult female survival is clearly the biggest proportional contributor to overall jaguar population growth in the absence of external perturbation of baseline demographic rates. New models were defined on the basis of a range of adult survival from a minimum of 75%, corresponding to a proportional factor of 0.833 relative to the baseline rate of 90%, to a maximum of 98%, corresponding to a proportional factor of 1.089. These proportional factors are then systematically applied to all adult female survival rates. Between these minimum and maximum values, intermediate survival values of 80% (factor = 0.889), 85% (factor = 0.944), and 95% (factor = 1.056) were also derived and applied to all adult female survival rates.

To maintain consistent proportionality among modified survival rates in other age/sex classes, we applied the same proportional factors to both adult male survival, with a baseline value of 75%, and to male and female cub survival, also with a baseline value of 75%. The resulting array of survival values are summarized in Table 2.

Table 2. Range of survival rates defining scenarios developed for this addendum. Adult female survival rate is given only for the youngest adult class (Age 3-5 years) as defined in the original datasets summarized in Miller (2013). Survival rates for older adults are modified by applying the same multiplicative factor listed in the table. Values in bold represent the baseline values as listed in Table 1.

Adult Scenario	Factor	♀	♂	Cub Scenario	Factor	♀, ♂
A1	0.833	75.0	62.5	C1	0.777	58.28
A2	0.889	80.0	66.68	C2	0.833	62.5
A3	0.944	85.0	70.8	C3	0.889	66.68
A4	**1.000**	**90.0**	**75.0**	C4	0.944	70.8
A5	1.056	95.0	79.2	**C5**	**1.000**	**75.0**
A6	1.089	98.0	81.68	C6	1.056	79.2
				C7	1.089	81.68
				C8	1.112	83.4

This set of adult and cub survival values can then be combined systematically to produce 48 unique model scenarios, e.g., A1C1, A3C6, A6C8, etc. that represent the full range of potential threats to individual jaguar survival.

Iterations and years of projection

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). Note that while a more recent and substantially updated Version 10 of *VORTEX* is now available (Lacy and Pollak 2014), an older version of the software was used in the current analysis. This decision was made in order to provide continuity to the original analyses described in Miller (2013). The original version 9.99b remains a robust and reliable platform to evaluate the questions outlined in the Introduction.

Results from Simulation Models[1]

Core population baseline model performance

The Jalisco core area baseline model showed a very slightly positive average rate of population growth, increasing at approximately 0.4% per year (Table 3). The baseline model resulted in a very low probability of population extinction across the 100 years of the simulation, and yielded a final population size of approximately 730 individuals. This model serves as a foundation upon which we can compare alternative models that explore variation in initial population size, carrying capacity, and cub/adult mortality and the impact of this variation on future jaguar core population viability in the Northwestern Recovery Unit.

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[1] As described on page 3 of this report, because of the close similarity in both initial population size and carrying capacity between the Jalisco and the Sonora core areas, and because of the identical demographic rates used for each core area, the Sonora core area population is not explicitly modeled in this analysis. These similarities allow us to confidently apply the general results of the Jalisco models to the Sonora core area.

Impact of initial population size on core population extinction risk

A systematic proportional decrease in the initial abundance of the Jalisco core population leads to a gradual decrease in average population growth rate and final population abundance, and an increase in the risk of population extinction over the time frame of the simulation (Table 3). When the initial population size is set to 140 individuals, or 40% of the current population abundance, the average growth rate becomes negative and the extinction risk begins to increase (Figure 2). In particular, extinction risk begins to increase sharply when the initial population size decreases further to less than approximately 100 animals, suggesting a type of threshold with respect to long-term population viability. When a population of just 35 individuals is simulated using the same demographic rates, the risk of that population declining to extinction is greater than 50% over 100 years. These data demonstrate the greater inherent instability of smaller populations that are more sensitive to annual fluctuations in demographic rates, as well as to the deleterious effects of inbreeding.

Table 3. Results of Jalisco core population simulation models, with systematic reduction in initial population abundance. N_0, initial population size; r_s (SD), mean stochastic population growth rate (standard deviation); P(E), probability of population extinction across the 100 years of the simulation; N_{100} (SD), mean final population size (standard deviation) across all simulations at 100 years. See accompanying text for more information on model structure and implementation.

N_0	r_s (SD)	P(E)	N_{100} (SD)
350	0.004 (0.120)	0.002	732 (569)
315	0.004 (0.120)	0.003	690 (568)
280	0.003 (0.121)	0.002	607 (513)
245	0.003 (0.121)	0.011	545 (494)
210	0.001 (0.126)	0.022	420 (420)
175	0.000 (0.129)	0.028	340 (382)
140	-0.002 (0.133)	0.064	252 (305)
105	-0.004 (0.143)	0.126	170 (228)
70	-0.007 (0.153)	0.242	101 (164)
35	-0.014 (0.181)	0.542	40 (81)

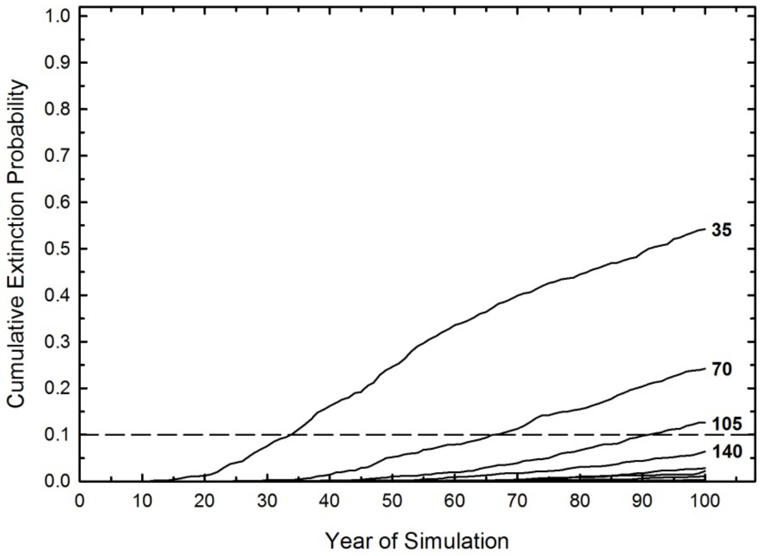

Figure 2. Cumulative extinction risk for simulated jaguar populations in an isolated Jalisco core area. Values next to selected risk trajectories indicate initial population size; lines below the labeled trajectories are for populations with initial abundances of at least 175 individuals. The horizontal dotted line denotes a cumulative extinction risk of 10% over the 100-year duration of the simulation. See accompanying text for more information on model structure and implementation.

We can identify specific risk thresholds that define population viability in the context of species recovery. As an example of this process, Figure 3 highlights a 10% risk as a type of threshold that is exceeded for jaguar populations initiated with approximately 110-120 individuals or fewer (extrapolated from the existing trajectories). The choice of whether or not to adopt a particular threshold or its value is, of course, at the discretion of the individual species management group.

Impact of carrying capacity uncertainty on core population extinction risk

As carrying capacity is systematically decreased in the set of models summarized in Table 4 and Figure 3, mean stochastic growth rate and mean final population size also decreases, but to a much smaller extent than those models just discussed where initial population size is modified. All carrying capacity scenarios – even one that includes a 70% decrease in the estimate of the parameter relative to the baseline value – yield a positive population growth rate and a very small extinction risk. Note that the three scenarios with the smallest carrying capacity values, just 30 – 50% of the baseline value, show a tendency toward population decline in later stages of the simulation. These are valid observations, despite the reported positive population growth rate; the early years of population growth are enough to offset the later years of slow population decline. Despite these (and other) statistical complications, it is clear that only very significant errors in carrying capacity lead to considerable change in long-term population dynamics of an isolated Jalisco core population. If the underlying growth rate of the population were expected to be higher than the current baseline value of 0.004, the differences most apparent in Figure 3 would be markedly smaller.

Table 4. Results of Jalisco core population simulation models, with systematic reduction in habitat carrying capacity. K, carrying capacity; r_s (SD), mean stochastic population growth rate (standard deviation); P(E), probability of population extinction across the 100 years of the simulation; N_{100} (SD), mean final population size (standard deviation) across all simulations at 100 years. See accompanying text for more information on model structure and implementation.

K	r_s (SD)	P(E)	N_{100} (SD)
2197	0.004 (0.120)	0.002	732 (569)
1977	0.004 (0.120)	0.005	710 (525)
1758	0.004 (0.120)	0.001	698 (473)
1538	0.003 (0.120)	0.020	639 (411)
1318	0.004 (0.120)	0.000	626 (357)
1098	0.002 (0.120)	0.004	518 (292)
879	0.002 (0.121)	0.006	464 (238)
659	0.001 (0.121)	0.003	367 (292)

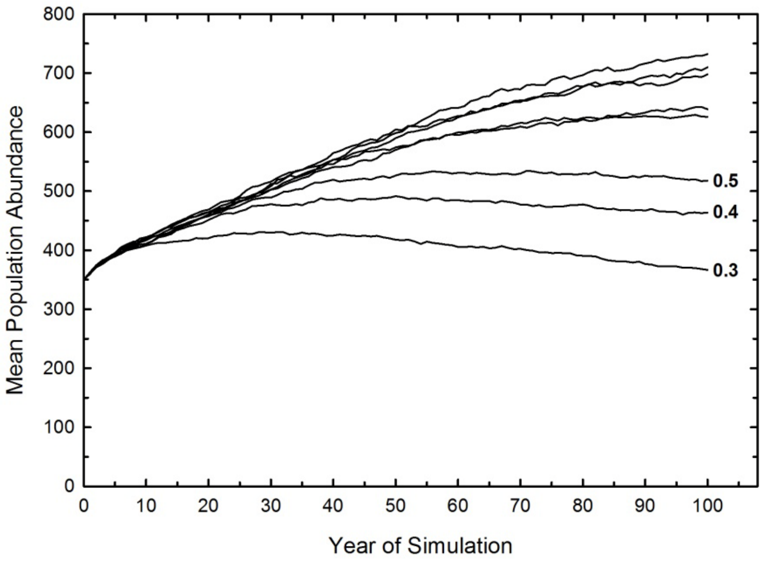

Figure 3. Mean abundance trajectories for simulated jaguar populations in an isolated Jalisco core area. Values next to selected risk trajectories indicate the carrying capacity for that specific scenario as a proportion of the original value (K = 2197individuals); lines above the labeled trajectories are for populations with carrying capacity values at least 60% of the baseline value. See accompanying text for more information on model structure and implementation.

Impact of cub and adult survival on core population viability

A total of 48 separate scenarios were constructed and simulated to help identify the survival conditions, applicable to both jaguar cubs and adults, which lead to favorable or unfavorable conditions for future population growth and stability. Our first look at the results of these simulations comes in the form of 3-dimensional surface plots of growth rate (Figure 4A) and extinction risk (Figure 4B) as a function of specific values for cub and adult survival across the range of values considered in this analysis (full tabular results of these analyses are found in Appendix A).

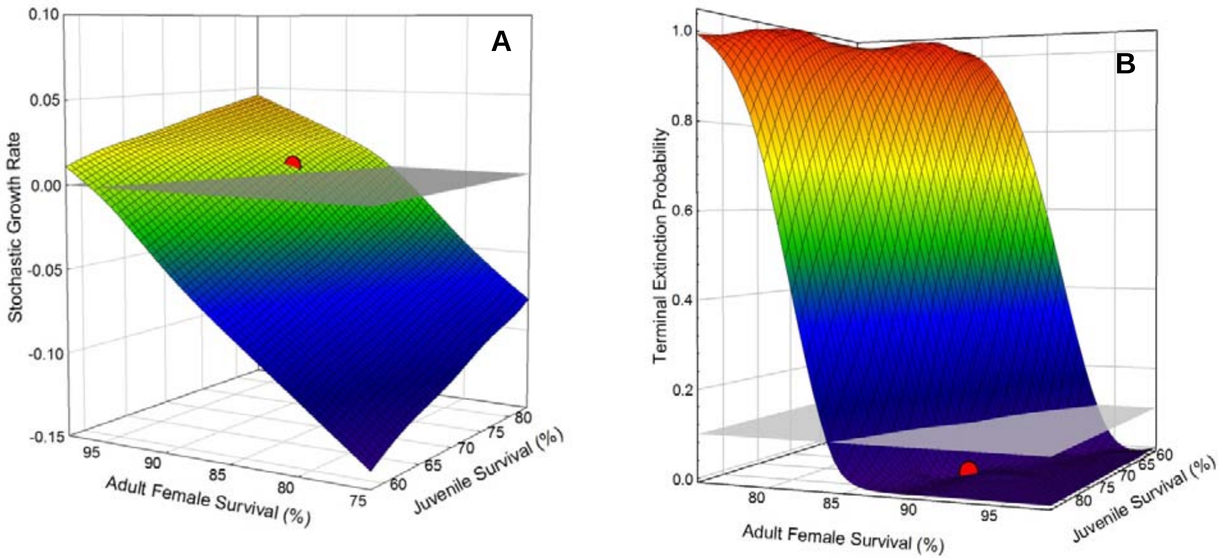

Figure 4. 3D surfaces depicting jaguar population performance in an isolated Jalisco core area, as a function of both cub (juvenile) and adult annual survival rates. **(A)** Mean stochastic growth rate surface across the range of simulated mean survival rates. Horizontal plane indicates mean population growth of 0.0. Red dot indicates mean stochastic growth rate of baseline Jalisco core population model. **(B)** Extinction risk surface across the range of simulated mean survival rates. Horizontal plane identifies extinction risk of 0.1. Red dot indicates extinction risk of Jalisco core population model. See accompanying text for more information on model structure and implementation.

Inspection of Figure 4A indicates that, under the range of survival values studied here, a relatively narrow range of values leads to positive population growth. Under conditions of low cub production – specifically, when annual cub survival values hover around 60% – only very high adult female survival of about 95% leads to positive growth (the upper left-hand corner of the surface). Alternatively, when cub survival is increased to approximately 83%, adult female survival of approximately 85% is required to generate long-term positive population growth (intersection of right-hand back panel with surface). As a frame of reference, the growth rate emerging from our baseline model is indicated in Figure 4A by the red dot, hovering just above the gray plane indicating $r = 0$. This baseline condition is in part defined by adult annual female survival of 90% and cub survival of 75%. When either survival rate declines, the surface indicates that stochastic population growth rate is likely to quickly decrease to a negative value. Moreover, the surface indicates that the population growth rate declines more rapidly per unit reduction in adult female survival compared to an equivalent unit reduction in cub survival. Quantitatively, a change of 1% in adult survival results in a change of 0.005 – 0.006 in the population growth rate, while an equivalent change of 1% in cub survival results in a change of just 0.001 – 0.002 in growth rate. This is very consistent with the results of the elasticity analysis reported earlier (detailed data available from the author), where the proportional sensitivity of our model to changes in adult female survival was calculated as approximately five times greater than the same value for female cub survival.

A similar picture emerges when examining the extinction risk surface (Figure 4B). As a frame of reference, the extinction risk emerging from our baseline model is indicated in the figure by the red dot, located below the gray plane indicating P(E) = 0.10. This baseline condition is in part defined by adult annual female survival of 90% and cub survival of 75%. The striking feature of this surface, however, is the abrupt transition from low to high extinction risk that results from relatively small changes in survival – particularly survival of adult females. For example, at the highest level of cub survival (corresponding to the front left-hand edge of the surface), the extinction risk is just 0.029 when adult female survival is 85% (growth rate $r_s = 0.026$), but jumps to 0.662 when adult survival declines to 80% (growth rate $r_s = -0.005$). Given an initial population abundance of 350 animals, corresponding to 134 adult females, this 5% increase in mortality equates to the additional loss of just 6-7 animals yearly. As expected, when cub survival is reduced to its minimum value of 58.28% (rear right-hand edge of surface), high extinction risk and low growth rates occur in the presence of much higher adult female survival rates: at 85% adult female survival, risk is 0.014 but increases to 0.583 when adult female survival decreases to 90%. As with examination of population growth rate, our simulated jaguar population is more sensitive with respect to extinction risk to changes in adult female survival, although the relationship is not quite as strong owing to the more stochastic nature of the extinction process.

We can perhaps distill the somewhat complicated information presented in the 3D surfaces down to a simpler set of data that identifies those conditions that lead to positive or negative long-term growth, or to a risk of extinction greater or less than some arbitrary threshold value – in this case, 0.10. This 10% risk value is used frequently in deriving case-specific definitions of population viability in conservation planning exercises, usually over a 100-year timeframe, and forms the basis of the IUCN’s definition of a “Vulnerable” species according to the Red List global classification system for threatened species (IUCN 2012). Figure 5 is an attempt at providing the type of simplification mentioned above. Panel A shows the combination of approximate survival values that give rise to a stochastic growth rate of 0.0 – effectively, this line is equivalent to the intersection of the growth rate surface of Figure 4A with the horizontal plane defining $r_s = 0.0$. As predicted, the threshold has a negative slope, meaning that as cub (juvenile) survival increases, the adult female survival rate necessary to confer positive growth decreases. Panel B shows the same general relationship for extinction risk, with the acceptable survival values decreased somewhat in accordance with the acceptable threshold risk being greater than zero.

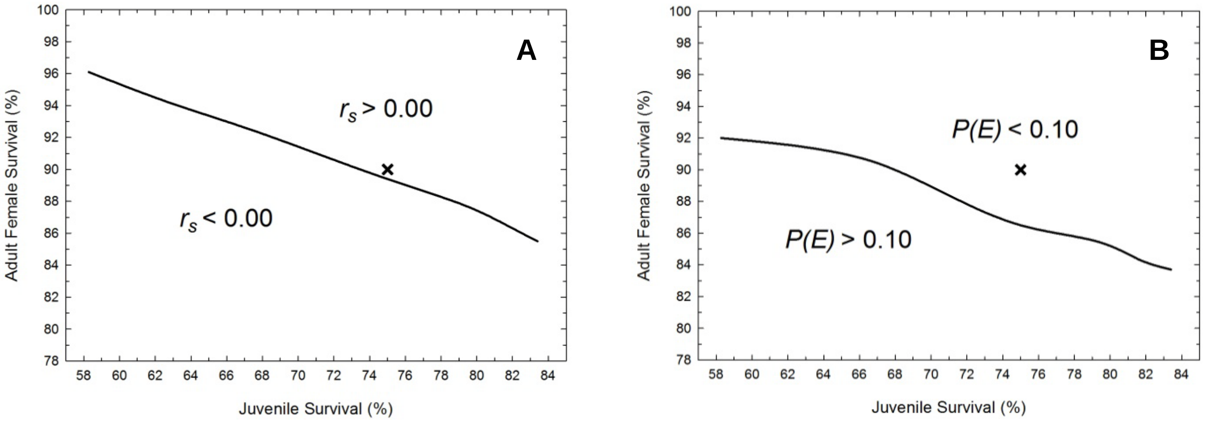

Figure 5. Plots identifying acceptable population outcomes for an isolated Jalisco core jaguar population, as a function of both cub (juvenile) and adult annual survival rates. **(A)** Mean stochastic growth rate plot across the range of simulated mean survival rates. Line indicates mean population growth of approximately 0.0. Black “X” symbol indicates mean stochastic growth rate of baseline Jalisco core population model. **(B)** Extinction risk plot across the range of simulated mean survival rates. Line identifies extinction risk of approximately 0.1. Black “X” symbol indicates extinction risk of Jalisco core population model. See accompanying text for more information on model structure and implementation.

Conclusions

We have created a new set of demographic simulation models, focusing on the Jalisco core area of the Northwestern Jaguar Recovery Unit. These models explore the long-term viability of this population under a variety of assumptions related to the size of the population, the habitat carrying capacity, and the demographic characteristics of the population, namely the rate of survival among cubs (juveniles) and adults. All of the model scenarios discussed above, and the underlying questions that formed the basis of this analysis (summarized below), address the fundamental desire among jaguar biologists and managers to explore and understand the sensitivity of extinction risk in Jalisco and Sonora core area populations to the assumption of demographic isolation. We can draw the following conclusions by revisiting the original questions that formed the basis of this latest effort.

- Can we obtain rough estimates of the minimum viable population size of each core area?

  As explained above, the present analysis is focused only on the Jalisco core area as defined solely by its current abundance (350 individuals) and its habitat carrying capacity (2179 individuals). However, the close similarity in both current size and habitat carrying capacity to the Sonora core area, itself defined by $N_0 = 300$ and $K = 1873$ individuals, means that the results obtained by analysis of the Jalisco core will be highly applicable to the Sonora area as well.

  Under our assumed conditions of the stochastic growth rate $r_s \approx 0.0$, an isolated core population of approximately 120 individuals – corresponding to an adult abundance of about 70-75 animals given the underlying demographic profile – appears to be the smallest population that persists with a sufficiently high probability, defined in this analysis as a 10% probability of population extinction over a 100-year timeframe. Due to the destabilizing effects of random variability in demographic rates and the deleterious impacts of inbreeding depression, smaller populations tend to decline in abundance over the long term, even if the mean expected demographic rates do not change over time. Since this abundance is defined in the context of the minimal conditions for long-term population growth, this could be considered a minimum viable population abundance for these populations, under the conditions simulated in this analysis. If survival within the population is more favorable, an abundance that confers long-term stability could perhaps be smaller.

It is critically important to understand that deriving an estimate of a viable population abundance is critically dependent on its underlying demographic stability. If field research indicates that a given population is in long-term decline due to unsustainable demographics, no population will be large enough to overcome these deterministic threats to its survival. Dedicated research is required to better understand mean rates of birth and death, and the forces influencing those rates over the long term, before a true estimate of population viability can be estimated with confidence.

- What are the potential consequences to population viability if our current estimates of habitat-specific carrying capacity are in error?

  In contrast to our analysis of initial population abundance, the impact of uncertainty in carrying capacity has a much smaller impact on long-term population viability projections. The true value for carrying capacity would have to considerably smaller – specifically, a reduction of perhaps as much as 60 – 70% of the current estimated value – for a significant effect to be manifest. While a detailed critique of the current estimation method for habitat carrying capacity in the Northwestern Jaguar Recovery Unit is far beyond the scope of this analysis, it may nevertheless be reasonable to argue that the extent of estimation error is not anywhere close to this magnitude. While the absolute value of long-term equilibrium abundance would likely change under a new carrying capacity, the associated estimate of long-term viability would likely not change appreciably.

- What are the critical levels of age-specific survival that influence extinction risk in isolated core populations?

  Estimating a critical value of one demographic parameter must always be done in the context of the underlying values of other parameters defining the growth potential of the population under analysis. The case of jaguars in the Jalisco core area, serving also in this analysis as a proxy for jaguars in the Sonora core area, is no exception. Critical values of adult female survival are defined in the context of the underlying cub survival, as demonstrated graphically in Figure 5. When cub survival is low, defined here as just 58%, adult female survival must be on the order of 92% to confer an acceptable (in the author's estimation) level of extinction risk (10%) over the time-course of the simulation. At the other end of the spectrum, a high rate of cub survival (83%) means that adult female can be as low as approximately 82 – 84% and still have a population that displays a low probability of population extinction. Additional analysis indicates that a population with those survival characteristics may actually have a negative growth rate (see Figure 5A), meaning that simple extinction risk is not always a complete descriptor of the demographic health of a population.

- What is the risk of core population extinction under a realistic "worst case scenario", e.g., when core populations are demographically isolated, cub production is low, and adult mortality is high?

  A precise definition of "low cub production" and "high adult mortality" is, sadly, not universal. In light of this, we must resort to more general insights. The results summarized in Figure 5, however, suggest that relatively small changes in survival among both cubs and adults, especially females, can dramatically increase the risk of extinction of jaguars in the Jalisco core area. This conclusion assumes a relatively low underlying growth rate, as with most of the conclusions drawn in this analysis. However, experts in jaguar population dynamics in Mexico suggest that both Jalisco and Sonora core populations may already be impacted by a combination of threatening factors that limit their growth to a considerable extent. In this case, it may be reasonable to conclude that these populations may be at considerable risk of future population declines if additional mortality occurs through hunting, etc. and dispersal of jaguars into these habitats through demographic connectivity is not possible. As discussed previously, the additional loss of as few as 10 adult females annually from one of these core populations may tip the demographic balance. Maintenance of metapopulation dynamics among these core populations and neighboring corridor habitats may therefore be a vitally important component of a successful management strategy for jaguars in the northern part of the species' range. The success of such a strategy must also depend, of course, on the responsible management of threats to survival and reproduction of jaguars in the presence of humans.

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Appendix A: Results of Survival Analysis

The following table gives the detailed results of the 48 scenarios comprising the survival analysis that was applied to the Jalisco core population. Column definitions are below:

Scenario	Name of scenario, defined by the combined levels of cub (juvenile) and adult survival
Surv (Cub)	Value of cub survival in the given scenario.
Surv (Adult)	Value of adult female survival in the given scenario. Other age/sex-specific survival values calculated as described in the report.
rs (SD)	Mean stochastic population growth rate (standard deviation)
P(E)	Probability of population extinction across the 100 years of the simulation
T(E)	Median time (years) to extinction in those scenarios where $P(E) \geq 0.50$
N_{100} (SD)	Mean final population size (standard deviation) across all simulations at 100 years.

Scenario	Surv (Cub)	Surv (Adult)	r_s (SD)	P(E)	T(E)	N_{100} (SD)
C1A1	58.28	75.00	-0.140 (0.197)	1.000	33	0
C1A2	58.28	80.00	-0.109 (0.198)	1.000	42	0
C1A3	58.28	85.00	-0.078 (0.178)	0.991	57	0.1 (1)
C1A4	58.28	90.00	-0.044 (0.156)	0.583	95	10 (21)
C1A5	58.28	95.00	-0.006 (0.117)	0.014		312 (317)
C1A6	58.28	98.00	0.011 (0.109)	0.000		1219 (598)
C2A1	62.50	75.00	-0.127 (0.195)	1.000	36	0
C2A2	62.50	80.00	-0.097 (0.188)	1.000	46	0
C2A3	62.50	85.00	-0.067 (0.176)	0.951	66	1 (3)
C2A4	62.50	90.00	-0.032 (0.144)	0.287		35 (47)
C2A5	62.50	95.00	0.005 (0.114)	0.000		780 (547)
C2A6	62.50	98.00	0.019 (0.110)	0.000		1740 (405)
C3A1	66.68	75.00	-0.118 (0.197)	1.000	39	0
C3A2	66.68	80.00	-0.088 (0.186)	1.000	51	0
C3A3	66.68	85.00	-0.055 (0.170)	0.835	78	3 (8)
C3A4	66.68	90.00	-0.019 (0.132)	0.093		116 (155)
C3A3	66.68	95.00	0.014 (0.114)	0.000		1399 (572)
C3A6	66.68	98.00	0.024 (0.112)	0.000		1963 (255)
C4A1	70.80	75.00	-0.109 (0.195)	1.000	42	0
C4A2	70.80	80.00	-0.078 (0.184)	0.991	57	0.1 (1)
C4A3	70.80	85.00	-0.046 (0.164)	0.626	91	10 (19)
C4A4	70.80	90.00	-0.007 (0.124)	0.027		311 (343)
C4A5	70.80	95.00	0.020 (0.115)	0.000		1802 (381)
C4A6	70.80	98.00	0.029 (0.114)	0.000		2007 (194)
C5A1	75.00	75.00	-0.098 (0.195)	1.000	47	0
C5A2	75.00	80.00	-0.068 (0.183)	0.959	66	1 (3)
C5A3	75.00	85.00	-0.033 (0.152)	0.330		33 (54)
C5A4	75.00	90.00	0.004 (0.120)	0.001		727 (551)
C5A5	75.00	95.00	0.025 (0.117)	0.000		1935 (240)
C5A6	75.00	98.00	0.035 (0.117)	0.000	51	2042 (176)
C6A1	79.20	75.00	-0.090 (0.194)	0.999	74	0
C6A2	79.20	80.00	-0.059(0.180)	0.874		2 (8)
C6A3	79.20	85.00	-0.022 (0.140)	0.134		95 (127)
C6A4	79.20	90.00	0.013 (0.119)	0.000		1300 (600)
C6A5	79.20	95.00	0.030 (0.119)	0.000		2000 (202)
C6A6	79.20	98.00	0.040 (0.117)	0.000	54	2056 (164)
C7A1	81.68	75.00	-0.085 (0.193)	0.997	82	0.03 (0.5)
C7A2	81.68	80.00	-0.052 (0.176)	0.768		6 (16)
C7A3	81.68	85.00	-0.014 (0.135)	0.067		190 (249)
C7A4	81.68	90.00	0.016 (0.119)	0.000		1568 (508)
C7A5	81.68	95.00	0.033 (0.120)	0.000		2023 (190)
C7A6	81.68	98.00	0.043 (0.118)	0.000	57	2072 (153)
C8A1	83.40	75.00	-0.080 (0.193)	0.994	88	0.1 (1)
C8A2	83.40	80.00	-0.047 (0.170)	0.662		9 (21)
C8A3	83.40	85.00	-0.008 (0.130)	0.029		278 (305)
C8A4	83.40	90.00	0.018 (0.120)	0.000		1707 (430)
C8A5	83.40	95.00	0.035 (0.120)	0.000		2034 (182)
C8A6	83.40	98.00	0.045 (0.118)	0.000		2086 (142)